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Faculty of Applied Ecology and Agricultural Sciences

Sabrina Elisabeth Dietz

Master thesis

An assessment of optimal foraging in honeybees through decoding of waggle dances in an urban landscape

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Abstract

A global decline of honeybees (*Apis mellifera*) and other pollinators which are essential for pollinating crops and wild flowers has been reported throughout the last decades. One major cause is the loss of available resources due to agricultural intensification. Especially urban areas seem to become an important habitat for pollinators. In 2017, Stange *et al.* developed a habitat suitability model for pollinators indicating habitat quality in terms of available floral resources and nesting sites for the City of Oslo, Norway. Our aim was to analyse whether the foraging patterns of honeybees match with highly suitable habitat patches as indicated by the ESTIMAP model. According to the optimal foraging theory honeybees should visit the closest and most rewarding habitat patches from the hive location, maximizing energetic intake per unit time. Hence, we hypothesised that patches which were frequently visited by the studied honeybees also had a high habitat suitability value and vice versa. We studied honeybee foraging patterns over the summer 2017 by decoding 506 waggle dances from three bee colonies located at two study sites in the urban area of Oslo. The waggle dance is a communication tool of successful foragers to indicate rewarding resource locations to their nestmates. We used this unique behavioural trait to analyse how the used foraging patches of our honeybees are correlated with values of the ESTIMAP model by applying a beta regression model. Moreover, we examined to what extent the foraging patterns of two bee colonies placed in the same environment overlapped.

After decoding the dances, the foraging patterns showed that visitation probabilities of used patches were only for one location correlated with the habitat suitability values of the ESTIMAP model. Furthermore, we ascertained that there was also only a mediocre overlap between the foraging patterns of the two hives located next to each other. In general, most of the foraging took place close to the hive locations. With a mean foraging distance of 688 m, 490 m and 425 m respectively, the mean foraging distances of the three urban bee colonies are much shorter than the foraging distances from their colleagues in rural areas.

Factors that lead to the moderate correlation between the visitation probabilities of the decoded waggle dances and the ESTIMAP values as well as of the foraging pattern of the hives placed in the same environment can be of various nature. First, by decoding waggle dances we did not have insight where honeybees of other hives or wild pollinators forage. Thus, high suitability habitat patches might have been exploited by other bees. Secondly, human error in

the process of decoding the waggle dances might cause some inaccuracy in plotting the foraging patterns of our honeybees.

Overall, our study raises more interesting questions about the resource selection of honeybees and suggests that next to the distance and the nectar-reward of the floral resources, also the exploitative competition by other bees might play a role in the resource selection of honeybees.

Acknowledgement

A bird asked a bee "You work so hard to make honey, but people steal it all. Don't you feel sad?" The bee replied, "No, they might have a way of stealing my honey but will never steal the Art of making it!" *Unknown author*

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1. Introduction

Wild and domestic bees are essential to the pollination of wild plants and crops, thus contributing to the maintenance and health of ecosystems, which in turn is vital to human food security and well-being (Klein *et al.* 2018). Pollination can be achieved by animals (invertebrates as well as vertebrates), wind or water (Barrows 2000). Around 78% to 94% (depending on the climate zone) of the global cultivated crops and wild plants need pollination by insects or other animals (Ollerton, Winfree & Tarrant 2011). In this system, bees are the most important group of pollinators, visiting more than 90% of the 107 main crop types (Klein *et al.* 2007). Over 16,000 bee species have been described worldwide (Michener 2000), of which up to 50 species are managed, and about 12 are commonly used for crop pollination (Potts *et al.* 2016). Bees, both managed and wild, are important contributors to pollination on all continents except for Antarctica (Ollerton 2017). Of all bee species, the European honeybee (*Apis mellifera*) is the most commonly managed bee in the world, although there is growing evidence highlighting the importance of wild pollinators and the significance of diverse pollinator assemblages in contributing to global crop production (Garibaldi *et al.* 2013). Healthy pollinator assemblages and populations are very important for agricultural services: only the honeybee can increase the yield of 96% of all animal-pollinated crop types (Potts *et al.* 2010) with an estimated economic value of € 153 billion per year representing 9.5% of the global production value for crops used for the human diet industry in 2005 (Gallai *et al.* 2009).

In addition to economic benefits, pollinators also provide in general, and maybe especially in urban areas, cultural ecosystem services. Cultural ecosystem services are immaterial benefits such as recreation, health benefits or the accumulation of knowledge that humans obtain from ecosystems (Niemelä *et al.* 2010). For instance, the presence of natural features such as parks or green zones in cities demonstrably increases the quality of life in cities (Chiesura 2004). Moreover, spending time in parks and urban forests can reduce stress and improve mental health (Hartig, Mang & Evans 1991). Pollinators' contribution to cultural ecosystem services is particularly conspicuous in urban areas where a growing majority of people now live. Honeybees can facilitate the bond between humans and the ecosystems in which they live. By beekeeping, enhancing pollinator health (e.g. through planting wild flowers) or studying and observing pollinators in their natural environment, people are encouraged to spend more time in natural areas of cities (Moore & Kosut 2013; Jørgensen 2014). Furthermore, pollinators and their products also benefit society indirectly as sources of inspiration for art, music, literature, religion, traditions, technology and education which contributes to an overall social and cultural identity (Potts *et al.* 2016).

Beekeeping can also cause conflicts, especially when honeybees are an introduced species (Paini 2004). In Norway, the honeybee is an important pollinator of many mass-flowering crops such as oilseeds, fruits (e.g. apples, plums), legumes (e.g. peas, beans) and berries (e.g. strawberries) (Totland *et al.* 2013; Åström *et al.* 2014). A subspecies, the European dark bee (*Apis mellifera mellifera*) has probably occurred locally in the South of Norway after the last Ice Age when climate conditions were favourable for pollinators (Milner 1996). Nevertheless, all honeybees found nowadays in Norway have been introduced, even though swarms can establish in the wild for short periods (Totland *et al.* 2013). In cold regions of the world it appears that most of wild honeybee colonies perish during the winter - almost always due to starvation (Seeley 1983). Thus, in Norway, honeybees would likely hardly persist without the facilitation by humans or would only be found at low densities. Winter feeding of colonies and a general care and maintenance of domesticated colonies is necessary to keep honeybee colonies healthy and viable. At the same time, this will almost certainly lead to far higher densities of domesticated honeybees than they would occur in a natural way which might result in a competition for resources with wild pollinators in Northern areas (Goulson 2004). Honeybees can outcompete native bees and other flower visitors (Wojcik *et al.* 2018). The effects of honeybees on wild bee populations generally depends on the landscape context and availability of flowering resources: homogeneous landscapes offer less foraging opportunities for pollinators and increase the potential for competition more than complex and heterogeneous landscapes (Herbertsson *et al.* 2016). Pathogens from honeybees present another risk for wild insect pollinators (Fürst *et al.* 2014). *Varroa destructor* is an exotic parasitic mite that can spread several harmful viruses to honeybees, including the deformed wing virus, viruses belonging to the acute bee paralysis virus complex and the slow bee paralysis virus which can also be spread to wild pollinators (McMahon *et al.* 2015). For instance, the honeybee is the likely source of the deformed wing virus in wild bumblebee populations (Fürst *et al.* 2014).

Although urban areas can support a notable high richness of pollinator species, the habitat suitability for a wide range of pollinators in urban areas remains generally unclear (Baldock *et al.* 2015). A review on the current knowledge about the effects of urbanization on bee species suggests that urban areas can be thoroughly positive for the abundance and richness of bees (Hernandez, Frankie & Thorp 2009). Especially, in an era of agricultural intensification, functionally important species in agricultural ecosystems i.e. pollinators suffer from the current farming procedures (Gallai *et al.* 2009). For instance, the species richness of bumblebees can increase in urban areas compared to the surrounding rural habitat. Also, several studies indicate that it is possible to find a higher abundance of cavity-nesting bee species in urban settings and fragmented habitats than in suburban areas or predominantly natural landscapes (Hernandez, Frankie & Thorp 2009). However, the effects of urbanization may also lead to a shift in bee communities from more specialized (e.g. short mouthparts pollinators) to more generalist species (e.g. honeybee) (Geslin *et al.* 2013). In response to potential deleterious effects of a high honeybee abundance on wild bee populations, Oslo municipality is considering implementing measures aimed at diminishing the conflict between wild pollinators and honeybees. The Oslo region is home to the highest biodiversity of red listed insects and pollinators in Norway (Henriksen, Hilmo & Kålås 2015). At the same time, the city is undergoing a rapid raise of beekeepers and honeybee colonies (Klima- og Miljødepartementet 2009). Thus, the Oslo Urban Environmental Agency has proposed eight "precautionary zones" within the area of Oslo (Stange *et al.* 2017). In these zones, beekeeping will be more strictly regulated. The largest of these suggested precautionary zones covers the entire coastline along the Oslo fjord as well as many islands located within the fjord containing habitat suitable for rare and threatened insect pollinator species.

To better understand how pollinators would use the urban area of Oslo, the ESTIMAP (Ecosystem Service Mapping Tool) model for the City of Oslo was created by researchers of the Norwegian Institute for Nature Research (Stange *et al.* 2017). Based on literature studies and advice from experts, scores that expressed the land unit's suitability for pollinators in terms of availability of floral resources and nesting sites were defined. To model the habitat suitability of the urban area of Oslo for pollinators, spatial data provided by the municipality was used to generate polygons based on 33 different landscape categories - amongst them 14 different types of forest. In accordance with experts on the local pollinator taxa, the landscape categories were valued 0 or given a value close to 0 if they were incapable of providing either floral resources or nesting sites. In contrast, if the landscape category represented the best possible habitat within Oslo it was given the highest habitat suitability score 1. For instance, land cover categories that are expected to offer a continuous availability of floral resources throughout the whole foraging season received the full habitat suitability value (Stange *et al.* 2017). The ESTIMAP model shows that in an urban setting, the patches of resources are usually very heterogenous and of different quality (Stange *et al.* 2017). However, this spatial and temporal distribution of resources is particularly important for central place foragers such as honeybees (Dukas & Edelstein-Keshet 1998). Central place foragers are animals which start their foraging excursions from a central location and return to that location between their searches for resources. The distance bee foragers have to fly to locate floral resources is a key determinant of survival of colonies, especially where resource patches are widely dispersed and distant from each other (Schmid-Hempel & Schmid-Hempel 1998). According to the optimal foraging theory, the optimal usage of the energy and time budgets available for an individual is straightforward: a foraging activity should be only continued if the resulting gain in energy per unit food exceeds the loss in time and energy spent per unit food (Goulson, 1999, MacArthur, 1966). Thus, in context of pollinators, foragers will maximise their net rate of energy intake by foraging close to the hive location while selecting the most nectar-rewarding floral resource in the area (Núñez 1982; Visscher & Seeley 1982). Variation in foraging distance and area depending on the distribution of resources has already been demonstrated for honeybees by means of decoded "waggle dances" of foraging bees (Beekman & Ratnieks 2000).

The waggle dance is a fascinating tool of communication that was decoded more than 50 years ago. Karl von Frisch showed that honeybees communicate the locations where rewarding food or other resources could be found using ritualized body movements which von Frisch called dances (Von Frisch 1967). These dances, performed by foragers that returned to their nest, had been depicted by many observers over several centuries (e.g. Aristotle around 350 B.C.) and had long been assumed to play an important role in communication about food (Dyer 2002). Thus, Von Frisch's discovery that honeybees can communicate spatial information was most certainly one of the seminal and major findings in behavioural biology in the twentieth century and was rewarded with a Nobel Prize in Physiology or Medicine in 1973 (Couvillon 2012). Honeybees perform the waggle dance to communicate rewarding locations where their nestmates can find either pollen, nectar, water or new nesting sites (Von Frisch 1967; Dyer 2002). The waggle dance consists of multiple circuits of alternating left-hand and right-hand loops, intersected by a straight segment in which the bee vibrates her abdomen from side to side. This straight segment is called the waggle run (Von Frisch 1967; Tautz *et al.* 2004). The distance and direction of the resource location are encoded in the duration of the waggle run and in the orientation of the dancing bee relative to vertical during respectively (Von Frisch 1967). The bees use a visual odometer to define the flight distance needed to the resource location. The distance measurements determined by this odometer are corresponding to the structure of the landscapes through which the honeybees navigate. When bees fly through a structured nature, the facets of the compound eyes of bees register images of objects. This "optical flow" helps them to determine their flight speed (Tautz 2008). Thus, the honeybee's sensation of the distance they flew during the foraging trip is not absolute, but highly dependent on the complexity of the landscape (Tautz *et al*. 2004). For instance, an experiment conducted by Tautz *et al.* (2004) indicated that the bees' sensation of distance travelled (as translated from the length of the waggle run) is shorter for flights over water (representing a highly monotonous landscape) than over land. In the orientation vector, the dancing bee communicates the direction of food relative to the sun and incorporates its determination of the current solar azimuth (Dyer & Dickinson 1994). The waggle runs will usually be repeated a variable number of times (1 to >100) in a single dance performance (Seeley, Mikheyev & Pagano 2000) while variation occur in dance durations and directions (Dyer 2002; De Marco, Gurevitz & Menzel 2008). Bees which follow the dance take then an average of the runs to derive a single distance and direction of the resource location (Tanner & Visscher 2008).

To assess the appropriate scale for the precautionary zones in the City of Oslo, to conserve wild pollinators as well as honeybees and to enhance both their pollination services, it is important to understand how far honeybee individuals are foraging and how foraging patterns of honeybees are distributed across the urban landscape of Oslo. Furthermore, it is important to know how resource availability might influence the observed foraging distances of honeybees from the three studied colonies. Since bees only dance to advertise the most profitable resource locations, the dances present filtered information about the most reward-promising foraging locations known to a colony at that time (Seeley 1994). Based on this knowledge, the optimal foraging theory and resource availability within the urban area of Oslo, we compared the *predicted* resource locations (as shown by the ESTIMAP) with the *actual* resources used by the bees which can be derived from the decoded waggle dances. This was accomplished by using three glass-walled observation bee hives at two locations in Oslo filming waggle dances from the 1^{st} of July 2017 till the 14^{th} of August 2017. Thus, the decoded waggle dances allowed us to investigate whether the frequency of visited resource patches matches the expected floral resource availability (as expressed by the ESTIMAP model). We predicted that patches which a high visitation frequency by our bees also had a high habitat suitability value and vice versa. Finally, to assess whether a small number of studied colonies are representative to make general statements about the foraging behaviour of honeybees in Oslo, we wanted to quantify if and to what extent the foraging pattern of two colonies placed directly next to each other can be considered correlated, thus to what degree the visited resource locations of both colonies overlap. Based on the optimal foraging theory and the fact that both colonies had access to the same resource locations we predicted that the foraging patterns of both colonies would overlap to a large degree.

2. Material and Methods

2.1 Study species and location

During the summer 2017, we studied three honeybee colonies in the urban area of Oslo, Norway. This study constituted a pilot stage designed to test waggle dance-based mapping within the context of a long-term surveillance of honeybee foraging behaviour in Oslo. Time and expense budgets were limited to utilize only three bee hives at two locations. The City of Oslo is located at the northernmost end of the Oslo fjord in the eastern part of Norway (59′ 55N, 10′45E). Its climate is characterised by mild winters (average January temperature = -3°C), warm summers (average July temperature = 18°C) and a relatively short growing season (177 frost-free days per year) (Stange *et al.* 2017).

We selected hive locations that provided variation in the availability of flowering resources in the immediate vicinity. We placed one hive on the peninsula of Bygdøy, surrounded by land characterized by agricultural fields, forests and residential zones. We placed two other bee hives in the Sogn Hagekoloni allotment gardens in the Ullevål district (hereafter Ullevål 1 & Ullevål 2) about 3 km directly north of the city's centre (see Figure 1). The two hives in Ullevål are placed closed together at a distance of around 20 cm and offered the possibility to evaluate whether the same foraging patterns emerged with regard to communicated resource locations and access to the same floral resources (for a picture of the setup of the hives see section Data collection). The allotment gardens in the immediate vicinity contained presumably higher abundance of ample floral resources than could be found on the Bygdøy peninsula, with low suitability foraging habitat to the south and moderate-to-highly suitable foraging habitat to the north of the Sogn location. Moreover, these two selected locations (Bygdøy and Ullevål) allowed us to test whether honeybee foraging patterns would mirror the distribution of the floral resources surrounding the hives as shown by the ESTIMAP model.

Each colony consisted of approximately 5,000 workers of mixed European race, predominantly *Apis mellifera carnica* (around 90%) (Jørgensen, personal communication). We controlled for the effects of genetic background by dividing bees and brood from one large colony onto two frames that were then divided and used in the observation hives at the Sogn location. Additionally, we used queens bred from worker eggs from the same hive to assure that the two queens have the same, or at least a similar genetic background. We housed colonies in glass-walled observation hives consisting of two vertically stacked Langstrothstyle deep frames and periodically removed bees over the study period to keep a consistent number of bees and to prevent swarming (Seeley 1995).

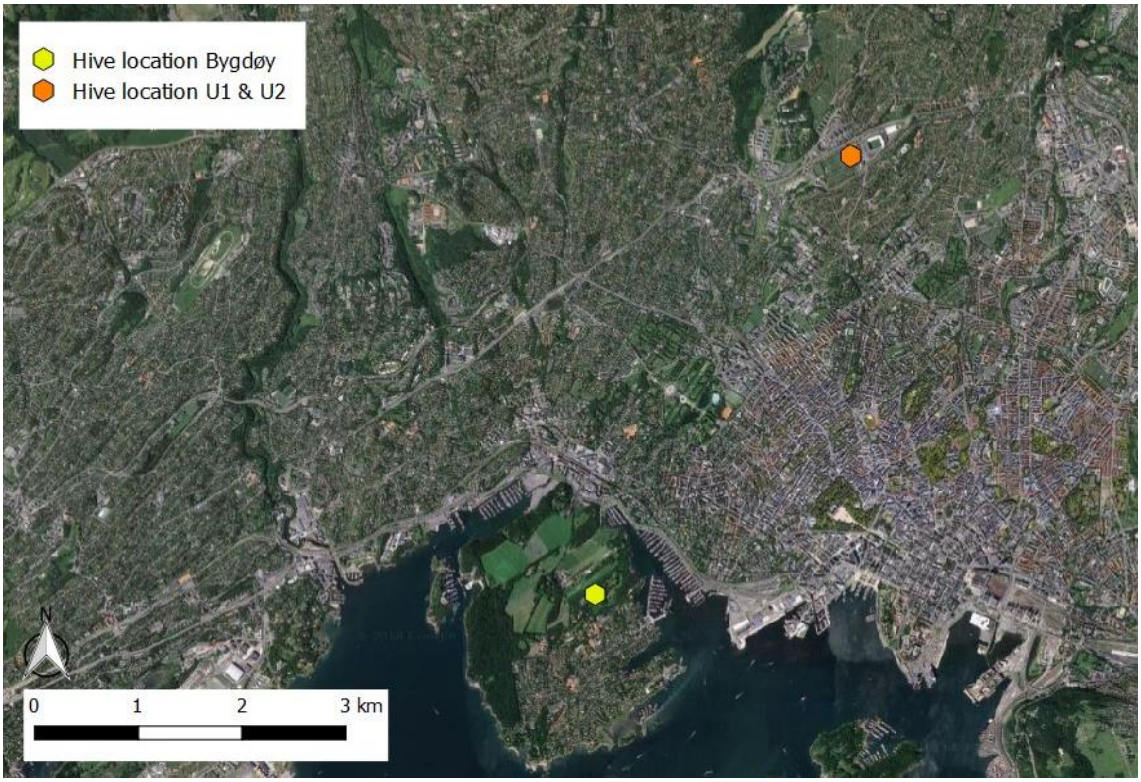


Figure 1 One bee hive is located on the peninsula of Bygdøy, the other two bee hives (U1 & U2) are located in the Sogn Hagekoloni allotment gardens in Ullevål.

2.2 Data collection

We filmed honeybee dances in observation hives on 28 days between July 1st to August 14th, 2017. We filmed only on days with suitable foraging weather (over 15 degrees, no strong wind or rain). On each of the days we recorded videos (25 frames per second) for one to two hours per hive, using a Canon EOS 700D camera positioned approximately 0.3 m from the glass case and focused on the lower frame where most dances occurred. Moreover, we covered the hives and camera with an awning during filming (see Figure 2) because direct sun exposure might redirect the bee´s impression of the foraging direction and would lead to errors in the foraging directions dancing bees communicate (Seeley 2009).

Figure 2 The bee hives Ullevål 1 + 2 and the camera are about to be covered with an awning (A). Once the awning is on top of the hives, the lid of the hives could be opened and the filming process of the dances on the lower frame could start (B).

We used a digital clock that was attached to the glass wall of the hive and visible within the video clip to document the exact time of each waggle dance. We stored all videos on external hard drives and processed them with a video editing program (Filmora Version 8.4.0, Wondershare Softare Co, Ltd.). We played the footage until we detected a bee performing a waggle dance. We decoded the waggle dances following the protocol of Couvillon *et. al*. (2012). The duration of the waggle run was measured by going frame by frame through the footage to detect the start and the end of the vibration of the bee´s body. The time was taken by the timer of the video editing program with a precision of 0.04 sec. To define the direction of the foraging location indicated by the dancing bee, we measured the angle towards the vertical of the hive with the open source software OnScreenProtractor (Version 0.5) which measures the angle as a clockwise heading from the vertical of the hive (see Figure 3). Time of the day (derived from the digital clock in the video frame) was used in the calculation of solar azimuth using the R function “sunPosition”. To obtain the final angle, we added the azimuth to the angle measured with the OnScreenProtractor.

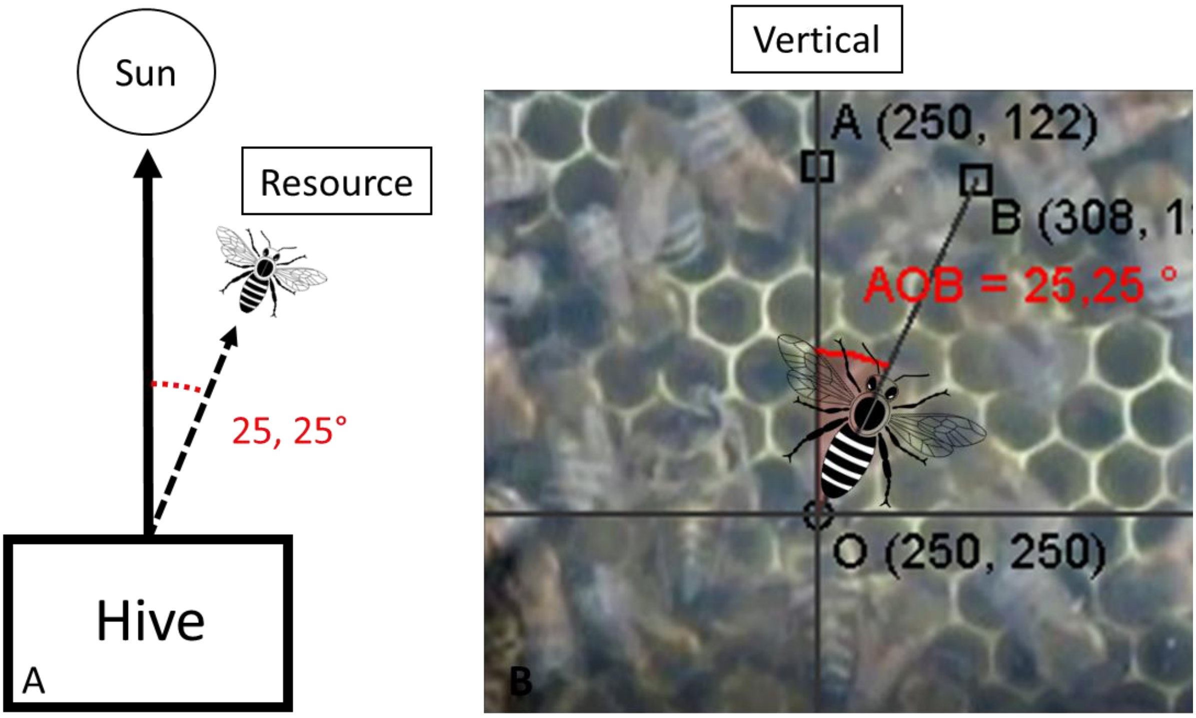


Figure 3 Angle of the dance towards the vertical of the hive (B) shows the direction of the resource in relation to the sun (A).

2.3 Data analysis

We translated observed waggle dances into communicated foraging locations by determining the duration (in seconds) and angular direction (degrees from vertical) for each dance. However, both components contain noise in their signals: waggle runs performed by different bees can differ slightly in their length and direction even though they aim to indicate the same foraging location (Towne & Gould 1988; Couvillon *et al.* 2012b). Translating and plotting the dances as specific points would therefore highly overestimate the accuracy of the foraging location (Schürch *et al.* 2013). We used a probabilistic approach, and applied a Bayesian duration to distance calibration model created by researchers from the University of Sussex, hereafter called the "Sussex calibration model" (Schürch *et al*. 2013). A calibration curve is a model representing the duration of the averaged waggle runs against the distance to the resource location (Scheiner *et al.* 2013). Generating a calibration curve specifically for the Oslo area was beyond the scope of this study and deemed unnecessary by the authors of the calibration model we used (Schürch, personal communication). Because we were interested in the honeybees' general foraging patterns, we did not differentiate between dances for nectar versus pollen. We quantified the error in the prediction of distances from run durations with

JAGS 4.3.0 from within R with the package *rjags* (Plummer 2016). Schürch *et al*. (2013) built first a linear model with duration as the response variable and distance as the predictor (see Figure 4) and reformulated the linear model then in a Bayesian framework.

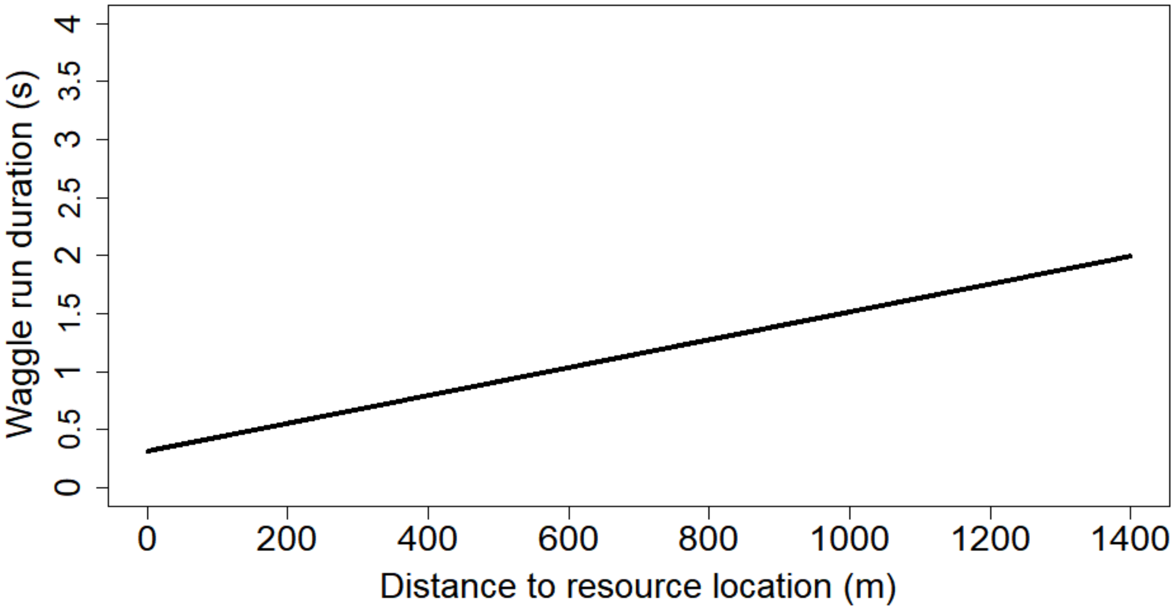


Figure 4 Linear duration to distance calibration model for the landscapes of Sussex. Model parameters can be acquired from Schürch et al. (2013).

The waggle run duration was modelled as a Normal distribution $N(\mu,\tau)$ with a Gamma prior for the precision $\tau \sim$ Gamma(0.01,0.01). To model unknown distances based on waggle run duration measurements, we assumed N (μx,τx) with a prior expectation for the mean $\mu x \sim$ Uniform(0, 14000) and $\tau x \sim$ Gamma(0.01,0.01). As suggested by Schürch *et al.,* we chose the non-informative uniform prior μ_x as the only prior so that the dances would range from 0 to 14 km. We used four MCMC chains and a burn-in of 300,000 iterations. We thinned the results by taking every 100th sample from an updated 100,000 iterations which resulted in a final sample size of 1000 simulations per dance. Thus, using a Bayesian linear calibration curve gave us the possibility to calculate new distances from known waggle run durations including an error distribution around the estimated distance.

To calculate the directional scatter for each dance, we used a von Mises distribution. We used therefore the *rvonmises* function from the *circular* package with a final sample size of 1000 and the concentration parameter κ set to 24.9 as estimated by Schürch *et al.* (2013) (Agostinelli & Lund 2017). A concentration parameter which is zero represents a circular distribution that is uniform, if it is greater than zero the distribution is ranging in a sector of the circle (Mardia 1975). Thus, for each initial heading as derived from the waggle dance we had now 1000 simulated headings ranging in a certain scatter. Finally, we combined the calibrated distance distributions from the calibration model with the directional component: we calculated the foraging locations by adding the simulated distance*simulated heading vectors to the coordinates of the hive location. This latter approach ensured us that one foraging location is not only plotted as a single point, but as a probability distribution which can be represented as a colour-coded probability cloud.

For all the dances, we determined the probability (from 0 to 1) that a specific bin (25m x 25m) has been visited as $pvisited = 1 - (1 - pvisited_1) * (1 - pvisited_2) * \cdots * (1 - pvisited_n)$ where $(1 - pvisited_i)$ is the probability that a certain square had not been visited according to a certain dance i. We chose the size of the bins so that the resulted probabilities would range from 0 to 1. We analysed then the relationship between the foraging probability and landscape attributes by first plotting the dance probability as a raster layer, converting simulated foraging locations to raster values which we created by using the *rasterize* function from the *raster* package in R (Hijmans 2017). This probability could be then visualized as a heat map. To project the dances on a map, we imported the raster layer into QGIS (QGIS Development Team 2018) and placed the raster layer on top of a Google satellite map. Additionally, we plotted the hive location, the 50th and the 99th foraging distance percentile. The resulting figure allowed us to have an overview of the urban area of Oslo in which the observed honeybees are foraging. For all the data analysis, we used the R version 3.4.1 (R Core Team 2017).

2.4 Landscape analysis

Since honeybees only perform the waggle dance when they return from a profitable location, the information retrieved from the waggle dance is a good indicator for suitable habitat available and known to the colony (Seeley 2014). The honeybee measures the profit based on the relative caloric reward since they must spend time and energy visiting flowers (Waddington & Holden 1979). The benefit to cost ratio depends on a complex of factors

(Waddington 1980). A major factor is the flight distance which is largely determined by the flower spacing around the hive. Therefore, the visitation probability is decreasing non-linearly with distance from the hive (Couvillon, Schürch & Ratnieks 2014a) as shown in Figure 5 where we exemplarily used the decoded distances of the Bygdøy hive. Thus, to evaluate the relative importance of habitat suitability as expressed by the ESTIMAP values to honeybees, we corrected not only for distance but also for 1/distance by adding it as a covariate in the model as conducted in a previous study using dance decoding to study honeybee foraging behaviour (Couvillon, Schürch & Ratnieks 2014a). Since our dependent variable, the visitation probability, assumes values from 0 to 1, we logit transformed the probability and used the following linear model to describe the relationship between the visitation probability and the distance to the hive: $p_{visited.logit} \sim distance + I(1/distance)$.

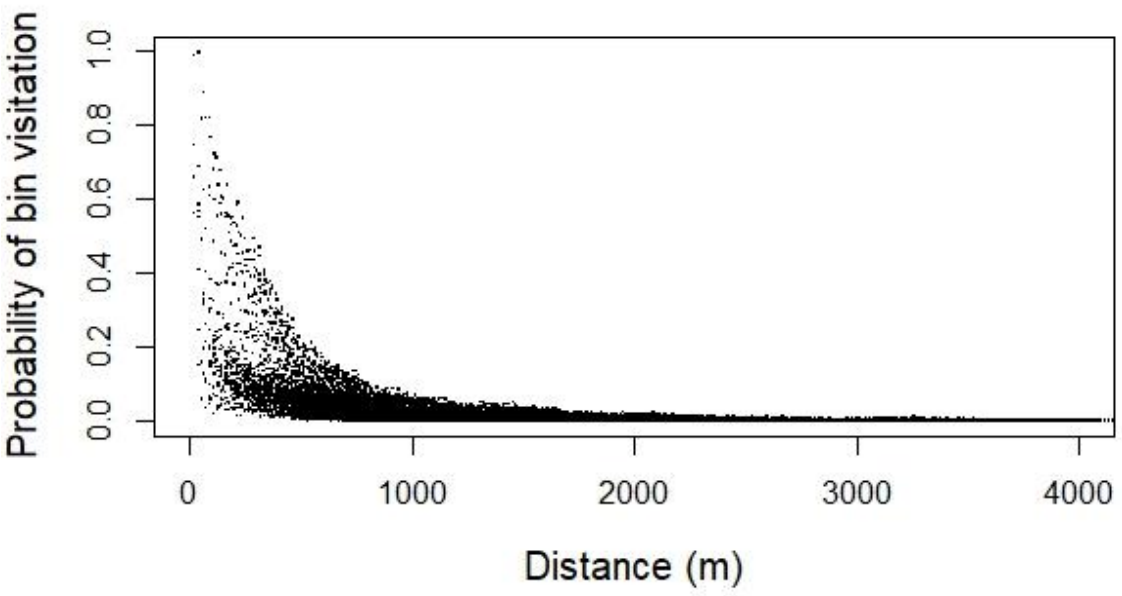


Figure 5 The black points represent the probabilities of each bin visited during the study period in relation to the distance from the hive location (here: Bygdøy location).

To explain the further procedure and the next steps of the spatial analysis of the decoded waggle dances, we used the data of the hive that was located on Bygdøy as an example. Results and values for the location Ullevål 1 and Ullevål 2 are given in the result section. Our ultimate goal was to know which areas are visited more, while taking into account the fact that bees value some resources more than others. For instance, Schürch *et al.* (2013) showed that a nature reserve 2 km to the south-east of their studied bee hive would without the correcting of distance not show up as an important foraging location since it is too far away – even though the nature reserve was frequently visited and represented a good habitat for pollinators. The residuals of the linear model expressed therefore the corrected measure for the variation in the visitation probability once distance is accounted for. When we plotted the residuals of the model for the Bygdøy dances, it was visible that areas with a high visitation probability are clustered together (see Figure 6), which is an indicator for spatial autocorrelation. In this context, the level of spatial autocorrelation showed to which degree the visitation probability of one bin is more similar with the visitation probabilities of its neighbouring bins than with the visitation probabilities of bins further away. To check for spatial non-independence of the 25m x 25m bins, we calculated the Moran's I value with the *Moran.I* function from the *ape* package (Paradis, Claude & Strimmer 2004). A Moran´s I value of 0.973 confirmed that the values of the visitation probability cluster spatially and indicated therefore a high degree of spatial non-independence of our data at this resolution. This occurred for two reasons. First, the method we used to plot the dances implies that we visualize honeybee visitation as a probability distribution. Second, adjacent areas tend to share similar land-use characteristics (Couvillon, Schürch & Ratnieks 2014a).

To deal with the spatial autocorrelation we adapted a blocking design, which is an approved method to correct for autocorrelation (Keitt *et al.* 2002; Couvillon, Schürch & Ratnieks 2014a). We used the *gstat* package in R to calculate the variogram to be able to apply the right block size (Pebesma 2004; Gräler, Pebesma & Heuvelink 2016). A variogram is a function that describes the level of spatial dependence of a random spatial field. The fitted variogram model provided us with a range of 423.61 m and a psill of 0.05. The range represents the distance limit beyond which the data are no longer correlated. Thus, we chose a block size of 400m x 400m (0.16 km^2) to minimize the spatial dependence as well as to incorporate the foraging resolution of the honeybees. A block side length of 400 m implies that the smaller bins must increase by a factor of 16. We created a random block raster with the *aggregate* function which can be laid over the raster of the ESTIMAP model (Figure 7).

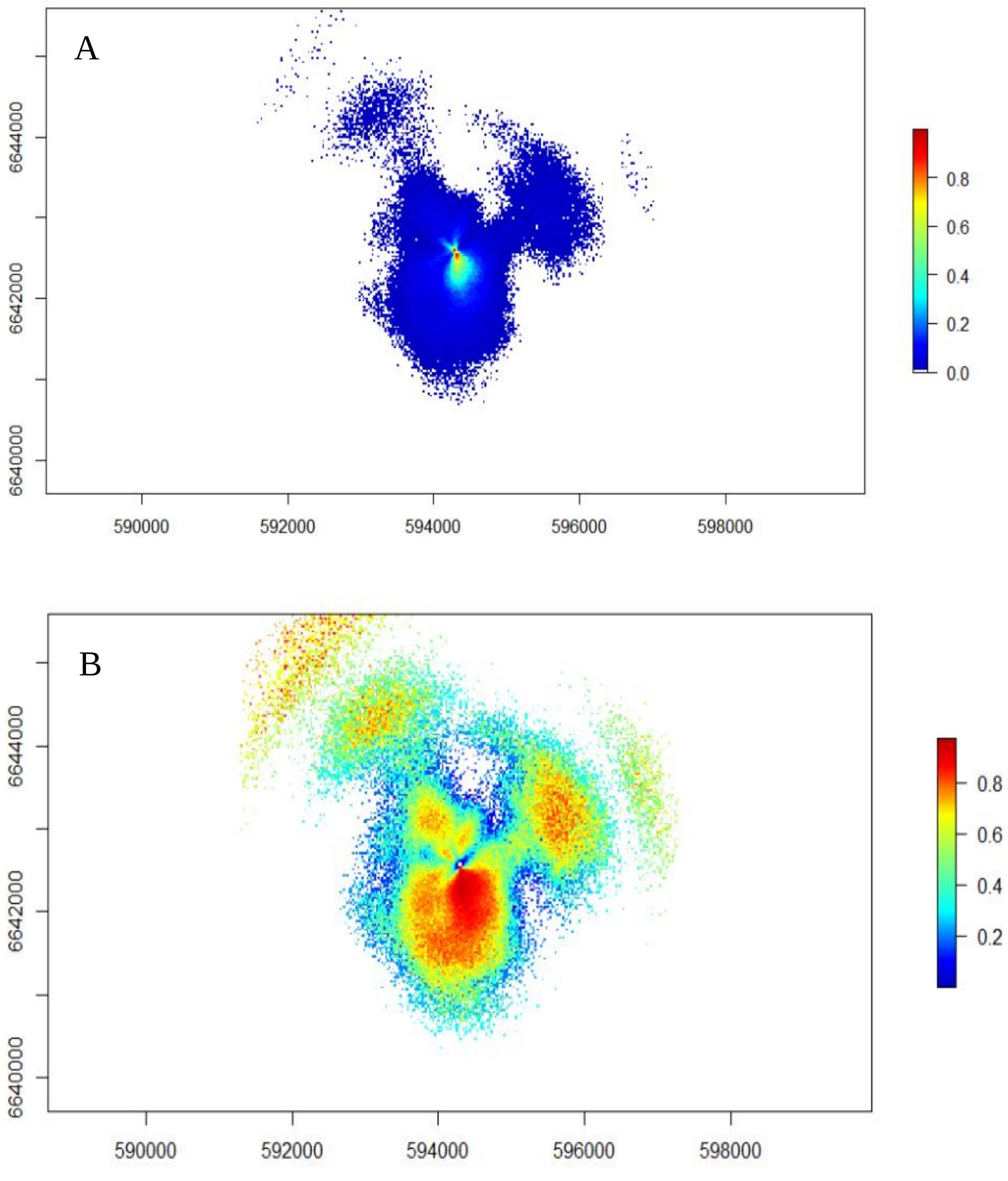


Figure 6 Visitation probabilities of 25 x 25m bins of the colony on Bygdøy before (A) and after (B) the linear model was corrected for distance.

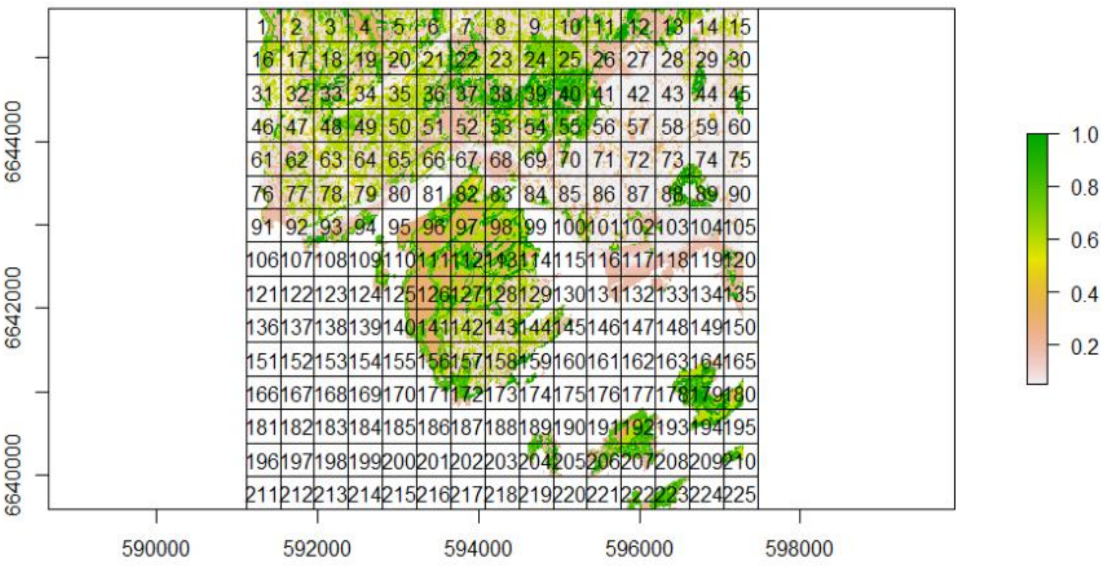


Figure 7 The random blocks on top of the ESTIMAP model representing habitat suitability values from 0 to 1.

Since we wanted to correct for spatial autocorrelation we fitted a model where each block has its own intercept by adding the block variable as a random factor in a linear mixed model. Thus, we expanded the previous model in the following way: $p_{visited.logit} \sim distance + I(1/distance) + (1|block)$. To build the linear mixed effect model, we used *lme4* package (Bates *et al.* 2015). A residual plot from the null model illustrates that, instead of grouping together, the colours – representing the visitation probability – are now randomly distributed across the map (see Figure 8). Since each block possess its own intercept, we could extract the visitation probability for each of the blocks. The 99th percentile for the distances of the dances is 2840 m for the Bygdøy location. Therefore, we decided that no block should be included in the analysis whose closest corner was beyond 2840 m. This resulted in 185 included bins compromising in total an area of 29.6 km². By ranking the blocks, we could asses which of the 185 blocks are the most visited by the honeybees of the three locations (see Figure 9).

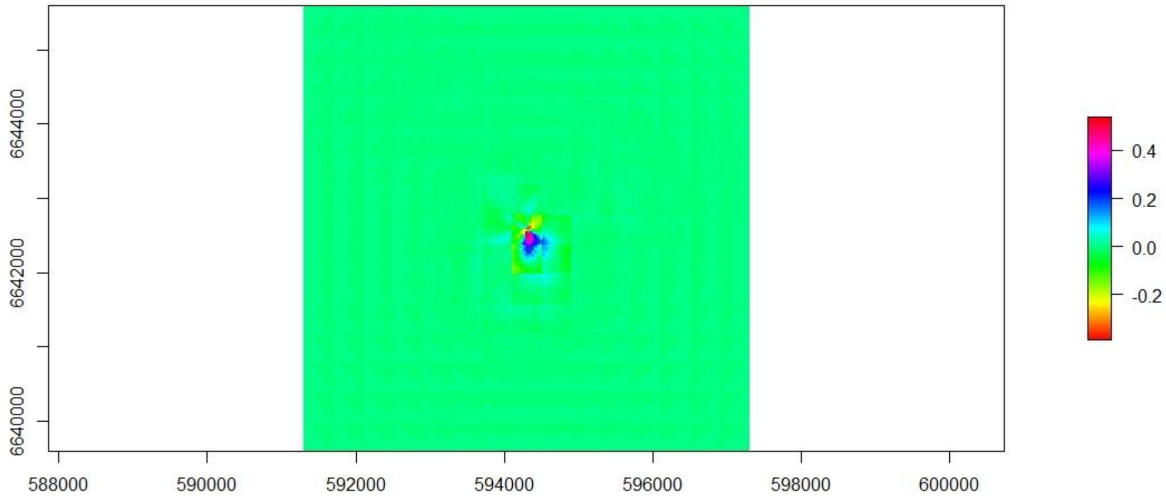


Figure 8 After implementing the blocking design, the residuals are more evenly distributed on the raster.

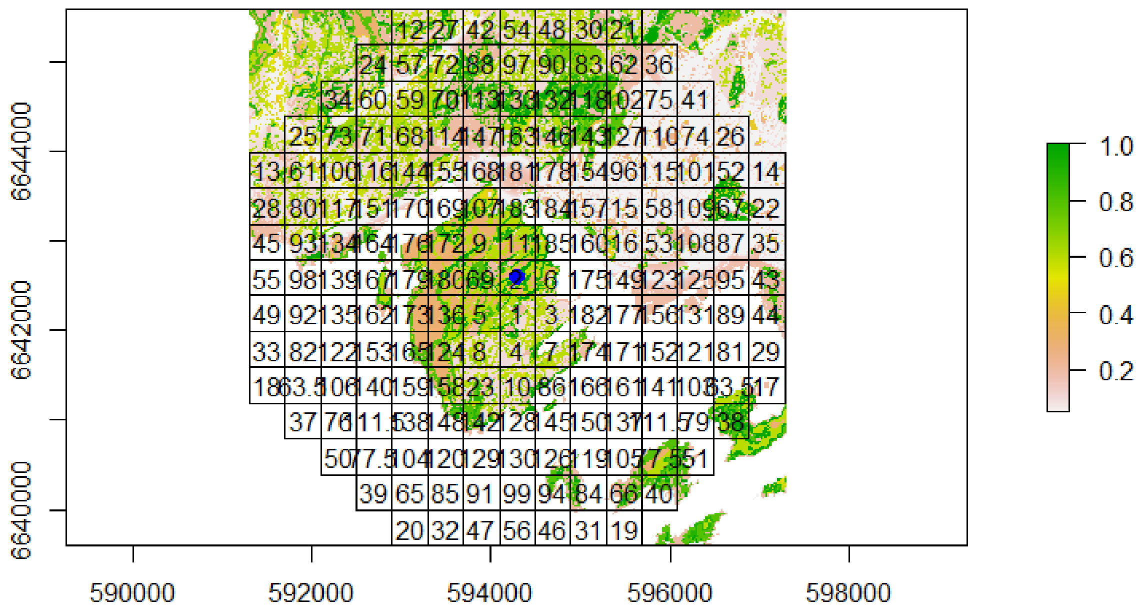


Figure 9 The number visible in each block indicates its rank relating to the visitation probability when the influence of distance has been removed. Rank number 1 is the most visited block, rank number 185 is the least visited block. The blue point shows the location of the bee hive.

2.5 Overlap analysis

Since we had a “replicate” design with two hives (Ullevål 1 and Ullevål 2) at one location, we wanted to quantify if and to what extent the visited resource patches of the two colonies can be considered similar. Thus, we compared the two visitation probability raster layers of Ullevål 1 and Ullevål 2 with the Jaccard coefficient. The Jaccard coefficient is a well-known measurement of similarity between two data sets (Kobayakawa *et al.* 2009). In this context, the coefficient is equal to the intersection between the two raster layers (Ullevål 1 ∩ Ullevål 2) divided by the union between the two raster layers (Ullevål 1 ∪ Ullevål 2). The comparison of two layers resulting in a similarity coefficient of 0.0 would indicate no common raster cells at all, whereas a value of 1.0 would show a complete overlap of the two raster layers. We imported the two raster layers in QGIS and used then the raster calculator to compute the intersection and the union. We computed one Jaccard coefficient for the whole raster layers where all visited raster squares are included, and we computed a second Jaccard coefficient where only the raster squares that lie within the 50th percentile foraging distances of the two hives are involved.

2.6 ESTIMAP analysis

To analyse whether the foraging locations of honeybees will be spatially distributed according to expected floral resource availability (as expressed by the ESTIMAP) we imported the ESTIMAP model into R. Since each block is now ranked from least visited to most visited we wanted to assess the mean ESTIMAP value for each of these ranked blocks. Therefore, we rasterized the model with the same block size factor as the rank raster while calculating the mean habitat suitability value for each new block. Thus, we ended up with a data frame containing information about the rank, the visitation probability, the habitat suitability value as given by the ESTIMAP and the distance of each block from the hive. To determine whether the ESTIMAP values can predict the probability of visitation, we used a beta regression model to analyse the mean ESTIMAP values of each block against the visitation probability of each block (Cribari-Neto & Zeileis 2009). Moreover, we tested whether the variable “distance” and the interaction between the ESTIMAP value and the distance have a positive influence on the model fit. The Akaike information criterion (AIC) was used for comparing the models. We then selected the model with the smallest AIC score. This determined an overall p value, as well as the sign of the parameter estimate which allowed us to understand whether the mean ESTIMAP value is increasing or decreasing with an increase in the probability of visitation and thus the ranking.

3. Results

We decoded a total of 506 waggle dances from the 01.07.18 to the 14.08.18. Recorded dances which were included in the data analysis ranged from 15 dances per hive per day to 1 dance per hive per day (see Appendix; AppTable 1 - AppTable 10). The probability distributions of all foraging locations with the 99th and 50th percentile foraging distances of the three studied bee colonies are shown in Figure 10 (for an enlarged view see Appendix; AppFigure 1 - AppFigure 3). The mean, the minimum and maximum foraging distance of all three bee hives are shown in Table 1.

Table 1 The mean with 95% CI, the minimum and maximum foraging distance of all three bee hives

Location	**Mean predicted distance (m)**	**95% CI**	**Min predicted distance (m)**	**Max predicted distance (m)**
Bygdøy (211 dances)	688.39	685.95;690.84	0.007	4039.79
Ullevål 1 (190 dances)	490.95	488.03;493.87	0.006	5236.82
Ullevål 2 (105 dances)	425.27	422.98;427.56	0.019	2741.46

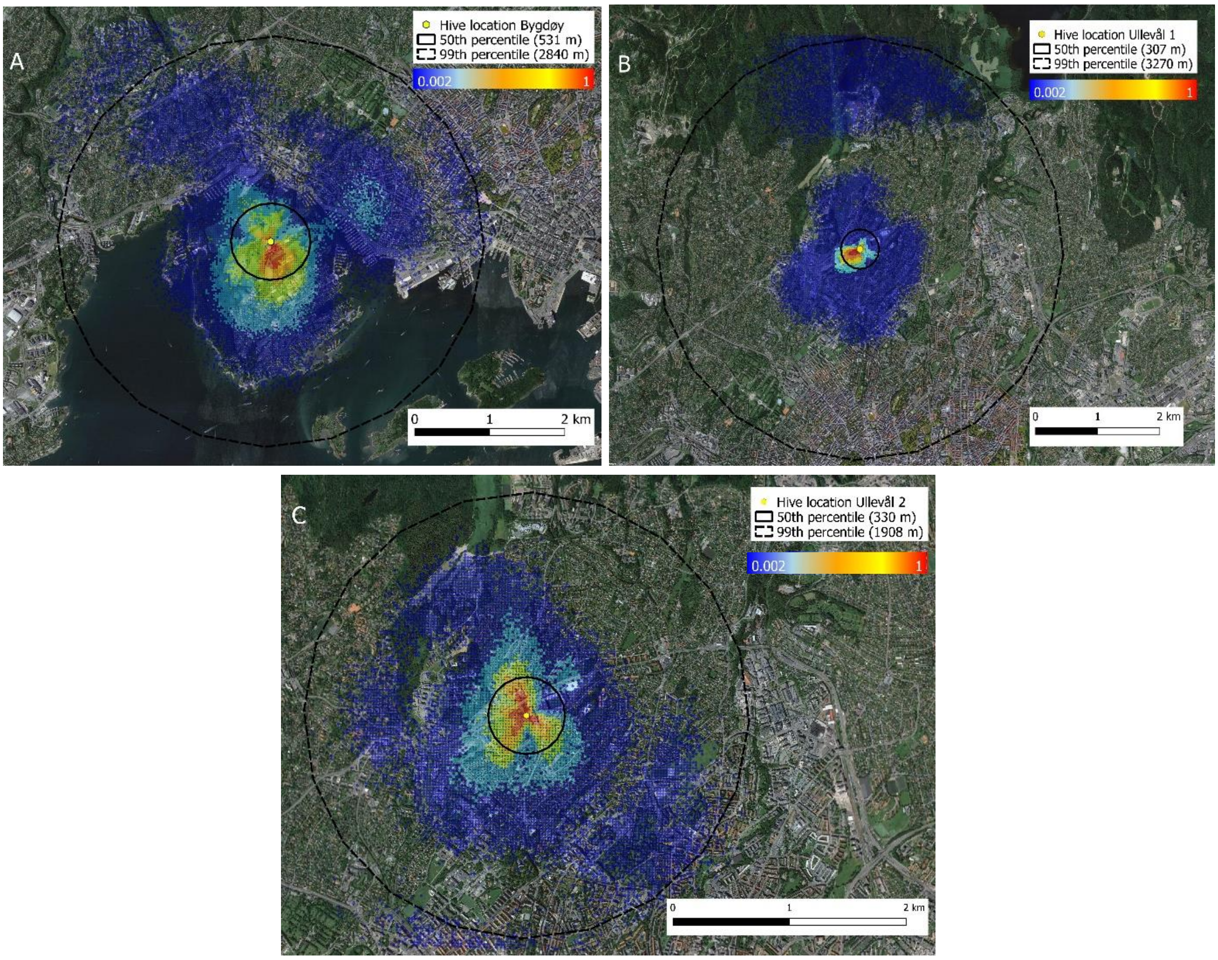


Figure 10 Honeybees of three observation hives were studied at two locations in Oslo (Bygdøy: A; Ullevål: B, C). Shown is the distribution of foraging locations and the probability that a bin (25m x 25m) has been visited. The colour code ranges from dark blue to red, where blue indicates a low probability and red a high probability of visitation.

3.1 Landscape analysis

The results showed that for all three bee colonies the linear models indicate that the dance probability decreases with an increase of distance from the hives (see Figure 11).

Since habitat patches with a high visitation probability were clustered together for all three bee hives, we calculated the Moran's I value. The Moran's I values of the three datasets of the 25 × 25 m bins containing the honeybee visitation probability indicate a high level of spatial autocorrelation, which means that there is no statistically independence between adjacent bins (Bygdøy: 0.973; Ullevål 1: 0.877; Ullevål 2: 0.954). To correct for this spatial autocorrelation, we applied a randomized blocking design. To apply the appropriate block size, we calculated a variogram for each of the three datasets. Fitting an exponential model to the variogram gave a good fit. The results of the variogram gave 423.6 m for the range of the Bygdøy location, 313.2 m for the range of Ullevål 1 and 215.6 m for the range of Ullevål 2. Therefore, we chose a block size of 400m x 400m for the location on Bygdøy, for Ullevål 1 we chose 300m x300m and for the Ullevål 2 location we chose 200m x 200m blocks. By using the blocking design, the distance beyond the data were spatially autocorrelated decreased to the following extent: for the location of Bygdøy, the psill is now 0.0003, and the range is 184.1 m, for Ullevål 1 the psill is now 0.0002 and the range is 119.4 m and for Ullevål 2 the psill is now 0.0002 and the range is 80 m. This implied that the range beyond the data are not spatially autocorrelated anymore decreased by 56.5% for Bygdøy, 61.9% for Ullevål 1 and by 62.9 % for Ullevål 2.

The 99th percentiles for the distances of the decoded waggle dances are 2840 m (Bygdøy), 3270 m (Ullevål 1) and 1908 m (Ullevål 2) respectively. We decided to exclude each block from the analysis whose closest corner was beyond the 99^{th} percentiles. Thus, we included 185 blocks for Bygdøy, 416 for Ullevål 1 and 332 for Ullevål 2 which we then used to investigate the effect of the habitat suitability of the blocks on the visitation probability with beta regression models (see ESTIMAP analysis). We estimated the foraging area of each bee colony according to the used blocks. The estimated foraging area of each bee colony was 29.6 km^2 for Bygdøy and, 37.4 km^2 and 13. 3 km^2 for the Ullevål 1 and Ullevål 2 colonies.

The five highest ranked blocks, which represent the blocks that are communicated the most often by dancing foragers as profitable areas, were for all the three locations in close vicinity to the hives – even when distance to the hives is factored out (see Figure 12, squares 1 - 5). For Bygdøy, these squares include mainly agricultural fields and residential areas. Interestingly, the block that covers mostly the allotment gardens (lower left block closet to the hive location outlined in red) is visited the most by bees of the Ullevål 1 hive and the second most frequently by the bees of Ullevål 2. The other squares contain mainly residential areas.

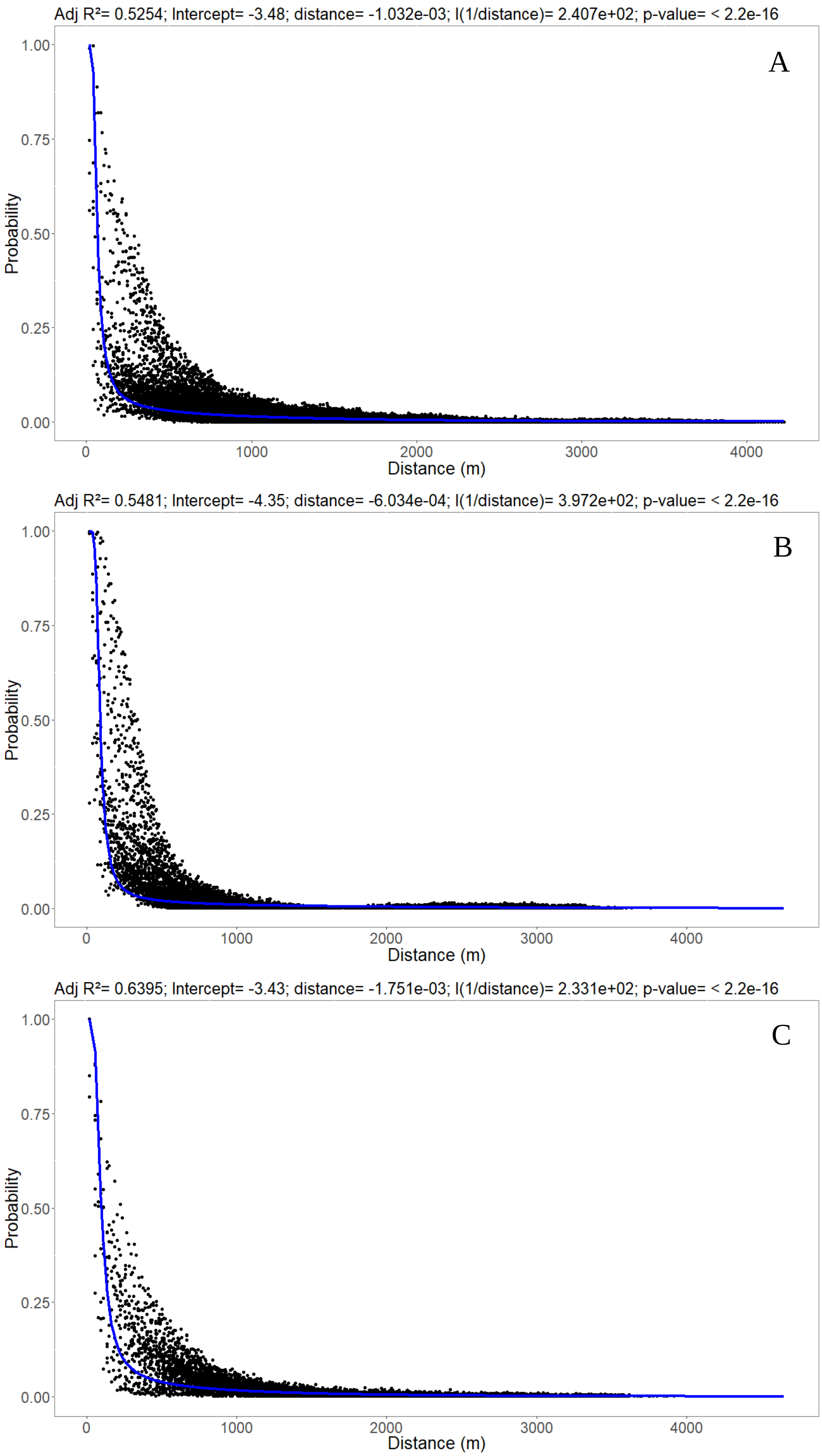


Figure 11 For all locations, the visitation probability of 25 m x 25 m bins is Inversely proportional to the distance from Hives (A: Bygdøy; B: Ullevål 1; C: Ullevål 2).

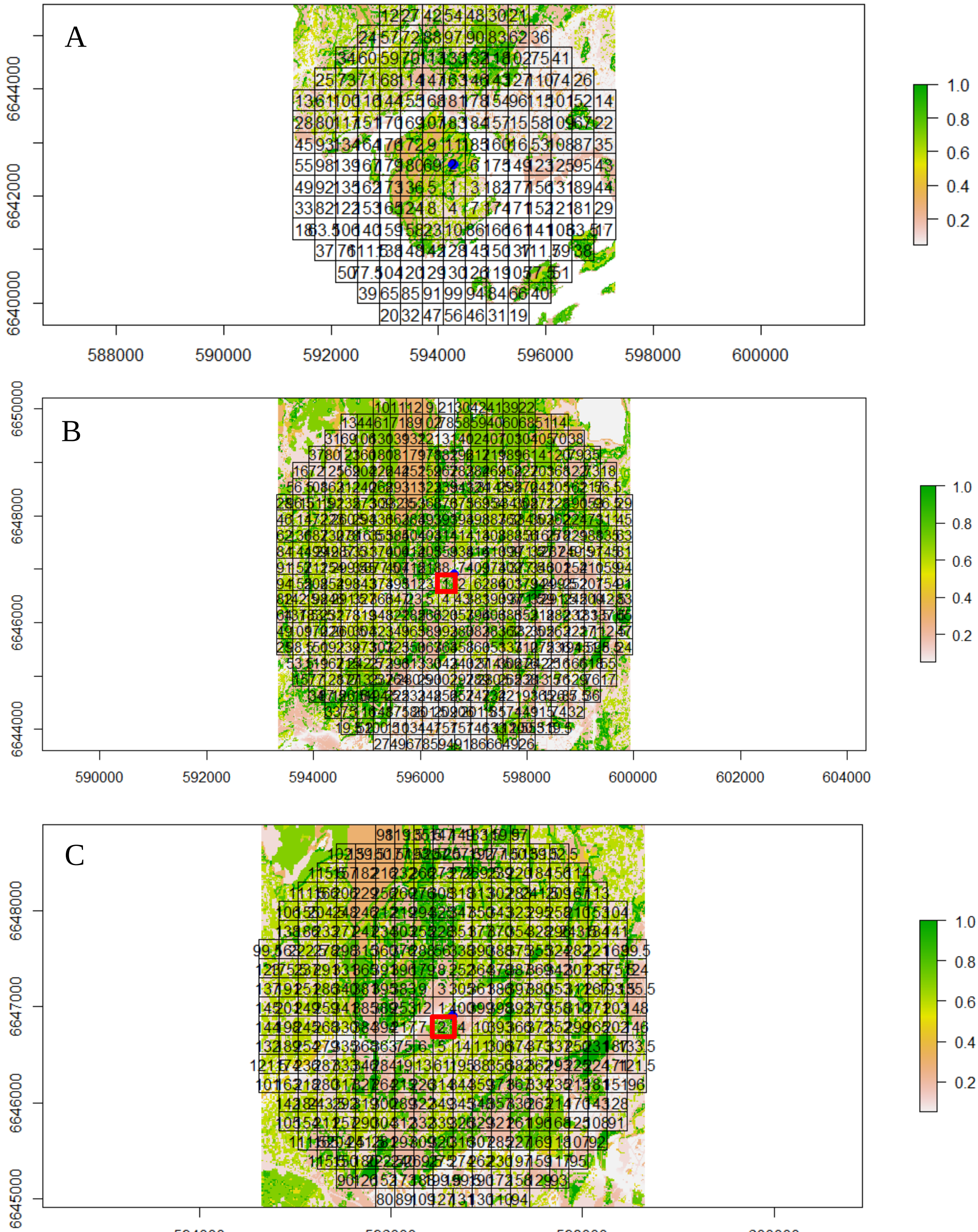


Figure 12 Ranking of the blocks from 1 to 185 for Bygdøy (A), from 1 to 416 for Ullevål 1 and from 1 to 332 for Ullevål 2. The blue point indicates the hive location. The squares outlined with red represent the square that covers the allotment gardens which are in close vicinity to Ullevål 1 and 2.

3.2 Overlap analysis

The Jaccard coefficient comparing the overlap between the raster layers of Ullevål 1 and 2 amounted to a value of 0.50. When looking at the area where 50% of all dances occurred, the Jaccard's coefficient value decreased to 0.39. Even though the colonies were placed in the same environment, were of equal size and had the same genetic background, foragers from Ullevål 1 and Ullevål 2 exploited different forage patches.

3.3 ESTIMAP analysis

Our results show that the foraging locations of the honeybees of all three colonies cover a wide spectrum of used habitat types in Oslo, with some blocks used more than others. The habitat suitability values of visited blocks ranged from 0.00 to 0.91. The mean ESTIMAP value of the patches which were used as a resource location accounted to 0.36. If focused on the five patches that had the highest visitation probabilities of each bee hives the mean ESTIMAP value increased to 0.42.

The best beta regression models with the lowest AIC scores had the the following formula: $visitationprob \sim ESTIMAPvalue + distance + ESTIMAPvalue * distance, data = dances, link = "logit"$. Overall, we found a significant effect of the ESTIMAP values on the visitation probabilities on Bygdøy and a non-significant effect of the ESTIMAP values on the visitation probabilities of the Ullevål locations. (Bygdøy: Pseudo R-sq.= 0.204, Log-likelihood= 750.378, AIC= -1490.756; Ullevål 1: Pseudo R-sq.= 0.431, Log-likelihood= 1624.536, AIC= -3237.073; Ullevål 2: Pseudo R-sq.= 0.518, Log-likelihood= 1454.034, AIC= -2896.069). By assessing the sign of the estimate (minus or plus value), we could then determine whether the ESTIMAP value is associated with a lower or higher visitation probability than expected. These values could be then be paired with the p value to allocate significance. For the dances of Bygdøy the ESTIMAP value is a significant predictor of the visitation probability: Each additional unit of the ESTIMAP value increases the estimated log-odds of the visitation probability by 0.089 meaning that the odds that the visitation probability will increase by 1.09 times while holding all other predicting variables constant. For the dances of Ullevål 1, each additional unit of the ESTIMAP value increases the estimated log-odds of the visitation probability by 0.030. However, the ESTIMAP value is not a significant predictor of the visitation probability in this model. For Ullevål 2, each additional unit of the ESTIMAP value decreases the estimated log-odds of the visitation probability by 0.029. Also, in this case the ESTIMAP value of the blocks is not a significant predictor. Thus, the visitation probabilities were not correlated with the expected availability of floral resources mapped around the two hives at Ullevål but were correlated on Bygdøy (see Table 2).

Table 2 Coefficients of the models for the locations of Bygdøy, Ullevål 1 and Ullevål 2

Bygdøy	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	3.416e-01	4.873e-03	70.101	< 2e-16 ***
ESTIMAPvalue	8.867e-02	1.325e-02	6.694	2.18e-11 ***
distance	9.487e-06	2.131e-06	4.451	8.55e-06 ***
ESTIMAPvalue:distance	-3.681e-05	6.030e-06	-6.104	1.03e-09 ***
Ullevål 1	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	7.995e-02	1.097e-02	7.289	3.12e-13 ***
ESTIMAPvalue	3.047e-02	2.190e-02	1.391	0.164
distance	-1.600e-05	3.839e-06	-4.168	3.07e-05 ***
ESTIMAPvalue:distance	-1.302e-05	8.333e-06	-1.562	0.118
Ullevål 2	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	6.026e-02	6.877e-03	8.762	< 2e-16 ***
ESTIMAPvalue	-2.926e-02	1.447e-02	-2.023	0.0431 *
distance	-2.612e-05	4.326e-06	-6.039	1.55e-09 ***
ESTIMAPvalue:distance	2.049e-05	9.833e-06	2.083	0.0372 *

4. Discussion

In this study, we analysed waggle dances of honeybees in three bee colonies in the City of Oslo to understand their foraging patterns. First, we examined how well the foraging patterns of two hives having the same access to resource locations were overlapping. Secondly, we investigated how well a habitat suitability model can predict profitable flight patterns of the studied honeybees. Our results showed that with a Jaccard coefficient of 0.5 the two foraging patterns of Ullevål 1 and Ullevål 2 only overlapped to a mediocre level. Furthermore, our results indicated that the visitation probabilities of the Bygdøy hive were correlated with the habitat suitability values of the ESTIMAP model. Thus, an increase in the ESTIMAP value led to an increase in the visitation probability. For Ullevål 1 and Ullevål 2 however, the ESTIMAP values did not play a significant role in predicting the visitation probability. In the following part, we address potential limitations of the study. We then discuss our findings and results, first in the frame of our predictions, and after that in the broader context of urban pollinator ecology and the conservation management of pollinators in cities.

4.1 Potential shortcomings

There are three main shortcomings of our work. First of all, since our time was limited to set up the study design in summer 2017, we were unable to create our own duration-to-distance calibration curve unique to the bee strains we used and the urban landscape of Oslo. To create a duration-to-distance calibration curve, worker bees have to be trained to feeders according to the standard training procedure by von Frisch (Von Frisch 1967; Schürch *et al.* 2013). This resulting distance calibration is not universally applicable; it is rather connected to the structure of the landscape through which the honeybee flies (Esch *et al.* 2001). However, our decoded dances that we created with the Sussex calibration model showed that the used duration-to-distance transformation reflected some important landmarks when plotted on the Google satellite map. For instance, most of the visited resource locations of Bygdøy are located within the area of the peninsula and depict therefore reasonably well its shoreline. Moreover, most dances of the Ullevål locations were within the limits of the allotment gardens while there were almost no dances within the area of the Ullevaal stadium which represents a highly unsuitable habitat for pollinators (see Figure 13). Although our results showed that the used Sussex calibration curve performed reasonably well, we still believe that a duration to distance calibration curve generated for the urban landscape of Oslo would produce a more accurate picture of the foraging patterns of our bees.

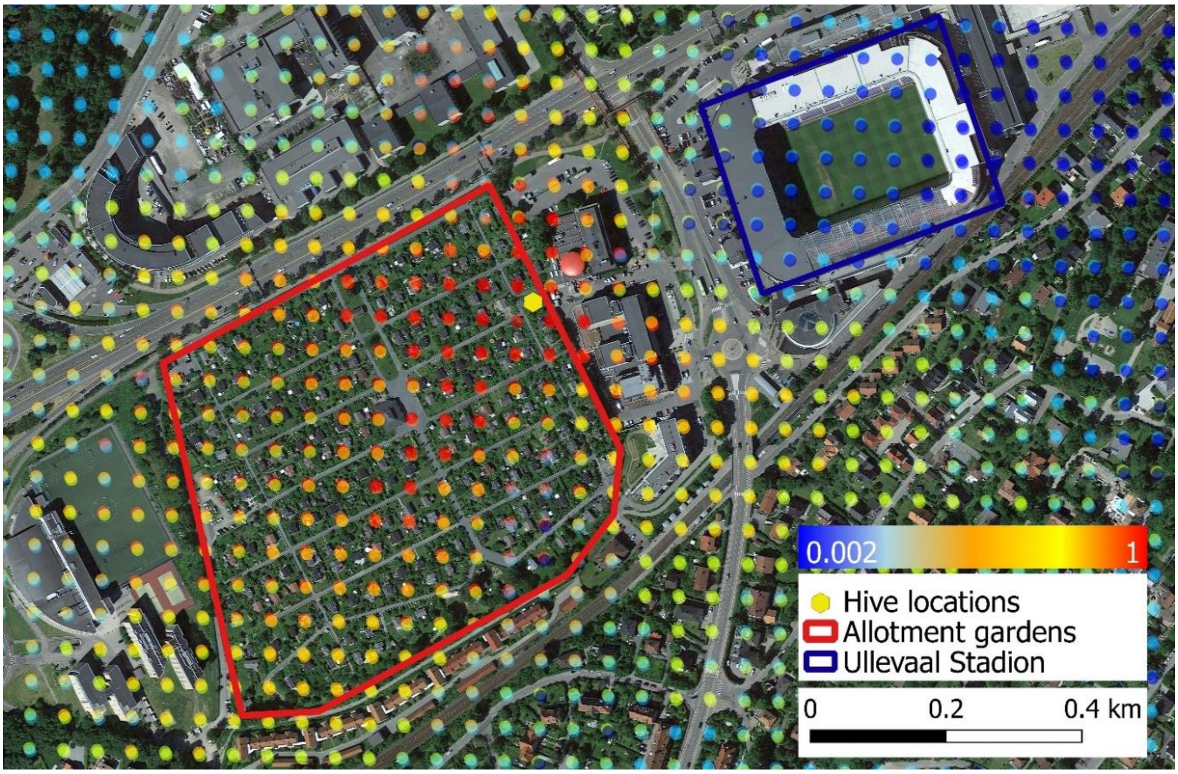


Figure 13 Within the boundaries of the Sogn Hagekoloni allotment gardens (red outline) it was possible to find the most predicted foraging locations while hardly any waggle dance indicated a suitable resource location within the boundaries of the Ullevaal Stadion (blue outline).

Secondly, various techniques have been applied throughout the time to decode waggle dances. During the lifetime of von Frisch, the waggle dances were analysed straight from the observation hive with the aid of stopwatches and protractors (Couvillon 2012). With the progress of modern technology, waggle dances can be analysed by going frame by frame through recorded videos (Couvillon *et al.* 2012a). Thus, by using the computer screen as a virtual observation hive, we were able to extract duration and direction of the waggle run manually. Although this approach allows measurements with higher precision, manual decoding from the videos is still prone to errors in the duration and direction measurements (Wario *et al*., 2017). For instance, Wario *et al.* (2017) ascertained that there was a standard deviation of 6.6° when letting eight trained researchers measure the angles of waggle runs. Hence, when discussing the results, the possible inaccuracy of the decoding process should be kept in mind.

The third limitation resulted from the nature of our statistical data analysis. To analyse the visitation probability (values from 0 to 1) we logit transformed the data so that the transformed visitation probability assumed values in the real line. In this way, we could then perform a standard linear regression analysis. This latter approach, nevertheless, has several shortcomings (Cribari-Neto & Zeileis 2009). First, the regression parameters of our linear model are only interpretable in terms of the mean of logit transformed visitation probability, and not in terms of the visitation probability mean itself. Secondly, regression models involving probability data are usually heteroscedastic: the data are more variable around the mean and show less variation around the lower limit (0) and upper limit (1) of the standard unit interval (0-1). Third, since the distributions of probabilities are normally not symmetric, the hypothesis testing based on the Gaussian approximations for interval estimation could be fairly inaccurate in smaller data sets (Cribari-Neto & Zeileis 2009). Thus, one should be aware of these limitations when interpreting and using the results of our regression model.

4.2 Discussion of the results

Our results clearly showed that most foraging from the urban colonies was at relatively short distances (mean predicted distance: 425m – 688m), indicating abundant high-quality forage within short distances around the two study locations. In general, honeybees possess a great potential to survey a wide range of landscapes for resource locations (Couvillon, Schürch & Ratnieks 2014a). One reason is their capability of performing long-distance foraging trips of around 10 km (Von Frisch 1967). Honeybees from a single location are therefore able to scout through a large area. So, how did our results align with previous studies which investigated honeybee foraging using waggle dances decoding? A study from Brighton showed that the foraging of bee colonies placed in the city centre was mainly local (monthly mean distances 0.5–1.2 km) and mostly within the area of the city (monthly means: 78–92 %) (Garbuzov, Schürch & Ratnieks 2015). In contrast with this, bee colonies placed in a rural area close to Sheffield showed a mean foraging distance of 5.5 km for the month of August (Beekman & Ratnieks 2000) while another study reported a mean foraging distance of around 2.2 km in the summer months (June – August) by bees placed in a rural area around Brighton (Couvillon, Schürch & Ratnieks 2014b). Thus, the distances published by Garbuzov *et al*. (2015) and our distances were shorter than those from studies where bee hives were located in rural areas and thus supported the idea that bees in urban areas need to fly shorter distances to fulfil their need for nutrients and other resources. Honeybees are very skilled in estimating their foraging economics and successful foragers perform the waggle dance only after assessing a visited location as a high-quality feeding location (Seeley 2009). The short distances advertised by our decoded dances, therefore, indicate that the urban area of Oslo provides a sufficiently high resource availability to meet the foraging needs of honeybees which can support honeybees on Bygdøy and in the Ullevål district.

4.2.1 Overlap analysis

With a Jaccard coefficient of 0.50, we found only a moderate level of foraging overlap between the two Ullevål colonies. Focusing on the 50^{th} percentile of the foraging distance, the result indicated an even smaller overlap with a Jaccard coefficient of 0.39. Therefore, we could conclude that the foragers of the two colonies exploited different patches in the study period even though they started their foraging from the same location.

The foraging patterns of a colony, defined as the patches where honeybees fly to for resources, is influenced by many factors such as the colony size, the nutritional needs of the colony, the distribution of pollen and nectar, chance factors, as well as the foraging patterns and densities of competing pollinators (Waddington *et al.* 1994). The observation that two bee colonies being located at the same place have two different foraging patterns is not novel (Beekman *et al.* 2004). According to Beekman *et al.* (2004), equal-sized colonies show no consistent difference in the intake and need of pollen and nectar. Hence, the finding that colonies use different foraging patches cannot be simply explained by different nutritional needs. The most likely explanation for the finding that colonies forage on different patches, even when placed in the same environment, is based on the availability and abundance of resource patches and on chance factors (Beekman *et al.* 2004). Especially when the number of available resource patches is large, as it is possible to find it in urban environments, different colonies will discover and exploit a different subset of all the available patches. When foraging honeybees from a colony are recruited by nestmates and actively exploiting a certain patch, it is more likely that they persist with this resource than to switch to an unknown patch even though other patches around have equal quality (Detrain & Deneubourg, 2008). Thus, a forager will remain exploiting that patch for as long as this particular location is rewarding and may also communicate the patch to her nestmates if she thinks the profit is sufficient enough (Seeley 1995).

The level of interspecific and intraspecific competition can alter the foraging behaviour and diet breadth, leading to a more generalist foraging behaviour of some pollinators (Morse 1977). Especially more generalist pollinators like the bumble bee (*Bombus terrestris*) can shift to a different subset of available plant species depending on the degree of intraspecific competition (Fontaine, Collin & Dajoz 2008). According to the optimal foraging theory, an increase or decrease of resource availability is correlated with an increase or decrease respectively in diet breadth (MacArthur & Pianka 1966). Hence, when resources are limited because of competition the diet breadth of some species can increase (Schoener 1971). As a result, the observed foraging patterns of our honeybee colonies were most likely not only based on the available forage but were also influenced by the way how the scouts of the colonies discovered different patches and by the potential competition caused by other honeybees and wild pollinators (see more details in ESTIMAP analysis). In other words, depending on some factors different foraging patterns could emerge from several bee colonies at the same location. Thus, we were not able to make any general statements about the foraging behaviour of honeybees in Oslo. For instance, we were unable to exclude that honeybees would not visit the islands in the Oslo fjord which represent excellent habitat for pollinators and host some rare and threatened insect pollinator species (Henriksen, Hilmo & Kålås 2015). Hence, although it seemed that our studied honeybees did not fly over the water towards the islands in the Oslo fjord, other colonies at the same site could utilize a foraging footprint that might extend further beyond the peninsula. Our results should be interpreted with this in mind. Moreover, our findings raised therefore more interesting questions and thoughts about the mechanism of resource selection of honeybees and might query study designs that use only one bee hive per study location to predict where honeybees are most likely to exploit resource locations. Questions such as “Are honeybees optimal foragers after all?” or “Do honeybees have an omniscient overview about available resource locations?” can be addressed in future studies based on the observation hives in Oslo and the ESTIMAP model.

4.2.2 ESTIMAP analysis

The ESTIMAP habitat suitability model did not appear to provide a very strong indicator of bee foraging probability. Evaluating the predictive power of a habitat suitability model is very important, both for applied and theoretical research questions (Hirzel *et al.* 2006). However, while model evaluators based on presence/absence data of the target species have received a lot of attention (Fielding & Bell 1997), evaluation of models based on presence-only data are more seldom. Their first step in evaluating a habitat suitability model usually consists of defining a habitat suitability threshold (often 0.5) that is supposed to separate unsuitable patches (habitat suitability value below threshold) where the species should be absent, from suitable patches (habitat suitability value above threshold) where it is supposed to be present (Hirzel *et al.* 2006). According to this threshold the ESTIMAP model performed rather poorly in predicting foraging presence since the mean ESTIMAP value of the patches where honeybee foraging took place accounted only for a value of 0.36 or 0.42 respectively if focused on the patches with the five highest visitation probabilities.

However, factors that lead to prediction errors can be of various nature. During the analysis of the ESTIMAP model, we came across three prominent reasons that might explain why the ESTIMAP model performed rather poorly in predicting the visitation probabilities of patches around the hive locations. First, many habitat suitability models - including the ESTIMAP model - produce maps showing a continuous scale of the habitat suitability for the target species. This type of output obviously contains more information than a map that predicts only the presence or absence of the target species which is certainly less convenient for wildlife and conservation management. However, studies showed that a continuous gradient can be sometimes misleading since actual presence data often exhibit a wide range of habitat suitability values (from 0 to 1). Hence, even good predictive models can suffer from uncertainty, making the usage of a continuous habitat suitability scale in some cases too ambiguous (Hirzel *et al.* 2006). Secondly, since all the dances were decoded manually, and we applied the Sussex calibration curve to translate the dances into real foraging locations, human error might cause a certain degree of inaccuracy that might lead to an insufficient plotting of the used foraging pattern.

A more important factor that the ESTIMAP model had not the strongest predictive power might be caused by a prediction error that is arising directly from the ecology of the target species (biotic errors) (Fielding & Bell 1997). Biotic errors can arise because not all behavioural-relevant processes of the target organism have been addressed in the model. Very common processes that are difficult to incorporate in a habitat suitability model are intra- and interspecific interferences. Unfortunately, these relevant data are in many cases difficult to acquire (Fielding & Bell 1997). Competition for nutrients or the intra- and interspecific competition between multiple species has the potential to reshape the presence of the target species (Austin & Gaywood 1994). A common example is the competition for nesting sites between the peregrine falcons (*Falco peregrinus*) and Golden Eagles (*Aquila chrysaetos*) at the coast of Southwest Scotland (Ratcliffe 2010). Peregrine falcons were outcompeted from their usual breeding sites on a particular cliff after Golden Eagles got re-established in 1945 in Scotland. Afterwards the Golden Eagles abandoned this cliff again and the falcons returned for breeding. Hence, depending on the presence of the Golden Eagle, the cliff was either occupied or avoided by the target species even though the cliff was constantly highly suitable as a breeding site (Fielding & Bell 1997).

In our study we were only able to visualize the visited patches of three hives. In fact, around the two locations where our three observation hives were placed also other bee hives were located. For instance, in the Sogn Hagekoloni allotment gardens there were three other bee hives each hosting around 60000 bees placed around the two observation hives in the summer months of 2017 (Larssen, personal communication). In these cases, we had no insight where honeybees of other colonies exploited resources around our two study locations. Moreover, we had also no information about the density and abundance of wild pollinators on Bygdøy and in the Ullevål district. Hence, we had no empirical data if and how the presence of other honeybees and wild pollinators might have influenced the foraging patterns of our studied colonies. Stange *et al*. (2017) used a pan trap design to achieve a validation of the ESTIMAP model. The results showed that the total bee abundance, bee species richness, and bumblebee abundance all increased significantly with an increase in the ESTIMAP habitat suitability scores (ESTIMAP values measured within an area of 50 m radius around the trap locations). However, solitary bees' abundance and the abundance of honeybees did not vary significantly with the habitat suitability as given by the ESTIMAP model (Stange *et al.* 2017). Thus, this method seems to be a better approach to evaluate a habitat suitability model for pollinators. At the same time, their results demonstrate that honeybee abundance is not correlated with the ESTIMAP values. The findings of Stange *et al*. (2017) and our findings might raise the hypothesis that honeybees as generalist foragers are less dependent on high quality resource locations. Moreover, one could question whether honeybees have an omniscient view of the resource locations and their nectar-rewards surrounding the hive location. An additional point to consider is the fact that the ESTIMAP model estimates suitability of a patch averaged over an entire growing season (Stange *et al.* 2017). Our filming, however, took place from the beginning of July to mid-August and captured therefore only half of the foraging season which starts in Norway around April (Jørgensen 2014). The foraging pattern and range of honeybees vary significantly during the foraging season (Couvillon, Schürch & Ratnieks 2014b). Decoding waggle dances over the full foraging season might therefore provide a different foraging pattern and a different match with the ESTIMAP model. However, these hypotheses and questions must undergo a more detailed and thorough research which was outside the scope of this study. Finally, we have learned and must admit that using the decoded waggle dances as presence data might be not the most appropriate method to validate a habitat suitability model for pollinators.

4.2.3 Our results in the context of urban pollinator ecology and the conservation management of pollinators in cities

Since land loss to urbanization is expected to increase throughout the upcoming years, urban pollinator ecology is an emerging research field. However, published studies of pollinator ecology in urban and suburban areas are still relatively rare (Hernandez, Frankie & Thorp 2009). The honeybee is only one species of pollinator, but our dance decoding data showed that studying honeybees´ foraging patterns could have a wider relevance. In particular, we know now that the bees of all three colonies foraged mostly in the vicinity of the hives and exploited also resource locations in residential areas. This shows that honeybee dance decoding could locate important areas that might support also other pollinator species since the honeybee is a quite generalist forager and would exploit resource patches where typically other insect pollinators would also forage (Biesmeijer & Slaa 2006). Residential gardens and other private sites in cities play a unique role in the suitability and conservation of bee habitats since the creation and maintenance of the gardens are conducted by individual owners or organizations (Hernandez, Frankie & Thorp 2009). In California, techniques in garden design and plant management were identified through e.g. surveys of urban bee habitats. These techniques appear to increase the environmental suitability of habitats for bees. For instance, the creation of habitats with a more stable availability of floral resources over the whole foraging period increased the establishment of new bee populations and successional populations of pollinators. To maintain both wild pollinators and honeybees, Oslo municipality should therefore promote conservation practices aiming at preserving the functionality of plant-pollinator networks at both public and private scale.

5. Conclusion and future perspectives

To our knowledge, this is the first study that compares the foraging patterns of honeybees with a habitat suitability map for pollinators in an urban setting. Our findings suggest that using the decoded waggle dances as species presence data might be not the most appropriate method to test a habitat suitability model for pollinators. However, we gained insight in the foraging behaviour of our three studied bee colonies: compared to colonies placed in rural areas, our urban honeybees showed relatively short mean foraging distances. Moreover, we know now that two colonies located in the same environment do not necessarily use the same resource patches. This finding gave interesting insight in the optimal foraging of honeybees. Next to the distance and the nectar-reward of the floral resources, also the exploitative competition by other bees might play a role in the resource selection of honeybees. However, we must keep in mind that both the use of the Sussex calibration curve and the manual decoding of the waggle dances might cause some inaccuracy in plotting the foraging patterns of our honeybees.

Urban areas are increasing rapidly in size and abundance. Even though the habitat suitability for pollinators of urban areas is likely to differ between cities, regions and climate zones, urban areas could have the potential to represent important source areas and refuges for pollinators. However, while there has been increasing interest in enhancing agricultural areas for pollinators, far less attention has been paid to how urban areas can be made more pollinator-friendly. Therefore, identifying suitable habitats in urban areas for pollinators as given by the ESTIMAP, gives us an idea on where pollinators are likely to forage and where potential conflicts between honeybees and other pollinators might occur. Addressing public and private landowners should be part of the strategy of the Oslo municipality to conserve wild pollinators while at the same time allow lively honeybee populations.

This current study was the start of long-term surveillance of foraging patterns of honeybees in the City of Oslo. In 2018, next to the two existing locations Bygdøy and Ullevål, there were two new locations established and each location was fitted now with three observation beehives meaning that data will be collected from 12 beehives at four different locations. This new approach will give us the chance to conduct a more thorough statistical analysis and to make more detailed statements about the resource selection of honeybees. Moreover, we will use a computer software that automatically detects and decodes waggle dances to reduce the inaccuracy caused by the manual decoding.

The waggle dance decoding is a very vivid demonstration of how scientists can use natural behaviours to study resource selection. Already in 2017, the waggle dance project gained attention and interest by a lot of citizens of Oslo. In the following years of the project, we can use this public recognition of the ecological value of pollinators (and in particular honeybees) as an important flagship group for raising public awareness of human impacts on biodiversity in the City of Oslo.

References

Agostinelli, C. & Lund, U. (2017) R package 'circular': Circular Statistics (version 0.4-93).

Åström, J., Dramstad, W., Debella-Gilo, M., Hovstad, K.A., Åström, S.C.H. & Rusch, G. (2014) Assessing Norwegian pollination deficits. Capacity building towards IPBES-implementation and methodological evaluation of the "Protocol to Detect and Assess Pollination Deficits in crops.

Austin, M. & Gaywood, M. (1994) Current problems of environmental gradients and species response curves in relation to continuum theory. *Journal of Vegetation Science,* **5,** 473-482.

Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P. & Memmott, J. (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences,* **282**.

Barrows, E.M. (2000) *Animal behavior desk reference: a dictionary of animal behavior, ecology, and evolution*. CRC press.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software,* **67,** 1-48.

Beekman, M. & Ratnieks, F.L.W. (2000) Long-Range Foraging by the Honey-Bee, Apis mellifera L. *Functional Ecology,* **14,** 490-496.

Beekman, M., Sumpter, D.J.T., Seraphides, N. & Ratnieks, F.L.W. (2004) Comparing foraging behaviour of small and large honey-bee colonies by decoding waggle dances made by foragers. *Functional Ecology,* **18,** 829-835.

Biesmeijer, J.C. & Slaa, E.J. (2006) The structure of eusocial bee assemblages in Brazil. *Apidologie,* **37,** 240-258.

Chiesura, A. (2004) The role of urban parks for the sustainable city. *Landscape and urban planning,* **68,** 129-138.

Couvillon, M.J. (2012) The dance legacy of Karl von Frisch. *Insectes sociaux,* **59,** 297-306.

Couvillon, M.J., Pearce, F.C.R., Harris-Jones, E.L., Kuepfer, A.M., Mackenzie-Smith, S.J., Rozario, L.A., Schürch, R. & Ratnieks, F.L. (2012a) Intra-dance variation among waggle runs and the design of efficient protocols for honey bee dance decoding. *Biology open***,** BIO20121099.

Couvillon, M.J., Phillipps, H.L., Schürch, R. & Ratnieks, F.L. (2012b) Working against gravity: horizontal honeybee waggle runs have greater angular scatter than vertical waggle runs. *Biology letters,* **8,** 540-543.

Couvillon, M.J., Schürch, R. & Ratnieks, F.L. (2014a) Dancing bees communicate a foraging preference for rural lands in high-level agri-environment schemes. *Current Biology,* **24,** 1212-1215.

Couvillon, M.J., Schürch, R. & Ratnieks, F.L.W. (2014b) Waggle Dance Distances as Integrative Indicators of Seasonal Foraging Challenges. *PLOS ONE,* **9,** e93495.

Cribari-Neto, F. & Zeileis, A. (2009) Beta regression in R.

De Marco, R.J., Gurevitz, J.M. & Menzel, R. (2008) Variability in the encoding of spatial information by dancing bees. *Journal of Experimental Biology,* **211,** 1635-1644.

Detrain, C., & Deneubourg, J. L. (2008). Collective decision-making and foraging patterns in ants and honeybees. *Advances in insect physiology, 35,* 123-173.

Dukas, R. & Edelstein-Keshet, L. (1998) The spatial distribution of colonial food provisioners. *Journal of Theoretical Biology,* **190,** 121-134.

Dyer, F.C. (2002) The biology of the dance language. *Annual review of entomology,* **47,** 917-949.

Dyer, F.C. & Dickinson, J.A. (1994) Development of sun compensation by honeybees: How partially experienced bees estimate the sun's course. *Proceedings of the National Academy of Sciences,* **91,** 4471-4474.

Esch, H.E., Zhang, S., Srinivasan, M.V. & Tautz, J. (2001) Honeybee dances communicate distances measured by optic flow. *Nature,* **411,** 581.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation,* **24,** 38-49.

Fontaine, C., Collin, C.L. & Dajoz, I. (2008) Generalist foraging of pollinators: diet expansion at high density. *Journal of Ecology,* **96,** 1002-1010.

Fürst, M., McMahon, D.P., Osborne, J., Paxton, R. & Brown, M. (2014) Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature,* **506,** 364.

Gallai, N., Salles, J.-M., Settele, J. & Vaissière, B.E. (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological economics,* **68,** 810-821.

Garbuzov, M., Schürch, R. & Ratnieks, F.L.W. (2015) Eating locally: dance decoding demonstrates that urban honey bees in Brighton, UK, forage mainly in the surrounding urban area. *Urban Ecosystems,* **18,** 411-418.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D. & Afik, O. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science,* **339,** 1608-1611.

Geslin, B., Gauzens, B., Thébault, E. & Dajoz, I. (2013) Plant Pollinator Networks along a Gradient of Urbanisation. *PLOS ONE,* **8,** e63421.

Goulson, D. (1999). Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in plant ecology, evolution and systematics*, *2*(2), 185-209.

Goulson, D. (2004) Keeping bees in their place: impacts of bees outside their native range. *Bee World,* **85,** 45-46.

Gräler, B., Pebesma, E.J. & Heuvelink, G. (2016) Spatio-Temporal Interpolation using gstat. *The R Journal*, **8,** 204-218.

Hartig, T., Mang, M. & Evans, G.W. (1991) Restorative effects of natural environment experiences. *Environment and behavior,* **23,** 3-26.

Henriksen, S., Hilmo, O. & Kålås, J. (2015) The 2015 Norwegian red list for species. *Norwegian Biodiversity Information Centre, Norway*.

Herbertsson, L., Lindström, S.A., Rundlöf, M., Bommarco, R. & Smith, H.G. (2016) Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology,* **17,** 609-616.

Hernandez, J.L., Frankie, G.W. & Thorp, R.W. (2009) Ecology of urban bees: a review of current knowledge and directions for future study. *Cities and the Environment (CATE),* **2,** 3.

Hijmans, R.J. (2017) raster: Geographic Data Analysis and Modeling.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *ecological modelling,* **199,** 142-152.

Jørgensen, R.R. (2014) *Bier og birøkting i by og bygd*. Kagge.

Keitt, T.H., Bjørnstad, O.N., Dixon, P.M. & Citron-Pousty, S. (2002) Accounting for spatial pattern when modeling organism-environment interactions. *Ecography,* **25,** 616-625.

Klein, A.-M., Boreux, V., Fornoff, F., Mupepele, A.-C. & Pufal, G. (2018) Relevance of wild and managed bees for human well-being. *Current Opinion in Insect Science*.

Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences,* **274,** 303-313.

Klima- og Miljødepartementet (2009) Lov om forvaltning av naturens mangfold (Naturmangfoldloven)

Kobayakawa, M., Kinjo, S., Hoshi, M., Ohmori, T. & Yamamoto, A. (2009) Fast Computation of Similarity Based on Jaccard Coefficient for Composition-Based Image Retrieval. pp. 949-955. Springer Berlin Heidelberg, Berlin, Heidelberg.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist,* **100,** 603-609.

Mardia, K.V. (1975) Statistics of directional data. *Journal of the Royal Statistical Society. Series B (Methodological)***,** 349-393.

McMahon, D.P., Fürst, M.A., Caspar, J., Theodorou, P., Brown, M.J.F. & Paxton, R.J. (2015) A sting in the spit: widespread cross-infection of multiple RNA viruses across wild and managed bees. *Journal of Animal Ecology,* **84,** 615-624.

Michener, C.D. (2000) *The bees of the world*. JHU press.

Milner, A. (1996) An introduction to understanding honeybees, their origins, evolution and diversity. *Available via Bibba electronic journal, URL:<* http://www.bibba.com.

Moore, L.J. & Kosut, M. (2013) *Buzz: Urban beekeeping and the power of the bee*. NYU Press.

Morse, D.H. (1977) Resource Partitioning in Bumble Bees: The Role of Behavioral Factors. *Science,* **197,** 678-680.

Niemelä, J., Saarela, S.-R., Söderman, T., Kopperoinen, L., Yli-Pelkonen, V., Väre, S. & Kotze, D.J. (2010) Using the ecosystem services approach for better planning and conservation of urban green spaces: a Finland case study. *Biodiversity and Conservation,* **19,** 3225-3243.

Núñez, J.A. (1982) Honeybee Foraging Strategies at a Food Source in Relation to its Distance from the Hive and the Rate of Sugar Flow. *Journal of Apicultural Research,* **21,** 139-150.

Ollerton, J. (2017) Pollinator diversity: distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics,* **48**.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos,* **120,** 321-326.

Paini, D. (2004) Impact of the introduced honey bee (Apis mellifera)(Hymenoptera: Apidae) on native bees: a review. *Austral ecology,* **29,** 399-407.

Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics,* **20,** 289-290.

Pebesma, E.J. (2004) Multivariable geostatistics in S: the gstat package. *Computers & Geosciences,* **30,** 683-691.

Plummer, M. (2016) rjags: Bayesian Graphical Models using MCMC.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution,* **25,** 345-353.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R. & Settele, J. (2016) Safeguarding pollinators and their values to human well-being. *Nature,* **540,** 220.

QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ratcliffe, D. (2010) *The peregrine falcon*. A&C Black.

Scheiner, R., Abramson, C.I., Brodschneider, R., Crailsheim, K., Farina, W.M., Fuchs, S., Grünewald, B., Hahshold, S., Karrer, M., Koeniger, G., Koeniger, N., Menzel, R., Mujagic, S., Radspieler, G., Schmickl, T., Schneider, C., Siegel, A.J., Szopek, M. & Thenius, R. (2013) Standard methods for behavioural studies of Apis mellifera. *Journal of Apicultural Research,* **52,** 1-58.

Schmid-Hempel, R. & Schmid-Hempel, P. (1998) Colony performance and immunocompetence of a social insect, Bombus terrestris, in poor and variable environments. *Functional Ecology,* **12,** 22-30.

Schoener, T.W. (1971) Theory of feeding strategies. *Annual review of ecology and systematics,* **2,** 369-404.

Schürch, R., Couvillon, M.J., Burns, D.D., Tasman, K., Waxman, D. & Ratnieks, F.L. (2013) Incorporating variability in honey bee waggle dance decoding improves the mapping of communicated resource locations. *Journal of Comparative Physiology A,* **199,** 1143-1152.

Seeley, T.D. (1983) The Ecology of Temperate and Tropical Honeybee Societies: Ecological studies complement physiological ones, offering a new perspective on patterns of honeybee adaptation. *American Scientist,* **71,** 264-272.

Seeley, T.D. (1994) Honey bee foragers as sensory units of their colonies. *Behavioral Ecology and Sociobiology,* **34,** 51-62.

Seeley, T.D. (1995) The Wisdom of the Hive Harvard University Press. *Cambridge, Massachusetts, London, England*.

Seeley, T.D. (2009) *The wisdom of the hive: the social physiology of honey bee colonies*. Harvard University Press.

Seeley, T.D. (2014) *Honeybee ecology: a study of adaptation in social life*. Princeton University Press.

Seeley, T.D., Mikheyev, A.S. & Pagano, G.J. (2000) Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *Journal of Comparative Physiology A,* **186,** 813-819.

Stange, E., Zulian, G., Rusch, G., Barton, D. & Nowell, M. (2017) Ecosystem services mapping for municipal policy: ESTIMAP and zoning for urban beekeeping. *One Ecosystem,* **2,** e14014.

Tanner, D.A. & Visscher, P.K. (2008) Do honey bees average directions in the waggle dance to determine a flight direction? *Behavioral Ecology and Sociobiology,* **62,** 1891-1898.

Tautz, J. (2008) *The buzz about bees: biology of a superorganism*. Springer Science & Business Media.

Tautz, J., Zhang, S., Spaethe, J., Brockmann, A., Si, A. & Srinivasan, M. (2004) Honeybee odometry: performance in varying natural terrain. *PLoS Biology,* **2,** e211.

Totland, Ø., Hovstad, K., Ødegaard, F. & Åström, J. (2013) State of knowledge regarding insect pollination in Norway–the importance of the complex interaction between plants and insects. *Norwegian Biodiversity Information Centre, Norway*.

Towne, W.F. & Gould, J.L. (1988) The spatial precision of the honey bees' dance communication. *Journal of Insect Behavior,* **1,** 129-155.

Visscher, P.K. & Seeley, T.D. (1982) Foraging Strategy of Honeybee Colonies in a Temperate Deciduous Forest. *Ecology,* **63,** 1790-1801.

Von Frisch, K. (1967) The dance language and orientation of bees.

Waddington, K.D. (1980) Flight patterns of foraging bees relative to density of artificial flowers and distribution of nectar. *Oecologia,* **44,** 199-204.

Waddington, K.D., Herbert, T.J., Visscher, P.K. & Richter, M.R. (1994) Comparisons of forager distributions from matched honey bee colonies in suburban environments. *Behavioral Ecology and Sociobiology,* **35,** 423-429.

Waddington, K.D. & Holden, L.R. (1979) Optimal Foraging: On Flower Selection by Bees. *The American Naturalist*, **114,** 179-196.

Wario, F., Wild, B., Rojas, R., & Landgraf, T. (2017). Automatic detection and decoding of honey bee waggle dances. *PloS one*, *12*(12), e0188626.

Wojcik, V. A., Morandin, L. A., Davies Adams, L., & Rourke, K. E. (2018). Floral Resource Competition Between Honey Bees and Wild Bees: Is There Clear Evidence and Can We Guide Management and Conservation?. *Environmental entomology*.

Appendix

AppTable 1 Average measurements for the dances 1-50 of the Bygdøy hive

	movie ID	dance.id	location	day	month	year	average.length	hour	minute	second	average.angle	Azimuth	heading	distance	heading.rad	easting	northing	duration
1	4556	4556_1	Bygdoy	1	7	2017	0.51	9	7	39	104.2	101.0	205.2	163.8	3.58141563	594224.279	6642442.83	0.51
2	4557	4557_1	Bygdoy	1	7	2017	4.03	9	25	53	208.0	105.3	313.3	3097.1	5.46846561	592040.769	6644715.82	4.03
3	4559	4559_1	Bygdoy	1	7	2017	0.9	9	35	18	206.8	107.6	314.4	488.8	5.48679157	593944.622	6642932.78	0.9
4	4559	4559_2	Bygdoy	1	7	2017	2.72	9	41	30	223.4	109.1	332.6	2005.4	5.80444149	593370.176	6644370.96	2.72
5	4560	4560_1	Bygdoy	1	7	2017	1.15	9	45	45	73.0	110.2	183.2	697.1	3.19657053	594255.695	6641894.97	1.15
6	4560	4560_2	Bygdoy	1	7	2017	2.3	9	50	16	220.9	111.3	332.3	1655.4	5.79885644	593523.214	6644056.02	2.3
7	4561	4561_1	Bygdoy	1	7	2017	0.63	10	1	19	100.6	114.1	214.7	263.8	3.7472219	594143.853	6642374.16	0.63
8	4561	4561_2	Bygdoy	1	7	2017	4.48	10	2	8	217.8	114.4	332.2	3472.1	5.79728564	592672.523	6645661.21	4.48
9	4562	4562_1	Bygdoy	1	7	2017	0.61	10	6	17	222.4	115.4	337.9	247.1	5.89694394	594200.921	6642819.88	0.61
10	4562	4562_2	Bygdoy	1	7	2017	0.57	10	9	40	185.8	116.3	302.1	213.8	5.27316327	594112.987	6642704.68	0.57
11	4562	4562_3	Bygdoy	1	7	2017	0.79	10	13	34	37.4	117.4	154.8	397.1	2.70089702	594463.383	6642231.86	0.79
12	4563	4563_1	Bygdoy	1	7	2017	0.49	10	21	36	83.3	119.5	202.8	147.1	3.53900412	594237.074	6642455.38	0.49
13	4563	4563_2	Bygdoy	1	7	2017	3.2	10	25	27	205.9	120.6	326.5	2405.4	5.69815094	592965.661	6644596.38	3.2
14	4587	4587_1	Bygdoy	2	7	2017	0.4	13	37	16	352.8	186.1	538.9	72.1	9.40575387	594295.371	6642518.93	0.4
15	4587	4587_2	Bygdoy	2	7	2017	0.62	13	38	8	319.2	186.4	505.6	255.4	8.82455923	594438.265	6642380.23	0.62
16	4587	4587_3	Bygdoy	2	7	2017	0.3	13	41	23	91.4	187.7	279.1	11.3	4.87121394	594305.108	6642589.22	0.3
17	4587	4587_4	Bygdoy	2	7	2017	0.39	13	42	53	324.3	188.2	512.5	63.8	8.94481242	594323.436	6642534.45	0.39
18	4588	4588_1	Bygdoy	2	7	2017	1.05	13	51	51	127.6	191.6	319.2	613.8	5.57161457	593893.206	6643055.82	1.05
19	4589	4589_1	Bygdoy	2	7	2017	0.98	14	2	46	179.8	195.7	375.5	555.4	6.55371134	594442.429	6643126.22	0.98
20	4590	4590_1	Bygdoy	2	7	2017	0.5	14	12	39	327.8	199.4	527.2	155.4	9.20155035	594328.406	6642439.44	0.5
21	4590	4590_2	Bygdoy	2	7	2017	0.84	14	16	32	128.2	200.8	329.0	438.8	5.74283137	594068.29	6642967.24	0.84
22	4591	4591_1	Bygdoy	2	7	2017	0.58	14	27	18	107.2	204.7	311.9	222.1	5.44333287	594128.649	6642739.26	0.58
23	4593	4593_1	Bygdoy	2	7	2017	1.1	14	41	27	108.0	209.7	317.7	655.4	5.5452601	593853.066	6643075.92	1.1
24	4594	4594_1	Bygdoy	2	7	2017	0.24	14	56	14	322.2	214.8	536.9	61.3	9.37119635	594290.72	6642652.16	0.24
25	4594	4594_2	Bygdoy	2	7	2017	0.5	14	59	3	279.1	215.7	494.9	155.4	8.6367618	594404.184	6642481.39	0.5
26	4594	4594_3	Bygdoy	2	7	2017	2.67	15	1	28	104.4	216.5	320.9	1963.8	5.6004125	593054.978	6644114.53	2.67
27	4595	4595_1	Bygdoy	2	7	2017	1.52	15	6	44	112.3	218.3	330.5	1005.4	5.76901131	593799.52	6643466.42	1.52
28	4595	4595_2	Bygdoy	2	7	2017	1.46	15	10	18	105.7	219.4	325.2	955.4	5.6751126	593748.183	6643375.16	1.46
29	4597	4597_1	Bygdoy	3	7	2017	0.67	9	29	42	41.2	106.3	147.5	297.1	2.57401158	594453.71	6642340.5	0.67
30	4598	4598_1	Bygdoy	3	7	2017	0.85	9	34	22	320.6	107.4	428.0	447.1	7.4700092	594708.528	6642758.48	0.85
31	4598	4598_2	Bygdoy	3	7	2017	0.31	9	39	23	201.9	108.6	310.5	-2.9	5.4185492	594296.219	6642589.11	0.31
32	4598	4598_3	Bygdoy	3	7	2017	0.49	9	41	16	25.5	109.1	134.6	147.1	2.34868957	594398.781	6642487.78	0.49
33	4599	4599_1	Bygdoy	3	7	2017	0.51	9	47	46	191.7	110.7	302.4	163.8	5.27805019	594155.757	6642678.77	0.51
34	4600	4600_1	Bygdoy	3	7	2017	1.15	10	3	27	82.8	114.7	197.5	697.1	3.44754887	594084.035	6641926.29	1.15
35	4600	4600_2	Bygdoy	3	7	2017	0.65	10	5	6	35.8	115.1	151.0	280.4	2.63474904	594430.12	6642345.84	0.65
36	4601	4601_1	Bygdoy	3	7	2017	0.57	10	12	16	240.4	117.0	357.5	213.8	6.23867941	594284.49	6642804.54	0.57
37	4601	4601_2	Bygdoy	3	7	2017	0.97	10	16	22	14.6	118.1	132.7	547.1	2.31622645	594695.995	6642219.92	0.97
38	4603	4603_1	Bygdoy	3	7	2017	0.48	10	30	9	181.3	121.9	303.2	138.8	5.29096563	594177.833	6642666.87	0.48
39	4603	4603_2	Bygdoy	3	7	2017	0.49	10	30	48	31.7	122.0	153.7	147.1	2.68239653	594359.191	6642459.15	0.49
40	4604	4601_1	Bygdoy	3	7	2017	0.56	10	43	12	236.6	125.5	362.1	205.4	6.31966269	594301.491	6642796.28	0.56
41	4604	4601_2	Bygdoy	3	7	2017	0.88	10	53	40	10.3	128.6	138.9	472.1	2.42338967	594604.646	6642235.53	0.88
42	4605	4605_1	Bygdoy	3	7	2017	0.91	10	54	31	210.6	128.8	339.4	497.1	5.92434561	594119.43	6643056.42	0.91
43	4632	4632_1	Bygdoy	4	7	2017	2.86	14	17	6	121.0	200.8	321.8	2122.1	5.61612047	592981.104	6644258.2	2.86
44	4632	4632_2	Bygdoy	4	7	2017	0.4	14	18	46	268.6	201.4	470.1	72.1	8.20426921	594361.706	6642566.26	0.4
45	4632	4632_3	Bygdoy	4	7	2017	1.22	14	29	26	121.0	205.3	326.3	755.4	5.69518388	593874.971	6643219.55	1.22
46	4632	4632_4	Bygdoy	4	7	2017	0.62	14	33	14	357.7	206.6	564.3	255.4	9.84836937	594189.014	6642358.16	0.62
47	4632	4632_5	Bygdoy	4	7	2017	1.19	14	38	47	328.1	208.6	536.7	730.4	9.3671821	594336.046	6641861.79	1.19
48	4632	4632_6	Bygdoy	4	7	2017	1.02	14	43	4	14.0	210.1	224.1	588.8	3.91128285	593884.281	6642168.2	1.02
49	4632	4632_7	Bygdoy	4	7	2017	0.47	14	44	4	271.7	210.4	482.2	130.4	8.41510499	594404.418	6642521.6	0.47
50	4633	4633_1	Bygdoy	4	7	2017	1.24	14	47	39	14.7	211.6	226.4	772.1	3.95055276	593735.344	6642058.07	1.24

AppTable 2 Average measurements for the dances 51-100 of the Bygdøy hive

51	4633	4633_2	Bygdoy	4	7	2017	0.4	14	53	23	151.1	213.6	364.7	72.1	6.36504125	594299.894	6642662.84	0.4
52	4633	4633_3	Bygdoy	4	7	2017	1.12	14	57	9	233.7	214.9	448.6	672.1	7.82954702	594965.883	6642607.42	1.12
53	4633	4633_4	Bygdoy	4	7	2017	1.93	15	7	56	112.5	218.4	331.0	1347.1	5.77651623	593640.304	6643768.84	1.93
54	4634	4634_1	Bygdoy	4	7	2017	0.4	15	12	23	310.8	219.9	530.7	72.1	9.26193874	594305.686	6642519.87	0.4
55	4634	4634_2	Bygdoy	4	7	2017	0.82	15	17	13	236.6	221.5	458.1	422.1	7.9948297	594711.904	6642531.75	0.82
56	4635	4635_1	Bygdoy	5	7	2017	0.59	9	34	8	28.1	107.4	135.5	230.4	2.36492114	594455.501	6642426.66	0.59
57	4635	4635_2	Bygdoy	5	7	2017	0.77	9	34	33	5.6	107.5	113.0	380.4	1.97292019	594644.072	6642442.11	0.77
58	4635	4635_3	Bygdoy	5	7	2017	0.95	9	37	27	2.8	108.2	111.0	530.4	1.93644281	594789.352	6642401.35	0.95
59	4635	4635_4	Bygdoy	5	7	2017	0.93	9	40	37	140.9	108.9	249.9	513.8	4.36087967	593811.664	6642414.11	0.93
60	4635	4635_5	Bygdoy	5	7	2017	0.62	9	43	16	285.3	109.6	394.9	255.4	6.89230522	594440.136	6642800.48	0.62
61	4636	4636_1	Bygdoy	5	7	2017	0.7	9	47	22	15.2	110.6	125.8	322.1	2.19597326	594555.164	6642402.5	0.7
62	4636	4636_2	Bygdoy	5	7	2017	0.96	9	50	34	20.2	111.4	131.7	538.8	2.29790049	594696.501	6642232.89	0.96
63	4636	4636_3	Bygdoy	5	7	2017	0.83	9	55	37	351.9	112.7	464.6	430.4	8.10862517	594710.537	6642482.58	0.83
64	4637	3637_1	Bygdoy	5	7	2017	0.83	10	1	22	4.2	114.2	118.4	430.4	2.06664437	594672.58	6642386.22	0.83
65	4638	4638_1	Bygdoy	5	7	2017	0.58	10	9	4	3.4	116.2	119.6	222.1	2.08723925	594487.119	6642481.34	0.58
66	4638	4638_2	Bygdoy	5	7	2017	0.75	10	11	45	117.5	116.9	234.4	363.8	4.09035363	593998.382	6642379.05	0.75
67	4639	4639_1	Bygdoy	5	7	2017	2.37	10	18	53	60.8	118.8	179.6	1713.8	3.1344368	594306.263	6640877.29	2.37
68	4639	4639_2	Bygdoy	5	7	2017	0.72	10	20	57	258.1	119.4	377.5	338.8	6.58774526	594395.582	6642914.16	0.72
69	4639	4639_3	Bygdoy	5	7	2017	0.75	10	26	22	253.6	120.8	374.4	363.8	6.53468725	594384.522	6642943.31	0.75
70	4639	4639_4	Bygdoy	5	7	2017	0.7	10	27	29	30.9	121.1	152.1	322.1	2.65377313	594444.961	6642306.49	0.7
71	4665	4665_1	Bygdoy	7	7	2017	1.1	9	47	35	227.1	110.7	337.8	655.4	5.89589675	594046.463	6643197.87	1.1
72	4665	4665_2	Bygdoy	7	7	2017	1.02	9	48	29	105.3	111.0	216.3	588.8	3.77462357	593945.701	6642116.33	1.02
73	4665	4665_3	Bygdoy	7	7	2017	0.47	9	51	48	155.6	111.8	267.4	130.4	4.66718495	594163.717	6642585.11	0.47
74	4665	4665_4	Bygdoy	7	7	2017	1.05	9	52	58	204.8	112.1	316.8	613.8	5.52972667	593874.094	6643038.62	1.05
75	4667	4667_1	Bygdoy	7	7	2017	0.54	10	7	4	331.2	115.7	446.9	188.8	7.79935283	594482.468	6642601.31	0.54
76	4668	4668_1	Bygdoy	7	7	2017	1.75	10	12	0	49.0	117.0	166.0	1197.1	2.89794469	594582.79	6641429.27	1.75
77	4668	4668_2	Bygdoy	7	7	2017	1	10	13	27	142.9	117.4	260.3	572.1	4.54256844	593730.146	6642494.31	1
78	4668	4668_3	Bygdoy	7	7	2017	0.82	10	15	17	93.4	117.9	211.3	422.1	3.68788071	594074.72	6642230.35	0.82
79	4668	4668_4	Bygdoy	7	7	2017	0.6	10	18	35	180.6	118.8	299.4	238.8	5.22464312	594085.896	6642708.02	0.6
80	4668	4668_5	Bygdoy	7	7	2017	0.63	10	18	47	8.5	118.8	127.3	263.8	2.22180414	594503.806	6642431.17	0.63
81	4669	4669_1	Bygdoy	7	7	2017	0.87	10	25	21	256.7	120.6	377.3	463.8	6.5847782	594431.753	6643033.82	0.87
82	4669	4669_2	Bygdoy	7	7	2017	0.71	10	32	41	308.7	122.6	431.3	330.4	7.5277796	594606.993	6642696.88	0.71
83	4670	4670_1	Bygdoy	7	7	2017	0.68	10	39	3	8.0	124.4	132.4	305.4	2.31081593	594519.537	6642385.06	0.68
84	4708	4708_1	Bygdoy	14	7	2017	0.81	9	53	56	230.4	112.7	343.0	413.8	5.98717747	594173.307	6642986.76	0.81
85	4752	4752_1	Bygdoy	17	7	2017	1.1	9	24	59	77.0	105.8	182.8	655.4	3.18993827	594262.326	6641936.35	1.1
86	4752	4752_2	Bygdoy	17	7	2017	0.75	9	32	25	325.1	107.6	432.6	363.8	7.55081794	594641.162	6642699.59	0.75
87	4752	4752_3	Bygdoy	17	7	2017	1.33	9	34	35	135.8	108.1	243.9	847.1	4.25598538	593533.621	6642217.67	1.33
88	4753	4753_1	Bygdoy	17	7	2017	1.56	9	39	40	176.4	109.3	285.7	1038.8	4.9871038	593294.2	6642872.78	1.56
89	4796	4796_1	Bygdoy	18	7	2017	2.84	14	40	15	125.4	207.7	333.1	2105.4	5.81334267	593340.781	6644468.27	2.84
90	4796	4796_2	Bygdoy	18	7	2017	1.17	14	40	20	297.6	207.7	505.3	713.8	8.81949778	594700.118	6642004.05	1.17
91	4796	4796_3	Bygdoy	18	7	2017	0.58	14	48	34	245.6	210.5	456.2	222.1	7.96149392	594514.801	6642567.17	0.58
92	4797	4797_1	Bygdoy	18	7	2017	0.8	15	0	23	290.5	214.5	505.0	405.4	8.81391272	594526.537	6642258.9	0.8
93	4798	4798_1	Bygdoy	18	7	2017	1.11	15	5	56	71.9	216.3	288.2	663.8	5.02968984	593663.384	6642798.09	1.11
94	4798	4798_2	Bygdoy	18	7	2017	0.78	15	9	6	350.6	217.3	568.0	388.8	9.91259749	594111.793	6642247.59	0.78
95	4801	4801_1	Bygdoy	18	7	2017	0.38	15	37	9	288.8	226.1	514.9	55.4	8.98652579	594317.516	6642540.82	0.38
96	4802	4802_1	Bygdoy	18	7	2017	2.1	15	43	16	312.1	227.9	540.0	1488.8	9.42477796	594294	6641102.25	2.1
97	4803	4803_1	Bygdoy	18	7	2017	0.61	15	54	23	140.1	231.1	371.2	247.1	6.47918578	594342.119	6642833.35	0.61
98	4803	4803_2	Bygdoy	18	7	2017	0.63	15	57	26	11.6	232.0	243.6	263.8	4.25232019	594057.674	6642473.89	0.63
99	4803	4803_3	Bygdoy	18	7	2017	0.39	16	1	27	281.5	233.2	514.6	63.8	8.98198793	594321.314	6642533.4	0.39
100	4804	4804_1	Bygdoy	18	7	2017	1.1	16	9	43	1.8	235.5	237.3	655.4	4.14149178	593742.522	6642236.82	1.1

AppTable 3 Average measurements for the dances 101-150 of the Bygdøy hive

101	4806	4806_1	Bygdoy	19	7	2017	1.88	9	47	3	128.5	111.4	239.8	1305.4	4.18599768	593165.303	6641935.14	1.88
102	4811	4811_1	Bygdoy	19	7	2017	0.68	10	38	31	44.6	124.9	169.5	305.4	2.95798402	594349.763	6642290.72	0.68
103	4811	4811_2	Bygdoy	19	7	2017	0.98	10	41	43	71.8	125.8	197.6	555.4	3.4492942	594125.782	6642061.67	0.98
104	4849	4849_1	Bygdoy	20	7	2017	1.39	14	12	45	20.3	197.9	218.3	897.1	3.80918109	593738.621	6641886.51	1.39
105	4850	4850_1	Bygdoy	20	7	2017	1.51	14	23	59	20.6	201.9	222.5	997.1	3.88318305	593620.509	6641855.76	1.51
106	4850	4850_2	Bygdoy	20	7	2017	0.37	14	27	45	310.6	203.2	513.8	47.1	8.96767623	594314.78	6642548.75	0.37
107	4850	4850_3	Bygdoy	20	7	2017	0.76	14	34	34	318.1	205.6	523.7	372.1	9.13941663	594398.743	6642233.96	0.76
108	4851	4851_1	Bygdoy	20	7	2017	1.08	14	38	1	307.3	206.8	514.1	638.8	8.97291222	594572.907	6642016.36	1.08
109	4852	4852_1	Bygdoy	20	7	2017	1.68	14	40	51	4.2	207.7	212.0	1138.8	3.69957442	593691.06	6641624.97	1.68
110	4853	4853_1	Bygdoy	20	7	2017	0.94	14	54	44	316.1	212.4	528.5	522.1	9.2240651	594398.087	6642079.4	0.94
111	4854	4854_1	Bygdoy	20	7	2017	1.24	15	3	52	312.6	215.4	528.0	772.1	9.21603658	594453.998	6641835.68	1.24
112	4854	4854_2	Bygdoy	20	7	2017	1.21	15	8	3	13.4	216.8	230.2	747.1	4.01722434	593720.279	6642112.48	1.21
113	4854	4854_3	Bygdoy	20	7	2017	1.06	15	13	12	119.4	218.4	337.8	622.1	5.89537315	594058.751	6643166.89	1.06
114	4855	4855_1	Bygdoy	20	7	2017	0.48	15	14	23	282.2	218.8	501.0	138.8	8.74375049	594381.356	6642483.2	0.48
115	4926	4926_1	Bygdoy	1	8	2017	2.38	9	53	17	306.5	114.6	421.1	1722.1	7.35010508	595802.058	6643422.46	2.38
116	4926	4926_2	Bygdoy	1	8	2017	2.18	9	54	5	313.2	114.8	428.0	1555.4	7.47018373	595736.259	6643173.42	2.18
117	4926	4926_3	Bygdoy	1	8	2017	2.18	9	54	39	318.3	115.0	433.3	1555.4	7.56198805	595783.579	6643038.75	2.18
118	4926	4926_4	Bygdoy	1	8	2017	1.19	9	55	37	34.0	115.2	149.2	730.4	2.60350765	594668.333	6641963.8	1.19
119	4927	4927_1	Bygdoy	1	8	2017	1.9	10	14	38	300.1	120.1	420.2	1322.1	7.33404805	595441.373	6643247.84	1.9
120	4929	4929_1	Bygdoy	1	8	2017	1.32	10	33	23	15.9	125.1	141.0	838.8	2.46073971	594821.956	6641939.26	1.32
121	4972	4972_1	Bygdoy	3	8	2017	2.01	9	46	38	335.9	113.3	449.2	1413.8	7.83966993	595707.605	6642611.23	2.01
122	4972	4972_2	Bygdoy	3	8	2017	1.32	9	47	39	213.1	113.5	326.6	838.8	5.7000708	593832.162	6643291.15	1.32
123	4972	4972_3	Bygdoy	3	8	2017	1.16	9	48	8	40.3	113.7	154.0	705.4	2.68710892	594603.677	6641957.19	1.16
124	4972	4972_4	Bygdoy	3	8	2017	1.15	9	51	18	320.2	114.4	434.6	697.1	7.58537546	594966.087	6642776	1.15
125	4972	4972_5	Bygdoy	3	8	2017	2.44	9	51	3	322.1	114.4	436.4	1772.1	7.61714045	596016.614	6643006.79	2.44
126	4976	4976_1	Bygdoy	3	8	2017	1.12	10	35	38	7.9	126.0	133.9	672.1	2.33734493	594778.108	6642124.81	1.12
127	4978	4978_1	Bygdoy	3	8	2017	0.72	10	50	25	58.0	130.2	188.2	338.8	3.28453512	594245.743	6642255.7	0.72
128	4978	4978_2	Bygdoy	3	8	2017	0.68	10	52	27	53.0	130.7	183.7	305.4	3.20616984	594274.291	6642286.22	0.68
129	4978	4978_3	Bygdoy	3	8	2017	0.5	10	58	58	35.3	132.6	167.9	155.4	2.92970968	594326.684	6642439.06	0.5
130	4979	4979_1	Bygdoy	3	8	2017	1.75	11	3	3	304.3	133.8	438.1	1197.1	7.64646199	595465.4	6642837.64	1.75
131	4979	4979_2	Bygdoy	3	8	2017	0.7	11	5	4	48.8	134.4	183.1	322.1	3.19604693	594276.47	6642269.39	0.7
132	4979	4979_3	Bygdoy	3	8	2017	1.18	11	7	20	167.8	135.0	302.8	722.1	5.28468244	593686.973	6642982.05	1.18
133	4980	4980_1	Bygdoy	3	8	2017	0.65	11	13	1	40.2	136.7	176.9	280.4	3.08801105	594309.018	6642310.99	0.65
134	4980	4980_2	Bygdoy	3	8	2017	0.62	11	13	31	48.7	136.9	185.5	255.4	3.2377603	594269.475	6642336.76	0.62
135	5001	5001_1	Bygdoy	4	8	2017	2.62	11	2	55	298.7	133.9	432.6	1922.1	7.54977075	596127.828	6643166.74	2.62
136	5002	5002_1	Bygdoy	4	8	2017	0.59	11	14	21	30.9	137.3	168.1	230.4	2.93442207	594341.395	6642365.51	0.59
137	5005	5005_1	Bygdoy	4	8	2017	0.89	11	59	52	16.7	151.4	168.1	480.4	2.93372394	594393.146	6642120.93	0.89
138	5007	5007_1	Bygdoy	4	8	2017	1.22	12	10	18	22.1	154.9	176.9	755.4	3.08766198	594334.72	6641836.68	1.22
139	5008	5008_1	Bygdoy	4	8	2017	1.59	12	22	2	16.4	158.8	175.2	1063.8	3.05781685	594383.012	6641530.98	1.59
140	5008	5008_2	Bygdoy	4	8	2017	1.79	12	24	38	36.3	159.6	196.0	1230.4	3.42049627	593955.264	6641408.13	1.79
141	5009	5009_1	Bygdoy	4	8	2017	2.01	12	32	47	28.5	162.4	190.9	1413.8	3.33148448	594027.151	6641202.66	2.01
142	5010	5010_1	Bygdoy	4	8	2017	0.51	12	45	49	325.8	166.9	492.7	163.8	8.59888816	594414.381	6642479.99	0.51
143	5011	5011_1	Bygdoy	4	8	2017	0.8	12	58	59	22.9	171.5	194.4	405.4	3.39292007	594193.177	6642198.32	0.8
144	5047	5047_1	Bygdoy	7	8	2017	1.29	12	5	0	30.5	153.5	183.9	813.8	3.21018409	594238.227	6641779.16	1.29
145	5047	5047_2	Bygdoy	7	8	2017	0.88	12	6	43	32.1	154.0	186.2	472.1	3.24910494	594243.343	6642121.64	0.88
146	5048	5048_1	Bygdoy	7	8	2017	0.82	12	11	6	10.6	155.5	166.1	422.1	2.89829376	594395.682	6642181.35	0.82
147	5049	5049_1	Bygdoy	7	8	2017	1.2	12	23	27	4.5	159.6	164.1	738.8	2.86373624	594496.635	6641880.58	1.2
148	5051	5051_1	Bygdoy	7	8	2017	1.43	12	43	15	40.0	166.3	206.3	930.4	3.59974158	593882.487	6641756.53	1.43
149	5062	5062_1	Bygdoy	8	8	2017	0.97	10	8	32	18.3	119.7	138.0	547.1	2.4082053	594660.212	6642184.57	0.97
150	5062	5062_2	Bygdoy	8	8	2017	1.73	10	9	20	299.3	119.9	419.3	1180.4	7.31764195	595308.668	6643194.18	1.73

AppTable 4 Average measurements for the dances 151-211 of the Bygdøy hive

151	5069	5069_1	Bygdoy	10	8	2017	0.57	9	45	22	65.0	114.3	179.3	213.8	3.12920082	594296.649	6642377.27	0.57
152	5070	5070_1	Bygdoy	10	8	2017	1.16	10	6	43	29.8	119.6	149.5	705.4	2.60874363	594652.344	6641983.38	1.16
153	5073	5073_1	Bygdoy	10	8	2017	1.56	12	53	53	7.6	170.2	177.8	1038.8	3.10232275	594334.781	6641553.05	1.56
154	5077	5077_1	Bygdoy	10	8	2017	1.4	13	36	24	10.3	184.8	195.1	905.4	3.40461377	594058.593	6641716.72	1.4
155	5105	5105_1	Bygdoy	11	8	2017	0.57	14	19	33	309.4	199.3	508.7	213.8	8.87831537	594405.079	6642408.38	0.57
156	5105	5105_2	Bygdoy	11	8	2017	0.62	14	19	58	285.6	199.5	485.1	255.4	8.46571954	594503.097	6642444.32	0.62
157	5105	5105_3	Bygdoy	11	8	2017	0.91	14	20	12	328.8	199.6	528.3	497.1	9.22057444	594394.802	6642104.24	0.91
158	5105	5105_4	Bygdoy	11	8	2017	1.1	14	24	23	343.2	200.9	544.2	655.4	9.49755819	594246.341	6641937.32	1.1
159	5108	5108_1	Bygdoy	11	8	2017	1.16	14	59	21	10.3	212.1	222.4	705.4	3.88231039	593817.972	6642070.41	1.16
160	5111	5111_1	Bygdoy	11	8	2017	0.66	15	15	34	320.1	217.1	537.2	288.8	9.37573421	594308.156	6642302.6	0.66
161	5112	5112_1	Bygdoy	11	8	2017	0.6	15	23	27	242.8	219.5	462.3	238.8	8.06813353	594527.296	6642540.26	0.6
162	5113	5113_1	Bygdoy	13	8	2017	0.68	11	11	46	54.6	138.0	192.6	305.4	3.36202774	594227.219	6642292.97	0.68
163	5113	5113_2	Bygdoy	13	8	2017	0.75	11	11	50	32.5	138.1	170.5	363.8	2.97613544	594353.911	6642232.22	0.75
164	5113	5113_3	Bygdoy	13	8	2017	0.57	11	12	69	47.4	138.5	185.8	213.8	3.24282175	594272.399	6642378.34	0.57
165	5113	5113_4	Bygdoy	13	8	2017	1.39	11	14	56	294.5	139.0	433.5	897.1	7.56530418	595153.963	6642846.39	1.39
166	5115	5115_1	Bygdoy	13	8	2017	0.65	11	39	9	41.2	146.2	187.5	280.4	3.27196875	594257.544	6642312.96	0.65
167	5117	5117_1	Bygdoy	13	8	2017	0.65	12	8	31	10.0	155.5	165.5	280.4	2.88782178	594364.4	6642319.56	0.65
168	5118	5118_1	Bygdoy	13	8	2017	1.63	12	13	57	30.7	157.2	187.9	1097.1	3.27947366	594143.212	6641504.33	1.63
169	5120	5120_1	Bygdoy	13	8	2017	0.64	12	44	25	16.4	167.3	183.6	272.1	3.20494811	594276.774	6642319.46	0.64
170	5125	5125_1	Bygdoy	13	8	2017	0.68	13	3	40	9.5	173.8	183.2	305.4	3.19761772	594276.898	6642286.06	0.68
171	5125	5125_2	Bygdoy	13	8	2017	0.67	13	6	6	4.1	174.6	178.7	297.1	3.11890337	594300.74	6642293.99	0.67
172	5147	5147_1	Bygdoy	14	8	2017	1.81	13	8	34	249.8	175.5	425.3	1247.1	7.42201264	595426.53	6643113.1	1.81
173	5147	5147_2	Bygdoy	14	8	2017	1.36	13	10	29	253.4	176.1	429.5	872.1	7.4960146	595110.803	6642896.55	1.36
174	5148	5148_1	Bygdoy	14	8	2017	1.63	13	21	9	2.3	179.8	182.0	1097.1	3.17702284	594255.138	6641494.61	1.63
175	5149	5149_1	Bygdoy	14	8	2017	1.95	13	33	26	251.4	183.9	435.3	1363.8	7.59741823	595613.111	6642937.06	1.95
176	5153	5153_1	Bygdoy	14	8	2017	1.81	14	8	36	1.7	195.7	197.4	1247.1	3.44545448	593920.864	6641401.05	1.81
177	5153	5153_2	Bygdoy	14	8	2017	1.96	14	17	56	237.6	198.8	436.4	1372.1	7.61679139	595627.668	6642913.4	1.96
178	5154	5154_1	Bygdoy	14	8	2017	1.03	14	32	12	321.6	203.4	525.0	597.1	9.16210591	594449.04	6642014.4	1.03
179	5157	5157_1	Bygdoy	14	8	2017	1.66	14	47	12	196.3	208.2	404.5	1122.1	7.05968229	595080.339	6643391.46	1.66
180	4861	4861_1	Bygdoy	21	7	2017	0.87	10	24	86	49.4	121.5	170.9	463.8	2.98241863	594367.506	6642133.11	0.87
181	4861	4861_2	Bygdoy	21	7	2017	1.08	10	29	18	103.1	122.6	225.7	638.8	3.93903359	593836.929	6642144.81	1.08
182	4862	4862_1	Bygdoy	21	7	2017	1.1	10	38	38	46.8	125.1	171.9	655.4	3.00074458	594386.009	6641942.07	1.1
183	4865	4865_1	Bygdoy	21	7	2017	1.54	11	7	34	56.6	133.5	190.1	1022.1	3.31804544	594114.585	6641584.79	1.54
184	4865	4865_2	Bygdoy	21	7	2017	1.42	11	9	10	63.7	134.0	197.6	922.1	3.44911967	594014.883	6641712.18	1.42
185	4865	4865_3	Bygdoy	21	7	2017	0.92	11	14	57	93.9	135.7	229.7	505.4	4.00814863	593908.82	6642263.77	0.92
186	4865	4865_4	Bygdoy	21	7	2017	2.37	11	17	29	275.2	136.5	411.7	1713.8	7.18499693	595638.354	6643653.85	2.37
187	4867	4867_1	Bygdoy	21	7	2017	2.23	11	27	42	272.2	139.6	411.8	1597.1	7.18778946	595549.596	6643577.99	2.23
188	4867	4867_2	Bygdoy	21	7	2017	1.34	11	29	46	33.3	140.3	173.6	855.4	3.03024065	594389.056	6641740.88	1.34
189	4867	4867_3	Bygdoy	21	7	2017	2.28	11	31	22	240.0	140.8	380.8	1638.8	6.64569019	594875.129	6644123.25	2.28
190	4868	4868_1	Bygdoy	21	7	2017	1.13	11	43	17	18.8	144.6	163.5	680.4	2.85274066	594487.818	6641938.77	1.13
191	4868	4868_2	Bygdoy	21	7	2017	0.99	11	43	42	116.0	144.8	260.8	563.8	4.55094602	593737.581	6642500.38	0.99
192	4904	4904_1	Bygdoy	22	7	2017	1.48	12	9	46	9.8	153.5	163.3	972.1	2.85064627	594572.851	6641659.77	1.48
193	4904	4904_2	Bygdoy	22	7	2017	3.51	12	12	0	275.1	154.3	429.4	2663.8	7.49357114	596786.61	6643530.39	3.51
194	4904	4904_3	Bygdoy	22	7	2017	1.66	12	13	32	8.2	154.8	163.0	1122.1	2.84418855	594622.814	6641518.18	1.66
195	4904	4904_4	Bygdoy	22	7	2017	0.87	12	16	59	90.5	156.0	246.5	463.8	4.30206207	593868.746	6642406.01	0.87
196	4905	4905_1	Bygdoy	22	7	2017	0.63	12	28	20	88.8	160.0	248.7	263.8	4.34115745	594048.216	6642495.32	0.63
197	4905	4905_2	Bygdoy	22	7	2017	0.9	12	32	32	13.8	161.4	175.2	488.8	3.05851498	594334.558	6642103.94	0.9
198	4906	4906_1	Bygdoy	22	7	2017	0.53	12	33	41	13.0	161.8	174.8	180.4	3.05101007	594310.32	6642411.32	0.53
199	4907	4907_1	Bygdoy	22	7	2017	0.81	12	41	55	79.6	164.8	244.4	413.8	4.26593376	593920.804	6642412.35	0.81
200	4907	4907_2	Bygdoy	22	7	2017	1.79	12	40	47	348.5	164.4	512.8	1230.4	8.950572	594855.848	6641496.35	1.79
201	4908	4908_1	Bygdoy	22	7	2017	1.46	12	52	56	44.0	168.8	212.7	955.4	3.71231532	593777.845	6641787.01	1.46
202	4908	4908_2	Bygdoy	22	7	2017	1.49	13	0	24	344.0	171.5	515.5	980.4	8.99717229	594700.572	6641698.86	1.49
203	4966	4966_1	Bygdoy	2	8	2017	2.03	14	25	31	224.1	201.6	425.7	1430.4	7.42969209	595597.584	6643179.86	2.03
204	4966	4966_2	Bygdoy	2	8	2017	0.65	14	26	19	309.5	201.9	511.4	280.4	8.92491566	594428.405	6642344.89	0.65
205	4966	4966_3	Bygdoy	2	8	2017	0.82	14	32	34	289.9	204.0	493.9	422.1	8.61948304	594598.337	6642298.54	0.82
206	4967	4967_1	Bygdoy	2	8	2017	0.73	14	47	27	318.7	208.9	527.6	347.1	9.20783353	594368.709	6642252.05	0.73
207	4968	4968_1	Bygdoy	2	8	2017	2.12	14	50	50	199.6	210.0	409.6	1505.4	7.14939221	595440.943	6643566.09	2.12
208	4968	4968_2	Bygdoy	2	8	2017	1.59	14	53	42	354.5	210.9	565.4	1063.8	9.86878972	593837.05	6641630.4	1.59
209	4970	4970_1	Bygdoy	2	8	2017	0.56	15	17	59	309.8	218.6	528.4	205.4	9.2219707	594335.375	6642389.79	0.56
210	4970	4970_2	Bygdoy	2	8	2017	0.71	15	22	19	328.3	219.9	548.2	330.4	9.56859309	594246.645	6642263.99	0.71
211	4970	4970_3	Bygdoy	2	8	2017	0.54	15	25	2	34.6	220.7	255.4	188.8	4.45722184	594111.362	6642543.36	0.54

AppTable 5 Average measurements for the dances 1-50 of the Ullevål 1 hive

	movie ID	dance.id	location	day	month	year	average.length	hour	minute	second	average.angle	Azimuth	heading	distance	heading.rad	easting	northing	duration
1	4565	4565_1	Ulleval 1	1	7	2017	0.68	12	41	20	9.9	164.9	174.8	305.4	3.05135913	596669.521	6646599.83	0.68
2	4567	4567_1	Ulleval 1	1	7	2017	0.35	13	4	4	210.1	173.5	383.7	30.4	6.69595568	596654.202	6646931.86	0.35
3	4568	4568_1	Ulleval 1	1	7	2017	0.34	13	17	45	191.4	178.8	370.2	22.1	6.46103436	596645.907	6646925.74	0.34
4	4569	4569_1	Ulleval 1	1	7	2017	0.41	13	32	20	185.5	184.3	369.8	80.4	6.45457664	596655.715	6646983.24	0.41
5	4578	4578_1	Ulleval 1	2	7	2017	0.76	10	12	2	246.9	117.0	363.9	372.1	6.35195128	596667.567	6647275.2	0.76
6	4607	4607_1	Ulleval 1	3	7	2017	0.79	14	28	5	355.5	204.9	560.4	397.1	9.78099966	596503.523	6646531.85	0.79
7	4607	4607_2	Ulleval 1	3	7	2017	0.69	14	31	26	265.7	206.1	471.8	313.8	8.23411435	596933.353	6646787.59	0.69
8	4608	4608_1	Ulleval 1	3	7	2017	0.54	14	35	16	258.9	207.5	466.4	188.8	8.13969203	596823.098	6646850.8	0.54
9	4627	4627_1	Ulleval 1	4	7	2017	0.47	11	1	12	93.9	130.9	224.8	130.4	3.92384922	596550.072	6646811.49	0.47
10	4627	4627_2	Ulleval 1	4	7	2017	0.85	11	6	0	322.9	132.3	455.2	447.1	7.94438969	597087.257	6646863.64	0.85
11	4628	4628_1	Ulleval 1	4	7	2017	0.56	11	8	6	38.5	133.0	171.5	205.4	2.99254154	596672.504	6646700.86	0.56
12	4628	4628_2	Ulleval 1	4	7	2017	0.75	11	13	55	85.6	134.8	220.3	363.8	3.84530941	596406.633	6646626.66	0.75
13	4628	4628_3	Ulleval 1	4	7	2017	0.59	11	14	13	328.6	134.9	463.4	230.4	8.08837935	596866.116	6646850.48	0.59
14	4629	4629_1	Ulleval 1	4	7	2017	0.74	11	20	11	319.5	136.7	456.2	355.4	7.96254111	596995.324	6646865.49	0.74
15	4630	4630_1	Ulleval 1	4	7	2017	0.46	11	29	36	103.8	139.7	243.5	122.1	4.24952766	596532.762	6646849.49	0.46
16	4630	4630_2	Ulleval 1	4	7	2017	0.5	11	31	6	110.0	140.2	250.2	155.4	4.36611566	596495.808	6646851.25	0.5
17	4630	4630_3	Ulleval 1	4	7	2017	0.63	11	35	55	34.7	141.8	176.5	263.8	3.079808	596658.285	6646640.75	0.63
18	4644	4644_1	Ulleval 1	6	7	2017	0.61	10	1	4	39.2	114.2	153.4	247.1	2.67698601	596752.711	6646683.11	0.61
19	4644	4644_2	Ulleval 1	6	7	2017	0.48	10	3	38	53.7	114.9	168.5	138.8	2.94122886	596669.615	6646768.03	0.48
20	4645	4645_1	Ulleval 1	6	7	2017	0.68	10	15	3	269.1	117.9	386.9	305.4	6.75302794	596780.276	6647176.32	0.68
21	4645	4645_2	Ulleval 1	6	7	2017	0.65	10	19	30	136.9	119.1	255.9	280.4	4.46629756	596370.032	6646835.69	0.65
22	4646	4646_1	Ulleval 1	6	7	2017	0.51	10	24	0	60.0	120.3	180.2	163.8	3.14578144	596641.314	6646740.25	0.51
23	4646	4646_2	Ulleval 1	6	7	2017	0.59	10	24	39	115.7	120.5	236.1	230.4	4.1214205	596450.662	6646775.62	0.59
24	4647	4647_1	Ulleval 1	6	7	2017	1.06	10	29	43	56.8	121.8	178.7	622.1	3.11837977	596656.439	6646282.08	1.06
25	4647	4647_2	Ulleval 1	6	7	2017	0.9	10	34	19	331.0	123.1	454.1	488.8	7.92571467	597129.493	6646868.97	0.9
26	4647	4647_3	Ulleval 1	6	7	2017	0.61	10	35	47	130.3	123.5	253.9	247.1	4.43086737	596404.643	6646835.36	0.61
27	4647	4647_4	Ulleval 1	6	7	2017	0.45	10	38	37	116.5	124.3	240.9	113.8	4.20380004	596542.647	6646848.61	0.45
28	4648	4648_1	Ulleval 1	6	7	2017	0.57	10	44	2	50.0	125.9	175.9	213.8	3.06933602	596657.431	6646690.81	0.57
29	4649	4649_1	Ulleval 1	6	7	2017	0.72	10	47	18	138.5	126.8	265.3	338.8	4.62966037	596304.409	6646876.01	0.72
30	4650	4650_1	Ulleval 1	6	7	2017	0.47	11	4	50	134.5	132.0	266.5	130.4	4.65165152	596511.824	6646896.08	0.47
31	4650	4650_2	Ulleval 1	6	7	2017	0.57	11	7	32	123.0	132.8	255.8	213.8	4.46490129	596434.763	6646851.64	0.57
32	4650	4650_3	Ulleval 1	6	7	2017	0.69	11	8	16	110.9	133.0	243.9	313.8	4.25633445	596360.316	6646765.82	0.69
33	4673	4673_1	Ulleval 1	7	7	2017	0.41	12	2	34	235.8	150.7	386.5	80.4	6.74604662	596677.907	6646975.96	0.41
34	4674	4674_1	Ulleval 1	7	7	2017	0.46	12	14	7	4.1	154.8	158.8	122.1	2.77228098	596686.069	6646790.15	0.46
35	4674	4674_2	Ulleval 1	7	7	2017	0.37	12	16	57	111.1	155.8	266.9	47.1	4.65810924	596594.986	6646901.45	0.37
36	4675	4675_1	Ulleval 1	7	7	2017	0.68	12	26	48	63.4	159.3	222.8	305.4	3.88772091	596434.683	6646679.73	0.68
37	4675	4675_2	Ulleval 1	7	7	2017	0.7	12	27	3	91.6	159.4	251.0	322.1	4.38060189	596337.483	6646799.09	0.7
38	4675	4675_3	Ulleval 1	7	7	2017	0.88	12	27	45	145.1	159.7	304.8	472.1	5.32011263	596254.443	6647173.56	0.88
39	4678	4678_1	Ulleval 1	7	7	2017	0.58	12	53	6	75.3	169.1	244.3	222.1	4.26383936	596441.886	6646807.69	0.58
40	4678	4678_2	Ulleval 1	7	7	2017	0.45	13	0	44	13.1	171.9	185.0	113.8	3.22833552	596632.145	6646790.68	0.45
41	4679	4679_1	Ulleval 1	7	7	2017	1.36	13	5	37	156.8	173.8	330.6	872.1	5.77023304	596214.024	6647663.85	1.36
42	4680	4680_1	Ulleval 1	7	7	2017	0.53	13	14	55	62.3	177.3	239.6	180.4	4.18111076	596486.452	6646812.59	0.53
43	4699	4699_1	Ulleval 1	13	7	2017	0.59	13	29	37	53.8	182.5	236.3	230.4	4.12386396	596450.349	6646776.09	0.59
44	4704	4704_1	Ulleval 1	13	7	2017	0.5	14	29	33	67.2	204.5	271.7	155.4	4.74240864	596486.653	6646908.66	0.5
45	4706	4706_1	Ulleval 1	13	7	2017	0.51	14	45	32	306.4	210.0	516.5	163.8	9.01410199	596707.374	6646753.87	0.51
46	4706	4706_2	Ulleval 1	13	7	2017	0.24	14	48	47	73.1	211.2	284.3	61.3	4.9610984	596701.365	6646888.92	0.24
47	4716	4716_1	Ulleval 1	14	7	2017	0.56	12	14	44	88.2	155.0	243.2	205.4	4.24394261	596458.713	6646811.25	0.56
48	4716	4716_2	Ulleval 1	14	7	2017	0.31	12	15	23	110.6	155.2	265.9	2.9	4.63995782	596644.909	6646904.21	0.31
49	4717	4717_1	Ulleval 1	14	7	2017	0.52	12	35	52	45.2	162.5	207.8	172.1	3.62592152	596561.876	6646751.71	0.52
50	4719	4719_1	Ulleval 1	14	7	2017	0.55	12	47	11	45.4	166.7	212.1	197.1	3.70201788	596537.241	6646737.06	0.55

AppTable 6 Average measurements for the dances 51-100 of the Ullevål 1 hive

51	4720	4720_1	Ulleval 1	14	7	2017	0.61	13	0	23	20.1	171.6	191.6	247.1	3.34474898	596592.148	6646662	0.61
52	4720	4720_2	Ulleval 1	14	7	2017	0.28	13	0	43	64.8	171.7	236.4	27.9	4.12648195	596665.26	6646919.44	0.28
53	4720	4720_3	Ulleval 1	14	7	2017	0.34	13	8	41	11.4	174.7	186.1	22.1	3.24718507	596639.672	6646882.04	0.34
54	4722	4722_1	Ulleval 1	14	7	2017	0.32	13	14	12	59.8	176.7	236.5	5.4	4.12822728	596637.482	6646901.01	0.32
55	4722	4722_2	Ulleval 1	14	7	2017	1.78	13	16	18	356.3	177.5	533.8	1222.1	9.31604395	596774.62	6645689.13	1.78
56	4722	4722_3	Ulleval 1	14	7	2017	0.46	13	16	37	212.2	177.6	389.9	122.1	6.80416609	596702.765	6647009.89	0.46
57	4722	4722_4	Ulleval 1	14	7	2017	0.46	13	19	34	38.8	178.7	217.5	122.1	3.79644019	596567.647	6646807.17	0.46
58	4722	4722_5	Ulleval 1	14	7	2017	0.49	13	20	27	15.3	179.1	194.3	147.1	3.39117474	596605.671	6646761.47	0.49
59	4733	4733_1	Ulleval 1	15	7	2017	0.75	10	5	18	188.8	115.7	304.5	363.8	5.31505117	596342.332	6647110.19	0.75
60	4735	4735_1	Ulleval 1	15	7	2017	0.47	10	21	43	115.4	120.1	235.5	130.4	4.10955226	596534.572	6646830.06	0.47
61	4735	4735_2	Ulleval 1	15	7	2017	0.63	10	23	57	13.4	120.7	134.0	263.8	2.3392648	596831.63	6646720.68	0.63
62	4736	4736_1	Ulleval 1	15	7	2017	0.69	10	33	21	145.1	123.2	268.3	313.8	4.68324198	596328.383	6646894.86	0.69
63	4736	4736_2	Ulleval 1	15	7	2017	0.55	10	36	46	13.2	124.2	137.4	197.1	2.39790786	596775.426	6646758.95	0.55
64	4736	4736_3	Ulleval 1	15	7	2017	1.05	10	41	23	109.2	125.5	234.7	613.8	4.09576416	596141.281	6646549.08	1.05
65	4737	4737_1	Ulleval 1	15	7	2017	1.38	10	44	34	111.1	126.4	237.4	888.8	4.14410978	595892.936	6646425.69	1.38
66	4760	4760_1	Ulleval 1	17	7	2017	1.64	12	47	35	65.9	166.8	232.7	1105.4	4.0615557	595762.553	6646234.28	1.64
67	4760	4760_2	Ulleval 1	17	7	2017	1.29	12	48	17	49.0	167.1	216.1	813.8	3.77148198	596162.656	6646246.41	1.29
68	4760	4760_3	Ulleval 1	17	7	2017	1.34	12	56	25	27.6	170.1	197.7	855.4	3.4503414	596382.067	6646089.03	1.34
69	4761	4761_1	Ulleval 1	17	7	2017	1.23	13	4	39	51.2	173.1	224.3	763.8	3.91494805	596108.49	6646357.48	1.23
70	4763	4763_1	Ulleval 1	17	7	2017	1.12	13	19	39	23.4	178.7	202.0	672.1	3.52626322	596389.798	6646281.03	1.12
71	4764	4764_1	Ulleval 1	17	7	2017	1.82	13	34	33	47.1	184.2	231.3	1255.4	4.03642296	595662.646	6646118.55	1.82
72	4764	4764_2	Ulleval 1	17	7	2017	0.72	13	39	18	212.6	186.0	398.6	338.8	6.95600973	596853.108	6647168.92	0.72
73	4764	4764_3	Ulleval 1	17	7	2017	0.29	13	40	20	14.2	186.3	200.5	19.6	3.49955968	596648.861	6646922.34	0.29
74	4765	4765_1	Ulleval 1	17	7	2017	0.83	13	44	19	186.8	187.8	374.6	430.4	6.53852698	596750.713	6647320.46	0.83
75	4765	4765_2	Ulleval 1	17	7	2017	0.69	13	45	10	162.8	188.1	351.0	313.8	6.12558208	596592.756	6647213.86	0.69
76	4766	4766_1	Ulleval 1	17	7	2017	0.75	13	53	26	34.0	191.2	225.1	363.8	3.92908521	596384.252	6646647.33	0.75
77	4771	4771_1	Ulleval 1	18	7	2017	0.8	9	38	47	218.9	109.3	328.2	405.4	5.72782154	596428.243	6647248.49	0.8
78	4771	4771_2	Ulleval 1	18	7	2017	0.67	9	42	37	202.3	110.2	312.5	297.1	5.45415391	596422.967	6647104.71	0.67
79	4775	4775_1	Ulleval 1	18	7	2017	0.26	10	16	45	54.3	119.0	173.3	44.6	3.02465559	596636.798	6646948.28	0.26
80	4776	4776_1	Ulleval 1	18	7	2017	0.81	10	32	9	350.0	123.1	473.1	413.8	8.25680363	597022.633	6646741.8	0.81
81	4777	4777_1	Ulleval 1	18	7	2017	0.62	10	34	57	111.3	123.9	235.2	255.4	4.10431627	596432.367	6646758.08	0.62
82	4777	4777_2	Ulleval 1	18	7	2017	0.88	10	41	25	99.8	125.7	225.5	472.1	3.93641559	596305.055	6646573.35	0.88
83	4778	4778_1	Ulleval 1	18	7	2017	0.95	10	49	3	188.8	127.9	316.7	530.4	5.52745774	596278.231	6647290.02	0.95
84	4778	4778_2	Ulleval 1	18	7	2017	0.8	10	52	1	339.6	128.7	468.3	405.4	8.17337689	597026.913	6646776.7	0.8
85	4778	4778_3	Ulleval 1	18	7	2017	0.48	10	57	54	97.9	130.5	228.3	138.8	3.98493575	596538.372	6646811.74	0.48
86	4779	4779_1	Ulleval 1	18	7	2017	0.78	11	1	40	219.5	131.6	351.1	388.8	6.12750194	596581.722	6647288.05	0.78
87	4822	4822_1	Ulleval 1	19	7	2017	1.47	14	52	56	19.8	211.9	231.7	963.8	4.04410241	595885.568	6646306.82	1.47
88	4822	4822_2	Ulleval 1	19	7	2017	0.54	14	53	28	10.7	212.1	222.8	188.8	3.88824451	596513.804	6646765.46	0.54
89	4823	4823_1	Ulleval 1	19	7	2017	0.47	15	9	57	34.7	217.5	252.2	130.4	4.40189491	596517.82	6646864.15	0.47
90	4823	4823_2	Ulleval 1	19	7	2017	0.45	15	11	42	355.4	218.1	573.5	113.8	10.0094633	596579.217	6646809.15	0.45
91	4826	4826_1	Ulleval 1	19	7	2017	0.74	15	32	11	7.7	224.5	232.1	355.4	4.05143279	596361.432	6646685.82	0.74
92	4826	4826_2	Ulleval 1	19	7	2017	0.72	15	38	46	8.2	226.5	234.6	338.8	4.09506602	596365.773	6646707.91	0.72
93	4827	4827_1	Ulleval 1	19	7	2017	1.3	15	47	45	19.0	229.1	248.1	822.1	4.33016187	595879.241	6646597.37	1.3
94	4830	4830_1	Ulleval 1	20	7	2017	0.58	9	21	0	126.8	105.2	232.0	222.1	4.04864027	596467.068	6646767.18	0.58
95	4830	4830_2	Ulleval 1	20	7	2017	0.88	9	21	17	123.9	105.3	229.2	472.1	4.00029465	596284.635	6646595.53	0.88
96	4830	4830_3	Ulleval 1	20	7	2017	1.16	9	22	59	355.4	105.7	461.1	705.4	8.04684052	597334.338	6646768.8	1.16
97	4830	4830_4	Ulleval 1	20	7	2017	0.62	9	26	8	352.4	106.4	458.8	255.4	8.00739608	596894.417	6646864.97	0.62
98	4830	4830_5	Ulleval 1	20	7	2017	0.89	9	26	33	94.1	106.5	200.6	480.4	3.50147955	596472.812	6646454.36	0.89
99	4830	4830_6	Ulleval 1	20	7	2017	0.44	9	31	21	142.8	107.7	250.5	105.4	4.37117711	596542.661	6646868.72	0.44
100	4830	4830_7	Ulleval 1	20	7	2017	0.88	9	32	21	8.6	107.9	116.5	472.1	2.03365764	597064.41	6646693.21	0.88

AppTable 7 Average measurements for the dances 101-150 of the Ullevål 1 hive

101	4831	4831_1	Ulleval 1	20	7	2017	0.96	9	35	0	7.8	108.6	116.4	538.8	2.03069058	597124.774	6646664.87	0.96
102	4833	4833_1	Ulleval 1	20	7	2017	1.03	9	52	38	117.3	112.9	230.2	597.1	4.01827154	596183.071	6646522.04	1.03
103	4833	4833_2	Ulleval 1	20	7	2017	0.73	9	55	59	155.5	113.8	269.3	347.1	4.69982261	596294.944	6646899.64	0.73
104	4833	4833_3	Ulleval 1	20	7	2017	0.6	9	57	44	350.0	114.2	464.2	238.8	8.10181839	596873.455	6646845.43	0.6
105	4935	4935_1	Ulleval 1	1	8	2017	4.16	11	59	54	199.7	151.2	350.9	3205.4	6.12366221	596132.828	6650068.72	4.16
106	4935	4935_2	Ulleval 1	1	8	2017	0.78	12	0	56	329.6	151.5	481.1	388.8	8.39642997	596974.944	6646703.31	0.78
107	4935	4935_3	Ulleval 1	1	8	2017	0.47	12	3	20	116.1	152.3	268.3	130.4	4.68341651	596511.638	6646900.22	0.47
108	4935	4935_4	Ulleval 1	1	8	2017	1.45	12	8	42	206.5	154.1	360.6	947.1	6.29365728	596651.918	6647851.03	1.45
109	4935	4935_5	Ulleval 1	1	8	2017	0.88	12	9	37	67.4	154.4	221.8	472.1	3.87079122	596327.464	6646551.96	0.88
110	4935	4935_6	Ulleval 1	1	8	2017	0.45	12	10	0	46.5	154.5	201.0	113.8	3.5081118	596601.236	6646797.81	0.45
111	4937	4937_1	Ulleval 1	1	8	2017	0.49	12	24	23	320.9	159.3	480.2	147.1	8.38089654	596769.133	6646830.04	0.49
112	4938	4938_1	Ulleval 1	1	8	2017	1.12	12	33	50	47.0	162.6	209.6	672.1	3.65751198	596310.438	6646319.4	1.12
113	4938	4938_2	Ulleval 1	1	8	2017	0.41	12	34	31	15.3	162.8	178.1	80.4	3.10860593	596644.652	6646823.63	0.41
114	4938	4938_3	Ulleval 1	1	8	2017	0.77	12	36	0	88.2	163.3	251.5	380.4	4.38950307	596281.242	6646783.29	0.77
115	4938	4938_4	Ulleval 1	1	8	2017	0.58	12	37	32	46.0	163.9	209.9	222.1	3.6629225	596531.395	6646711.42	0.58
116	4938	4938_5	Ulleval 1	1	8	2017	0.78	12	40	58	108.9	165.0	273.9	388.8	4.78045682	596254.15	6646930.44	0.78
117	4983	4983_1	Ulleval 1	3	8	2017	0.78	12	5	51	78.5	153.3	231.8	388.8	4.04602227	596336.414	6646663.7	0.78
118	4983	4983_2	Ulleval 1	3	8	2017	3.3	12	11	41	192.2	155.3	347.5	2488.8	6.06432102	596101.64	6649333.38	3.3
119	4983	4983_3	Ulleval 1	3	8	2017	1.15	12	13	50	8.3	156.0	164.3	697.1	2.8672269	596830.865	6646232.99	1.15
120	4983	4983_4	Ulleval 1	3	8	2017	2.77	12	14	25	194.0	156.2	350.2	2047.1	6.11214304	596293.567	6648921.21	2.77
121	4984	4984_1	Ulleval 1	3	8	2017	3.21	12	18	34	191.5	157.6	349.0	2413.8	6.09189722	596183.089	6649273.72	3.21
122	4984	4984_2	Ulleval 1	3	8	2017	5.36	12	19	58	199.6	158.0	357.6	4205.4	6.24129741	596465.895	6651105.73	5.36
123	4984	4984_3	Ulleval 1	3	8	2017	3.78	12	24	40	215.4	159.6	375.0	2888.8	6.5444611	597388.202	6649694.71	3.78
124	4984	4984_4	Ulleval 1	3	8	2017	0.48	12	25	44	18.9	160.0	178.9	138.8	3.1216959	596644.76	6646765.28	0.48
125	4985	4985_1	Ulleval 1	3	8	2017	0.53	12	30	20	329.5	161.6	491.0	180.4	8.56991569	596778.121	6646785.59	0.53
126	4987	4987_1	Ulleval 1	3	8	2017	0.57	12	55	0	78.6	170.1	248.7	213.8	4.34045932	596442.865	6646826.32	0.57
127	4990	4990_1	Ulleval 1	3	8	2017	4.23	13	22	19	174.9	179.7	354.6	3263.8	6.18806486	596332.019	6650153	4.23
128	4990	4990_2	Ulleval 1	3	8	2017	0.76	13	24	55	20.5	180.6	201.1	372.1	3.51038072	596507.869	6646556.93	0.76
129	5012	5012_1	Ulleval 1	4	8	2017	3.67	13	45	3	187.7	187.7	375.4	2797.1	6.55109335	597382.429	6649601.3	3.67
130	5012	5012_2	Ulleval 1	4	8	2017	0.72	13	50	5	41.1	189.4	230.5	338.8	4.02280939	596380.65	6646688.48	0.72
131	5012	5012_3	Ulleval 1	4	8	2017	0.3	13	51	45	61.8	190.0	251.8	11.3	4.39456452	596652.687	6646907.52	0.3
132	5013	5013_1	Ulleval 1	4	8	2017	0.63	13	57	10	5.1	191.9	197.0	263.8	3.43829863	596564.887	6646651.77	0.63
133	5013	5013_2	Ulleval 1	4	8	2017	0.77	13	57	26	183.1	192.0	375.1	380.4	6.54725362	596741.293	6647271.23	0.77
134	5014	5014_1	Ulleval 1	4	8	2017	3.7	14	5	21	154.2	194.7	348.9	2822.1	6.09015189	596100.62	6649673.67	3.7
135	5014	5014_2	Ulleval 1	4	8	2017	0.58	14	7	34	2.3	195.5	197.8	222.1	3.45243579	596574.073	6646692.56	0.58
136	5015	5015_1	Ulleval 1	4	8	2017	0.57	14	11	5	75.5	196.7	272.2	213.8	4.75078622	596428.408	6646912.21	0.57
137	5015	5015_2	Ulleval 1	4	8	2017	3.53	14	19	25	179.4	199.5	378.9	2680.4	6.61322707	597510.676	6649439.75	3.53
138	5016	5016_1	Ulleval 1	4	8	2017	1.19	14	23	15	41.6	200.8	242.4	730.4	4.23032904	595994.82	6646565.37	1.19
139	5019	5019_1	Ulleval 1	4	8	2017	0.75	14	56	14	357.4	211.6	569.0	363.8	9.93144704	596465.484	6646585.95	0.75
140	5026	5026_1	Ulleval 1	5	8	2017	0.56	11	51	38	19.7	149.0	168.7	205.4	2.94419592	596682.286	6646702.57	0.56
141	5027	5027_1	Ulleval 1	5	8	2017	1.38	12	3	48	5.3	152.9	158.2	888.8	2.76180901	596971.477	6646078.58	1.38
142	5027	5027_2	Ulleval 1	5	8	2017	0.66	12	3	58	99.1	153.0	252.1	288.8	4.39910238	596367.305	6646815.01	0.66
143	5028	5028_1	Ulleval 1	5	8	2017	0.66	12	20	9	117.6	158.3	276.0	288.8	4.81623607	596354.806	6646933.93	0.66
144	5029	5029_1	Ulleval 1	5	8	2017	0.67	12	23	32	112.3	159.4	271.7	297.1	4.74205958	596345.047	6646912.81	0.67
145	5029	5029_2	Ulleval 1	5	8	2017	1.21	12	26	27	91.5	160.4	251.9	747.1	4.39700798	595931.764	6646672.27	1.21
146	5092	5092_1	Ulleval 1	11	8	2017	0.51	10	53	26	43.2	132.5	175.7	163.8	3.06619443	596654.335	6646740.72	0.51
147	5127	5127_1	Ulleval 1	13	8	2017	0.55	14	30	5	59.8	202.8	262.6	197.1	4.58306008	596446.563	6646878.58	0.55
148	5136	5136_1	Ulleval 1	14	8	2017	0.29	10	21	31	295.8	124.4	420.2	19.6	7.33387352	596625.006	6646894.27	0.29
149	5138	5138_1	Ulleval 1	14	8	2017	0.56	10	30	45	130.2	126.8	257.0	205.4	4.48584524	596441.832	6646857.86	0.56
150	5138	5138_2	Ulleval 1	14	8	2017	0.62	10	33	47	81.2	127.7	208.9	255.4	3.64546921	596518.679	6646680.33	0.62

AppTable 8 Average measurements for the dances 151-190 of the Ullevål 1 hive

151	5138	5138_3	Ulleval 1	14	8	2017	0.67	10	35	33	85.6	128.1	213.7	297.1	3.72959408	596477.208	6646656.81	0.67
152	5138	5138_4	Ulleval 1	14	8	2017	0.46	10	36	12	105.0	128.3	233.3	122.1	4.07132955	596544.155	6646830.99	0.46
153	5139	5139_1	Ulleval 1	14	8	2017	0.57	10	54	6	117.8	133.3	251.0	213.8	4.38130002	596439.859	6646834.52	0.57
154	5140	5140_1	Ulleval 1	14	8	2017	0.65	10	55	36	108.3	133.7	242.0	280.4	4.22317319	596394.476	6646772.22	0.65
155	5140	5140_2	Ulleval 1	14	8	2017	0.56	10	56	57	111.1	134.1	245.2	205.4	4.27937279	596455.542	6646817.81	0.56
156	5140	5140_3	Ulleval 1	14	8	2017	0.65	10	59	34	121.6	134.8	256.4	280.4	4.4755478	596369.411	6646838.2	0.65
157	4885	4885_1	Ulleval 1	21	7	2017	0.44	14	16	28	43.3	199.2	242.5	105.4	4.23294703	596548.469	6646855.37	0.44
158	4885	4885_2	Ulleval 1	21	7	2017	0.92	14	17	34	14.1	199.6	213.8	505.4	3.73064128	596361.206	6646483.76	0.92
159	4885	4885_3	Ulleval 1	21	7	2017	0.57	14	23	29	207.7	201.7	409.4	213.8	7.14450529	596804.173	6647043.24	0.57
160	4886	4886_1	Ulleval 1	21	7	2017	0.34	14	32	29	3.7	204.8	208.5	22.1	3.63953509	596631.453	6646884.6	0.34
161	4888	4888_1	Ulleval 1	21	7	2017	0.64	14	56	3	203.5	212.8	416.2	272.1	7.26458395	596868.176	6647055.24	0.64
162	4891	4891_1	Ulleval 1	22	7	2017	0.64	9	31	48	337.4	108.0	445.4	272.1	7.77352196	596913.203	6646925.87	0.64
163	4891	4891_2	Ulleval 1	22	7	2017	0.61	9	35	36	122.1	108.9	231.0	247.1	4.03153604	596450.007	6646748.47	0.61
164	4891	4891_3	Ulleval 1	22	7	2017	0.7	9	39	2	131.7	109.8	241.4	322.1	4.21374841	596359.136	6646749.97	0.7
165	4892	4892_1	Ulleval 1	22	7	2017	0.57	9	50	14	147.7	112.5	260.2	213.8	4.54117218	596431.375	6646867.58	0.57
166	4892	4892_2	Ulleval 1	22	7	2017	0.68	9	50	22	126.2	112.6	238.8	305.4	4.16714812	596380.868	6646745.6	0.68
167	4892	4892_3	Ulleval 1	22	7	2017	0.47	9	52	32	86.0	113.1	199.1	130.4	3.47547414	596599.261	6646780.79	0.47
168	4893	4893_1	Ulleval 1	22	7	2017	1.14	9	56	2	352.7	114.0	466.7	688.8	8.14597522	597301.597	6646705.74	1.14
169	4893	4893_2	Ulleval 1	22	7	2017	0.58	9	57	21	7.6	114.3	122.0	222.1	2.12860356	596830.419	6646786.45	0.58
170	4894	4894_1	Ulleval 1	22	7	2017	0.33	9	59	32	103.6	114.9	218.5	13.8	3.81336988	596633.442	6646893.24	0.33
171	4895	4895_1	Ulleval 1	22	7	2017	1.22	10	21	53	117.2	120.7	238.0	755.4	4.15336002	596001.58	6646503.35	1.22
172	4895	4895_2	Ulleval 1	22	7	2017	1.15	10	22	39	322.8	120.9	443.7	697.1	7.74420042	597334.887	6646980.37	1.15
173	4895	4895_3	Ulleval 1	22	7	2017	0.33	10	23	0	149.7	121.0	270.7	13.8	4.72495535	596628.251	6646904.17	0.33
174	4896	4896_1	Ulleval 1	22	7	2017	0.8	10	27	30	5.1	122.3	127.4	405.4	2.2226768	596964.284	6646658.04	0.8
175	4897	4897_1	Ulleval 1	22	7	2017	0.58	10	30	37	106.8	123.1	229.9	222.1	4.01251195	596472.124	6646760.95	0.58
176	4912	4912_1	Ulleval 1	31	7	2017	0.58	13	30	14	20.2	182.4	202.6	222.1	3.53586253	596556.69	6646698.96	0.58
177	4912	4912_2	Ulleval 1	31	7	2017	0.88	13	33	36	7.9	183.6	191.5	472.1	3.34195645	596548.043	6646441.36	0.88
178	4912	4912_3	Ulleval 1	31	7	2017	1.25	13	40	21	293.7	186.0	479.8	780.4	8.37321709	597319.557	6646516.74	1.25
179	4914	4914_1	Ulleval 1	31	7	2017	3.11	13	56	14	173.7	191.6	365.3	2330.4	6.37586229	596857.667	6649224.42	3.11
180	4916	4916_1	Ulleval 1	31	7	2017	0.97	14	13	56	316.4	197.8	514.2	547.1	8.97430848	596880.194	6646411.49	0.97
181	4918	4918_1	Ulleval 1	31	7	2017	0.29	14	39	36	96.2	206.5	302.7	19.6	5.28328618	596658.478	6646893.42	0.29
182	4961	4961_1	Ulleval 1	2	8	2017	0.87	11	24	31	23.5	140.1	163.6	463.8	2.85570772	596772.781	6646459.07	0.87
183	4961	4961_2	Ulleval 1	2	8	2017	0.42	11	24	0	156.2	139.9	296.1	88.8	5.16774538	596562.293	6646943.03	0.42
184	4962	4962_1	Ulleval 1	2	8	2017	0.92	11	38	25	90.0	144.4	234.4	505.4	4.09157537	596230.891	6646610	0.92
185	4962	4962_2	Ulleval 1	2	8	2017	0.84	11	44	12	73.6	146.2	219.8	438.8	3.83658276	596361.034	6646567.01	0.84
186	4962	4962_3	Ulleval 1	2	8	2017	0.31	11	44	33	76.6	146.3	222.9	2.9	3.89016437	596643.985	6646906.14	0.31
187	4962	4962_4	Ulleval 1	2	8	2017	0.32	11	45	33	153.6	146.6	300.3	5.4	5.24087468	596637.322	6646906.73	0.32
188	4962	4962_5	Ulleval 1	2	8	2017	0.98	11	46	14	80.9	146.9	227.8	555.4	3.97551097	596230.675	6646530.77	0.98
189	4962	4962_6	Ulleval 1	2	8	2017	1.22	11	47	40	290.5	147.3	437.8	755.4	7.64052787	597380.273	6647064.02	1.22
190	4963	4963_1	Ulleval 1	2	8	2017	0.64	11	48	58	197.4	147.7	345.1	272.1	6.02330578	596572.084	6647166.95	0.64

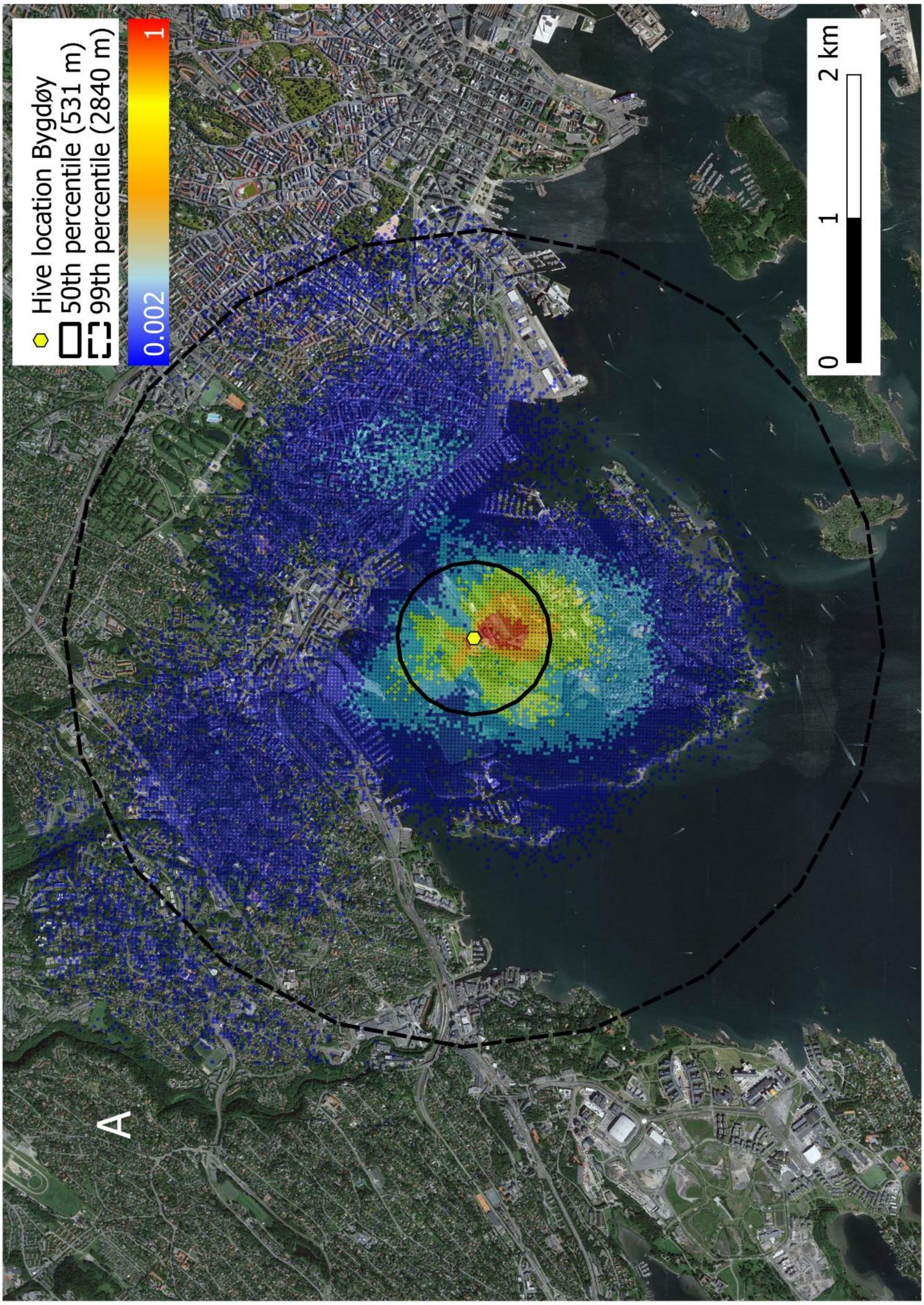
AppTable 9 Average measurements for the dances 1-50 of the Ullevål 2 hive

	movie ID	dance.id	location	day	month	year	average.leng	hour	minute	second	average.angl	Azimuth	heading	distance	heading.rad	easting	northing	duration
1	4818	4181_2	Ulleval 2	19	7	2017	0.29	13	52	0	155.4	190.5	346.0	19.6	6.03796655	596646.754	6646882	0.29
2	4613	4613_1	Ulleval 2	3	7	2017	0.3	13	52	0	91.1	191.7	282.8	11.3	4.93526753	596652.972	6646898.51	0.3
3	4785	4785_2	Ulleval 2	18	7	2017	0.34	13	57	48	88.8	192.7	281.5	22.1	4.91327638	596620.361	6646905.41	0.34
4	4571	4571_3	Ulleval 2	1	7	2017	0.35	14	5	23	89.0	196.8	285.8	30.4	4.988151	596612.733	6646909.28	0.35
5	4583	4583_2	Ulleval 2	2	7	2017	0.35	14	16	28	55.2	200.8	256.0	30.4	4.46856648	596612.483	6646893.66	0.35
6	4574	4574_1	Ulleval 2	1	7	2017	0.35	14	32	15	75.9	206.6	282.5	30.4	4.93125327	596612.309	6646907.6	0.35
7	4660	4660_2	Ulleval 2	6	7	2017	0.35	10	52	13	257.9	128.2	386.2	30.4	6.73958891	596655.405	6646928.3	0.35
8	4661	4661_1	Ulleval 2	6	7	2017	0.36	10	56	14	114.7	129.4	244.1	38.8	4.25982511	596607.151	6646884.06	0.36
9	4847	4847_1	Ulleval 2	20	7	2017	0.36	10	58	48	170.3	130.9	301.2	38.8	5.25675717	596608.851	6646921.07	0.36
10	4686	4686_2	Ulleval 2	7	7	2017	0.37	11	4	14	231.8	131.8	363.6	47.1	6.34566809	596644.94	6646947.99	0.37
11	4724	4724_1	Ulleval 2	14	7	2017	0.38	11	7	34	0.8	133.1	133.9	55.4	2.3361232	596681.964	6646862.61	0.38
12	4724	4724_2	Ulleval 2	14	7	2017	0.38	11	15	36	156.2	135.5	291.7	55.4	5.09129996	596590.514	6646921.5	0.38
13	4691	4691_2	Ulleval 2	13	7	2017	0.39	11	30	21	130.4	140.1	270.5	63.8	4.72111563	596578.252	6646901.56	0.39
14	4842	4842_1	Ulleval 2	20	7	2017	0.39	15	14	39	357.9	218.9	576.8	63.8	10.0667101	596603.83	6646849.94	0.39
15	4692	4692_1	Ulleval 2	13	7	2017	0.39	15	16	0	44.8	220.1	264.9	63.8	4.62337719	596578.502	6646895.33	0.39
16	4694	4694_1	Ulleval 2	13	7	2017	0.41	15	32	47	347.8	225.3	573.1	80.4	10.0024819	596598.084	6646833.63	0.41
17	4572	4572_1	Ulleval 2	1	7	2017	0.41	15	36	30	111.9	227.8	339.7	80.4	5.92835987	596614.061	6646976.41	0.41
18	4687	4687_1	Ulleval 2	7	7	2017	0.41	15	43	33	235.3	229.3	464.6	80.4	8.10792704	596719.838	6646880.8	0.41
19	4820	4820_3	Ulleval 2	19	7	2017	0.41	9	51	6	227.9	112.4	340.3	80.4	5.93935544	596614.892	6646976.71	0.41
20	4724	4724_4	Ulleval 2	14	7	2017	0.43	9	53	14	233.3	112.6	345.8	97.1	6.03569762	596618.218	6646995.13	0.43
21	4790	4790_1	Ulleval 2	18	7	2017	0.43	9	54	8	235.7	113.1	348.8	97.1	6.08823203	596623.193	6646996.24	0.43
22	4616	4616_1	Ulleval 2	3	7	2017	0.45	9	57	17	231.3	113.2	344.5	113.8	6.01300834	596611.64	6647010.62	0.45
23	4785	4785_1	Ulleval 2	18	7	2017	0.46	10	8	55	358.6	116.9	475.5	122.1	8.29921513	596752.181	6646848.42	0.46
24	4691	4691_3	Ulleval 2	13	7	2017	0.46	10	9	34	98.7	116.7	215.4	122.1	3.75856654	596571.366	6646801.42	0.46
25	4621	4621_1	Ulleval 2	4	7	2017	0.46	10	22	55	6.3	120.0	126.3	122.1	2.20382725	596740.428	6646828.78	0.46
26	4571	4571_2	Ulleval 2	1	7	2017	0.47	10	30	46	109.7	122.1	231.8	130.4	4.04584774	596539.497	6646820.37	0.47
27	4657	4657_1	Ulleval 2	6	7	2017	0.48	10	34	38	229.2	123.2	352.4	138.8	6.15054028	596623.649	6647038.53	0.48
28	4845	4845_2	Ulleval 2	20	7	2017	0.48	10	34	54	237.0	124.1	361.0	138.8	6.3011622	596644.494	6647039.73	0.48
29	4621	4621_2	Ulleval 2	4	7	2017	0.49	12	0	16	69.9	150.0	219.9	147.1	3.83797903	596547.653	6646788.16	0.49
30	4682	4682_1	Ulleval 2	7	7	2017	0.49	12	3	39	95.0	151.1	246.2	147.1	4.29612795	596507.477	6646841.53	0.49
31	4788	4788_1	Ulleval 2	18	7	2017	0.52	12	6	25	187.9	152.2	340.1	172.1	5.93656292	596583.539	6647062.85	0.52
32	4729	4729_2	Ulleval 2	14	7	2017	0.54	12	10	58	328.2	153.7	481.9	188.8	8.41109073	596802.209	6646801.2	0.54
33	4845	4845_1	Ulleval 2	20	7	2017	0.54	12	19	52	301.3	157.0	458.3	188.8	7.99866943	596828.778	6646873.79	0.54
34	4583	4583_1	Ulleval 2	2	7	2017	0.55	12	27	35	330.1	159.8	489.9	197.1	8.55019347	596793.218	6646774.61	0.55
35	4820	4820_1	Ulleval 2	19	7	2017	0.55	12	39	36	161.4	163.9	325.3	197.1	5.67825419	596529.918	6647063.11	0.55
36	4725	4725_2	Ulleval 2	14	7	2017	0.56	12	42	0	44.5	164.8	209.3	205.4	3.65332319	596541.41	6646721.9	0.56
37	4656	4656_3	Ulleval 2	6	7	2017	0.56	12	52	28	101.8	168.9	270.7	205.4	4.72460629	596436.599	6646903.51	0.56
38	4697	4697_1	Ulleval 2	13	7	2017	0.56	13	6	33	29.6	173.9	203.5	205.4	3.55209409	596560.025	6646712.65	0.56
39	4614	4614_1	Ulleval 2	3	7	2017	0.58	13	8	27	329.4	175.1	504.5	222.1	8.80518608	596770.964	6646720.2	0.58
40	4783	4783_1	Ulleval 2	18	7	2017	0.59	13	25	47	291.3	180.9	472.2	230.4	8.24179379	596855.306	6646813.86	0.59
41	4945	4945_1	Ulleval 2	1	8	2017	0.61	13	26	35	143.8	181.1	324.9	247.1	5.67074927	596499.961	6647103.18	0.61
42	4682	4682_3	Ulleval 2	7	7	2017	0.62	13	28	16	26.5	182.4	208.8	255.4	3.64459654	596518.874	6646677.22	0.62
43	4622	4622_1	Ulleval 2	4	7	2017	0.62	13	30	23	149.3	183.4	332.7	255.4	5.80653589	596524.814	6647127.95	0.62
44	4950	4950_1	Ulleval 2	1	8	2017	0.63	13	40	44	148.0	186.2	334.1	263.8	5.83166863	596526.918	6647138.32	0.63
45	4782	4782_1	Ulleval 2	18	7	2017	0.63	13	46	31	13.0	188.6	201.5	263.8	3.51718751	596545.25	6646655.64	0.63
46	4783	4783_2	Ulleval 2	18	7	2017	0.64	13	53	57	143.1	191.3	334.4	272.1	5.83568289	596524.265	6647146.29	0.64
47	5021	5021_1	Ulleval 2	4	8	2017	0.64	14	11	34	134.2	196.9	331.0	272.1	5.77721436	596510.133	6647138.99	0.64
48	4687	4687_2	Ulleval 2	7	7	2017	0.65	14	13	30	258.3	199.3	457.6	280.4	7.98662666	596919.953	6646863.91	0.65
49	4691	4691_1	Ulleval 2	13	7	2017	0.65	14	20	24	171.7	201.3	372.9	280.4	6.50903091	596704.794	6647174.3	0.65
50	4783	4783_3	Ulleval 2	18	7	2017	0.67	14	24	33	13.6	202.3	215.9	297.1	3.76764226	596467.925	6646660.26	0.67

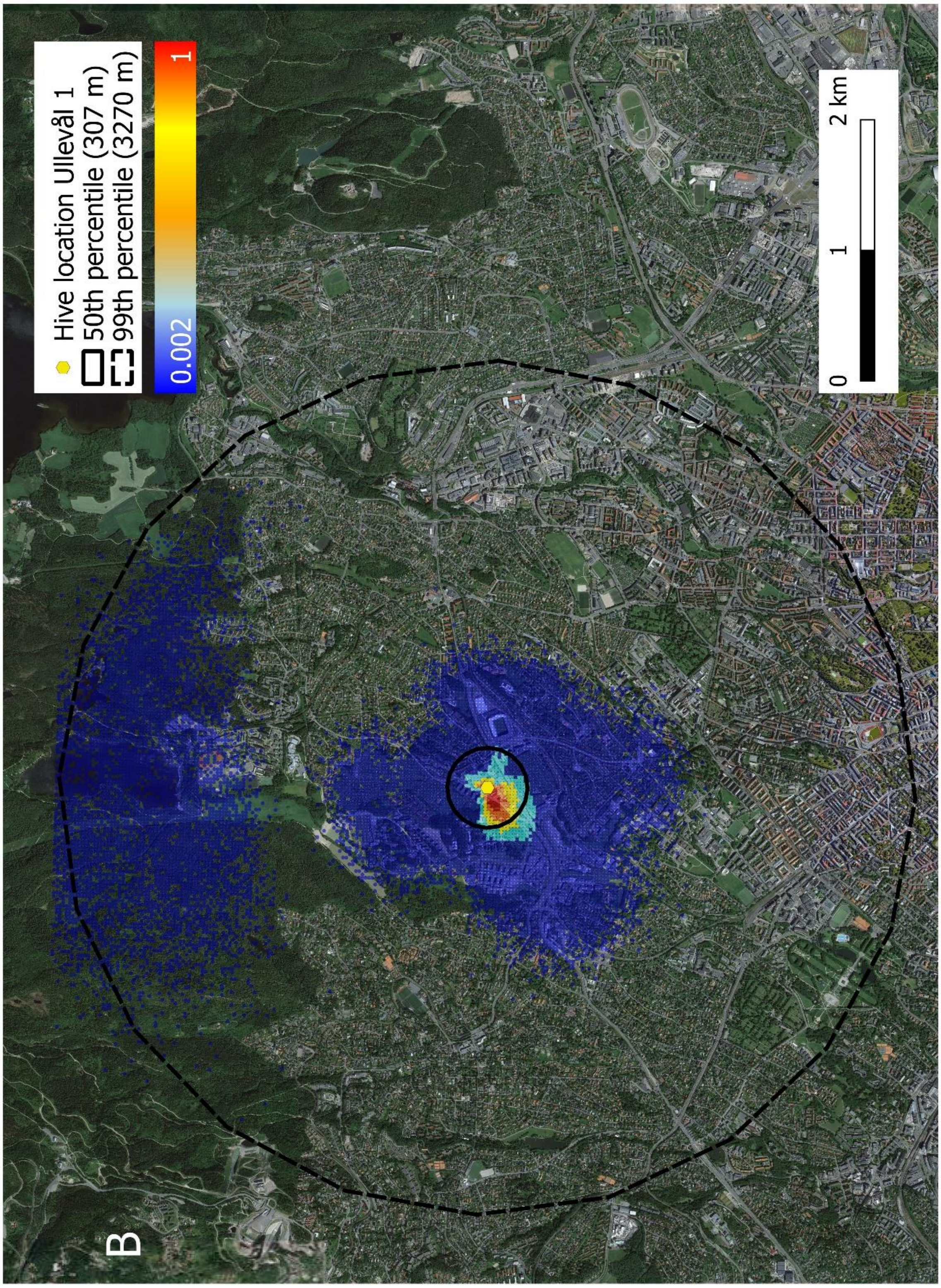
AppTable 10 Average measurements for the dances 51-105 of the Ullevål 2 hive

51	4573	4573_1	Ulleval 2	1	7	2017	0.68	14	25	59	11.7	204.4	216.1	305.4	3.77165651	596462.05	6646654.23	0.68
52	4620	4620_4	Ulleval 2	4	7	2017	0.68	12	11	19	354.9	153.9	508.8	305.4	8.8795371	596800.396	6646639.87	0.68
53	4998	4998_1	Ulleval 2	3	8	2017	0.69	12	14	43	90.1	156.3	246.3	313.8	4.29944408	596354.623	6646775.09	0.69
54	4696	4696_1	Ulleval 2	13	7	2017	0.7	12	19	34	351.8	156.7	508.5	322.1	8.87465018	596810.384	6646626.44	0.7
55	4993	4993_1	Ulleval 2	3	8	2017	0.7	12	32	18	336.9	162.2	499.1	322.1	8.7104147	596853.009	6646657.66	0.7
56	4781	4781_1	Ulleval 2	18	7	2017	0.72	12	37	0	121.2	163.0	284.2	338.8	4.9600512	596313.586	6646984.04	0.72
57	4818	4181_1	Ulleval 2	19	7	2017	0.72	12	47	16	155.7	166.7	322.4	338.8	5.62659244	596435.22	6647169.32	0.72
58	4900	4900_1	Ulleval 2	22	7	2017	0.74	12	49	13	155.5	167.5	323.0	355.4	5.63723895	596428.055	6647184.81	0.74
59	4748	4748_1	Ulleval 2	15	7	2017	0.74	13	3	35	160.3	172.7	333.0	355.4	5.81229547	596480.755	6647217.73	0.74
60	4820	4820_2	Ulleval 2	19	7	2017	0.76	13	8	22	139.4	174.4	313.8	372.1	5.47736679	596373.58	6647158.68	0.76
61	4582	4582_1	Ulleval 2	2	7	2017	0.76	13	16	23	337.6	178.2	515.8	372.1	9.00171015	596794.762	6646561.72	0.76
62	4586	4586_1	Ulleval 2	2	7	2017	0.78	13	22	7	37.9	180.4	218.3	388.8	3.80987922	596401.114	6646595.88	0.78
63	4613	4613_2	Ulleval 2	3	7	2017	0.78	13	32	40	20.3	184.3	204.6	388.8	3.57164178	596479.924	6646547.65	0.78
64	4615	4615_1	Ulleval 2	3	7	2017	0.78	13	33	29	44.9	184.6	229.5	388.8	4.0053561	596346.436	6646648.48	0.78
65	4620	4620_1	Ulleval 2	4	7	2017	0.79	13	36	31	66.7	185.7	252.4	397.1	4.40538556	596263.483	6646781	0.79
66	4582	4582_3	Ulleval 2	2	7	2017	0.8	13	38	38	293.8	186.7	480.5	405.4	8.38648159	596991.283	6646695.17	0.8
67	4571	4571_1	Ulleval 2	1	7	2017	0.8	13	43	2	66.0	188.4	254.4	405.4	4.44029215	596251.499	6646792.04	0.8
68	4683	4683_2	Ulleval 2	7	7	2017	0.8	13	48	4	16.4	189.9	206.3	405.4	3.59991612	596462.625	6646537.42	0.8
69	4820	4820_4	Ulleval 2	19	7	2017	0.8	14	18	40	78.4	200.2	278.6	405.4	4.8619637	596241.11	6646961.41	0.8
70	4686	4686_1	Ulleval 2	7	7	2017	0.84	14	32	6	150.7	206.0	356.7	438.8	6.22471678	596616.362	6647339	0.84
71	4624	4624_1	Ulleval 2	4	7	2017	0.86	14	33	23	292.9	206.7	499.6	455.4	8.72018854	596936.983	6646554.03	0.86
72	4687	4687_3	Ulleval 2	7	7	2017	0.86	14	47	56	91.2	211.5	302.6	455.4	5.28171538	596258.419	6647146.5	0.86
73	4682	4682_2	Ulleval 2	7	7	2017	0.87	11	16	39	211.4	135.6	347.0	463.8	6.0562925	596537.679	6647352.86	0.87
74	4729	4729_1	Ulleval 2	14	7	2017	0.88	11	30	24	217.1	140.1	357.2	472.1	6.23466515	596619.103	6647372.53	0.88
75	4682	4682_4	Ulleval 2	7	7	2017	0.88	11	40	25	261.7	143.2	405.0	472.1	7.06805987	596975.638	6647234.99	0.88
76	4584	4584_1	Ulleval 2	2	7	2017	0.89	11	44	15	28.3	144.6	172.9	480.4	3.01767428	596701.38	6646424.27	0.89
77	4660	4660_1	Ulleval 2	6	7	2017	0.9	11	44	37	252.3	144.6	396.9	488.8	6.92790993	596935.728	6647291.64	0.9
78	4959	4959_1	Ulleval 2	2	8	2017	0.9	11	49	56	209.0	148.0	357.0	488.8	6.23082543	596616.421	6647389.08	0.9
79	4620	4620_3	Ulleval 2	4	7	2017	0.94	12	8	34	123.2	152.9	276.0	522.1	4.81780687	596122.815	6646955.94	0.94
80	4684	4684_1	Ulleval 2	7	7	2017	0.95	12	11	31	50.9	153.9	204.7	530.4	3.57286351	596420.272	6646419.15	0.95
81	4815	4815_1	Ulleval 2	19	7	2017	0.96	12	17	31	252.9	156.1	409.0	538.8	7.13787304	597048.415	6647254.66	0.96
82	4954	4954_1	Ulleval 2	2	8	2017	0.98	12	41	56	352.9	165.5	518.4	555.4	9.04743778	596846.643	6646384.66	0.98
83	4694	4694_2	Ulleval 2	13	7	2017	1	13	5	45	56.8	173.6	230.4	572.1	4.02088953	596201.33	6646536.19	1
84	4696	4696_2	Ulleval 2	13	7	2017	1	13	40	40	292.6	186.7	479.3	572.1	8.36449044	597141.14	6646621.47	1
85	4731	4731_1	Ulleval 2	14	7	2017	1.02	13	55	39	20.7	192.2	212.9	588.8	3.71510785	596322.551	6646406.45	1.02
86	4728	4728_1	Ulleval 2	14	7	2017	1.07	14	9	53	143.7	197.4	341.1	630.4	5.95349261	596437.901	6647497.46	1.07
87	4724	4724_3	Ulleval 2	14	7	2017	1.07	14	11	10	343.7	197.8	541.5	630.4	9.45113243	596625.388	6646270.8	1.07
88	4953	4953_1	Ulleval 2	2	8	2017	1.08	14	28	29	29.2	202.7	231.9	638.8	4.04689494	596139.552	6646506.61	1.08
89	4693	4693_1	Ulleval 2	13	7	2017	1.12	14	29	6	154.3	204.3	358.6	672.1	6.2592743	596625.931	6647572.89	1.12
90	4582	4582_2	Ulleval 2	2	7	2017	1.13	14	29	38	298.3	205.6	503.9	680.4	8.7941905	597043.187	6646351.44	1.13
91	4624	4624_2	Ulleval 2	4	7	2017	1.17	14	36	4	247.3	207.7	455.0	713.8	7.94107356	597353.045	6646838.92	1.17
92	4725	4725_1	Ulleval 2	14	7	2017	1.18	11	25	41	80.5	138.6	219.2	722.1	3.82523812	596185.915	6646341.19	1.18
93	4657	4657_2	Ulleval 2	6	7	2017	1.29	12	0	31	198.9	150.0	348.9	813.8	6.08962829	596485.475	6647699.55	1.29
94	4656	4656_2	Ulleval 2	6	7	2017	1.32	12	5	58	50.6	151.9	202.6	838.8	3.53533893	596320.213	6646126.43	1.32
95	4620	4620_2	Ulleval 2	4	7	2017	1.33	12	21	47	74.8	157.6	232.4	847.1	4.05544705	595971.226	6646383.69	1.33
96	4786	4786_1	Ulleval 2	18	7	2017	1.42	12	25	17	188.1	158.8	346.9	922.1	6.05507077	596433.479	6647799.2	1.42
97	4683	4683_1	Ulleval 2	7	7	2017	1.48	14	0	1	337.1	194.3	531.4	972.1	9.27415605	596787.864	6645939.92	1.48
98	4623	4623_1	Ulleval 2	4	7	2017	1.58	14	44	17	3.4	210.5	213.9	1055.4	3.73360834	596053.041	6646025.2	1.58
99	4848	4848_1	Ulleval 2	20	7	2017	1.76	13	38	33	134.7	185.6	320.3	1205.4	5.589766	595871.533	6647828.04	1.76
100	4698	4698_1	Ulleval 2	13	7	2017	1.78	14	40	0	125.8	208.1	334.0	1222.1	5.82905064	596105.891	6647999.21	1.78
101	4659	4659_1	Ulleval 2	6	7	2017	1.83	15	16	44	47.3	221.1	268.4	1263.8	4.68394011	595378.761	6646865.05	1.83
102	4663	4663_1	Ulleval 2	6	7	2017	1.88	10	47	28	344.1	126.9	470.9	1305.4	8.21892998	597861.445	6646435.1	1.88
103	4663	4663_2	Ulleval 2	6	7	2017	1.94	10	6	4	24.8	115.5	140.2	1355.4	2.44764974	597508.888	6645859.05	1.94
104	4656	4656_1	Ulleval 2	6	7	2017	2.38	10	24	22	13.0	120.4	133.4	1722.1	2.32739656	597894.254	6645718.87	2.38
105	4816	4816_1	Ulleval 2	19	7	2017	2.87	11	13	50	54.2	135.3	189.5	2130.4	3.30652627	596292.214	6644799.49	2.87

AppFigure 1 Shown is the distribution of foraging locations and the probability that a bin (25m x 25m) has been visited for the hive on Bygdøy. The colour code ranges from dark blue to red, where blue indicates a low probability and red a high probability of visitation.



AppFigure 2 Shown is the distribution of foraging locations and the probability that a bin (25m x 25m) has been visited for the Ullevål 1 hive. The colour code ranges from dark blue to red, where blue indicates a low probability and red a high probability of visitation.



AppFigure 3 Shown is the distribution of foraging locations and the probability that a bin (25m x 25m) has been visited for the Ullevål 2 hive. The colour code ranges from dark blue to red, where blue indicates a low probability and red a high probability of visitation.