

Modelling foraging strategies of honey bees as agents in a dynamic landscape representation

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Abstract

Introduction: Both intrinsic colony mechanisms and external environmental variables affect the honey bee colony development rates and response and a key aspect of this is the use of resources within the landscape by honey bees. Although several models have been developed to explore the foraging behaviour of bees, none fully considered the spatial and temporal dynamics of landscape resources and the role of the colony in the process.

Methodology: Here, we introduce a new honey bee foraging model being developed as a part of the ApisRAM honey bee colony model. Based on agent-based modelling, we used a dynamic ALMaSS landscape model enhanced with floral resource modelling to assess the impacts of weather conditions and resource availability on the possible foraging behaviour of honey bees. Several possible mechanisms (defined, based on honey bee traits) for scouting and foraging were investigated, separately for nectar and pollen collection, including prioritising foraging polygons for nectar foraging according to their *distance* to the colony, the *quality* or the *energetic efficiency* and, for pollen foraging, according to their *distance* to the colony and pollen *quantity*.

Results: If model foraging bees prioritised the polygons, based on their distance from the colony, the number of unsuccessful flights increased compared to other tested strategies and the total amount of sugar collected showed a high variability. Contrary to expectations, the energetic efficiency strategy did not provide the colony with the highest amount of sugar. Overall, the tested strategies provide different outcomes on the collection of resources, the number of performed flights and their success rate, evidencing that the model's outcome at the colony level arises from the individual types of behaviour.

Conclusions and Relevance: Variability in the mass of collected nectar and pollen was found mostly when scout bees applied the *distance* strategy. This higher variability in sugar collection means that model bees were not able to find the most profitable foraging sites at the landscape level, but only at the local level. Other strategies showed less dependence on the surrounding landscape (i.e. *quality* or *random*), but it comes at a cost (i.e. lower production for both nectar and pollen collection). These outputs help us evaluate which strategies could be used for future model development and confirm the models' ability to create dynamic responses. These responses at the colony level were only possible thanks to the implementation of a dynamic landscape model and dynamic spatiotemporal resource model, as well as implementing a social communication mechanism for bees to share information about the resources. Plant nectar production and quality information is essential to predict honey bee foraging distribution. In future model development, the implementation of pollen quality should also be explored to evaluate if it influences the overall pollen collection.



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Key words: Honey bee, foraging model, floral resource model, ALMaSS, agent-based model

Introduction

Honey bee colonies are under stress due to land-use/land-cover changes causing loss, fragmentation and degradation of habitats and as a result of changes to the spatial and temporal distribution, diversity and abundance of flower resources (Tscharntke et al. 2005, Alaux et al. 2017). Some level of infectious or parasitic agents almost always occur in honey bee colonies (e.g. *Varroa destructor* and *Nosema ceranae*). Colonies may also suffer from poor beekeeping management practices (Rortais et al. 2017, Stanimirović et al. 2019) and are exposed to pesticides and other chemicals (Zioga et al. 2020, Xiao et al. 2022). Understanding the mechanisms behind each stressor and how they interact with each other has been a challenge for the scientific community: although the impact of a certain stressor (e.g. the active ingredient of a plant protection product) can be measured on an individual bee, the complex behavioural system within the colony hinders the assessment of how these individual impacts transfer to the colony level (EFSA, Scientific Committee et al. 2021).

Seeley (1995), in his book *Wisdom of the Hive*, identified the need to model this complex honey bee colony system and predict its response to stimuli using computer simulations more than 25 years ago. Recently, the European Food Security Agency (EFSA) endorsed the development of a mechanistic model of the honey bee colony as a basis for the environmental risk assessment of multiple stressors to bees at the European scale (EFSA 2016, EFSA, Scientific Committee et al. 2021). The ApisRAM model, currently under development (Duan et al. 2022), uses an agent-based modelling (ABM) approach to deal with complex systems with dynamic feedback mechanisms and interactions amongst many agents (Grimm et al. 2005, Stillman et al. 2014). ABMs are based on a bottom-up approach, in which relevant information regarding the individual level (bottom) is gathered to formulate theories about its behaviour. This information is then used to create a digital representation of the individual (i.e. an agent). The model outcome (emergent properties) will then be the result of those agents' behaviour, based on their intrinsic characteristics and interactions with the external environmental conditions (Grimm et al. 2005). In ApisRAM, the agents (bees) interact with and react to both other bees and the resources in the colony, the hive's physical and chemical properties and the external environment. This model is composed of several sub-models that entail specific mechanics of the colony, such as the foraging behaviour (Duan et al. 2022).

The foraging sub-model simulates the interactions between the foraging individual agents and the environment, based on the coded behavioural rules for the acquisition and transportation of food (i.e. nectar and pollen) into the colony in each specific scenario. Over and above bee behaviour, such an approach also requires detailed modelling of patterns of food resources and stressors (e.g. pesticide loads) in space and time and of interactions with other environmental variables (e.g. weather). The modelling of honey bee foraging behaviour is not a novel idea. Several other models have been developed, exploring the metabolic costs of foraging (Schmid-Hempel et al. 1985), the exploitation of the

most rewarding resources (Camazine and Sneyd 1991), the behavioural rules and states while foraging, including the impact of foraging recruitment (de Vries and Biesmeijer 1998, Sumpter and Pratt 2003, Dornhaus et al. 2006) and the role of feedback mechanisms (i.e. nectar receivers) that control foraging (Schmickl and Crailsheim 2004). However, these models do not fully integrate the various impacts of environmental conditions on foraging. The landscape representation in which bees were modelled was rather simplistic and, in most cases, included only a few food sources (Camazine and Sneyd 1991, de Vries and Biesmeijer 1998, Schmickl and Crailsheim 2004). Weather variables were not fully contemplated, either because the simulations spanned over only a few hours (de Vries and Biesmeijer 1998, Dornhaus et al. 2006, Baveco et al. 2016) or because no interlinks were considered between the modelled landscape and the weather variables (Becher et al. 2014). Notably, none of these previous foraging models integrated the spatial and temporal dynamics of landscape resources. They also did not fully consider the role of the colony in the foraging process (which impacts the forager bees' numbers and behaviour) either because a limited number of foragers was modelled or because the foragers were not modelled at an individual level. Furthermore, studies evaluating honey bee colony's strength, production and health status rarely considered the impact of the environmental conditions (Hatjina et al. 2015, Odoux et al. 2015, Dupont et al. 2021). Landscape structure was usually defined using very broad land-use categories (e.g. urban, grassland, forest; Lecocq et al. (2015), Sponsler and Johnson (2015)) and without a quantitative assessment of the available resources for bees. However, bees can actively adapt and respond to changes in the environmental conditions around the hive. Changes in environmental conditions may lead to shifts in their foraging patterns, impact bees' diet (diversity of collected resources), accumulation of resources, colony size, and energy spent for thermoregulation (Simone-Finstrom et al. 2014, Sponsler and Johnson 2015, Danner et al. 2016). Therefore, including environmental conditions is essential if we want to reflect feedback loops in the complex bee colony system and predict exposure to (and effects of) single or multiple stressors on its strength, production and health status.

The foraging sub-model developed within the ApisRAM aims to overcome these limitations by performing a much more detailed simulation of the bees and the environment in which they are foraging. The environment in which the colony and the bees are modelled is implemented as a detailed, spatiotemporal landscape representation within the Animal, Landscape and Man Simulation System (ALMaSS). Detailed simulation of the bees requires, however, knowledge of the mechanisms driving foraging preferences and distribution. The most accepted theory on foraging behaviour shows that, at the colony level, the most profitable resources are the ones that are selected for foraging (SchmidHempel et al. 1985, Seeley 1994). Nevertheless, the individual mechanisms that lead each bee to a certain polygon (i.e. scout bees) are still poorly understood (Grüter and Farina 2009).

As stated above, several honey bee models have been developed to explore the known honey bee colony foraging mechanisms. This paper aimed to test different foraging mechanisms which model honey bees could implement in a complex landscape. We evaluated how different theoretical foraging strategies (mechanisms) affect honey bees' collection of resources (for both pollen and nectar). These foraging strategies were defined based on honey bee traits/behaviour that

possibly determine their foraging ability and communication. The main goal of this data exploration study was to find out how bees' individual decisions could lead to different colony outcomes. Additionally, we assessed potential caveats/challenges in developing modelling approaches for such a complex foraging system.

These goals were achieved by performing computer simulations in which the number of forager bees and their strategies were independent of in-hive mechanisms, for example, the number of brood cells or receiver bees. Bees were only affected by their behaviour (the strategy applied) and environmental characteristics. In the future, the results obtained from these simulations will be used to create the final foraging sub-model of ApisRAM, in which the nectar and pollen production from the colony will also be influenced by in-hive colony dynamics, emerging from the individual honey bee foraging decisions (bottom-up approach). Therefore, the developed strategies are not the final foraging model. Instead, lessons from these extensive simulations will be used for a robust overall model development.

Material and methods

Defining the modelling environment

ALMaSS landscape and floral resource model

To properly model the impacts of environmental conditions on foraging activities, a detailed, spatio-temporal landscape representation within the ALMaSS modelling environment was used (Topping et al. 2003, Topping et al. 2015). This landscape representation combines detailed land-use/land-cover mapping with information on farming systems, farm practices, weather, and plant growth (Fig. 1). The ALMaSS landscape simulation typically operates on a 10 by 10 km window, with a spatial resolution of 1 m.² Each 1 m² belongs to one single landscape element (being a polygon of rather homogeneous properties) of a specific land-use/land-cover type (e.g. forest, building, field in rotation, river, etc.) to which information on habitat type and its plant composition is linked. To account for crop diversity, fields are also mapped, each belonging to a given farm unit (managed by the same farmer). Farm units are classified into different types (e.g. cattle, pig or arable farms), based on the structure of crops grown and the animals kept on the farm. Each farm type has an associated crop rotation plan, which allows realistic modelling of patterns of crop types changing in space and time. Crop husbandry is described by country-specific management plans consisting of time windows and probabilities of occurrence of different farming operations, including soil cultivation practices and fertiliser and pesticide applications. Associated vegetation growth models for all modelled vegetation types and crops supply vegetation height, green, and total biomass daily, driven by weather conditions, for example, mean daily temperature. Such a structure reflects the dynamic character of an agricultural landscape, allowing it to map patterns of vegetation changing in space and time together with associated management actions.

The spatio-temporal pattern of floral resources available for bees was simulated with floral resource models incorporated into the ALMaSS landscape representation (Ziółkowska et al. 2021). These models described pollen, nectar and sugar production levels and their changes throughout the year for all vegetated polygons in a landscape (Fig. 2). The floral resource models relat-

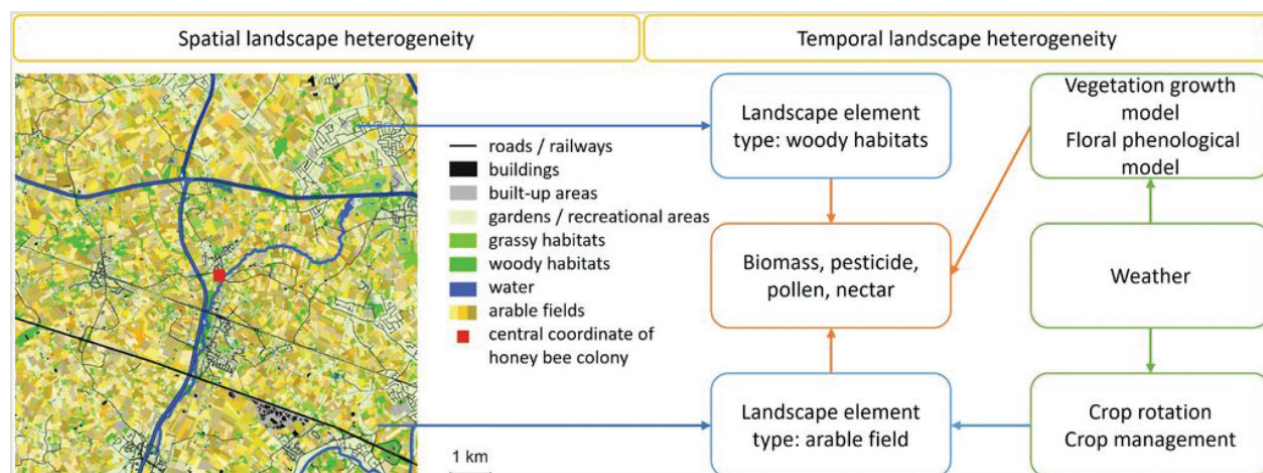


Figure 1. Components in ALMaSS landscape model. The blue arrow represents the access to landscape information at a 1 m resolution. In this example, one element has woody habitats,² while the other is an arable field. The information about each element depends on its type and the temporal factors described in the green boxes. The orange box shows some of the factors derived from the landscape element type, its management and the weather.

ed flowering time and, therefore, the production of resources, to accumulated growing degree-days (GDD), based on daily average temperatures. For annual crops, GDDs were accumulated from the sowing date and crop-specific thermal requirements for growing (i.e. base and maximum temperatures) were used. For other vegetated landscape elements, floral resource models were generated by superimposing models for individual plant species composing that element, i.e. they summarised the production of all plant species from a given habitat. Here, the production of resources by individual plants was related to GDDs being accumulated starting from the beginning of the year and the same thermal requirements for growing were applied to all plant species composing a given landscape element type. Floral resource models provided information on nectar and pollen quantity (mg/m³) and quality for each day of the simulation (Fig. 3). The quality of nectar was defined as the quantity of sugar (mg/m³). In contrast, the quality² of pollen was not considered in this study. The daily available resources were traced per square metre using resource maps for the simulated landscape. When a model bee foraged at a location, the foraged amount was depleted from the corresponding map. This resource information, together with hourly weather data (e.g. wind speed, rainfall, temperature and solar radiation), were provided to the modelled foraging bees.

Landscape development

The foraging strategies (see below) were tested using a dynamic ALMaSS landscape representation of a 10 km by 10 km area located near Ringkøbing, Denmark. Details of the landscape generation process can be found in an open GitLab repository (<https://gitlab.com/ALMaSS/b-good-wp5>). To make the simulation results comparable, in this study, the same crop rotations were used for the simulations, i.e. the same field grew the same crop across all the simulations.

For each general landscape element type identified in the study area, we defined the type of associated floral resource habitat. The detailed description of plant composition, density of flowers and floral resources (nectar, sugar and pollen)

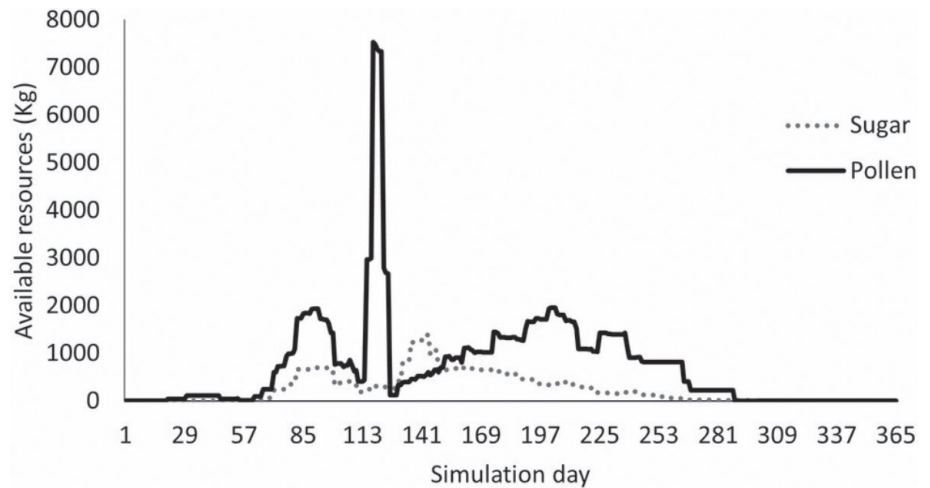


Figure 2. The total mass of floral resources (i.e. sugar and pollen) in the studied landscape available to bees in all the simulations. The mass of floral resources was calculated, based on the production and phenology of the individual plant species comprising the habitats present in the studied landscape and the landscape composition. Pollen availability started on simulation day 20 and nectar was available from day 39.

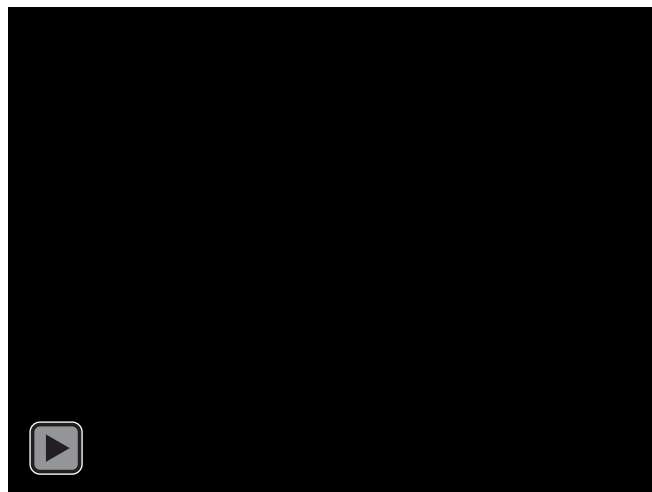


Figure 3. Example of nectar (in yellow on the left side) and pollen (in blue on the right side) spatial and temporal distribution through the season. In each snapshot, a brighter colour indicates a higher amount of the resource in the polygon. A total of 12 snapshots were taken every 30 days, starting on day 15 of the simulation.

produced by each plant composing each of the habitats is available in the GitLab repository (<https://gitlab.com/ALMaSS/b-good-wp5>). In addition, all documentation and input files related to the generation of floral resource models can be found in the GitLab repository (https://gitlab.com/ALMaSS/floral_resource_models).

Defining the foraging model rules

Environmental conditions for foraging and scouting

Low temperatures (< 10°C), darkness, rain, and strong winds (> 25 m/s) prevent foraging or scouting behaviour (Wenner 1963, Hennessy et al. 2020) and these thresholds were included in the foraging model. Under favourable environmental conditions, possible foraging or scouting activities were defined by the hourly

solar radiation and temperature (Vicens and Bosch 2000, Clarke and Robert 2018). If the average solar radiation in an hour was higher than the threshold, the model bees would fly out for foraging or scouting for that hour. That threshold of radiation (R) was defined by the equation from Vicens and Bosch (2000):

$$R = 2261.9e^{-0.164t}$$

in which t is the hourly environmental average temperature ($^{\circ}\text{C}$). In our model, hourly weather data were used to calculate the available foraging hours per each day for these simulations (Fig. 4).

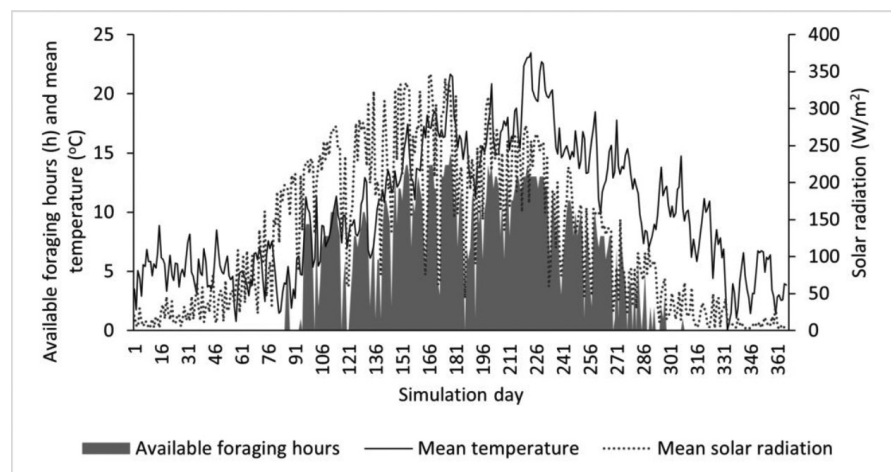


Figure 4. Available foraging hours and weather variables (temperature and solar radiation) for each simulation day throughout the year. Rain and wind variables are not shown, but were used to calculate the number of available foraging hours.

Individual model bee behaviour

Specific foraging simulation rules were defined for individual model bee behaviour. Each model bee had an imposed maximum flying distance of 20 km per day for foraging/ scouting activities. When this threshold was reached in a day, foraging or scouting activity stopped. Additionally, in each foraging flight, a scouter/forager was allowed to carry 50 mg of nectar (Chatterjee et al. 2021) or 8 mg of pollen (García-García et al. 2004) (defined as *full crop*). When successful at finding a suitable resource polygon, model bees started to collect resources in one square metre within the polygon. If, in that square metre, they could not reach a full crop, model bees then performed searching flights (Reynolds et al. 2007) in the surrounding square metres until reaching a full crop or until searching locally a maximum area of 25 m². The flight was considered unsuccessful if model bees still could not reach a full crop. Model bees that performed successful flights memorised information about their relative position to the colony (including distance), resource quantity (nectar or pollen mg/m) and quality (sugar mg/m^{2.2} for nectar).

Scouts behaviour

When favourable environmental conditions occurred for the first time in a year, the model bees initiated exploration of the landscape surrounding the hive through scouting activity. They selected a random direction and flew in that chosen direc-

tion. Every 10 m, the bees would make a random turn, with a higher likelihood of maintaining their previous flying direction. On the initial day of the simulation, when weather conditions permitted foraging, only 25% of the total number of foraging bees performed scouting flights. This rule was in line with the findings of Seeley (1983), indicating that not all forager bees participate in scouting behaviour. In subsequent simulation days, the activation of scouting behaviour followed the rules described in the „social information“ section. The model scout bees randomly foraged for 20 to 140 minutes (based on Seeley (1983)) for a single scouting trip, visiting several polygons in the scouting path. When returning to the colony, these bees shared one scouted polygon’s information to recruit other foragers. The choice of which polygon’s information to share was made according to the strategy set in each simulation (see *Selected scouting/foraging strategies* section below).

Recruits behaviour

Recruit model bees were defined as those that did not yet have information about a foraging location and were waiting for floral resource information to find a suitable polygon to forage (Fig. 5). These could be new forager bees that were just added to the foraging force each day (in these simulations, this number was set to increase at the same pace each day - see *Simulation setup and runs*) or old foragers that performed unsuccessful flights. The new daily recruits always waited for social information until the scout bees returned to the colony and only then did they choose where to forage according to the observed waggle dances. Foragers having unsuccessful flights searched for social information immediately after returning to the colony.

Foragers behaviour

Forager model bees were defined as those engaged in foraging activities in a known polygon (Fig. 5). These bees would fly out to the polygon and perform

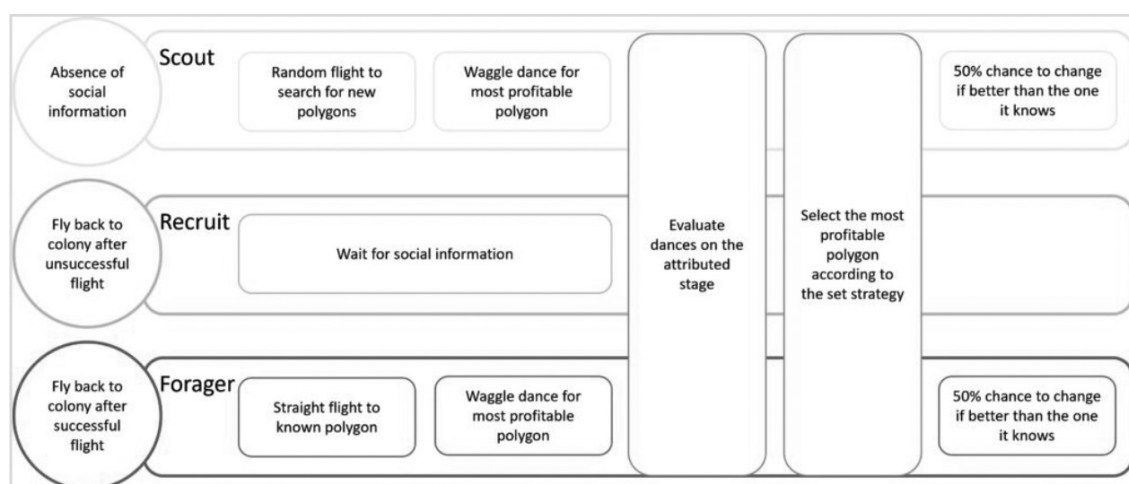


Figure 5. Scout, recruit and foragers behaviour rules. Without private and social information, model bees become scout bees. When there is no private information because they never performed a foraging flight or because the flight was unsuccessful, model bees become recruits and will search for social information. If model bees have private information, they are considered forager bees even if no social information is available in the colony. In the presence of social information, scout and forager bees can change foraging locations (50% chance).

direct flights between the polygon and the colony. When arriving at the colony after a successful flight, these bees then performed waggle dances to recruit other bees and observed other waggle dances (more details in the *Social information* section). If a model forager bee performed an unsuccessful flight, then it became a recruit bee (Biesmeijer and Seeley 2005).

Social information

The waggle dance behaviour (Frisch 1993) was implemented differentially in space in the colony to mimic the communication of social information. When arriving at the colony after a successful flight, scouts and foragers were randomly assigned to one frame side, hitherto referred to as a *stage*. This way, a 10-frame honey bee colony was composed of 20 stages. Recruit bees were also randomly assigned to a stage (in the next steps of model development, bees' spatial distribution will be influenced by other in-hive mechanisms) to observe the waggle dances. All model bees in the same stage (recruits, scouts and foragers) observed the waggle dances on the stage. Since honey bees have some preference over their private information (Grüter and Ratnieks 2011), but without a clear threshold (e.g. resource quality or polygon distance) for what causes bees to abandon their own polygon (private information) in favour of other polygons (social information), model bees had a 50% chance of moving to a new polygon if it was better (according to the set strategy, see below) than the one they knew. Since model recruit bees had no private information, they selected the most profitable polygon (according to the set strategy, see below). If a model recruit bee did not find any social information in its stage, it automatically became a scout bee (based on Beekman et al. (2007)).

Selected scouting/foraging strategies

Scouting strategies

We tested the following scouting strategies:

1. Distance strategy: Prioritise the closest polygon

Despite their ability to detect colours and patterns (Avarguès-Weber et al. 2012), honey bees have poor stereo vision, hindering their perception of objects that are far away (Srinivasan 2021). Furthermore, at the beginning of the season, smaller colonies tend to forage closer to the colony (Beekman et al. 2004). Therefore, model bees selected the closest polygons to forage in in this strategy.

2. Quality or quantity strategy: Prioritise the polygon with better quality (nectar) or quantity(pollen)

Honey bees possess several taste gustatory sensilla (mostly located on the distal segment of the antennae, on the mouthparts and on the tarsi of the fore-legs (de Brito Sanchez 2011)). The peripheral taste detection allows honey bees to rapidly access sugar content in nectar (Jung et al. 2015). Therefore in this strategy, model bees were made to select flower rewards with the most

sugar content to represent the assumption that this sensory apparatus is used to select high sugar returns.

As for pollen, it has been suggested that honey bees make their choices, based on fatty and amino acids content (Cook et al. 2003, Zarchin et al. 2017), but no clear factor has been identified. Pollen foragers are believed to go through a multimodal stimulus, with gustatory, olfactory, visual and mechanosensory cues while collecting pollen from a flower (Nicholls and Hempel de Ibarra 2016). Considering that honey bees could perceive a positive reward with less handling time and it is not clear which pollen traits fully drive pollen foraging behaviour, model bees preferred to forage on polygons with more pollen quantity (per m).²

3. Random strategy: Randomly choose a polygon from the whole landscape

As we do not yet fully understand the mechanisms driving foraging choices by scout bees (Grüter and Farina 2009), a random strategy was also tested. In this strategy, model bees randomly selected a polygon from the ones they had visited during their scouting trip.

Foraging strategies

For the foraging model bees, besides the strategies used by scout bees (i.e. distance, quality or quantity and random), an extra strategy was set only for nectar collection, since we cannot measure the energetic gain of pollen collection.

4. Energetic efficiency: Prioritise the polygon providing higher energetic efficiency

Other than the direction and distance of available resources, honey bees can transmit information on the profitability (balance between energy gained from the resource and the energy spent to collect it) of resources by performing more intra-dance circuits during the waggle dance (Seeley et al. 2000). In the model, bees had access to this information via the waggle dance and prioritised polygons that provided a higher energetic gain. The energetic gain was calculated, based on the values from table 1 of Baveco et al. (2016) and assuming the same flower handling time between foragers:

$$\text{Energetic gain} = (\text{quality} * 17.2) + (\text{distance} * (-0.0168))$$

where the *energetic gain* is the amount of sugar reaching the hive (in mg), *quality* is the amount of sugar per m² (mg/m²), 17.2 (J/mg) is the energetic value of sugar and *distance* is the distance from the colony to the resource polygon (m).

Simulations to explore the influence of scouting and foraging strategies

Simulation setup and runs

In all the simulations performed, the total daily number of modelled bees was predetermined and varied with time to represent a typical honey bee colony

(i.e. from approximately 1000 to 9600 forager bees). This daily number was obtained from fieldcollected data on colony strength from the EFSA OC/EFSA/SCER/2017/02 project (Dupont et al. 2021): 34% of all adult bees were assumed to be foragers, from which 30% were pollen foragers.

A total of 1200 simulations (one-year simulation for each run) were performed to test the scout-forager strategies in a dynamic landscape with a different spatio-temporal resource distribution around the colony. We explored different flower pattern scenarios around the colony by placing the colony in 100 different landscape locations (regular grid of 100 cells of 1 km x 1 km with the colony placed in the centre of each cell).

Simulation outputs

For each simulation, daily data on nectar, sugar and pollen in the landscape and resources collected were obtained, as well as the number of foraging flights and those that were successful (i.e. in which model bees collected nectar or pollen). Such daily data were used to calculate the yearly amount of resources collected by the colony, the mean number of daily foraging flights and the percentage of successful flights. For each of those outputs, data were pooled together to calculate the variation of the model outputs, represented using box-plots for the respective strategy.

Results

Sugar collection

The amount of sugar collected by model bees throughout the year depended on both scouting and foraging strategies (see Fig. 6), for all evaluated colony parameters (i.e. total amount of sugar collected, mean number of daily foraging flights and their success).

Regardless of the strategy used by the foragers, the highest variability was observed when scout model bees employed the distance strategy. Although in this strategy, the colony was, on average, the most successful in collecting sugar (with the mean total amount of sugar collected varying from 91 to 125 kg depending on the foraging strategy), it was at the expense of a large number of daily flights with a lower success rate. When the distance foraging strategy was coupled with the quality or random scouting strategy, the observed mean amount of sugar collected by the colony was still relatively high (mean total amount of collected sugar of 91 and 109 kg, respectively) and less dependent on the colony's location (as the variability of the parameter decreased). When these strategies were coupled, the mean number of daily flights decreased only slightly (from on average 6 to 5), but the foraging success rate increased significantly, resulting in a relatively high total sugar collection. Other combinations of strategies further increased the foraging success rate. Still, because the daily number of flights decreased significantly, these strategies resulted in, on average, a very low total amount of sugar collected (on average at least half compared to the previously described combination of strategies).

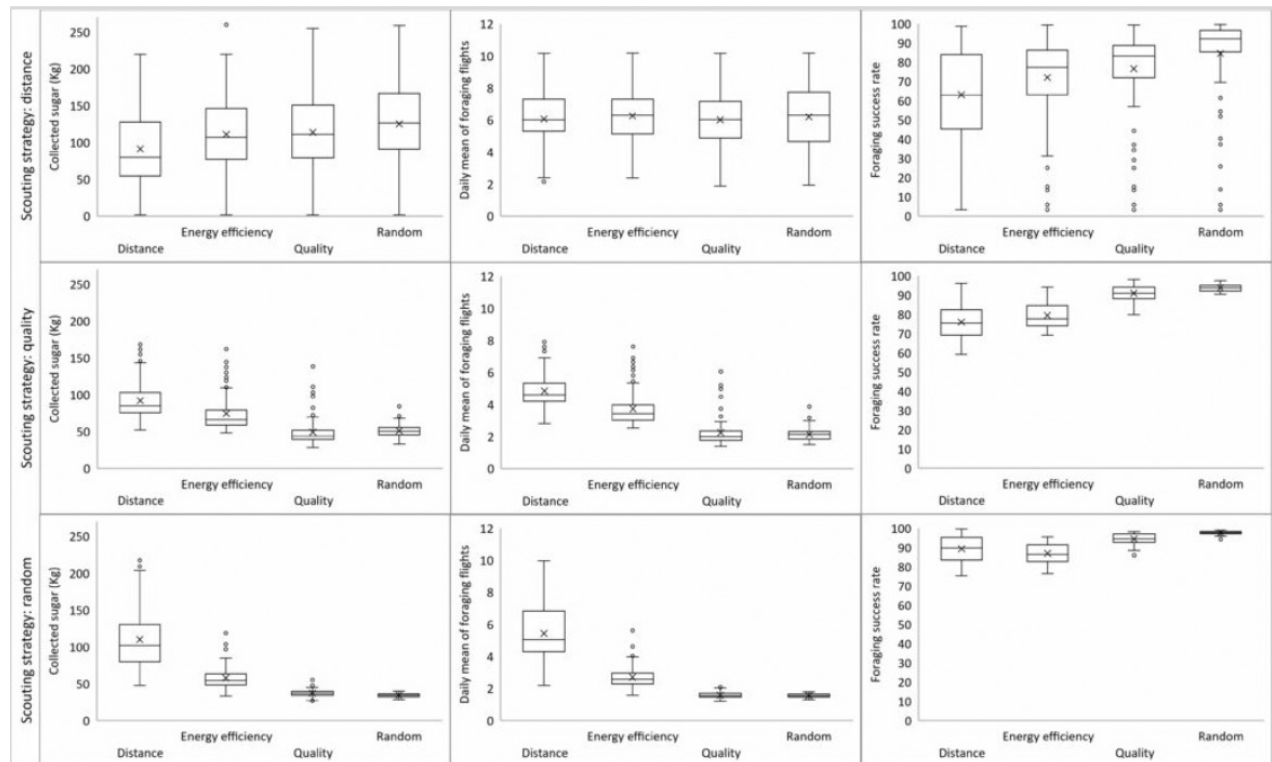


Figure 6. Results of the implementation of different scouting and foraging strategies on the performance of model colonies in terms of nectar collection. For each scouting strategy (i.e. distance, quality or random), four different foraging strategies (i.e. distance, energy efficiency, quality and random) were tested. The total amount of sugar collected, the mean number of daily foraging flights and their success were evaluated for all combinations of scouting and foraging strategies.

Pollen collection

Similar to sugar, pollen collection varied considerably depending on the scouting and foraging strategy used (see Fig. 7). Interestingly, the foraging success rate for all combinations of scouting and foraging strategies was very high (> 81%) and higher than for sugar collection. In addition, on average, the model foragers made more flights to collect pollen than to collect nectar. The colony collected the highest average amount of pollen when the distance strategy was used by scout or forager bees (between 26 and 34 kg on average). In these cases, the number of daily flights performed was always high (on average 7 to 8 daily mean foraging flights), but in the case of the foraging distance strategy, their success rate was lower (on average 82 to 95%, depending on the scouting strategy). When either scout or forager bees used quantity or random strategies, the amount of pollen collected by a colony was much lower (on average between 6 and 13 kg, depending on the combination of strategies). This result was consistent with the low number of foraging flights and the low variability of the observed results.

Discussion

In this study, for the first time, a dynamic ALMaSS landscape model with spatially and temporally varying patterns of floral resources was used to evaluate different scouting and foraging strategies of honey bees. Each mapped element in the ALMaSS landscape model had associated information on habitat type and its plant composition, allowing model bees to evaluate available floral resources from each

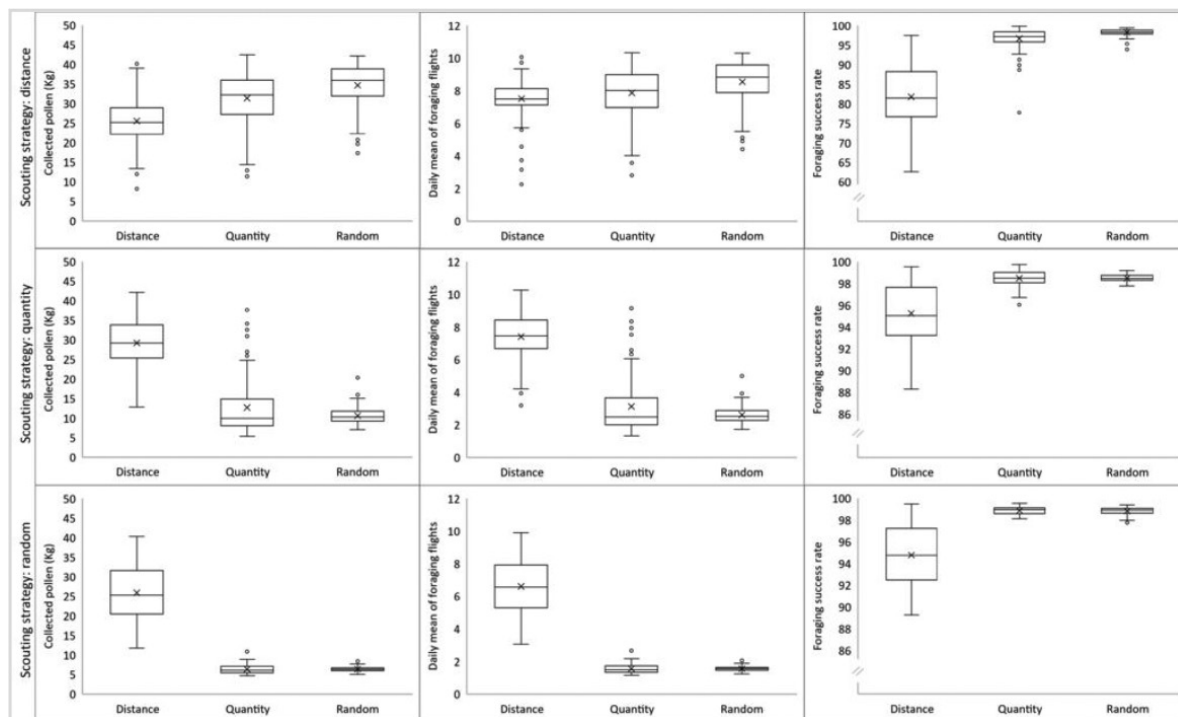


Figure 7. Results of implementing different scouting and foraging strategies on the performance of model colonies in pollen collection. Three different foraging strategies (i.e. distance, quality or random) were tested for each scouting strategy (i.e. distance, quantity and random). The total amount of collected pollen, the mean number of daily foraging flights, the number of foraging flights and their success were evaluated for all combinations of scouting and foraging strategies.

landscape square metre and for each simulation day. The quantity and quality of floral resources available to model bees depended on the distribution of habitats within a landscape and their composition, but were also determined by weather conditions, which defined the number of available foraging hours per day and the time of flowering. This combination of factors was used to evaluate the outcome of foraging strategies in terms of the amount of sugar and pollen collected.

Foraging rules and individual bee behaviour

In our model, scouting model bees had a random flight behaviour and a random time-frame to perform their flights. These assumptions were inspired by the approach to flight rules implemented in the BEESCOUT model (Becher et al. 2016). However, unlike our model, in the BEESCOUT model, bees could only recruit other bees if the „recruitment“ feature was activated or later by integrating the probability data into the BEEHAVE model. In our model, scouting bees were able to visit multiple polygons and bring back information to the colony about the most profitable polygon. This behaviour was chosen to allow foragers to explore the landscape. If the bees simply flew randomly in the landscape until they found a suitable polygon, then the closest and largest polygons would have the highest probability of being found by the model bees. By allowing the model bees to explore the landscape and visit more polygons, there is a higher chance of finding more suitable foraging sites and bringing more and better information back to the colony to better deal with the landscape complexity.

Nevertheless, the time available for scouting was set, based on evidence from a small number of samples (n = 8) investigated by Seeley (1983). In ad-

dition, in our model, the number of scouts for the first day of the simulation was set at 25%, although in reality, it can vary between 5% and 35% (Seeley 1983). In future model developments, these numbers could be used to evaluate the scout activation behaviour. Unfortunately, the parameterisation of our model was limited due to the limited number of available studies on foraging behaviour. This highlights the need for more fundamental behavioural studies in honey bee colonies using modern technology (e.g. GPS tracking) to collect more accurate data (e.g. Wario et al. (2017), Siefert et al. (2021)).

In the model, recruits (unemployed foragers) can also activate scouting behaviour (Biesmeijer and Seeley 2005, Beekman et al. 2007) when communication is scarce (no waggle dances). This allows for continuous scouting behaviour and creates a dynamic fluctuation in the number of model scout bees in a simulation. Overall, as the drivers of scouting behaviour are still unclear and there is a knowledge limitation for model development, we believe that the implemented scouting mechanisms are a good solution to model this behaviour: they allow a dynamic number of scouting model bees (except on the first day) and avoid over-representation of closer and larger polygons amongst foraging sites.

On the other hand, the social information flow mechanisms still have room for improvement. Honey bees can shift their foraging patterns at the colony level when presented with a low- or high-quality nectar source, increasing foraging effort to visit the most rewarding sources (Seeley et al. 1991, Seeley 1995). Individual bees make their decision by comparing social information with their personal information (Grüter et al. 2008, Grüter and Ratnieks 2011) and are more prone to abandon a previous foraging location if the new location has better profitability (Camazine and Sneyd 1991, Seeley 1994). This behaviour ultimately leads the colony to select the most rewarding patches when food is abundant and to lower its foraging thresholds when resources are scarce (Seeley et al. 1991). We believe that the implementation of social information flow mechanisms with several stages for information flow in which model bees are spatially distributed (as in Schmickl and Crailsheim (2004)) embraces part of this behaviour. In our model, bees can observe and compare a set of dances with their private information. We allowed them to make individual decisions by implementing a 50% chance of switching to a more profitable polygon than the one the model bee already knows. However, this threshold is only theoretical, as little is known about the main drivers of this change. What is the relationship between sugar content and the probability of changing? Is this behaviour similar for all forager bees or does experience also play a role? These questions need to be investigated to model this behaviour better.

Nevertheless, even considering this drawback, we could capture the colony behaviour described above as an emergent property of the behaviour and decisions of individual model bees (as in individual agent-based models; Topping et al. (2003), Stillman et al. (2014)). We obtained a heterogeneous and dynamic distribution of honey bees in the landscape, leading the colony to progressively forage on the most profitable polygons (according to the strategies tested).

Implementation of strategies for nectar and pollen collection

In general, implementing the scouting *distance* strategy (i.e. when bees prioritised foraging polygons according to their distance from the hive) resulted in the highest average amounts of total sugars collected at the colony level. This strate-

gy could, therefore, be beneficial to honey bee colonies and is consistent with our knowledge of honey bee behaviour. Honey bees can detect the colour, shape and scent of flowers (Srinivasan 2010) and their vision has *regional* specialisations to account for the specificities of the foraging tasks (e.g. the dorsal rim of the eye is specialised in the perception of polarised light to aid their navigation, while the front-ventral region is specialised in colour vision to aid in flower recognition; Srinivasan (2010)). However, they have poor stereo vision, preventing them from seeing long distances. It has also been observed that smaller colonies tend to forage closer to the hive at the beginning of the season (Beekman et al. 2004).

However, in the scouting *distance* strategy, high variability in total sugar collected at the colony level was observed regardless of the foraging strategy used. This may indicate that the landscape context, i.e. the distribution and quality of resource polygons in the immediate vicinity of the hive, played an important role in this strategy. By prioritising the closest polygons, model foragers were able to explore habitats away from the colony only after the closest resources were depleted. Furthermore, we observed an increase in the total number of daily foraging flights performed and a decrease in their success rate, as these model bees were most likely foraging in closer, but smaller polygons, which were depleted more quickly, activating the search for new resources more often than in other strategies.

Since bees can also evaluate nectar quality (Seeley et al. 1991) and communicate this information by sharing food with other bees (Farina and Wain-selboim 2005) and by performing more intra-dance circuits during the waggle dance (Seeley et al. 2000), one of the scouting strategies tested was the *quality* strategy. When scout bees prioritised polygons according to the quality of the available nectar (i.e. sugar content), both the average and the total amount of sugar collected by the colony and its variability were reduced. This strategy was, therefore, less context-dependent than the scouting *distance* strategy and, at the same time, resulted in good foraging success (from 60% to

99%) despite the strategy used by the model foragers. When the scouting *quality* strategy was coupled with the foraging *distance* strategy, the number of daily foraging flights increased and their success rate decreased (similar to the results obtained for the scouting *distance* strategy).

Honey bees can also communicate information about the profitability of a resource (Seeley et al. 2000) by assessing the energetic gain of their visit (the ratio between the distance travelled and the reward received Camazine and Sneyd (1991), Seeley and Tovey (1994)); hence, higher sugar collection was expected when the foraging *energy efficiency* strategy was used. Other in silico foraging models exploring the interaction between the colony and the landscape have included this profitability principle (Schmickl and Crailsheim 2004, Becher et al. 2014, Baveco et al. 2016); similarly, our study included the evaluation of nectar quality (sugar/m) and distance in the 2 *energy efficiency* strategy. In this strategy, model bees may have higher *efficiency* when foraging on nearby resource polygons, even if these have lower sugar availability (sugar/m) due to distance costs. However, the 2 highest *energy* would be obtained from nearby polygons with higher sugar concentrations. In this case, forager model bees would spend less time travelling, allowing them to make several high-return foraging flights on the same day. If, in real life, forager bees do use this strategy, it is a good way to avoid leaving the fate of the colony in the hands of the scout

bees. Therefore, using the *energy* strategy to drive social information decisions may be the most efficient and safest strategy for the entire colony, regardless of the strategies used by the scout bees. However, when this strategy was applied, the average total amount of sugar collected decreased compared to the foraging *distance* strategy, but the bees performed fewer and more successful foraging flights. Most probably, the implementation of a 20 km daily budget has limited the number of foraging trips performed in other strategies (besides the *distance* strategy). For future model development, the effect of the daily flight budget on model's outcome needs to be explored.

Interestingly, when the scouting *quality* or *random* strategy was coupled with the foraging *random* strategy, it resulted in low amounts of sugar collected, with little influence from the colony position and, thus, surrounding resources. Here, model foragers performed fewer flights, but with a high success rate. Most likely, because the colony did not concentrate on a few profitable polygons, the model bees always had enough social information to visit a polygon with resources, leading them to perform successful flights even if they were not profitable for the colony in terms of time and energy.

Regarding pollen collection, when model scout bees used the *distance* strategy, similar results were obtained for nectar foraging, i.e. the amounts of pollen collected were high, but highly dependent on the resources close to the colony location. Studies on honey bee pollen foraging behaviour show that bees adapt their foraging distances to the availability of pollen in their surroundings (Danner et al. 2016), suggesting that they prefer to forage near the colony when sufficient pollen is available. By analysing waggle dances, Couvillon et al. (2014) showed that bees prefer to forage closer to the colony at the beginning of the season and increase their foraging distances later as resources become scarcer, demonstrating that the colony adapts to the dynamics of resource availability in the landscape. This dependence on the surrounding landscape was reduced when model foragers focused on polygons with more pollen (*quantity* strategy) or chose them randomly (*random* strategy). Nevertheless, the total amount of collected pollen was reduced when foragers applied these strategies unless they were coupled with the scouting *distance* strategy (i.e. scout bees prioritised the closest polygons).

Interestingly, the highest pollen collection was achieved when the scouting *distance* strategy was combined with the foraging *random* strategy. In this case, the model foragers always had social information, as they were only distributed to a few closest polygons announced by the scout bees. This leads to a slower depletion of resources in these polygons (also because bees can only carry 8 mg of pollen per flight) and to an extremely high foraging success rate. However, for future model development, the amount of pollen collected cannot be used as the sole proxy for colony success; rather, pollen quality must also be taken into account. There is an important relationship between pollen availability and diversity and healthy colony growth (Mattila and Otis 2006, Keller et al. 2015a, Keller et al. 2015b, Requier et al. 2016), as bees require essential amino acids mainly for healthy larvae and hypopharyngeal gland development (Brod-schneider and Crailsheim 2010). Pollen quality was not implemented in our model and, consequently, we could not consider the need to collect pollen from diverse resources that might arise from the internal needs of the colony. Despite these limitations, we believe that the strategies tested allowed the model

bees to explore most of the available pollen diversity. They were able to fly in several random directions and bring this information back to the colony, as well as regularly switch foraging to new polygons in case of unsuccessful flights, resource depletion or the end of flowering. Furthermore, even if pollen quality is implemented, the available information on honey bee foraging mechanisms driving pollen selection is even more limited than for the nectar (see Nicholls and Hempel de Ibarra (2016)). In particular, honey bees have been shown to adapt their foraging range to compensate for the lack of pollen diversity close to the colony (Danner et al. 2017), meaning that a minimum pollen diversity threshold should be explored in future model development.

The most important lesson from our simulations comes from the behaviour of the model scout bees. Despite the „supposedly“ minor role of scouts (as scouting only occurs when social information is scarce), the choice of the scouting strategy influenced the annual resource collection of the whole colony for both nectar and pollen. Therefore, foraging models must include a reliable implementation of the scouting strategies.

Future testing and model development

We believe that, in the future development of the honey bee foraging model, nectar foraging should not be determined by the distance of the polygon from the colony, as such a strategy does not incorporate information about the profitability of the resource polygon. Furthermore, we need a better understanding of how bees weigh private versus social information in order to adjust the probabilities of switching resource polygons when private information is available. There is, therefore, a need to support new studies to report on internal colony mechanisms, as the few existing studies (although important) are outdated and lack replicability. The implementation of pollen quality and pollen diversity in the landscape needs to be further explored.

Duan et al. (2022) completed the first step in developing the ApisRAM model (i.e. the formal model), which described the possible approaches to implementing the different components of the honey bee colony model. In this study, one of these components, the foraging strategies, was studied separately from the others. In the future development of the ApisRAM model, forager model bees will not only influence and be influenced by other foragers (as tested in this study by implementing the waggle dances), but also by other model bees performing other tasks in the colony, i.e. food processing (e.g. Schmickl and Crailsheim (2004)) or brood rearing (Seeley 1995). In the foraging submodel, the next step is to use field-collected data from the EFSA OC/EFSA/SCER/2017/02 project (such as the daily number of foragers, colony population, weather, resource supply and honey gain) to validate the tested strategies. We aim to develop a reliable foraging model that can accurately predict the distribution of bees and their use of resources within a landscape. This will allow us to correctly predict possible exposure pathways to pesticides and/or other stressors.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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