1290

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COMPARING WAGGLE DANCE DECODING METHODS TO STUDY HONEY BEES' USE OF FLOWER RESOURCES IN AN AGRICULTURAL LANDSCAPE

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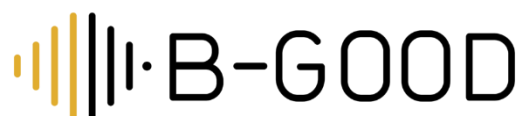
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Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

4

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

5

Resumo

O comportamento de forrageamento das abelhas melíferas desempenha um papel crucial nos serviços de polinização, tornando imperativo compreender a sua relevância ecológica e identificar locais de forrageamento chave. Este estudo teve como objetivo explorar a importância de diferentes modelos usados para decifrar as danças vibratórias das abelhas melíferas e obter informações sobre o seu comportamento de forrageamento. Três modelos - von Frisch e Jander (1957), Schürch et al. (2019) e Kohl e Rutschmann (2021) - foram comparados para avaliar o seu desempenho na descodificação das danças das abelhas melíferas. O estudo foi realizado com a *Apis mellifera iberiensis*, uma subespécie de abelha melífera nativa da Península Ibérica. Observações e gravações das danças vibratórias foram realizadas num apiário com diversas fontes de recursos florais, incluindo culturas temporárias de sequeiro e irrigadas, pastagens, florestas e áreas agroflorestais. Os resultados indicaram que o modelo de Kohl e Rutschmann (2021) tinha limitações, com aplicabilidade confiável apenas em danças com menos de três segundos. No entanto, a maioria das danças analisadas estava dentro deste intervalo, sugerindo aplicabilidade prática em cenários do mundo real. Por outro lado, o modelo de Schürch et al. (2019) mostrou potencial superestimação das distâncias de forrageamento devido à sua linearidade. A comparação das distâncias de forrageamento por mês revelou que as abelhas melíferas forragearam mais longe da colónia durante a primavera e mais perto da colónia durante o verão. Os meses de primavera, com temperaturas mais moderadas, provavelmente facilitaram jornadas de forrageamento mais longas. Por outro lado, os meses de verão, caracterizados por temperaturas elevadas, levaram as abelhas a procurar fontes de água próximas. Através da análise de concordância entre os modelos percebeu-se que, embora a concordância entre os modelos tenha sido observada nos meses de primavera, a mesma, durante os meses de verão, poderá ter sido prejudicada pelo número limitado de danças analisadas. Pastagens e pastagens permanentes surgiram como os locais mais visitados pelas abelhas melíferas ao longo da temporada, o que pode ser explicado pela diversidade de recursos florais disponíveis e pela menor exposição a produtos químicos. Essas áreas podem ser benéficas para apoiar colónias de abelhas melíferas, garantindo um fornecimento confiável de alimento. Este estudo destaca que a escolha do modelo durante a temporada de maior atividade das colónias pode não afetar a precisão na previsão dos padrões de forrageamento das abelhas. Assim sendo, os investigadores podem utilizar qualquer um dos modelos propostos para extrapolar os locais de forrageamento das abelhas durante a temporada de maior atividade das colónias. No entanto, pesquisas adicionais utilizando tecnologias avançadas e considerando fatores adicionais podem aprimorar a nossa compreensão do comportamento de forrageamento das abelhas melíferas e contribuir para estratégias eficazes de conservação. As descobertas têm valiosas implicações para a gestão de habitats, esforços de conservação e otimização das práticas de uso do solo para apoiar

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

6

colónias de abelhas melíferas e sustentar os serviços de polinização em paisagens agrícolas. Ao identificar áreas de forrageamento cruciais e compreender as preferências de forrageamento das abelhas melíferas, os formuladores de políticas podem implementar medidas direcionadas para proteger e melhorar estes habitats.

Palavras-chave: Waggle dance; Comportamento de forrageamento; Serviços de polinização; *Apis mellifera*

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

7

Abstract

Honey bee foraging behaviour plays a crucial role in pollination services, making it imperative to understand their ecological relevance and identify key foraging locations. This study aimed to explore the significance of different models used to decode honey bee waggle dances and gain insights into their foraging behaviour. Three models – von Frisch and Jander (1957), Schürch et al. (2019), and Kohl and Rutschmann (2021) – were compared to evaluate their behaviour in decoding waggle dances. The study was conducted with *Apis mellifera iberiensis*, a honey bee subspecies native to the Iberian Peninsula. Observations and recordings of waggle dances were performed in an apiary with diverse floral resources, including temporary rainfed and irrigated crops, pastures, forests, and agroforestry areas. Results indicated that the Kohl and Rutschmann (2021) model had limitations, with reliable application only to dances below three seconds. However, most dances analysed fell within this range, suggesting practical applicability in real-world scenarios. In contrast, the Schürch et al. (2019) model exhibited potential overestimation of foraging distances due to its linearity and faulty development. Comparison of foraging distances by month revealed that honey bees foraged further away from the colony during spring and closer to the colony during summer. Spring months, with more moderate temperatures, likely facilitated extended foraging journeys. Conversely, summer months, characterized by high temperatures, prompted bees to seek nearby water sources. Concordance between models was observed in the spring months, indicating consistent output trends. However, during summer months, the low number of analysed dances might have affected the models' agreement. Grass grazed and Permanent pastures emerged as the most visited land uses by honey bees throughout the season, which can be explained by the diverse availability of flower resources and lower chemical inputs. These areas may be beneficial to support honey bee colonies, ensuring a reliable food supply. Overall, the study demonstrated that the choice of model during the active season may not significantly impact the accuracy of predicting honey bee foraging patterns. Consequently, researchers can use any of the proposed models to extrapolate where honey bees were foraging during the productive period. Nonetheless, further research using advanced technologies and considering additional factors can enhance our understanding of honey bee foraging behaviour and contribute to effective conservation strategies. The findings hold valuable implications for habitat management, conservation efforts, and optimizing land practices to support honey bee colonies and sustain pollination services in agricultural landscapes. By identifying crucial foraging areas and understanding honey bee foraging preferences, policymakers can implement targeted measures to protect and enhance these vital habitats.

Keywords: Waggle dance; Foraging behaviour; Pollination services; *Apis mellifera*

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

8

Table of Contents

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

9

I - INTRODUCTION

Plant pollination is a vital process for the survival of terrestrial ecosystems (Cranmer et al., 2012). It falls under the category of regulating services, one of the four types of services provided by ecosystems (Balvanera et al., 2017; Egoh et al., 2007; Harrison et al., 2014). These services include provisioning (such as food), regulating (such as water quality regulation and pollination), cultural (for example, recreation), and supporting (such as nutrient cycling) services (Balvanera et al., 2017; Egoh et al., 2007; Harrison et al., 2014). These services have a high socio-economic value for humans, and, overall, pollination services value range widely from approximately 166 billion euros to ~330 (230–560) billion euros annually (Porto et al., 2020).

Several groups of pollinators such as wasps, flies, butterflies, beetles and thirps (Nabhan & Buchmann, 1997) are responsible for this service, with honey bees playing a major role due to their worldwide distribution and domestication (Molina-Montenegro et al., 2023). They enhance the quality and quantity of many major crops, including widely grown oilseeds, which are crucial inputs in the food (such as confection markets and cooking oils) and fuel industries (biodiesels) throughout Europe (Kleftodimos et al., 2021).

Landscape and pollination services

The landscape has undergone significant changes, primarily driven by urbanization (Antrop, 2004), agricultural intensification (Hietala-Koivu, 2002), and the impacts of deforestation and reforestation (Zipperer et al., 2012). Urbanization is a dynamic process, leads to functional, morphological, and structural transformations in urban areas and surrounding rural landscapes (Antrop, 2004). It results in the polarization of space, fragmentation of landscapes, and the emergence of multifunctional land uses (Antrop, 2004). Urban land use contributes to deforestation and fragmentation, creating an inhospitable environment for species and reducing ecosystem benefits for both species and humans (Zipperer et al., 2012). Additionally, agriculture has played a transformative role in altering the structure and character of landscapes through modernization practices (Hietala-Koivu, 2002).

The significant changes in landscapes resulting from agricultural intensification since the 1940s have led to substantial habitat losses, which previously supported greater diversity of insect pollinators (Patrício-Roberto & Campos, 2014). The environment in which pollinators nest and feed have a significant impact on their development as it regulates the availability of nesting and foraging resources in space and time (Kleftodimos et al., 2021; Pufal et al., 2017). Drastic landscape changes have therefore influenced the richness, abundance, and composition of pollinator

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

10

communities (Aguirre-Gutiérrez et al., 2015; Kennedy et al., 2013; Senapathi et al., 2017). From these, the decline of bee's abundance and richness is of serious concern thanks to their important role as providers of pollination services (Senapathi et al., 2017). The problem is even exacerbated in tropical areas because these regions have a higher proportion of plant species that rely on animal pollination compared to temperate regions (Boscolo et al., 2017). Furthermore, habitat fragmentation increased the risk of extinction for isolated plant and animal populations due to reduced gene flow, inbreeding depression, and increased vulnerability to environmental disturbances (Cranmer et al., 2012; Leimu et al., 2010).

Biodiversity losses pose a threat to pollination services, with an estimated 3 to 8% decrease in global crop production expected without these services (Aizen et al., 2009; Deguines et al., 2014). To compensate for this decline in food production and quality, there would need to be a shift in human diets and an expansion of agricultural areas (Breeze et al., 2016; Potts et al., 2016). While wind-pollinated cereals remain the primary source of calories for human consumption worldwide, there has been a rising reliance on crops that need animal pollination (Aizen & Harder, 2009; Breeze et al., 2016; Potts et al., 2016). Consequently, the urgency of pollination biology has grown, as it becomes essential for safeguarding and sustaining the global food supply (Bailes et al., 2015) by protecting pollinator communities.

Pollination: Providers of pollination services

In the field of terrestrial biology, plant-pollinator interactions play a crucial role in connecting food webs within complex ecosystems (Raguso, 2004). These interactions are generally considered mutually beneficial, with plants receiving reproductive advantages through pollen transfer and fertilization, while providing resources such as nectar, pollen, and oils that enhance the fitness of pollinators (Couvillon, 2012; Raguso, 2004).

Various families provide pollination services (Sentil et al., 2022). For example, *Apidae* which consists mainly in stingless honey bees, orchid bees, bumble bees and honey bees (Michener, 1990); The *Andrenidae* family includes mining bees, which are a particularly significant component of northern temperate ecosystems and critical pollinators in natural and agricultural settings (Bossert et al., 2022); The *Scoliidae*, a small family of aculeate wasps (Haichun et al., 2002), are known as ectoparasitoids or relatively primitive wasps that attack soil-dwelling scarabaeid larvae (Inoue & Endo, 2006); The *Tiphiidae*, comprising thiphiid wasps, consists mostly of species that are parasitoids of grub larvae of scarabaeid beetles (Bogusch, 2007); The *Halictidae*, also known as sweat bees, are a diverse group of metallic and non-metallic bees that are typically more abundant than most bees, with the exception of *Apis* (honey bee) species (Buckley et al., 2016); The

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

11

Sphingidae, also known as hawkmoth, includes about 1400 species (Kawahara et al., 2009), along with several other families of pollinators.

Amongst this diverse set of pollinators, *Apis mellifera* (from the *Apidae* family) is the most common pollinator of monocultures worldwide (Decourtye et al., 2010; Mashilingi et al., 2022) and contributes to the preservation of wild plant populations (Hung et al., 2018) that are essential for biodiversity and ecosystem functioning (Potts et al., 2016). Therefore, a drastic decrease in the population of these bees is a serious threat to the stability and harvest of food production (Decourtye et al., 2010; Mashilingi et al., 2022). Furthermore, they also produce honey and other beekeeping products, support cultural values (Kleftodimos et al., 2021; Potts et al., 2016; Pufal et al., 2017), and have been used as a focal species in environmental risk assessment as the representative species of all other insect pollinators (EFSA, 2013).

The health and sustainability of honey bee colonies and beekeeping practices rely on landscapes that offer an abundance of nutritious pollen and nectar-producing flowers (Decourtye et al., 2010). However, honey bees face numerous challenges. Pesticide exposure has been associated with an increased risk of disturbance and colony loss, particularly when combined with other stressors such as poor nutrition or pathogen and parasite loads (Boscolo et al., 2017). Despite the increase in the number of honey bee hives worldwide (Kluser et al., 2010; Pankiw & Page Jr, 2000), there are unexpected regional collapses occurring during the winter season (Brodschneider & Gray, 2022), with *Varroa destructor*, a parasitic mite, appointed as the major cause of these winter losses (Schüler et al., 2023). Besides this parasite and pesticides, pollution, habitat degradation and climate change have also been appointed as negative factors affecting the health of honey bees (Decourtye et al., 2010; Mashilingi et al., 2022).

Honey bee colony: Social organization and foraging behaviour

Foraging behaviour is a key element in social insect societies, showcasing sophisticated decision-making abilities in challenging and unexpected situations (Abou-Shaara, 2014; Tereshko & Lee, 2002). While each individual follows a few simple rules, interactions among colony members result in collective behaviour that enables informed decision-making in challenging and changing environments (Tereshko & Lee, 2002). In various circumstances, such as construction activities, foraging patterns, synchronization of activities, task allocation, and dynamic division of labour, insect societies have demonstrated remarkable success in behaviour (Tereshko & Lee, 2002).

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

12

The honey bee colony can be seen as a complex system, where individuals interact within a society and exhibit a range of behaviours crucial for reproduction, survival, foraging, and defence against predators and diseases (Abou-Shaara, 2014; Tereshko & Lee, 2002; Uzunov et al., 2014). In order to forage successfully, bees must learn and remember the colour, shape, and scent of these nutrient-rich flowers, as well as how to get there (Srinivasan, 2010). Since blooming flowers are capable of changing every few days, bees need and have developed the ability to quicky learn (and relearn) impressions of colour, smell, shape, and pathways (Srinivasan, 2010).

Bee colonies are known to select and prioritize different patches of flowers, opting for the most profitable ones that offer abundant or closer nectar sources to the nest (Seeley, 1994). As worker bees mature beyond 21 days of age, they transition to performing out-colony tasks, including water, nectar, pollen, or resin collection (Abou-Shaara, 2014). Forager bees can be categorized into two groups: scout bees that search for optimal food sources and reticent bees that wait in the hives for scouts to return and provide information about food sources through dance communication (Abou-Shaara, 2014). Reticent bees typically constitute a significant proportion (40-90%) of the total foraging population, and this organization is essential for saving time and effort for bee foragers (Abou-Shaara, 2014).

Understanding the social organization and foraging behaviour within honey bee colonies sheds light on their complex decision-making processes, resource allocation, and communication strategies. This knowledge is crucial for beekeepers and researchers seeking to promote colony health and productivity, as well as for developing effective conservation strategies for these vital pollinators.

The waggle dance for foraging communication

In 1973, Karl von Frisch won the Nobel Prize in Physiology for discovering that bees communicate through a dance known as the waggle dance. Honey bees use this dance to communicate where other bees can locate foraging areas (Couvillon, 2012). Since its discovery, the waggle dance has been the subject of extensive investigation, leading to a wide range of applications and research fields, spanning from basic science neurobiology to applied foraging ecology (Couvillon, 2012). The study of the waggle dance has provided valuable insights into honey bee foraging behaviour and communication, contributing to our understanding of their remarkable navigation abilities and social organization (Couvillon, 2012).

During the waggle dance, a returning forager bee moves in a straight line across the honeycomb while vigorously vibrating its abdomen from side to side (Couvillon, 2012). This waggle run occurs in the central part of the dance, resembling a pendulum with a frequency of approximately 13Hz (Landgraf et al., 2011) (Figure 1). The bee maintains a tight grip on the comb

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

13

while moving forward in a straight line (Landgraf et al., 2011). After the waggle run, the bee circles backward, alternating rotations from left to right until it reaches the initial point of the dance (return phase) (Couvillon, 2012). This circuit can be repeated multiple times (from 1 to 100) within a single dance session, with each repetition (waggle run) communicating the approximate distance and direction of a valuable resource (nectar, pollen, water, or a new nest site) relative to the hive location (Couvillon et al., 2012). In the waggle run, the duration of the run conveys the distance to the resource, while the angle of the dancer's torso relative to the vertical indicates the direction (Schürch et al., 2019).
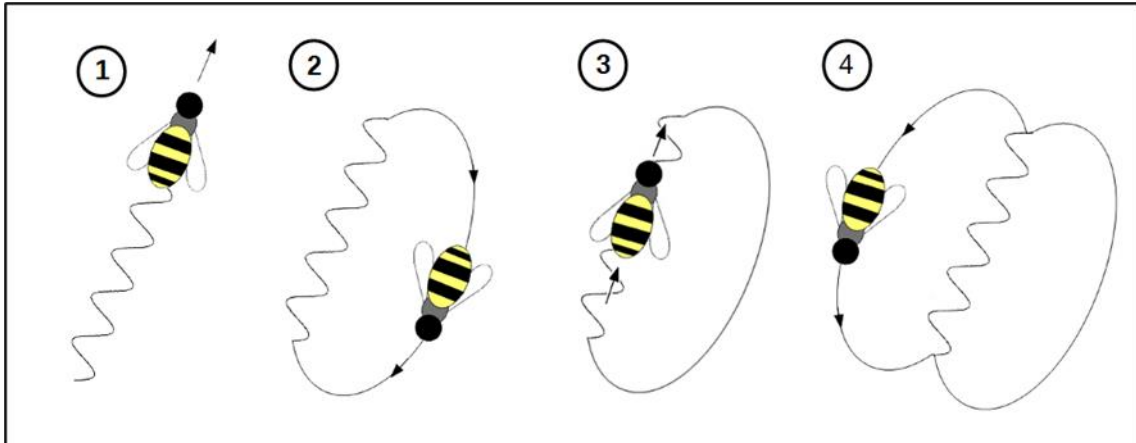

Figure 1. Illustration of the Waggle Dance. The dancer starts by running in a waggle pattern (1), then turns to one side (2) to make a circle back to where she started the waggle phase (return phase). After that, she starts another waggle phase (3) and then returns to the initial point again (4).

Notably, the transmission of resource profitability is through the number of repetitions of the waggle and return phase circuits within the dance (Seeley et al., 2000; Wario et al., 2015). Higher-quality resources are associated with a greater number of circuits, leading to a higher recruitment rate (Seeley & Towne, 1992). Additionally, the "liveliness" of the dance, specifically the quickness of the return phase, also indicates the profitability of the resource. Higher-quality resources result in a faster return phase (Seeley et al., 2000). Ecologists studying waggle dances rely on these aspects to decode and locate foraging locations (Couvillon, 2012). However, the inclusion of the return phase in estimating distance, as done by von Frisch, introduces noise to the data if the rapidity of the return phase is related to resource quality (Couvillon, 2012; Michelsen et al., 1992).

Despite this remarkable behaviour, the waggle dance exhibits variation between subsequent waggle runs (De Marco et al., 2008; Dyer, 2002). It seems that there is a certain subjectivity in dance that is linked to the perception that each individual experiences during their flight (De Marco & Menzel, 2005). To deal with this variation, it is believed that dance followers (recruits) calculate an average of several dances to derive a single distance and direction (Couvillon,

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

14

2012). Furthermore, to deal with this imprecision, honey bee workers need to rely on dead-reckoning to locate the precise position and use other senses to help them find the announced patch (Cartwright & Collett, 1983; Cheeseman et al., 2014). On the other hand, dead-reckoning alone is not precise enough for larger-scale movements (Cartwright & Collett, 1983), thus, honey bees utilize information from landmarks to achieve the necessary level of precision in their navigation (Cartwright & Collett, 1983; Kheradmand et al., 2020).

How bees estimate distance

Bees' ability to efficiently estimate distances and navigate their flights during foraging is crucial for their success and for the success of the colony. At first, it was believed that bees determine the distance to resources by measuring the energy they use during their foraging flights (von Frisch, 1967). However, this hypothesis was disproven when additional weight was imposed on a honey bee, since it did not result in an over-estimation of the distance travelled (Couvillon, 2012). This contradictory finding prompted the formulation of the optic flow hypothesis by Esch & Burns (1996). Which suggests that bees measure the distance travelled by integrating the optic flow generated by the visual panorama (Kheradmand & Nieh, 2019; Srinivasan et al., 1996). Bees utilize various visual cues to control their flight in real-time, ensuring they stay on track, maintain a safe speed, avoid obstacles, and land accurately (Kheradmand & Nieh, 2019; Srinivasan et al., 1996). The hypothesis received strong support from a sophisticated experiment, which demonstrated that bees use the information passing through their retinas during flight to determine distances (Srinivasan et al., 2000). The experiment involved training bees to navigate through tunnels containing black stripes that ran parallel to their flight path, creating a consistent visual "landscape" for the bees. As a result, the bees perceived less optical detail and, upon returning to the hive, performed dances suggesting significantly shorter distances than anticipated. In contrast, bees trained to fly through tunnels with patterned stripes experienced a visually detailed "landscape", causing them to produce dances indicating much greater distances than expected when they returned to the hive. Importantly, the tunnels used in both cases were of the same length. Further experimental evidence supports the optic flow hypothesis. Bees flying close to the ground indicate larger distances in their waggle dances compared to bees flying the same distance at a significant height, since they experienced reduced image motion (Esch & Burns, 1996). Furthermore, when bees fly over water, in which compared to land provide less mean visual contrast, also underestimate the flown distance (Tautz et al., 2004).

Compared to the circumstance during outside flying in a natural setting, the proximity to the tunnel's walls and floor substantially magnifies the perception of the optic flow of the bees, even though they had flown the same distance as in the previous condition (Tautz et al., 2004).

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

15

These studies suggest that the bee's ''odometer'' is driven by the optic flow (image motion) that is experienced during flight (Couvillon, 2012; Srinivasan et al., 2000; Tautz et al., 2004). Generally, the "odometer" is quite robust to the majority of contrasts at the spatial landscape level, which is an advantage to animals that are frequently foraging over several and variable environments (Couvillon, 2012; Si et al., 2003).

How bees estimate the angle

The angle at which the waggle phase is performed by bees on the opposite way of gravity provides information about the direction from the hive to the food source, as they rely on a dance-sun reference system (Hu et al., 2023). Bees have natural knowledge about specific patterns of the sun's movement in terms of space and time (Dyer & Dickinson, 1994). This knowledge helps bees with limited experience to create an internal understanding that not only remembers the parts of the sun's path they have observed before, but also predicts how the sun moves at different times of the day (Dyer & Dickinson, 1996).

Despite bees' ability to use the sun as a reliable reference for their dances, an intriguing peculiarity arises from the position of the sun, particularly its presence directly overhead at solar noon, impacting the accuracy of their dance (Couvillon, 2012). While some imprecision appears unavoidable, bees display compensatory traits that seem to address this issue (Couvillon, 2012). Notably, von Frisch referred to one of these behaviours as "noontime laziness" (von Frisch, 1967), where dancing either ceases or becomes disoriented just before and after solar noon (Couvillon, 2012). Moreover, the sun's zenith is associated with highest level of directional inaccuracy (Gardner, 2007). To potentially mitigate this imprecision, bees have developed a foraging break, acting as an adaptive mechanism (Couvillon, 2012). This phenomenon's explanation might be linked to two factors: challenges in orienting their dances accurately when the sun is at its highest point and reduced inclination to dance, resulting in decreased foraging activity (Gardner, 2007).

Other cues besides the Waggle Dance

Karl von Frisch, the discoverer of the waggle dance, initially recognized the importance of flower colour and aroma for honey bees. In the late 1960s, the role of odour became a topic of debate among scientists. Some believed that odour alone was sufficient for foragers, equipped with an olfactory landscape, to locate flowers accurately, challenging the necessity of the dance (Johnson, 1967; Wenner, 1967; Wenner et al., 1969). However, by the mid-1970s, most scientists became convinced of the existence of the waggle dance language (Couvillon, 2012; Esch et al., 2001; Seeley, 1991; Sherman & Visscher, 2002; Srinivasan et al., 2000). Nevertheless, the odour

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

16

and colours have been identified as complementary cues to the waggle dance. Bees acquire knowledge by forming associations between floral cues, such as colours and scents, and the reward they receive upon visiting a flower (Menzel, 1990, 1999). Thus, the odour emitted from a dancing bee's body during its waggle dance even has the potential to trigger the recollection of a foraging location that is different from the one being communicated through the dance (Grüter et al., 2008; Reinhard et al., 2004). For honey bees, the learning process for scents is quicker compared to that to colours (Kunze, 2001).

Waggle Dance interpretation

Foragers follow multiple waggle dances and successfully move to a known food source when a previously rewarding food source becomes unrewarding (Grüter & Ratnieks, 2011). Although the use of dance communication may diminish as bees gain their own foraging experience, it remains important for novice foragers (Couvillon, 2012). Inexperienced foragers rely on waggle dance information to locate food sources, but as they acquire their own experiences, they use the dance less or only to reactivate and validate their own memories (Biesmeijer & Seeley, 2005).

Nevertheless, to follow the dances, bees need to deal with the noisy communication of the dances that display inherent inaccuracies and imprecisions (Schürch et al., 2019). This inefficiency in dance recruitment was one of the initial objections levelled against the communication (Grüter & Farina, 2009a, 2009b; Johnson, 1967; Riley et al., 2005; Wenner, 1967). Later, it was suggested that this directional imprecision is adaptive, as it "tunes" the dance to match the spatial distribution of resources (Couvillon, 2012). For example, a 4º angular scatter can disperse recruits over a nearby flower patch, while a smaller scatter can effectively direct recruits to a patch farther from the hive (Couvillon, 2012). Evidence supporting this hypothesis includes the consistent dispersal of recruits within a certain range (100-1,000 m) (Couvillon, 2012; Towne & Gould, 1988).

The assumption is that floral resources are usually found in larger patches and benefit from a broader spread of recruited bees, while new nest sites are fixed points and require more precise directions (Couvillon, 2012). Dances for nest sites are indeed more accurate than dances for food (Couvillon, 2012). Interestingly, nest locations that are close by (<30 m) lack or have insufficient directional information in the dance, contrary to the tuned-error hypothesis (Beekman et al., 2005). This could be attributed to performance and physical limitations during the dance, as shorter waggle runs lead to greater angular divergence due to the bee's rapid movement to circle back (Couvillon, 2012).

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

17

Models for Waggle Dance decoding

Three major models have been proposed in the ongoing effort to decode the visual section of the honey bee's waggle dance, despite the additional clues that provide greater specificity to those observing the dance.

Proposed model of von Frisch & Jander (1957).

Karl von Frisch, the renowned discoverer of the spatial information content of the waggle dance, along with his colleague Rudolf Jander, proposed a model for the understanding of the waggle dance function. They aimed to address this matter by training bees to feeders situated at relatively long distances and determining the duration components of the resulting dances (von Frisch & Jander, 1957). In their study, they observed that the distance-circuit duration curves stemmed from a non-linearity in the waggle dance duration signals. Von Frisch & Jander (1957) determined that the mean waggle duration of dances performed by honey bees foraging a feeder located 4.5 km away was approximately 4 seconds.

Proposed model of a Universal Calibration by Schürch et al. (2019).

In the experiment done by Schürch et al. (2019), honey bees foraged at predetermined locations, allowing the calibration of both the honey bees' waggle run duration to distance and their angular precision. After that, it developed a universal calibration of a linear model using previously published individual data (Schürch et al., 2016; Wenner, 1962). They estimated that every kilometre the bees travelled, they would extend the duration of their waggle runs by approximately 1.18 seconds. The estimated range of this extension was between 1.12 and 1.25 seconds. Thus, and according to this study, the universal calibration, which was developed by combining existing calibrations, can be used in future research settings to generate distances from decoded waggle dances regardless of location or honey bee population.

Four previously published studies on bee populations, conducted over a 50-year period in three different locations (two in Sussex, UK, one in Michigan, USA, and one in Virginia, USA), served as the foundation for the creation of the universal calibration by Schürch et al. (2019). Due to the inclusion of individually marked bees foraging at known distances (i.e., individual calibration data) rather than aggregated data (von Frisch, 1967), these four studies were the only ones that were available to be used. This universal calibration integrates the individual data, including the individual variance, of numerous studies, populations, and geographies, which could lead to an increased variability in the model's output. Nonetheless, the authors believe that the individual differences between bees, even within the same hive/experiment/feeder, are so great that even if there are statistical disparities between calibrations due to differing intercepts, the biological importance of these changes was minimal. To put it another way, any bee might be allocated to any

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

18

population and area because bees dance so differently for the same location (i.e., there is such a wide variety in their duration).

Counter-Proposal model by Kohl & Rutschmann (2021)

Even more recently, Kohl and Rutschmann (2021), trained bees to visit sugar feeders up to 1.7 km from the colony and both the waggle phase and the return phase of the dance were timed. From their experiments, they concluded that the return phase was indeed not useful for the decoding of distance in the waggle dances. Furthermore, the distance function of the waggle phase was found to be non-linear, meaning that the increase in waggle duration levels off beyond a certain distance from the hive (Kohl & Rutschmann, 2021). Thus, for closer distances, a simple linear model effectively represented the connection, with the slope of waggle duration significantly flattening after around 1 km from the hive (Kohl & Rutschmann, 2021).

This segmented distance function suggests that bees perceive distance differently before and after a certain threshold distance, which may have adaptive value (Kohl & Rutschmann, 2021). It also helps bees balance the trade-off between communication precision and range (Kohl & Rutschmann, 2021). Interestingly, older studies trained bees to fly much farther distances than recent investigations, leading these recent studies to suggested that a straightforward linear relationship exists (e.g., Schürch et al., 2013). On the other hand, in older studies, the non-linearity relationship was not clearly found since most studies focused on the relationship between distance and the length of the entire dance circuit instead of only the waggle phase (Kohl & Rutschmann, 2021).

The use of Waggle Dance decoding

Waggle dances have been used in several studies to analyse the foraging patterns of honey bees throughout the year. These dances serve as filtered information indicating the most lucrative feeding locations known to the colony at any given time (Grüter et al., 2010). Bees' foraging activities vary in response to resource availability and colony needs, depending on factors such as the season, competition, weather, and time of day (Camazine, 1993; Couvillon et al., 2014; Dreller et al., 1999; Fontaine et al., 2008; Hassan et al., 2017; Seeley, 1995; Steele et al., 2022).

The analysis of the foraging patterns of the honey bees have reported that the summer season is particularly challenging for obtaining food, as observed in waggle dances promoting patches at longer distances in August and July (Couvillon et al., 2014). During this period, honey bees travel further and fly over larger areas compared to spring and autumn to collect resources (Couvillon et al., 2014). These seasonal patterns have been observed in several studies (Couvillon et al., 2014; Danner et al., 2016; Leong & Roderick, 2015). Nevertheless, it seems that the longer distances flown in agricultural areas are not solely due to presence of distant high-quality sites;

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

19

Samuelson et al. (2022) found that bees (foraging in the summer period) returned with nectar of similar quality, suggesting other factors influence their foraging behaviour. In complex landscapes, the same physical distance can induce greater optic flow, leading bees to perceive it as further, resulting in longer central waggle runs (Srinivasan et al., 2000; Tautz et al., 2004). This finding indicates that the relative distances flown in complex landscapes may be overestimated, while those in simpler landscapes may be underestimated (Samuelson et al., 2022; Schürch et al., 2019).

Nonetheless, the dance decoding process does not entail these other factors that influence their perception of direction and distance, and this is probably the main reason why the decoding models have such differences within themselves. Nevertheless, the decoding of the waggle behaviour plays a crucial role in understanding honey bee foraging behaviour in the landscape as dance communication influences foraging strategies and resource selection in honey bee colonies (Shackleton et al., 2023).

Aim of the study

The primary objective of this study is to explore the ecological relevance associated with different models by conducting a comparative analysis of their outcomes. Furthermore, this study aims at using these models output to identify the most common land use patches that honey bees visit during the beekeeping season (march to august). Specifically, the study focuses on examining the waggle dances of honey bees as a means to gain insights into their foraging behaviour and the model's ability to identify key forage locations. This research holds particular significance in light of the increasing reliance of global agriculture on pollination services and the concerning decline in available forage for bees.

To accomplish the study's objective, the methodology involves an in-depth analysis of honey bee waggle dances. These waggle dances are then used to find foraging patches according to each model presented above (the von Frisch & Jander (1957) model, the Schürch et al. (2019) model, and the Kohl and Rutschmann (2021) model). By comparing the results obtained from each model, the research seeks to ascertain if models' output are in concordance with each other, thereby contributing to a deeper understanding of how humans can use the waggle dance to study foraging patterns.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

20

II – MATERIAL AND METHODS

Experimental model and subject details

The honey bee subspecies chosen for the purposes of this study was *Apis mellifera iberiensis*, which is native to the Iberian Peninsula. A colony that fulfilled the criteria of being healthy, well-nourished, and free from disease was obtained from a local beekeeper. The hive was installed at the study location one year prior to the experiments to allow for acclimatization. Hive maintenance, including pest and disease treatments, as well as artificial feeding, was conducted in accordance with established local beekeeping practices.

Observation hive and waggle dance recordings

The recording and assessment of waggle dances were performed in an apiary installed in Idanha-a-Nova, Portugal, known for its abundant floral resources, including temporary rainfed and irrigated crops, improved pastures, Holm oak forests, Eucalyptus forests, Holm oak agroforestry areas, and Cork oak forests. In this landscape, at the beginning of the season, primary resources consisted of *Echium plantagineum*, *Salix* sp., *Jasione montana*, *Trifolium* spp., *Quercus* sp., *Anthemis* sp., *Chamaemelum* sp., *Brassica barrelieri*, and *Diplotaxis catholica*. During the middle of the season, the main resources included *Echium plantagineum*, *Jasione montana*, *Trifolium* spp., *Retama sphaerocarpa*, *Rubus ulmifolius*, and *Asteraceae*. Towards the end of the season, the available resources mainly comprised various *Asteraceae* species, such as *Carlina* spp., *Dittrichia* spp., among others, along with a few small herbaceous species with limited individuals and flowers (Dupont et al., 2021).

The observation hive used in this study was a modified Langstroth hive designed for this study by the authors. It incorporated a 4-frame observation hive, integrated with a Langstroth hive consisting of 10 frames. The hive entrance was positioned on both sides of the top of the hive. A recording box, housing a camera, was connected to the observation hive, ensuring minimal direct sunlight exposure. The recording setup included a Raspberry Pi 3 model B+ with a Raspberry Pi Camera Module v2 (Sony IMX219 8-megapixel sensor), attached to a movable wooden shelf. An LED light fixed on top of the recording box, positioned at a 45º angle to avoid direct light on the recorded frames. Inside the hive, a pendulum made of fishing line and iron weight as a gravitational reference, was used, which appeared as white lines on the recorded video.

The observations were conducted every 21 days during the beekeeping season. The time interval for recordings varied approximately between 09:00 and 17:00, while the video analysis

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

21

specifically focused on the period from 12:00 to 14:00. Meteorological data, including temperature (ºC), relative humidity (%), rainfall (mm), solar radiation (w/m2), wind speed (Km/h), and direction (°), were collected using the WatchDog 2900-131ET Weather Station. Waggle dance recordings were specifically conducted on sunny days without rain or residual wind.

Waggle dance decoding

To assess the summer foraging patterns of the honey bees, data from March to August were analysed. A total of 361 recordings of waggle dances were thoroughly assessed, amounting to eleven hours and 40 minutes of video footage. The selection and analysis of the waggle dances followed the methodology established by Couvillon et al. (2012), which requires a minimum of six uninterrupted waggle runs for decoding. The videos were observed in slow motion (0.13X) to decode the waggle dances, and only four consecutive waggle runs, excluding the first and last run, were considered for each complete dance.

The number of registered and decoded waggle dances varied across the months, with 64 dances in March, 39 dances in April, 209 dances in May, 17 dances in June, 14 dances in July, and 18 dances in August. May had the highest number of recorded dances due to two recording periods conducted in this month, as recordings were made every 21 days. Despite lower detection and decoding of dances in other months, an average of two hours of recorded dances per month was analysed.

The waggle run duration in milliseconds, which determines the distance, and the angle of orientation relative to gravity, indicating the direction to the resource patch (von Frisch, 67), were measured using Media Player Classic Home Cinema (MPC-HC X64 v1.7.13) and a protractor, respectively, with a maximum error of approximately 1°. Mean duration values and measured angles of four consecutive waggle runs were used to represent the waggle dance. Subsequently, the endpoint coordinates of each waggle dance were calculated, using three different formulas: von Frisch and Jander (1957), Schürch et al. (2019) and Kohl and Rutschmann (2021) (Table 1).

Table 1. Model's formulas used to calculate the distance-duration for each dance. The Schürch universal model is the only linear model that was considered in this study. The models are ordered in chronological order (from oldest to newest)

Author	Model	Formula
Von Frisch and Jander (1957)	non-linear	$d \leq 1.4$km: $tw = 0.1096 + \frac{1.7208}{0.6272}(1 - e^{-0.6272} * d)$ $d > 1.4$km: $tw = 0.7198069 + 0.70947 * d$
Schürch et al. (2019)	linear	$d = \frac{tw}{1.38} - 0.12$
Kohl and Rutschmann (2021)	non-linear	$tw = 0.1993 + \frac{2.0018}{0.6717} * (1 - e^{-0.6717*d})$

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

22

Identifying key foraging areas

In this study, it was used the Geographic Information System (GIS) software, specifically QGIS 3.30.3 version, known for its versatility in visualizing and analysing spatial data. The landscape land use types were obtained based on Corine level 3 land cover class and were corrected based on the field assessments (Figure 2). The data collected from the waggle dances (from the different models) was layered against the developed landscape to pinpoint which land use type were being visited by the honey bees.

By performing this analysis, it was possible to identify which food-resource areas (land use types) were being visited by honey bees in each month, according to the different models, providing insights into the foraging preferences and resources allocation. Then, to evaluate models' concordance within each month, the Kendall concordance coefficient was used. In each month, land use types with only one visit were removed from the analysis.
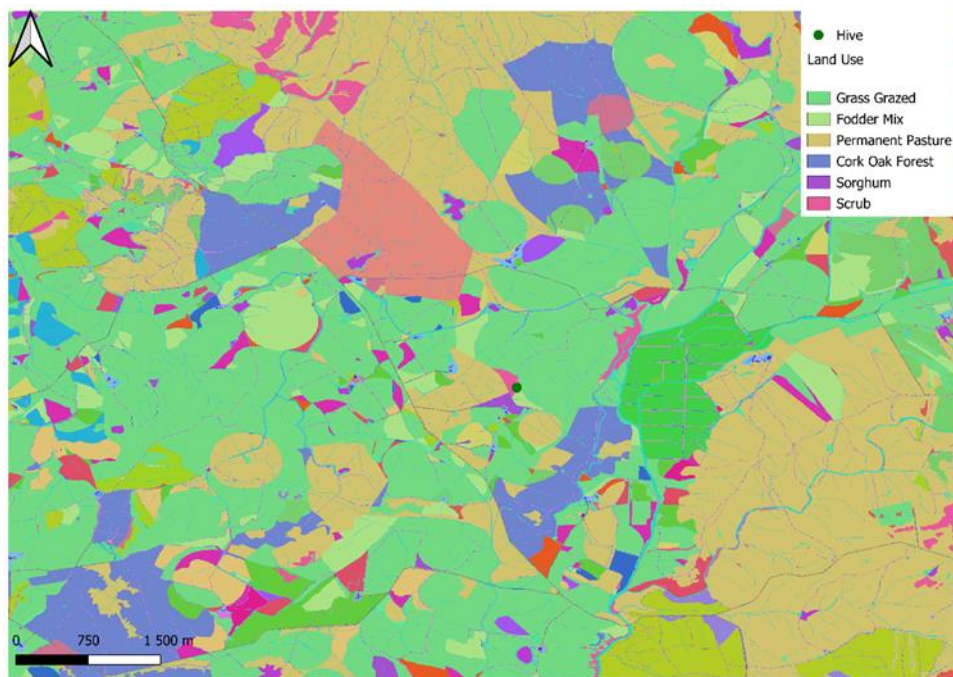

Figure 2. Land cover map of the most common land use types in the study area. The observation hive location pinpointed in green. Grass Grazed - area where animals feed on naturally growing grass in pastures; Fodder Mix - combination of different animal feeds; Permanent Pasture - land used for long-term grazing or hay production with perennial plants; Cork Oak Forest – woodland dominated by cork oak trees; Sorghum – versatile grain crop for human and animal consumption; Scrub – low, stunted vegetation of shrubs and small trees in arid regions.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

23

III – RESULTS

Models' performance

The three tested models predict similar distances until it starts to vary at approximately 1.5 s of dance time (Figure 3). Therefore, in this study, most of the decoded waggle dances (62%) will pinpoint to similar areas. On the other hand, the variability within the different models will play a major role on 38% of the obtained data. It was found that the Kohl and Rutschmann model's formula could only be reliably applied to dances below approximately 3 seconds.
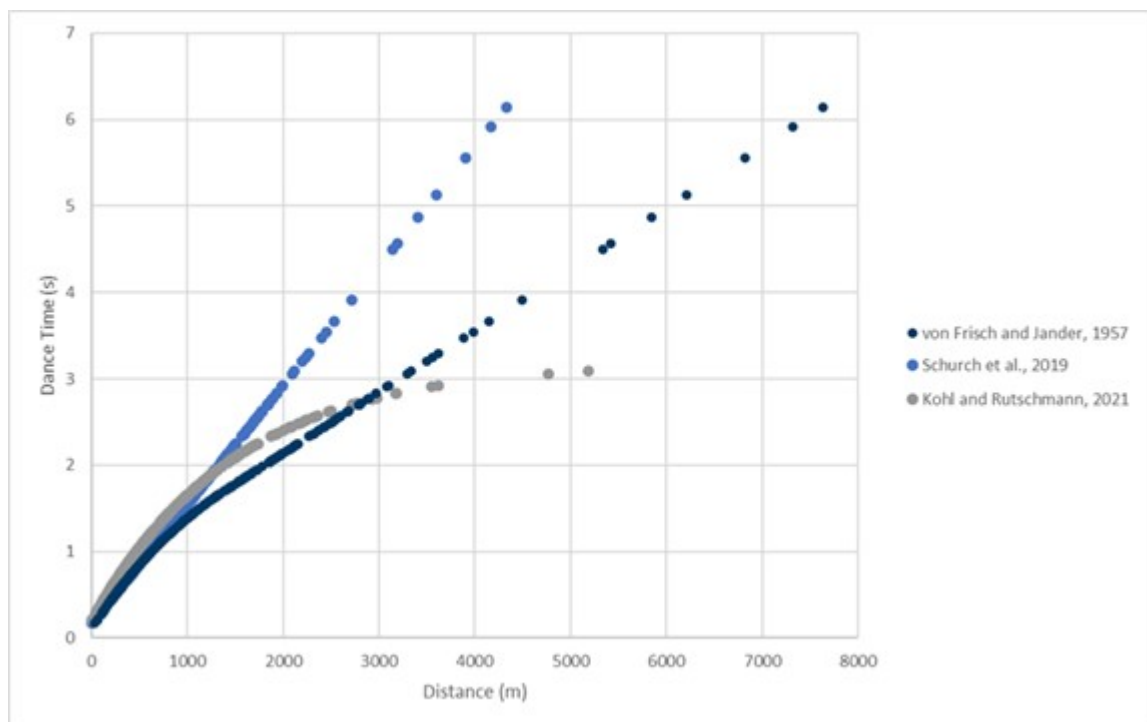

Figure 3. Comparison between the Dance Time (s) of the honey bees with the distance (km) within the three different models.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

24

The analysis of the three models used to study bee foraging patterns reveals interesting trends and variations in distance measurements (Figure 4). The von Frisch and Jander model consistently indicates that bees are foraging further away from the colony, with higher quartiles, median, and maximum distances. On the other hand, the Kohl and Rutschmann model consistently suggests that bees are foraging closer to the colony, displaying lower distances values across all measurements. The Schürch et al. (2019) model generally falls in between these two models.

When examining the data by month, March, April and May stand out as months with outliers in all models (Figure 4). In July, all models indicate remarkably close foraging distances, with the Kohl and Rutschmann model reflecting the closest range.
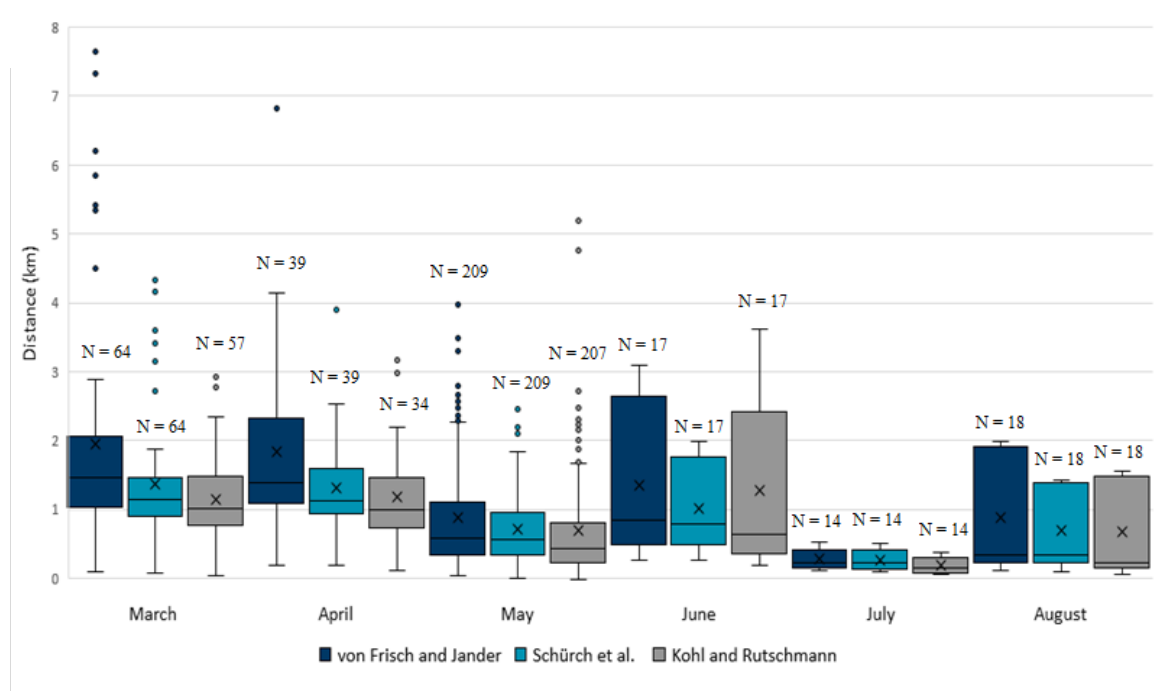

Figure 4. Boxplot graph, with the distances (km) calculated by each model for each month. Each colour corresponds to one model. Above the bars there is the number of dances analysed.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

25

In the month of March (Figure 5), Grass Grazed was the most visited land use type in all models more than 40% of the times, followed by Almond Plantation, Cork Oak Forest, Permanent Pastures and Fodder Mix. There are several land use types that were only being visited according to the output of one (i.e., Pond, Walnut Plantation, Eucalyptus Forest, Montado, Holm Oak, Ryegrass, Small Road, Urban Vegetation, Deciduous Forest, Sorghum and Yellow Lupine) or two models (e.g., Set Aside and Track). Nevertheless, these account for a small percentage of the waggle dance analysis, and overall, the models have a good agreement with a high degree of significance (W=0.67, p<<0.001).
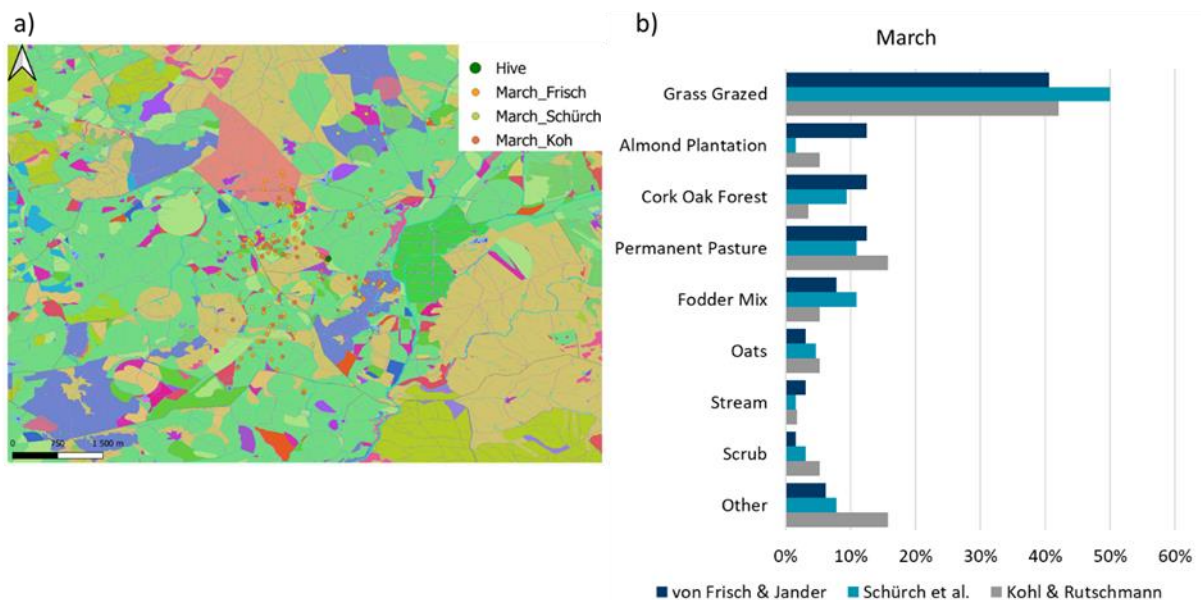

Figure 5. (a) Land cover map of the study area, with the honey bee waggle dance positions using all three models in the month of March and (b) the most commonly visited land use types in March according to each model.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

26

Concerning the month of April (Figure 6), the two most visited land types were Grass Grazed and Permanent Pasture, ranging from approximately 50% to 20% of the visits, respectively. There is only one land type (i.e., Set Aside) that was being visited according to two models and several other that were only visited according to one model (i.e., Cork Oak Forest, Fodder Mix, Eucalyptus Forest, Track, Urban Vegetation, Agroforestry and Maize). Once again, these other land use types account for a small percentage of the waggle dance analysis, and overall, the models have a good agreement with a good degree of significance (W=0.76, p<<0.005).
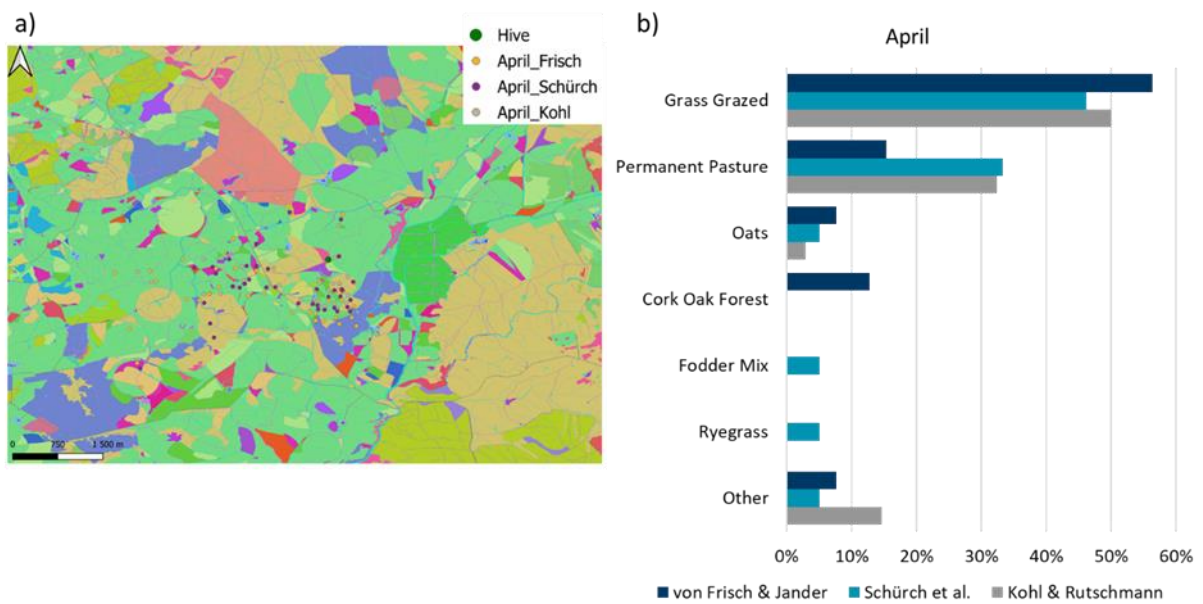

Figure 6. (a) Land cover map of the study area, with the honey bee waggle dance positions using all three models in the month of April and (b) the most commonly visited land use types in April according to each model.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

27

The month of May was the one with the most types of land use being visited (Figure 7a). The most visited land uses being Grass Grazed, Permanent Pasture, Fodder Mix, and Sorghum (Figure 7b). There are three land use types (i.e., Decidious Forest, Oats and Building) that were being visited according to two models, while several other land use types, were only visited according to the output of one single model (i.e.,Agroforestry, Olive Grove, Fresh Water, Maize, Pond, River, Winter Rey, Winter Wheat). These other land use types account for a small percentage of the waggle dance analysis (around 5%), and overall, despite the diversity of land use types according to the several models, there is a very good agreement within the models with a high degree of significance (W=0.82, p<<0.001).

Figure 7. (a) Land cover map of the study area, with the honey bee waggle dance positions using all three models in the month of May and (b) the most commonly visited land use types in May according to each model.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

28

June, on the other hand, was the month with the least land use types visited (Figure 8), with only two being visited according to all models (i.e., Grass Grazed and Permanent Pasture). The remaining land types (Figure 8 - Other) were only visited according to a single model and represent a low percentage of the waggle dances. There is a very good (perfect) agreement within the models with a high degree of significance (W=1, p<<0.001).
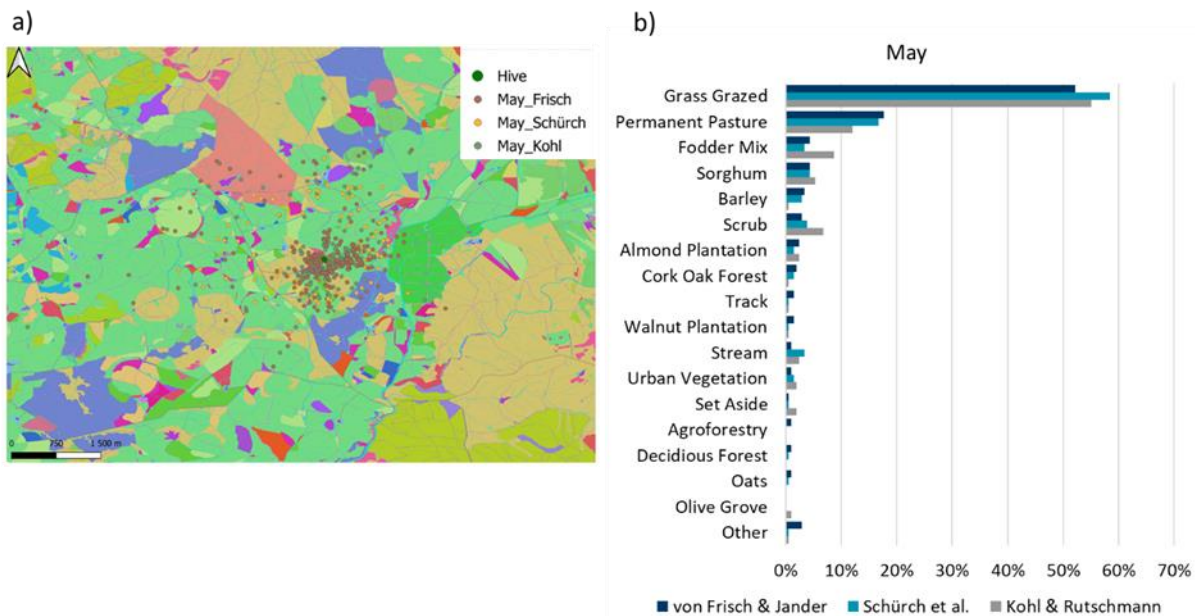

Figure 8. (a) Land cover map of the study area, with the honey bee waggle dance positions using all three models in the month of June and (b) the most commonly visited land use types in June according to each model.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

29

In July there was only three land use types visited according to all models (Figure 9). Once again, Grass Grazed had the most rate of visits (ap. 50%), with Permanent Pasture and Fodder Mix following (ap. 18% considering all models). Scrub was being visited according to two models, while Stream and Sorghum, were only visited according to one model (Figure 13). In this month, there is no agreement within the models (W=0.67, p>0.05).
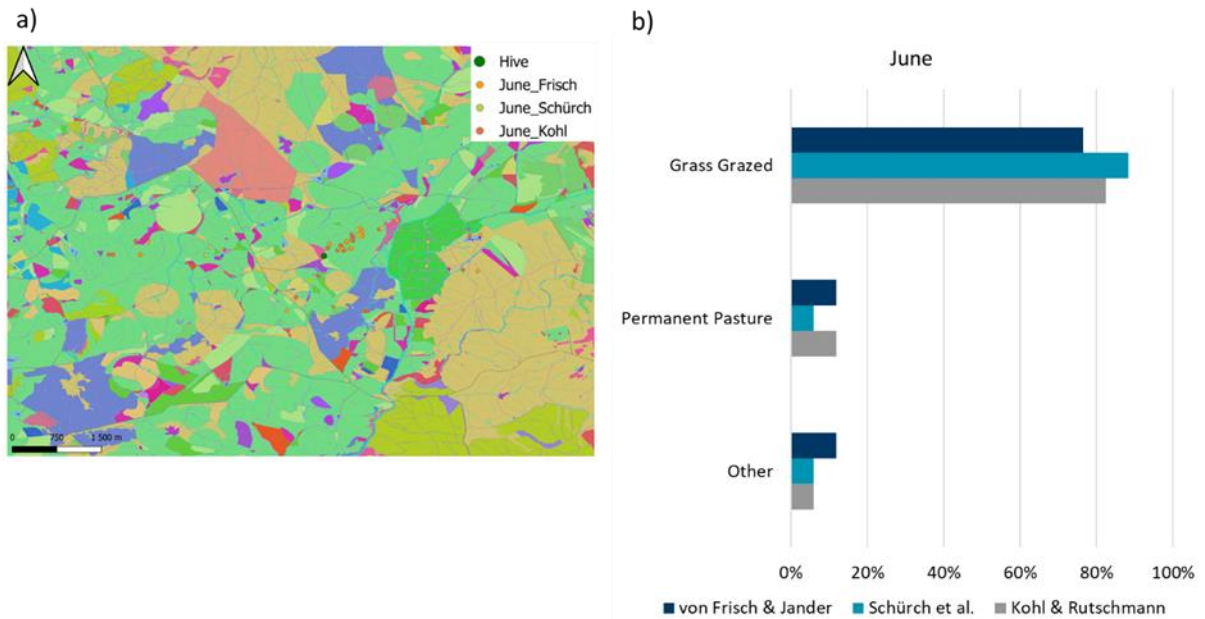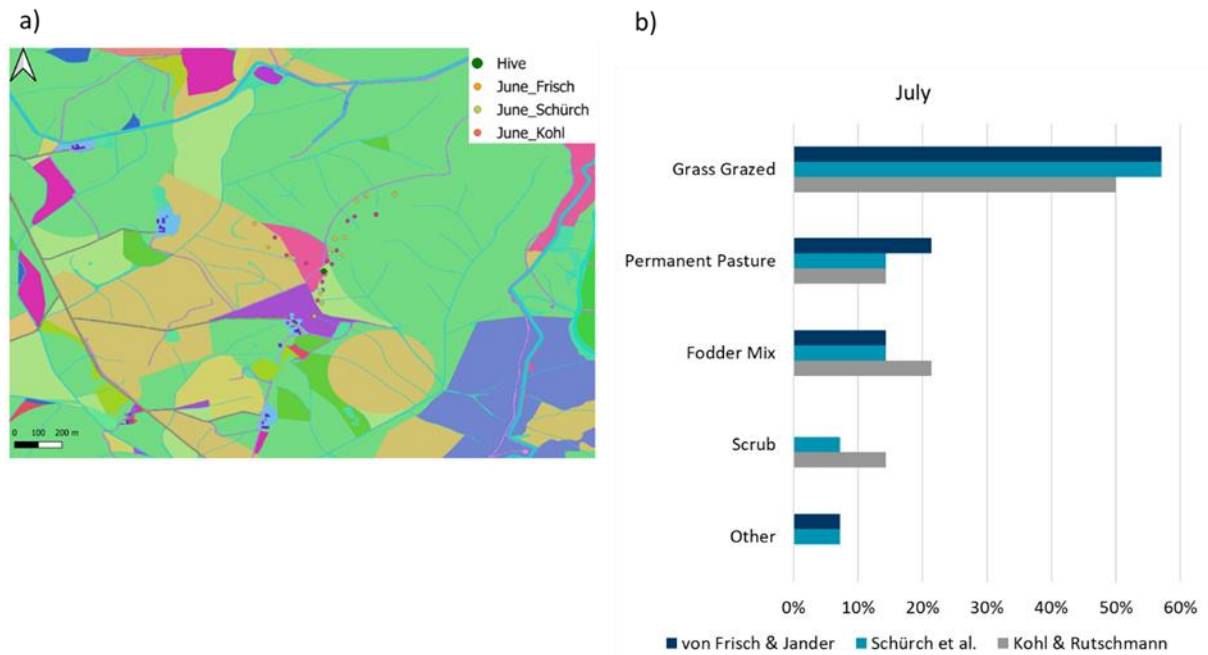

Figure 9. (a) Land cover map of the study area, with the honey bee waggle dance positions using all three models in the month of July and (b) the most commonly visited land use types in July according to each model.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

30

In the last month of this study, August, the visitation rate in the Grass Grazed continued high (ap. 60%), while Cork Oak Forest, Fodder Mix, Permanent Pasture were being visited according two models. The three remaining land uses (i.e., Oats, Stream and Scrub) were only visited according to one model. (Figure 10). Once again, there is no agreement within the models (W=0.78, p>0.05).
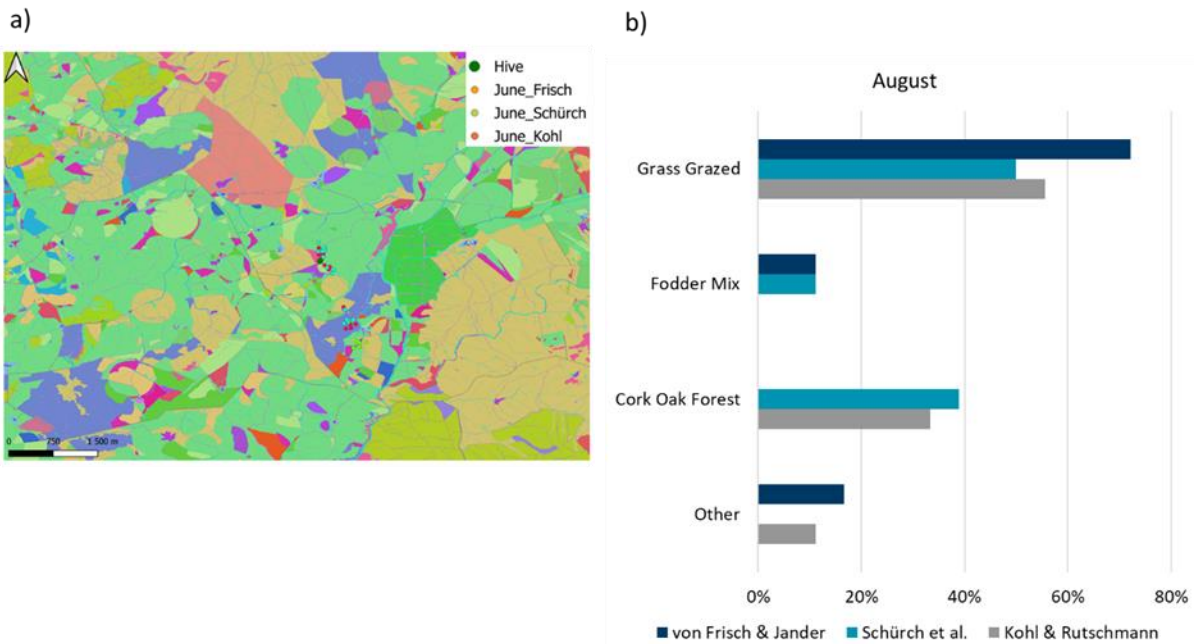

Figure 10. (a) Land cover map of the study area, with the honey bee waggle dance positions using all three models in the month of August and (b) the most commonly visited land use types in August according to each model.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

31

When considering the whole season and models' output, Grass Glazed and Permanent Pasture emerged as the most attractive land types for honey bees (Figure 11). Grass Grazed emerged as the most visited land use, accounting for 54.3% of the total visits from March to August, while Permanent Pasture and Fodder Mix received relatively high percentages of visits of 15.4% and 5.9%, respectively (Figure 11). Cork Oak Forest, Scrub, Sorghum, Almond Plantation and Stream margins, range from 4 % to 2% of visitation by honey bees (Figure 11). There are also several other land types, including Oats, Barley, Set Aside, Urban Vegetation, that had lower visitation rates, each accounting for less than 2% of the total visits (Figure 16).
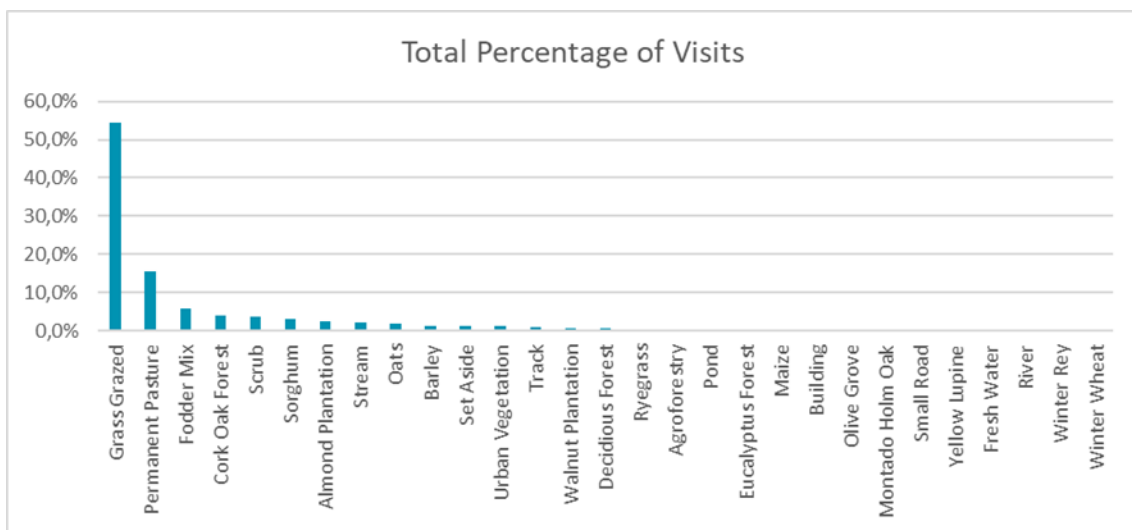

Figure 11. Total percentage of honey bee visits according to all the models, considering every land use
type visited from March to August.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

32

IV – DISCUSSION

The objective of this study was to investigate the ecological significance of various models in understanding honey bee waggle dances and their foraging behaviour. Given the increasing reliance of global agriculture on pollination services, the concerning loss of bee forage availability, and exposure to pesticides, accurately identifying crucial honey bee foraging sites is of utmost importance. Interestingly, in the busiest months (Spring) the models are in concordance with each other, meaning that the output is similar independently of the model that was used. The same does not happen in the summer months, but the output could be compromised by the lower number of waggle dances that was analysed. Furthermore, it was possible to verify which land uses have more ecological relevance for honey bees.

By comparing three different models – von Frisch and Jander (1957), Schürch et al. (2019) and Kohl and Rutschmann (2021) – this study aimed to evaluate these models' behaviour while decoding waggle dances. The study highlighted limitations and challenges associated with the Kohl and Rutschmann (2021) model. The model's formula could only be reliably applied to dances below approximately three seconds, beyond which its performance became impossible. This occurs because when calculating the distance with a duration of approximately three seconds, using the formula, the presence of logarithmic equation yields a negative value, rendering it impossible to solve. The limitation of the model lies in its restricted practical application, particularly in real-worlds scenarios with longer dance durations. In this study, this limitation resulted in the inability to convert fourteen dances into coordinates, potentially affecting the overall accuracy of the model's predictions. Nevertheless, most of the decoded dances allowed to have a good set of data for models' behaviour comparison. According to various other studies (Kohl & Rutschmann, 2021; Schürch et al., 2013, 2016, 2019; Si et al., 2003; Srinivasan et al., 2000) that have used different methods and models for waggle dance decoding, the majority of the dances were found to be shorter than three seconds, showing that these models' caveats aren't a limiting factor in real world. On the other hand, in most of those studies, honey bees were trained to fly distances that never exceeded 1.5 km (for models' development). The other two models do not have these limitations but the Schürch et al. (2019) model could be exaggerating bees foraging distances because of the model's linearity and faulty development (bees were trained to visit feeders relatively close to the colony) (Kohl & Rutschmann, 2021).

Our results indicate that the median foraging distances are much higher in spring months compared to summer months. These findings align with the study by Steele et al. (2022), which revealed that honey bees predominantly forage locally throughout the foraging season (April – October). The median foraging distance in their study was 0.78 km, with 95% of distances falling

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

33

within 2 km. Moreover, they found that the highest mean foraging distances were observed in May and October in 2018, and in September and May in 2019. This suggests that dance analysis in spring and early autumn months may indeed report higher foraging distances. Furthermore, Silliman et al. (2022) reported that the months with the highest median communicated foraging distances were April, May, June, and August. Aligning with the notion that spring and early summer months might involve longer foraging distances for honey bees. However, the results from Couvillon et al. (2014) and (Beekman et al., 2004) present contrasting perspective, indicating that bees may cover longer distances during summer months. According to Couvillon et al. (2014), the communicated forage distance is higher in the summer months (July and August) with an average of approximately 2.1 km and lower in spring months (March and April) with an average of approximately 0.5 km. Beekman et al. (2004) also found that forage distances in July were smaller (approximately 0.6 km) compared to August (between approximately 1.4 km to 2.9 km). Lastly, Danner et al. (2016) found that in both spring and summer, specific factors significantly influenced pollen foraging distances. In spring, the Oilseed Rape area within 2000m significantly influenced pollen foraging distances, with distances decreasing from 1324 m to 435 m with increasing Oilseed Rape area. In summer, Semi-Natural Habitats area within 200 m around the hive reduced mean pollen foraging distances from 846 m to 469 m. From all these studies, Danner et al. (2016) was the only study to mechanistically link the foraging distances with the landscape or colony needs, which is more ecologically relevant than the analysis of the foraging months.

In our study, honey bees foraged far away from the colony during spring and closer to the colony in the summer months. Since honey bees are ectothermic creatures, meaning their body temperature is influenced by the external environment (Heinrich, 1996), we believe summer temperatures influenced their foraging behaviour. In many regions, spring months often have more moderate and favourable temperatures for honey bees compared to the hot summer months (Salehizadeh et al., 2020). Because of that, honey bees may be more active and efficient in cooler temperatures as it can allow them to conserve energy and fly longer distances. During the summer, high temperatures can be challenging for honey bees, as excessive heat can cause them to overheat and dehydrate quickly. Also, during the spring season, honey bees embark on extensive foraging journeys in search of nourishing food. They venture far and wide, diligently exploring the landscape to collect nectar rich in sugars. However, as summer arrives, the scarcity of food resources becomes apparent. Instead of nectar, their primary requirement shifts to water, vital for regulating the hive's temperature amidst the sweltering heat (Kovac et al., 2018). Honey bees, ever resourceful, diligently seek out nearby water sources. Unlike nectar, which can vary in quality, water is a necessity with no qualitative assessment. Honey bees transition from extensive exploration to a focused pursuit of precision, directing their efforts towards locating the nearest water sources. To share this critical information with their hive mates, honey bees engage in their dance language,

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

34

indicating the locations of nearby water sources (Hasenjager & Leadbeater, 2019). Through these remarkable dances, they ensure the hive's hydration and survival during the summer months, displaying their remarkable adaptability and cooperative instincts.

Independently of the models that were used to decode the waggle dances, the foraging distance trends can also be used to understand how foraging availability is changing through time. When bees forage over larger distances, it may indicate that resources closer to the hive are scarce or insufficient to sustain the colony's needs. This suggests that environmental changes or human activities may be impacting resource availability, leading to potential implications for colony health (de Jongh et al., 2022; Hristov et al., 2020; Van Espen et al., 2023).

When comparing the three models, it was found that during March, April, May, and June there was concordance within the models, meaning that the rate at which the different land use types were used, were similar within the different models. The only two months where the three methods did not agree, according to the Kendall concordance coefficient, were July and August most probably due to the low number of dances. Thus, if just one of the methods decoded one waggle dance into a different land use, the remaining data would lose agreement. In other words, the methods are similar (concordant) in showing major foraging trends of honey bees. However, in months with a lower sample size, dances for land uses with small patches may skew the data. Interestingly, in the month of June, despite the lower number of waggle dances analysed, the models are in agreement, suggesting that the low number of dances in some months could really be a caveat of this study.

Nevertheless, during months when there is flowering and a greater interaction between the colony and the landscape (spring), the methods yield consonant results. Therefore, during the most important foraging months – the productive period (Hatjina et al., 2014; Odoux et al., 2014) – one could use any of the proposed models to extrapolate where the honey bees were foraging. Studying these preferred foraging areas helps identify key habitats and land uses that support colonies development. Such information can be valuable for effective habitat management and conservation efforts, as it allows researchers and policymakers to focus on protecting these critical foraging areas. In this study, almost every month, all three models consistently identified grass grazed as the most visited land type by honey bees. These areas are usually filled with herbaceous plants like *Trifolium spp.*, *Echium sp.* and *Vicia spp.* (Dupont et al., 2021). Furthermore, these areas have a low input of pesticides and species (as identified above) that offer a continuous offer of nectar and pollen during the most important period of colonies development.

Even so, one should have in mind some of the caveats of this analysis. These models' outputs are good to explore the major trends on the colonies foraging behaviour, showing a certain agreement on the overall land use types. But, for an in-depth analysis of the polygons and plant species visited by honey bees there are other methods (e.g., pollen capture followed by

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

35

palynological analysis) that most probably will yield better results (Dimou et al., 2006; Lau et al., 2019), since in this study the focus was only the different land use types.

Considering the output of all models, the most visited soil use categories were Grass grazed, Permanent pastures, and Fodder mixes which often contain a diverse array of flowering plants, including wildflowers and clovers (Michaud et al., 2012), which tend to have a high nutritional value for honey bees (Davidson et al., 2020). These areas of uncultivated forage land (including pastures, grassland, hay land, and roadside ditches) had been shown to benefit the yearly survival of apiaries and increase honey yield (Evans et al., 2018; Smart et al., 2016). They can offer a continuous supply of nectar and pollen throughout the season, providing reliable food source for the bees (Harris & Ratnieks, 2022), which are essential for their nutrition (Brodschneider & Crailsheim, 2010). Furthermore, Fodder mixes can be intentionally designed to provide a beneficial habitat for pollinators. Land management practices in grass grazed areas and permanent pastures may be more conductive to supporting honey bee populations (Smart et al., 2016). These areas usually have lower levels of disturbance, such as tiling or frequent mowing, which can disrupt bee habitats and their foraging behaviour. Fodder mixes, which are specially cultivated to provide forage for livestock, can also include flowering plants that are beneficial for honey bees. Furthermore, honey bees are sensitive to pesticides and other chemicals commonly used in agriculture and these areas often have lower chemical inputs compared to intensively managed crop fields. This lower exposure to pesticides can make these areas safer to honey bees. On the other hand, there were uncommon land uses that were visited in this study since they are not usually part of the honey bees' diet, such as barley and oats (DeGrandi-Hoffman et al., 2016), which are both cereal grains and belong to the same family (Bendich & McCarthy, 1970). These visits can be explained by the presence of some wild flowers in these areas or by the dance decoding inaccuracies.

The performed study can provide valuable insights into bees foraging behaviour in this specific landscape and overall, for the use of these models. Even so, some additional future experiments are recommended to increase the reliability of the study and to allow more robust conclusions regarding the visited land uses as well as the visited flowers:

1.   Like several authors have done in the past, bees can be trained in this specific landscape to access which model best reflects their actual foraging behaviour. Such an experiment would add robustness to the predictions and show the model's accuracy in a real-world scenario, different from the ones in which it was developed, to offer more confidence in its application.

2.   Investigating the flora blooming in each location where the bees forage would help us understand the reasons behind their visits to specific land uses. This additional information can shed light on the foraging preferences of honey bees and provide valuable context for their behaviour (Ghosh et al., 2020). To complement the landscape analysis, analysing the collected

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

36

pollen (Dimou et al., 2006; Lau et al., 2019) over time can give insights into floristic diversity that indeed reaches the colonies, helping to understand the colonies resources allocation and preferences.

3.   Additionally, incorporating advanced technologies, such as GPS tracking or video analysis (Cagnacci et al., 2010; Weimerskirch et al., 2002), which can provide more precise data on honey bee foraging behaviour, would enable a more comprehensive understanding of their movement patterns and validate waggle dance analysis methodologies.

Despite the significant contributions of this study, there are some limitations to acknowledge. The study focused solely on honey bee waggle dances and their relationship to foraging distances, overlooking other factors that might influence foraging behaviour, such as resource quality or the presence of competition. Future studies should aim to consider these additional factors to obtain a more holistic understanding of honey bee foraging dynamics.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

37

V – CONCLUSION

The findings of this study have important implications for understanding honey bee foraging patterns in this type of agricultural landscapes but most importantly showed how the different waggle dance decoding methods have the same output trends. These indicates that the choice of model during the active season, in which there is a high interaction between the colony and the landscape, does not significantly impact the accuracy of predicting honey bee foraging patterns. Meaning that with the use of any of these models, researchers can have an overall idea of the bees' use of the landscape and use that information to support conservation efforts and optimize land management practices to ensure the availability of adequate floral resources for honey bee colonies. Further research, incorporating advanced technologies and considering additional factors, will enhance our knowledge of honey bee foraging behaviour and contribute to the development of effective strategies for their conservation and the maintenance of pollination services.

Comparing waggle dance decoding methods to study honeybees' use of flower resources in an agricultural landscape.

38

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50

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51