
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's project in Biology
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Preface

This project is a part of a pilot project for *Research project on field data collection for honey bee colony model evaluation* - a project performed by Aarhus University financed by EFSA, the European Food Safety Authority. It is included in the EFSA-program where the purpose is to try identifying causes for the unusual weakening of numbers of bees and colony losses particularly in Western Europe, e.g. studying pesticides' effects on honey bees¹.

It is one of two reports about honey bee waggle dance. This report examines how to measure waggle dance simply and how waggle dance affects honey bees' behavior in foraging for resources. The other part, written by Julie Ørnholm Frederiksen, examines our decoded waggle dances in relation to pollen resources².

We have collaborated in the antecedent research process and in performing the field study, for then independently writing our own reports with different angles on the subject.

¹ <http://www.efsa.europa.eu/en/topics/topic/bee-health>

² Frederiksen, J.Ø. 2018. 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. Bachelor report. Aarhus University.

Resumé

Der er et ønske fra forvaltningen af pesticider om at kortlægge biers adfærd for at afdække risikoen for forgiftninger. Det er dog svært at følge biers flyveruter gennem landskabet, og gennem observationer bestemme hvor de trækker hen. Formålet med undersøgelsen var at undersøge hvordan vi kunne måle bidans simpelt, og hvad bidansens betydning er for biers adfærd under fødesøgning. Vi havde et observationsstade med honningbier, *Apis mellifera*, placeret i Hinnerup, Aarhus, hvor vi filmede bidans over to dage i maj 2018. Samtidig kortlagde vi de omkringliggende abundante blomsterressourcer indenfor en radius af tre kilometer, samt indsamlede pollenprøver fra hjemkomne bier. Danseoptagelserne blev afkodet ved brug af en hertil udviklet Excel makro og resultaterne sammenholdt med ressourcekortlægningen og pollenanalyse. Hvorvidt bidansen har betydning for biernes fødesøgning blev belyst vha. litteraturen. Resultaterne viste, at vi på simpel vis kunne måle bidans vha. vores model, men at denne formentligt kræver justering ift. kalibrering, hvis den skal være helt nøjagtig frem for blot indikerende. Aflæsningerne viste et tydeligt mønster hvor bierne hovedsageligt koncentrerede deres fouragering indenfor tre kilometer svarende til nærliggende rapsmarker. Diskussion af bidansens betydning, belyser, at honningbier er i stand til at afkode information fra dansene, men at det er usikkert hvorvidt de overhovedet gør brug af det. Bidansen er kun for særligt profitable ressourcer, og derfor giver afkodning et indblik i, hvilke nærliggende ressourcer bierne vurderer som sådanne. Vi lykkedes med at afkode bidanse med et simpelt set-up, som viste en klar sammenhæng mellem bidans og fordelingen af ressourcer i landskabet. Dette studie står i kontrast til behovet for fuldautomatiske metoder og komplicerede statistiske analyser.

Abstract

There is a desire from the management of pesticides to map bees' behavior to detect the risk of poisoning. But it is difficult to follow bees' foraging routes through landscapes and decide through observations where they forage. The purpose of the study was to examine how to measure waggle dance simply and the waggle dance's importance for honey bees' behavior in relation to foraging. We had an observation hive containing honey bees, *Apis mellifera*, installed in Hinnerup, Aarhus. We recorded waggle dances over two days in May 2018, mapped the nearby abundant resources within a radius of three kilometers and collected pollen from homecoming bees. Records of dances were decoded by using an Excel macro, invented for this task. The results were compared to the mapped resources and pollen analysis. To what degree waggle dance has influence on the bees' behavior during foraging was examined by using existing literature. The results revealed, that we in a simple manner were able to decode waggle dance with our model, but it probably requires calibration if it is to be accurate instead of indicative. The decoding showed a clear pattern of bees mostly concentrating their foraging within three kilometers, corresponding to nearby oilseed rape fields. Discussion of waggle dances' importance for foraging indicates that honey bees indeed are able to decode information within dances, but it is unsure how they use this. Dances are used for particularly profitable resources and therefore decoding provides an insight into which nearby resources the bees consider as such. We succeeded in decoding the waggle dance with a simple set-up, which revealed a clear correlation between waggle dance and distribution of resources in the surrounding landscape. This study is in contrast to the need for full-automatic methods and complicated statistical analysis.

Introduction

For animals living in social groups, communication is often an important and bearing element. For decades, the waggle dance of honey bees (*Apis mellifera*) has for many biologists been a fascinating feature. Here, the dancer vibrates her abdomen moving in a linear direction (waggle run) for then turning to either left or right to circle back to start (return phase). The average orientation of the bee's body relative to gravity approximates the direction to resources, and the duration of the waggle run approximates the distance (Von Frisch 1967a). This ability of the forager to communicate to its nestmates where resources are located has long been known. To which extent the nestmates are recruited, and actually follow the instructions, and even, as an observer, how to ascertain this as best as possible, is though still some of the most puzzling questions. This is for same reason what will be examined in this project.

It is widely known that honey bees are counted as economically savvy foragers. Dances are only advertising the most profitable foraging locations (Seeley 1994; 2012). Hereby is profitability and distance outweighed to determine whether to recruit other bees from the colony to this specific location (Schmid-Hempel & Schmid-Hempel 1987, Schmid-Hempel 1987, Seeley 1994). However, in which environments does the communication system seem to be especially beneficial? Studies indicate that dance communication plays a significant role in shaping how much colonies invest in exploring new resources vs. using some of them already known (Donaldson-Matasci & Dornhaus 2014). It seems further to be particularly useful in environments with many types of resources that vary in quality or is being ephemeral (Sherman & Visscher 2002, Dornhaus & Chittka 2004, Donaldson-Matasci & Dornhaus 2014). Waggle dance can thus improve the foraging-efficiency of the colony. It also means that if we can decode the dances correctly, we most likely get a processed and quite accurate message about only the most profitable locations relative to the current circumstances. This knowledge of space use may be interesting to analyse in relation to e.g. pesticide use in agriculture, climate change, etc.

Studies show that honey bees can fly over 10 kilometres for foraging if necessary (Eckert 1933 cited in Seeley 1995, Beekman & Ratnieks 2000). Still usually the foraging takes place within 1-3 km of the hive, if only good resources are available (Visscher & Seeley 1982, Couvillon et al. 2014b, Garbuzov et al. 2014). However, what is counted for a profitable location or resource may vary widely according to e.g. season, size of colony or potential nutrient deficiency. Just as the

recruiting success seems to do too. So, for the individual bee assessing the resource, what factors are then in play? And more importantly; to what extent does the waggle dance actually recruit following foragers? Unfortunately, and what might matter the most, is the fact that decoding is not so straightforward, even though we increasingly know a lot about it. It is so, that waggle dance of various bees, and even the same bee, exhibits noise in the directing of both direction and distance (Schweiger 1958). At the same time, there is an intra-dance variation making the decoding hampered and difficult to put on formula (Schürch & Couvillon 2013). Not just for biologists “eavesdropping”, but most probably also for the bees. It is further suggested that waggle dances might as well not just recruit foragers to the specific location danced for, but also re-activate memories of the recruiter (Grüter et al. 2008). This making the bee follow its own knowledge from earlier experience, rather than information contained in the dance (Grüter et al. 2008).

However, many researchers have through time been trying to decode the bees’ waggle dances. Gradually there are both very technologically, full-automatic methods, and vice versa very low-skilled, completely manual methods as well. In this project, we wanted to elaborate a simple and relatively cheap set-up and method, based on other previously used methods, to record and decode honey bees’ waggle dance. To further support our data, we mapped nearby resources within a radius of three kilometres from our observation hive and collected pollen from the same days as recording took place. This allows us to conduct whether we succeed to decode the dances correctly. The overall purpose of this project is therefore to examine how waggle dance can be measured in a simple manner, comprising whether our decoding data seems reliable. Hence, I also want to investigate what exactly the waggle dance’s importance is for the honey bees’ behaviour in relation to foraging, by examining the literature.

I will in the discussion be focusing on following themes:

- How is our semi-manual model useful as method?
- Are waggle dances reliable?
 - How effective is waggle dance in recruiting foragers?
- Why do honey bees even dance and for what?

As mentioned in preface, this project is part of a bigger investigation – for more analysis on the mapping of resources and pollen collection see Julie Ø. Frederiksen’s report.

Materials and methods

Study organism and location

We used a honey bee colony of Buckfast (a cross between *Apis mellifera ligustica* and *Apis mellifera mellifera*), which are generally known for being easy to handle. They were held in a combined observation hive and located on a farm in Hinnerup, Aarhus (latitude: 56.272307, longitude: 9.98722). The colony was placed in a permanent and private owned apiary consisting of four hives. Our colony was queenright, consisted of brood of all ages and about 5000 workers on six frames of Norwegian measure. Honey and pollen were visible in the combs during field days.

The surrounding landscape was mostly arable farmland with adjacent woods and some few and small urban areas with different types of gardening. The experimental area covered a circular area up to 3 kilometers in radius.

The experiment was conducted in early May (7th and 8th 2018), in a year with a bit delayed spring flowering. The abundance of flowering patches and number of flowering species was generally sparse for our particular area. It was mostly composed of oilseed rape, *Brassica napus*, wild cherry, *Prunus avium* and dandelions, *Taraxacum officinale*. But other plant species, especially different species of fruit trees, were flowering too.

The weather was ideal with no clouds, high sun and temperatures around and above 20°C. In addition, there was hardly any wind, also being ideal for this type of experiment.

The observation hive and set-up

The hive was custom made and consisted of an observation hive with two+two vertical frames on top of each other, a polystyrene isolated door and non-reflective glass. And then a normal sized box with room for 10 frames and the possibility to expand with ordinary supers if the colony was to grow. This was not necessary during our field days.

Because dances are mostly performed 4-18 cm from entrance opening with 94% of the dances within 24 cm of entry (Seeley & Towne 1992), the entrance was placed on the upper side in the right corner of the observation hive section. This is guiding the bees to a ‘dancefloor’, making it easier for recording. Furthermore, we built a tent of canvas fabric (figure 1), surrounding the observation hive. Daylight was therefore not visible for the bees, but still it was possible for diffuse light to come in. This was done to minimize errors of confusing the bees and thereby risk unreliable dances. Because when celestial cues as the sun, blue sky or even a bright artificial light source such

as a lamp is visible, this will make the bee orient its dances to this apparent azimuth (von Frisch 1973, Dyer 2002, Sherman & Visscher 2002). Without these, the bee will instead use gravity as reference point, with directly upward on the vertical frame equaling the sun's position (von Frisch 1973, Dyer 2002).

The camera used for filming was a webcam of type Sandström full HD 1080P placed on a tripod right in front of the hive. It was installed in such a height that only the upper frame was recorded, and the wooden edges visible for reference as plumbline when later decoding the films. We only recorded the upper frame, due to no sign of dances on the lower, supporting the dancefloor-observations by Seeley (Seeley & Towne 1992). The webcam was connected to a laptop computer through a USB-wire, allowing us to record the dances through Windows MovieMaker.



Figure 1: The observation hive with tent in front and stabilizing ropes. Photo: Annika S. Jeppesen



For avoiding condense water on the glass, due to temperature difference between the inside and outside of the hive when we needed the isolating door open for filming, we placed a small transportable oven in front, between hive and camera. This generated warm air which prevented condense, allowing us to record the dances through the glass.

Figure 2: Inside of the tent with the observation hive, oven, camera and laptop.

Photo: Annika S. Jeppesen

Data collection

Recording

The experiment was conducted over two coherent days, 7th and 8th may 2018, from 9:30 AM to 16:00 PM. Waggle dances were recorded during 10 minutes, then a twenty minutes' break and then again recording in 10 minutes etc. This was repeated regularly through the day with exactly the same procedure and intervals for both days, only temporarily interrupted midway due to leaving the location for mapping floral resources.

This procedure resulted in seven videos each day, making it a total of 14 videos each of 10 minutes. We did not use a clock on the hive, but every film was named after time at day and interval, allowing us to still determine the solar azimuth, as the sun moves 15 degrees per hour.

Furthermore, we had decided to record through the day from morning to afternoon, so we would be able to see if there were diurnal shifts in dances and resources used, and in order to get a diverse and complete picture of the colony's foraging as indicated by the dances.

Mapping

Within a circular area with a radius of 3 kilometres from the hive we mapped the floral resource availability. We had chosen 3 kilometres because of honey bees normally foraging within this zone. To produce the map we printed an updated orthophoto from Danmarks Miljøportal³ with natural habitats, such as e.g. meadows and watercourses, which were likely to contain wild flowers. We then visited these habitats within the specified area within the three-kilometre zone following this map. Within each habitat in the area, we categorized the available, and spatial most abundant, resources in different categories for herbs, shrubs and trees. This is because honey bee colonies are thought to only dance for large resources (see introduction). The floral resources found were identified to genus or species level and marked on our map. This allowed us to compare our dance directions with the surrounding environment later on (figure 7).

For further information about this method, see Julie Ø. Frederiksen's report.

³ arealinformation.miljoportal.dk

Pollen collection

We had two procedures for pollen collection.

On day one, we captured 22 bees bearing pollen with an insect net. We tried to cool them down with cooling elements, but this did unfortunately not succeed well enough. This forced us to bring them home for freezing allowing us to then collect the pollen.

On day two, we captured 38 bees. We now had more and better cooling elements, why we captured the bees near the entrance to the hive with an insect net, transferred them to a vial if they carried visible large pollen, and placed them on the ice-cold cooling elements. After a few minutes the bees were so cold that they lay completely still, making us able to remove the pollen on their hindlegs. For this removing-procedure we used the tip of a nail file. This allowed us to gently remove the pollen without damaging the pollen bags. After removal, we placed the bees on a black mat placed in the sun, letting the heat carefully wake them up. Pollen was collected in a vial. After a few minutes in the sun the bees flew away.

The pollen was then through the following week dried on paper, transferred to Eppendorf tubes and sent to QSI in Germany for analysis. For more information, see report by Frederiksen, J.Ø.

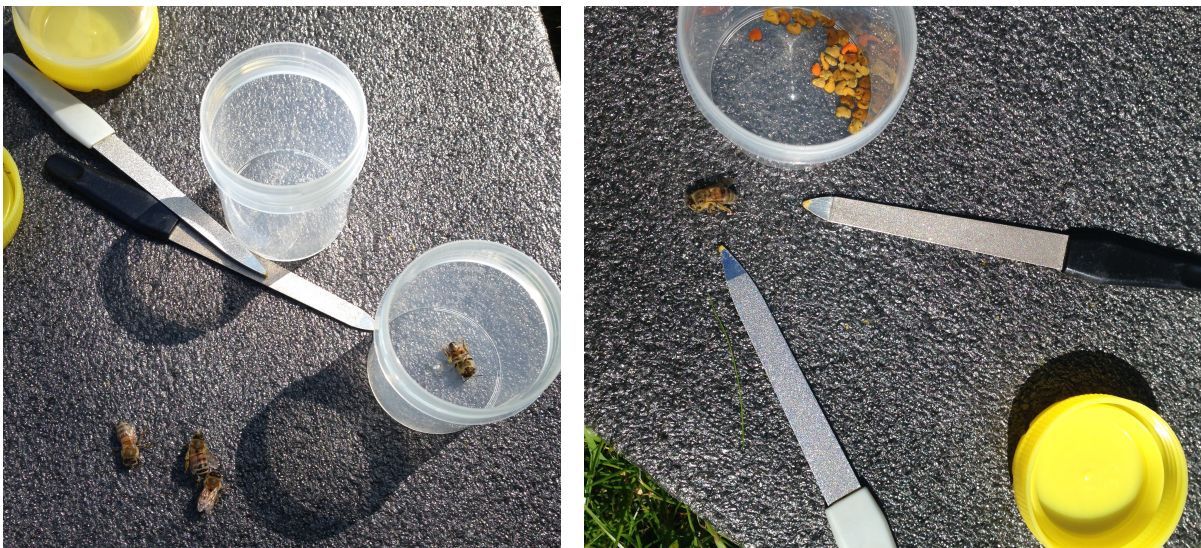


Figure 3 and 4: The bees after pollen collecting, ready for being warmed up by the sun. Collected pollen pellets can be seen in the vial (right, above), and the files were those used for prying off the pollen.
Photos: Annika S. Jeppesen

Decoding honey bee waggle dances

For the analysis, we used a newly developed semi-automatic method; an Excel macro named LetsDance. It was invented for this task by our supervisor Peter B. Sørensen. Here, we measured dances by measuring duration, which encodes distance to resources, and angle, which encodes the direction.

Each of our ten minutes' videoclips were played in e.g. QuickTime Player v.10.4, but any playback tool would have been useful for this. The film was stopped every time we observed a dancing bee, for which we first recorded the time of waggle runs by use of a stopwatch. We then cut out the specific dancing bee with a snipping tool, pasted the picture in our Excel macro and measured the angle by placing a vector pointing in the dancing direction (figure 5).

We only measured the waggle runs, not the return phases. This is because the important information lay within the waggle part of the dance (Michelsen et al. 1992), whereas the return phase, or the quickness of this, often is noisy because it depends on the bee's eagerness and the resource-quality (Seeley et al. 2000). We did not measure for dancing bees which were not reasonably constant in direction or time spent wagging. Neither did we measure runs where the dancing bee bumped into a nestmate, disturbing the dance.

When decoding, one of the possible, and here used methods, to deal with the variability incorporated in dances, is to take a mean of angle and mean of duration of four consecutive waggle runs, but not include the first nor the last, because these are proved to be significantly more vary than the middle runs (Couvillon et al. 2012). This too, because it is recommended to have an equal number of left- and right turned circuits (waggle phase+return phase) to equalize any angular bias (Couvillon et al. 2012). Nonetheless, inter-dance waggle runs vary, so most of all, it is just important to decode enough dances to obtain a good average. This made us partly ignore whether we had measured the same bee before or not, since it for the statistics was more important to measure as many dances as possible, and not so much whether it was for the same bees. It is important to notice, that we did not on purpose measure the same bee twice. But, if it moved to another part on the frame and began to dance again, then we most likely did.

Moreover, we had distributed the recordings, making my partner, Julie Ø. Frederiksen, decode the first seven Monday-recordings and I the following seven Tuesday-recordings. This resulted in respectively 97 and 130 measured dances, in total 227 decoded dances.

The time at day for the dance was noted in hour and minutes. Duration of waggle run, which was recorded in milliseconds, was automatically converted to flight length by one second equaling one

kilometer. This calibration is for simplicity an average of previous studies (seen in Schürch 2013), because the honey bee “odometer” is thought to be relative to landscape (Srinivasan et al. 2000). Besides, the duration is very variable due to intra- and inter-variabilities (Schürch et al. 2013), but also due to factors such as weather. Windy weather can e.g. make the bee grade distances as longer (von Frisch 1976b). In our field days, the wind speed was around 4 m/s and from a south/east direction.

The angle-measurements were set in relation to time and the solar azimuth. We had the GPS-coordinates for the hive and these were noted as well for the further calculations.

The decoding took us approximately 5 hours each, spread over four days. It could might as well have been done at fewer days, but we had the time and wanted to minimize bias as cause of being tired and unfocused. Which is indeed likely when during the same thing concentrated for hours. Even though one film was only 10 minutes in real time, it often took 30-45 minutes to decode it. This included playing the film twice to see if we missed any dance or whether our measuring was still the same.

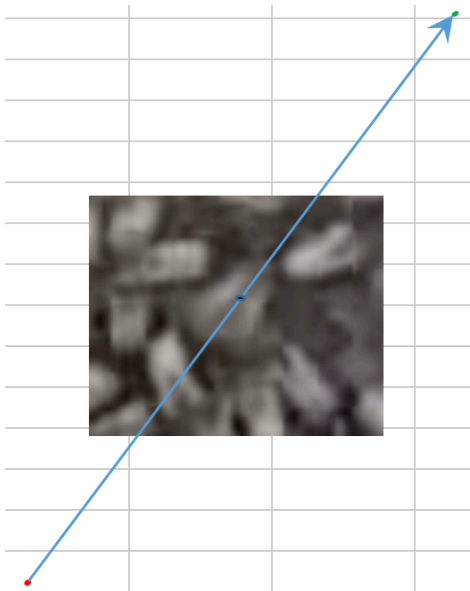


Figure 5: A decoding in our LetsDance-macro, with the arrow pointing in dance-direction for measuring the angle.

Analysis

To calculate a geographic point from information in dance

The angle to vertical on the frame, and therefore relative to gravity, corresponds to the angle to the sun. Time at day gives the geographic angle of the sun's position in relation to north and south. The angle to the sun can therefore be translated as the angle in relation to north-south. Time spent wagging gives the distance (von Frisch 1973, Dyer 2002). By use of coordinates, angle, time spent dancing and time at day, we ended up with endpoints for our bees' resource-location.

We presupposed 1 km/sec, meaning one second spent waggle dancing equaling one kilometer to resource danced for, based on mean predicted distances from Schürch et al. 2013.

Our data were further analysed in Microsoft Excel by Peter B. Sørensen. The thereby resulting UTM endpoints were afterward sent to our GIS-expert (Mette Balslev Greve) and plotted into ArcGIS. We compared this resulting orthophoto-map to our resource map made in the field days, by afterwards drawing our resource locations onto it (figure 7). For this we used Microsoft Paint but any drawing-program could have been useful.

Data from the two days have separated colours, respectively blue and orange, allowing to distinguish the patterns from one another.

Results

The decoding of the 227 waggle dances took us approximately five hours each, resulting in an average of 22,7 decoded dances pr. hour. Almost all of our decoded waggle dances resulted in coordinates within our three-kilometer zone, showing that foraging occurred nearby the hive as expected. More interestingly they resulted in a relatively clear pattern, independent of which day, showing that the foraging was divided in overall three groups (figure 6). When compared to our resource map it became visible, that these three foraging-spots all were more or less covered by oilseed rape fields (figure 7).

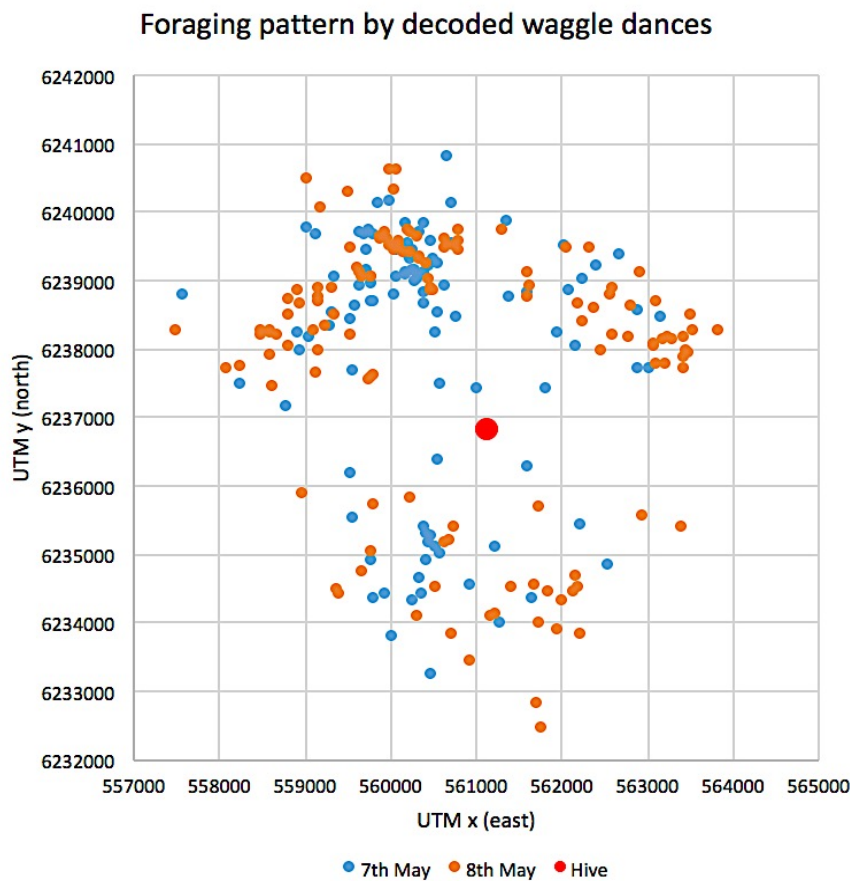


Figure 6: Showing the foraging pattern by decoded waggle dances for 7th and 8th May 2018. The two days are separated by color, respectively blue and orange, allowing to distinguish the patterns from one another.



Figure 7: The foraging pattern plotted onto our resource map. The decoded waggle dances for 7th and 8th May 2018 are separated by color, respectively blue and orange. Yellow: *Brassica napus*, oilseed rape. Pink: *Prunus avium*, wild cherry. Orange: *Taraxacum officinale*, dandelions. (Frederiksen, J.Ø 2018)

Compared to the resource map it became clear that our model may was imprecise, meaning there is a deviation between our mathematical decode-model and the data. Though direction and distance seemed more or less reasonable by grouping the points in areas of the most concentrated resource patches, e.g. avoiding the forest-belt in mid, still many points lay outside the plotted areas. Thus, our LetsDance model worked, conveying dances to geographic points, but it might needs to be calibrated. This could potentially be distance changed from 1 km/sec to 750-800 m/sec as found in other studies by e.g. Schürch et al (2013), due to many points lying to far north and south respectively. Another potential reason for displacement could be factors such as wind, even though it is unclear to what extent it effects (see discussion). Still, it is possible that some of those points outside the marked rape fields can be for private gardens, diverse nature fences and other resources

such as single trees. If they were not highly spatial abundant we did not map them, allowing the endpoints to be more or less correct even though we cannot locate for what.

Our decoding indicates that most of the foraging was less than three kilometers from the hive. This would be even clearer if our calibration was changed from 1 km/sec to e.g. 750 m/sec.

We see the bees concentrate on oilseed rape resources but only the most rewarding. This results in ignoring the oilseed rape fields neighboring the hive, which were fields almost not flowering, contrary to those highly flowering farther away.

Pollen analysis

Table 1: Results from QSI pollen analysis. Four pollen-types were identified and their abundance in approximate percent for 7th and 8th May 2018 respectively is calculated. Pollen from 7th May derives from 22 bees and 8th May from 38 bees.

| Pollentype | 7/5-18 | 8/5-18 |
|------------------------------|---------------|---------------|
| Acer spec. (Maple) | 02 | 09 |
| Pirus/prunus (Fruit blossom) | 50 | 51 |
| Brassica (Rape) | 46 | 34 |
| Taraxacum (Dandelion) | 02 | 06 |

Data validates that oilseed rape is a highly used resource in our two field days and thus correlates well with our decoding. Fruit blossoms are the most used, even though it does not clearly appear from our map and decoding. Further about the pollen analysis and thereto the specific abundances is examined in Julie Ø. Frederiksen's report.

Overall, our data show a correlation between a simple decoding of waggle dance and the distribution of resources in the surrounding landscape. This is even though we may need to adjust our calibration and lacked to map some potential resources. I argue that it therefore works well for the purpose of *indicating* important resources in landscapes. This is in contrast to references problematizing the use of waggle dance and/or argue that complicated statistical models are highly necessary for decoding waggle dances (e.g. Schürch et al. 2013, Couvillon et al. 2014b;2014c, Garbuzov et al. 2014)

Discussion

Our results clearly show our method works, resulting in a decoded forage pattern very reliable. Our dance decoding matches our resource mapping and collected pollen. It indicates that the honey bees foraged on nearby (~2,5 kilometres away) abundant resources. Especially some oilseed rape fields which we had previously categorized as high coverage. These were even some of the most flowering through the field days, making our analysis even more trustworthy and interesting. On the other hand, the pollen analysis showed that pollen from *Prunus* sp. was slightly more abundant in our samples. An explanation for this lacking match between samples and mapping could be that fruit blossom trees are more difficult to correlate with dance data, due to their spatial scattered distribution and the uncertainties in dances. Further, due to our interest in only spatially large resources, we did not map those resources not locally abundant. Trees graded as “few” will therefore not appear on our map. Hence, we argue that some of the endpoints far outside rape fields, in villages or near nature fences most possibly are correlated to those. For same reasons, we do still feel confident in our results.

It was not in our interest to train bees to reach known places such as feeders, and thereby experimentally control for the efficiency of dance language. Furthermore, we did not analyse dances for pollen or nectar separately, which we could have done by investigating the dancing bee more closely and see what it carried (Couvillon et al. 2014a). The reason for not doing this, is due to more interest in where the bees indicated profitable resources, compared to specifics on type of profit. Pollen collection is thus a simple method to obtain some control for comparison and we did indeed see a conceivable match to the decoding. If we had been more interested in how they graded the resources, and not only where they have been, we should not have limited our focus to only measuring waggle phases, but include the return phase too. When interested in the grading, then measuring dance rate is an often-used method and counted as the best indicator of the bees' subjective evaluation (Waddington 1982; 2001). Here, the number of reversals and duration is measured all together: The higher the dance rate, the greater subjective value evaluated by the bee (Waddington 1982; 2001).

How is our semi-manual model useful as method?

The work field of decoding waggle dances is growing and seems to be divided into full-automatic and to relatively manual methods. Early techniques used protractors and stopwatches for measuring

the angle and duration directly in the observation hive. This is obviously of high risk for errors, due to not being able to repeat measures or validate by e.g. double-check. Besides, we experienced many dances at the same time, impossible to manually measure all when not able to rewind. Nowadays, the most widespread technique is to employ digital video recordings and analyse the dances on screens afterwards. It is thus possible to pause, rewind and overall handle many more dances. This is often combined with more complicated statistical analysis tools and e.g. probability-distributions for mapping (Schürch et al. 2013). In another extreme, a completely automatized method is being developed for detecting, decoding and mapping dances in real-time (Wario et al. 2017). There is a growing tendency arguing that these more complicated techniques are highly necessary for decoding and mapping, due to e.g. the uncertainties in dances (Schürch et al. 2013, Couvillon et al. 2014b;2014c, Garbuzov et al. 2014). Our purpose was to combine different methods, but most of all keeping it relatively simple and cheap, making nearly everyone able to decode waggle dances. We wanted to see whether it is actually possible to deduce reliable data from a simple set-up and analysing tools. To this we succeed very well.

An aspect to keep in mind, however, is the time used for our semi-manual decoding compared to the need for e.g. automatic decoding. We, two persons, used altogether 10 hours for 227 dances, equalling an average of 22,7 decoded dances per hour. This was for 14 ten-minute recordings, covering two days. If we had recorded throughout the season, this could suddenly have been challenging in relation to man hour, unless the film is to be decoded during the period and not altogether in the end of it. In contrast, the full-automatic method developed by Wario et al., has greater potential when interested in recordings throughout the whole day, even months, and not just a few hours as we. This would be far too time-consuming to do manually. I argue though, that our few hours of “snapshots” are enough to get a trustworthy indication of how foraging is distributed in the area, why it for our study was not even necessary with full-day recordings.

Interestingly, the full-automatic method by Wario et al. is able to filter only relevant activity from the hives in real-time, due to being able to detect dances and only record these. This will undoubtedly reduce the amount of stored data, but also allow to only focus on the relevant; the dances. The risk is to blindly trust this, due to not completely knowing what might had been missed.

When using automatic decoding, it will further make greater demands to the whole set-up, e.g. well-defined and special light, well-defined placement of hive and frames, and also greater demands for the recordings, e.g. high speed and resolution (Wario et al. 2017). This is far less important in (semi)-manual decoding, why it is easier to manage. Furthermore, our semi-manual method can be

conducted directly in the field. In the full-automatic method there is (still) a need for laboratory-conditions, at least indoors, due to need of being able to control e.g. the light. This leads to some locational constraints when planning a study. Additionally, our method was conducted with a combined observation hive, which possibly heightens the relevance in results by making it even more realistic. This allowed us to not disturb the established colony, by moving parts of it to typical small indoor observations hives. This means further, that the bees in our study are free to expand, if the study covers more than a few days. These elements therefore also need to be considered when choosing method. Besides, if establishment of the automatic method is more expensive and/or has higher demands for set-up, it might be more realistic to use our simple method when interested in a few recordings from multiple hives, while the automatic may be beneficial when only interested in a few, but many recordings from same.

However, one of the most important considerations necessary when comparing manual to automatic is the level of induced error. Human error against technical. Never can one be completely sure, and it is important to check up on methods and moreover not simply rely on the technique. The full-automatic method from Wario et al. has an accuracy close to human performance, but sometimes still fails to e.g. recognize dancing bees (Wario et al. 2017). On the contrary, the advantage is that decoding does not have to be divided between several persons, as manually decoding often is, due to the number of recordings. I do argue that the possible minor uncertainties due to human error in time taking and determining angle, are not crucial. Small deviations are to be expected, just as the waggle dance is imprecise as it is. Depending on how accurate data is needed, this is not necessarily a problem. In our simple study the indications we got are enough to determine where the bees focus their foraging. The risk with relying fully on automatic is to not be aware of these deviations.

Are waggle dances reliable?

One of the main difficulties about decoding waggle dances is the lack of precise understanding of dances. We cannot differentiate between adjacent habitats (Schürch & Couvillon 2013), nor which species of flower the bee is actually dancing for (Schürch et al. 2013). We are only able to decode to a certain extent, but we cannot locate the exact foraging position. So, for our study, in the beginning of spring and by mapping the surrounding area together with pollen collection, we could better get a reasonable idea of where they went, and whether it was reliable. The great abundance of fruit blossom-pollen in our samples does illustrate these limitations due to being difficult to locate

exactly where these come from. They do, however, most likely derive from single trees around the landscape, difficult to pinpoint from single dance points. Conversely, the oilseed rape, which pollen were also abundant in the pollen analysis, are much easier to locate. This is due to their spatially large distribution and the clustering of endpoints from the decoded dances.

It is further so, that there is an incorporated variability in the dances (Schweiger 1958, Schürch & Couvillon 2013). This probably makes it just as difficult for the watching bees, as for the biologists, to decode the exact positions danced. Moreover, each honey bee possesses its own calibration making their indication of distance inaccurate leading to both intra- (Couvillon et al. 2012) and inter-dance variation (Schürch et al. 2016). As considered by Couvillon *et al.* a bee dancing for a nearby location is also necessitated to turn her body almost immediately, which results in less angular precision than for greater distances (Beekman et al. 2005, Couvillon et al. 2012). These points can thus be in accordance to our results with indicated inaccuracies in our mapped endpoints regarding to both distances and angles. We were able to see a reliable pattern, but it did not match perfectly to the mapped resources. It is therefore reasonable to ask, whether this is due to our calibration as hypothesised in results, or the bees struggling to convey exact information through dance? Most probably the answer is a combination. It has formerly been shown, that bees probably dance the best, meaning as precise as they can, and that, at least the intra-dance uncertainties, are non-adaptive (Preece & Beekman 2014). Even though, it is still unknown what the reason for the inter-dance variation is (Schürch et al. 2016). Still, it has the potential consequence that the recruited bees may not find the correct locations (Preece & Beekman 2014), here “correct” meaning the location described in the dance.

It is previously hypothesised that also external factors such as wind potentially can influence the bees distance-rating, thereby indicating a distance too far or too short. The honey bee odometer is thought to be visually driven (Srinivasan et al. 2018), and therefore it is possible that wind will influence how fast the images of the world moves by. In our field days, the wind speed was 4 m/s. von Frisch declared errors were established at all wind speeds above 1 m/s (von Frisch 1967b). He noticed this in his early studies, wherein bees flying against wind tended to signal a too large distance in their dances and vice versa for bees with tailwind. This meaning our slightly imprecise endpoints may also be correlated to the bees’ error in determining the correct distance, even though it is unclear to what extent it plays a role. Moreover, we do not know whether it affects the angle too. I do argue though, that it is more a potential difficulty for the biologists eavesdropping than for the bees. This depends on how the bees actually estimate the distance. If they use the same method,

it will result in the bees reaching the location danced for anyway. For us decoders, not yet able to integrate wind factors in decoding, due to not fully understanding how bees' assess this, we can only map the distance and angle danced. Until we know how, we can bear in mind to compare the data to weather forecasts, to see if there could be a potential correlation.

How effective is waggle dance in recruiting foragers?

The waggle dance does normally proceed inside a dark hive, so how do the bees even follow the dance if they cannot necessarily see it? For this, it has for example been hypothesized that it may have something to do with the wing movement: i.e. wing beats convey information about the foraging distance (Lopuch & Tofilski 2017). Furthermore, also vibratory (Tautz 1996), tactile by touching with their antennae (Rohrseitz & Tautz 1999) and auditory (Michelsen et al. 1986) cues, most probably play a role, as well as olfactory (Thom et al. 2007). But no matter how bees actually transfer the information within the dance to each other, it has still been noted, that the dance language may not be as effective in recruiting new foragers than first thought by e.g. von Frisch (Esch & Bastian 1970, Gould et al. 1976). As considered by Grüter and Farina (2009) both empirical and theoretical work suggests that a bee following a dance only needs to watch five to six waggle runs to be able to decode the dance and then being able to find the location (Esch & Bastian 1970). But in reality, as further stated by Grüter & Farina, the follower often needs to watch many more: Sometimes up to 50 waggle runs and even making small search trips before *might* succeeding in finding the resource (Esch & Bastian 1970, Mautz 1971, Grüter et al. 2008). Other studies found that bees following many waggle runs and most importantly; appearing to be especially active in this, also tended to use dance information to a higher degree than less active followers (Wray et al. 2010). It is still unclear why it is so: Whether there is just variance in how good or bad learners they are, generally has trouble with decoding, or might sometimes just simply ignore the information, for reasons we do not necessarily know.

In 2005, Biesmeijer and Seeley also studied to which extent honey bees acquired information through waggle dance. They were focusing on the bees' entire careers as foragers, starting from the novice who needs to find her first food source to the very experienced one. Between those is the experienced forager who has been interrupted in its foraging, e.g. due to rain or nightfall. The team ended up concluding that foragers not only use waggle dance to start working at new and unfamiliar resources, but also use it to resume their work at old and already familiar ones.

The first was mostly the case for the unexperienced and interrupted bees, whereas the latter was for the interrupted and experienced (Biesmeijer & Seeley 2005). Even more interestingly, they found evidence that bees overall more often used waggle dance for reactivating private information, meaning depending on own experience, rather than for recruitment for new resources (Biesmeijer & Seeley 2005). These private memories may be triggered through spatial information in dances or cues such as odours. This is leading the bee to ignore the information in the dance and follow its own memory and self-acquired navigational information instead. Actually, it has been investigated, that the dancing bee releases chemicals (Thom et al. 2007), and followers make contact to bodyparts probably smelling of the source danced for (Diaz et al. 2007). In continuation, it has been hypothesised that this type of cue is a component in the waggle dance especially important in activating own memories (Grüter & Farina 2009). However, a study in 2008 showed, that 93% of all foragers with private information about a location tended to ignore dances - but it was further proposed that the bees might also be able to switch their strategy and suddenly follow the social information in dances instead, if only the quality of the private information and known patch is below a certain threshold (Grüter et al. 2008). This was supported by a study in 2011 demonstrating that experienced foragers, with plentiful private information, flexibly could shift to relying on social information (Wray et al. 2011). Furthermore, these did to a higher degree rely fully on social information when foraging errors due to private information were costlier than following instructions (Wray et al. 2011).

As an interesting point to the difficulties for the bees to find what is danced for, it has been proposed that honey bee foragers adjust their crop contents before leaving the hive to find the guided location (Harano et al. 2013). This, with a positive correlation between distance and crop content (Harano et al. 2013). The team carrying out the study, found that dance followers were leaving the hive with a larger amount of honey, needed as energy source, than the dancers (Harano et al. 2013). This may indicate that followers indirectly prepare to search some extra for the specific target after arriving to the general area indicated, due to not being able to decode the dance perfectly. This is because the information is only approximate. Followers then may require more energy to find the food, compared to the dancer who already knows the route. This explanation is further supported by evidence pointing to the fact that bees reduce their honey load every time they repeat the same route (Harano et al. 2013).

Why do honey bees even dance and for what?

Why bees even communicate about where to find great resources is surprisingly still not fully understood. It is, however, strongly hypothesized and accepted, that it has to be due to being greatly beneficial for the entire colony. To further support this, one must remember that honey bee colonies do also consist of a group of scouts, which are those finding resources on their own, not following a dance as recruits. In 1983, Seeley suggested that the proportion of scouting bees are higher when resources are sparse, and conversely rarer when resources are great and dances therefore common (Seeley 1983). This hypothesis was further supported by Biesmeijer & Seeley, with a detected decreasing in scouts when resources were abundant due to season (Biesmeijer & Seeley 2005). It has previously been shown that honey bees whose follows a dance instead of searching on its own can collect more nectar (Seeley & Visscher 1988). This therefore supports the theory that communication makes food gathering more efficient, since the bees can focus on the most rewarding resources (Seeley 1986, Seeley et al. 1991) instead of allocating a lot of energy into food search, for resources not meaningful. Furthermore, the effect and level of advantageousness of waggle dance communication varies through environments. It is shown to be greatest in environments where floral species richness is high and the patches contain many flowers (Donaldson-Matasci & Dornhaus 2012). This again making the colony able to maximize its collection by concentrating on few, but greatly rewarding, resources. It is further noteworthy that it is possible some studies even underestimate the contribution of waggle dance for a colony's foraging success. This is because they fail to include those bees reactivating private information through dances, probably making the waggle dance even more efficient than calculated, as hypothesized by Biesmeijer & Seeley (2005). However, waggle dance being beneficial seems to correlate well with our data, with resources, here especially oilseed rape fields varying a lot in profitability, from almost not flowering to full bloom. It is strikingly how many of our bees visited, or at least danced for, the most flowering, but remove, fields, instead of those less flowering but nearby.

As a continuation, it is also important to bear in mind that it is not all foragers which perform waggle dances. It is exactly only those who visited the most profitable locations. Hence, decoding and following the dances makes us able to sort out the most notable resources and locations from those less meaningful to the colony at that time. Even between the waggle dances there is also differences. It is therefore, at least in theory, possible to rank the most important from those less. As

mentioned, the rate of return phase tells something about how much the individual bee grades the resource it is dancing for. This is even though we are not entirely sure exactly how they grade, and to which extent it can be translated as the colony's opinion. Similarly, patches rated as relatively better quality will generate more dances with more repeated waggle runs, which incidentally, is also believed to increase the number of recruitments (Couvillon et al. 2014b).

In our study, we clearly see more dances related to oilseed rape than fruit blossom, even though fruit blossom was a bit more abundant in our pollen analysis. This could potentially be a slight indication of the colony valuing oilseed rape as more profitable and therefore generating more dances. Choice test studies have previously been made, where bees have been offered feeders with pollen of different concentration (Beekman et al. 2016). It was observed, that dancers returning from a feeder containing higher pollen concentration were more likely to dance (Beekman et al. 2016). This result indicates and supports that honey bees indeed perform subjective evaluations of the resource. Studies also indicate that honey bees forage to balance the colony's nutritional deficiencies and specifically targets nutritionally complementary resources (Hendriksma & Shafir 2016). Waggle dances are thus hypothesised to help the colony to better complement its nutritional needs, hereby especially regarding essential fatty acids (Zarchin et al. 2017). They have been shown to affect colony foraging effort to specific pollens (Donaldson-Matasci & Dornhaus 2014), and since dances differ regarding what pollen was found, it is proposed that waggle dances help balancing the diet for the colony (Zarchin et al. 2017).⁴

Furthermore, honey bees are sensitive to foraging economics and very great at finding resources. They will therefore not unnecessarily forage on resources far away from the hive if closer options, in at least equal quality, are present (Seeley 1995;2012, Seeley et al., 2000). As mentioned in the introduction, bees are able to search an area for up to more than 10 kilometres. But normally they will stay within a radius of 1-3 kilometres. Previous studies have further shown that forage profit tends to decrease with increasing flight distance, which is based on a detected notable decrease in dance probability (Waddington 1982, Seeley et al. 1991).

In many temperate habitats, as the field site we used in Jutland, Denmark, spring is a season of great flower abundance. In contrast to this, summer has earlier been found to might be the most challenging season (Couvillon et al. 2014b). Bees then may need to go search farther from the hives, because of lack of resources, which will generate dances for more distant locations (Couvillon et al. 2014b), contrary to our ~2,5 km in this study.

⁴ For further reading of this topic, please see report written by Julie Ø. Frederiksen

Due to foraging ranges up to c. 10 kilometres which equals c. 100 km², and the fact that bees only dance for those resources valued as “best” (relative to perspective), decoding has huge potential in conservation tasks and land management issues. Knowing that bees will not search for patches distant from the hives if not necessary, means the dancing bees can be seen as indicators of resource-availability in a specific area (Couvillon et al. 2014b). This too, because honey bees are generalist foragers. Resources used by them, will thus account for a lot more pollinators and flower-visiting insects (Garbuzov & Ratnieks 2013). Due to the theory that waggle dances also help the colony to reach a balanced diet (Zarchin et al. 2017), this definitely has potential to be highly relevant in conservation tasks too. It means decoding dances might not only lead to the most profitable resources, but may also tell something interesting about what the colony needs.

Conclusion

In this study, we succeeded in recording and decoding waggle dances with a simple set-up and method. Our analysis showed a convincing pattern of waggle dance and the distribution of resources in the surrounding landscape. This pattern was supported by comparison with our resource-mapping and pollen analysis, showing that the colony concentrated its energy on oilseed rape fields and fruit blossoms. Together with decoding we argue they foraged on three specific nearby areas with oilseed rape fields, focusing on those flowering the most. The fruit blossoms were more difficult to correlate with our dance data, due to resources not mapped, their spatial scattered distribution and uncertainties in dances. Endpoints far outside rape fields are thought to be those.

As it is now, our model may have its limitations when the landscape is full of closely spaced resources. It is a prerequisite to our model, that angle to vertical equals the angle to the sun, and distance is 1 sec/km. The model may need to be calibrated regarding distance-measuring, but until knowing what exactly influences this, 1 sec/km is useful for indicating. Thus, the model works well in a landscape where it is possible to separate the resources from each other, as our three dominating areas with oilseed rape fields.

Our method is in contrast to the need for full-automatic methods and complicated statistical analysis. It does indeed take some man hours to decode by our semi-manual method, but this can be taken care by sensible planning and is outweighed by the easier and cheaper set-up. Furthermore, the full-automatic method is not necessarily more accurate than human performance. Thus, the need for such method only depends on the type of study. If reliable indications of resources used and how these are distributed is useful enough, then our method is highly recommendable. The

advantages are the simplicity and the possibility to use it everywhere. There are no locational nor practical constraints.

It is apparent from the examination of literature, that analysing decoded waggle dances is not necessarily straightforward. In general, dances definitely trigger the recruits to forage. Whether this foraging then is based on own memories or information from the dance, varies. The waggle dance contains many variabilities which can make it just as difficult for the bees, as for the biologists, to decode the location danced for. These can be due to both internal and external factors, as emphasized regarding to our model. Consequently, we still do not know the bees foraging pattern to a full extent just by decoding waggle dances. However, to a greater extent waggle dance does give an overall picture of where the, for the colony, profitable resources are located, which are in accordance with our results.

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