Project Report

Unraveling Beehavior: Investigating survival regimes of Western honey bee colonies under environmental stressors

Pablo Alves[1], **Bartek Golik**[2], **Jonas Schäfer**[3], **Kaleem Ullah**[4] **and David Klein Leunk**[5]

[1] *pablo.rodriguez.alves@student.uva.nl (15310191)*
[2] *bartek.golik@student.uva.nl (15309037)*
[3] *jonas.schafer@student.uva.nl (14039982)*
[4] *kaleemullah@student.uva.nl (12560081)*
[5] *david.herder@student.uva.nl (12992976)*

Abstract

Eusocial species exhibit a division of labor into reproductive and non-reproductive parts of the population. The non-reproductive group may divide work further into different tasks, which enables further specialization on the individual level aiming to increase efficiency for the collective - a behaviour known as polyethism. A prime example of an eusocial species exhibiting polyethism is the Western honey bee. Here, task specialization of an individual bee is temporal and may revolve around the gathering of specific resources. Given the limited knowledge of an individual bee, it is fair to assume that for tens of thousands of individual honey bees to be effective and aligned towards colony-level interests such as hive survival, there must be some type of coordination system. For the foraging behavior of honey bees, this coordination is assumed to emerge in a decentralized manner from honey bees individual perception of their environment. With various biological sensing capabilities and known methods of communication such as the infamous waggle dance, honey bees are both sophisticated organisms and exhibit complex adaptive capabilities on a colony level. For instance, it has been shown that a bee colony can respond and recover from sudden loss of forager bees or increase their foraging activity in response to scarce resource conditions. Despite this, there is a lack of consensus about how varying adaptation capabilities emerge through individual-based mechanisms. To this end, we propose an agent-based model aiming to capture how individual bee behaviour can lead to such emergent phenomena. We specifically focus on the adaptation of foraging activity in response to the availability of resources and changing weather conditions, factors that are known to play a key role in bee polyethism and stressors likely to worsen in light of anthropogenic pressures such as climate change. Using our model of bee swarms, resources and hive agents and 14 parameters, we we are able to observe communication-based effective foraging as well as colony survival tipping points in response to resource availability and storm events. We establish high and low likelihood survival regimes across the parameter space, evaluate parameter correlations for colony survival and growth, and explain causal mechanisms underpinning these emergent behaviors.

Keywords: *Western honey bee, foraging activity, resource scarcity, weather conditions, survival outcomes, agent-based model*

Course: Agent Based Modelling (2023/2024) **Group:** 5 **Tutor:** *Debraj Roy*

Contents

1. Introduction

1.1. Background information

The Western honey bee is the paramount example of a eusocial and polyethic species, dividing labour into reproductive and non-reproductive groups, as well as further specializing its non-reproductive work. Research on their resulting foraging behaviour dates back more than a century [1], with a lack of scientific consensus on the mechanism underpinning emergence of its specialized roles and foraging dynamics [23]. Forager bees play a critical role for the colony survival, since adequate nutrition is a colony's basis for growth and development [10]. Bees exhibit an age-correlated specialization, with bee workers adapting to colony needs by shifting among the critical tasks required for survival [23]. This behavior is complex and impacted by many factors, including seasonality[1] [11]. Still, under a conservative interpretation of current knowledge, the honey bee behavioral ontogeny can be separated into an initial nest phase and a subsequent foraging phase [5].

1.2. Motivation for an ABM approach

Although honeybees, as small insects, posses a simple physiology compared to larger animals, a bee colony is capable of numerous complex behaviours - from swarming decisions to adaptation of bee roles based on the changing environment and current colony needs. From multiple studies we know that, within a colony consisting of up to 80.000 individuals, there is a complex communication system utilizing antenna touching, waggle dancing and pheromone signalling [3]. By design, a system of ODEs or a Markov Chain model will not be able to fully capture these local interactions between many individuals. These reasons suggest agent-based modelling as an optimal approach. This is further supported by the fact that it has already been applied to other eusocial species such as ants [7], [20] or meerkats [16], [18]. Bees are discrete individuals that only perceive and interact with their local environment. Inside the nest, bees feed the queen, nurse the brood and process the food. Outside, they engage in foraging, mostly for nectar and pollen. Forager bees process their local surroundings and are known to be very effective at gathering resources given limited information and often exclusively visit certain flower species during one trip (flower constancy). As we emphasize the study of foraging bees, it is safe to assume that bees do not have complete, but only local information and don't know the state of the hive while foraging. Each individual bee has an internal state which encapsulates its stored information and labour specialization (polyethism). Each may also perform actions stochastically and can be genetically diverse, thus bee population are generally heterogeneous. One might question whether the existence of a queen bee raises concerns about a central supervisor excerpting control over the hive. However, its influence over the hive is understood to be limited to the reproductive system which is largely disconnected from our focus of study. All these particularities further support ABMs as the optimal method.
The assumption that bees behave using a predefined set of rules is consistent with the literature. At the highest level of detail, this would correspond to mirror the information processing in an individual bee brain. We can thus reduce this set to encapsulate their core behavior with a focus on elements relevant for foraging behavior. In ABMs such rules are in turn used to uncover emergence of complex behaviors similar to those observed in nature.

1.3. Related Work

Given the utility for biology [8], it is not surprising that ABMs have also been previously used to study bee behavior. Our literature review considered the following models[2]: *BeeKeeper* (2021), developed as part of a PhD thesis [22]; *Towards a Complete Agent-Based Model of a Honeybee Colony* (2018) [21]; *Bee++* (2017), An Object-Oriented, Agent-Based Simulator for Honey Bee Colonies [17]; *BEEHAVE* (2014), a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure [13] and *HoPoMo* (2007), a model of honeybee intracolonial population dynamics and resource management [9].
These models, although promising, were deemed unfit for the purposes of our work due to several reasons. First, the complexity of these models far exceeded the constraints of the project, and oftentimes made very sophisticated modelling choices. Secondly, the focus of these models did not map easily with the intended focus of the work (see 1.4), which was established before the literature review was completed due to predetermined deadlines. Thirdly, the implementation of these models was often not accessible, or it was only available in low-level programming languages. Preliminary efforts were invested into implementing these models, which were eventually discarded due to difficulties replicating their results. Therefore, we decided to create our own model from scratch instead, encapsulating an adequate level of complexity and parameterization, always based on reviewing the theory driving these models to help us frame our modelling decisions.

[1]For a more detailed review of the social physiology of honey bee colonies, see [3]
[2]For an advanced discussion of computational methods for the study of bees, see [14]

1.4. Problem statement

The focus of this research is to modelling beehive survival dynamics outcomes with a bottom-up ABM based on local information encoded at a bee level. In particular, it will focus on two areas:

1. Resource density and distribution effects on colony survival
2. Extreme weather event effects on colony survival

Weather events and resource availability are known to play a key role in bee behavior, constituting an adaptation challenge at the individual and colony level. By analyzing robustness to resource scarcity and storm events, we aim to study how foraging behavior and bee actions bring about emergent adaptation which would then impact bee colony survival. These are expected to manifest in the form of emergent foraging dynamics such as oscillations and stabilization in foraging activity states in response to external perturbations and classification of hostile regimes.

Report structure

The rest of this project report is structured as follows: Section 2 defines the model created using the ODD specification [12]. Section 4 details the experiments conducted on the model. Section 5 presents its results as well as sensitivity analysis conducted on the model. Finally, Section 6 provides a thoroughly discussion of the model dynamics obtained and presents a series of conclusions and lines of future work.

2. Model overview

2.1. Purpose

The purpose of this educational model was to create a minimalistic model capable of studying distribution of labor in bee colonies. Among all the different tasks a bee performs during its life, this model exclusively captures foraging dynamics. Foraging activity, a multifaceted phenomena tied to many factors, was studied in detail (see Sections 1.1 and 1.3). In particular, this model attempts to understand the mechanisms driving individual decision making during foraging activity. Units were discarded in order to focus on the intricacies of the emerging behaviors[3]. Our subsequent study will then examine two key factors impacting colony survival: resource scarcity and weather events.

[3]This is consistent with bottom-up ABM approaches, which do not aim to produce a fully realistic representation of the system (here the bee colony) [8], and that would otherwise exceed the scope of the project.

Activity (state)	Behaviour & tasks
In-hive	
RESTING	• (Randomly) inspecting hive's nectar levels • (Randomly) share perceived nectar level with a neighbour • Rest, don't take any action
DANCING	• Recruit nearby bees to forage from the resource
Outside the hive	
EXPLORING	• Move around the space, looking for resource
FOLLOWING	• Approach the resource destination communicated by waggle-dancing bee
CARRYING	• Successfully carry the resource back to the hive
RETURNING	• Return to hive without the resource

Table 1. Overview of all six bee activities considered in the model with the related behaviour.

2.2. Entities, state variables, and scales

Bees

Bee agents are the only mobile entities in the model and their be(e)haviour heavily depends on their current activity (state). In-hive activities include waggle dancing and resting. Outside the hive bees perform one of four activities, all related to foraging behaviour. An overview of activities is given in table 1 and a detailed description is provided in section 3.2. Bees are defined by a set of 14 parameters (table 2), which can be split into 5 groups, based on the part of agent's behaviour they govern. The precise meaning of these parameters is given as a list below.

1. FIELD_OF_VIEW: radius in which a bee can interact with other bees, through waggle dance or nectar communication
2. FOOD_CONSUMPTION: amount of nectar consumed by each bee in the hive at a single simulation step
3. SPEED_IN_HIVE: distance covered at each step within the hive
4. SPEED_FORAGING: distance covered at each step outside the hive
5. RESTING_PERIOD: minimal number of steps a bee will stay in the hive after coming back from a foraging trip
6. P_NECTAR_INSPECTION: probability of inspecting nectar levels at each step by in-hive bees
7. P_NECTAR_COMMUNICATION: probability of communicating perceived nectar levels at each step by in-hive bees
8. P_ABORT: probability of aborting a foraging trip
9. P_FOLLOW_WAGGLE_DANCE: probability of an in-hive to follow waggle-dancing bee's directions
10. EXPLORING_INCENTIVE: scale parameter for the exponential distribution governing how likely the bee is to start foraging based on a perceived nectar level
11. CARRYING_CAPACITY: amount of nectar carried back to the hive from a successful foraging trip
12. P_BIRTH: probability for a new bee agent to emerge in hive at each step
13. P_DEATH: probability a bee agent will die at a simulation step
14. DEATH_STORM_FACTOR: multiplicative factor for the death probability during storm

Additionally, the state variables of a bee agent, which are used to further describe their state within the dynamical system and fully specify their subsequent behavior dynamics at the individual level, include:

1. RESOURCE_DESTINATION: the resource found through exploration or communicated through waggle dance by another bee
2. PERCEIVED_NECTAR: current amount of nectar a bee perceives to be in the hive

Hive

Thee beehive is a singular stationary entity located in the center of 2-dimensional space domain. It is not so much an active agent that interacts with other entities, but rather a spatial boundary which allows bees to communicate. Only inside the hive can bees rest, waggle dance and share information about stored nectar between each other. It is also where new bee agents emerge. Hive boundaries are defined by a constant RADIUS, set by default at 5. Hive is defined by a single state variable NECTAR, the quantity of nectar stored at a given time.

Resource

Resources are stationary entities distributed across the model space, where bees can gather nectar to be stored in the hive. They are defined by a single state variable, QUANTITY, which defines how much nectar can the foragers extract from the resource before complete depletion. Quantity of resource is non-replenishable. An important, although implicit attribute of the resource is its position (distance) with regards to the hive. Resource boundaries are defined by a constant RADIUS, also set by default at a value of 5.

Weather

Weather is an exogenous factor in the model environment that can shut down bees' foraging activity and increase their chance of dying. A simplistic approach is taken to weather modelling, where there are only two states - SUNNY or RAIN. By default, the weather is in SUNNY state. At each step, it has a P_STORM chance to switch to RAIN state for STORM_DURATION steps. Both of these values are model parameters.

Parameter	Default Value	SA Range
General parameters		
FIELD_OF_VIEW	1.0	0.25 - 2
FOOD_CONSUMPTION	0.0001	0.000025 - 0.0002
Movement		
SPEED_IN_HIVE	1.0	0.25 -2
SPEED_FORAGING	5.0	1 - 15
In-hive behaviour		
RESTING_PERIOD	5	1 - 15
P_NECTAR_INSPECTION	0.2	0.05 - 0.4
P_NECTAR_COMMUNICATION	0.3	0.1 - 0.8
Exploration & Recruitment		
P_ABORT	0.025	0.005 - 0.04
P_FOLLOW_WAGGLE_DANCE	0.7	0.3 - 1
EXPLORING_INCENTIVE	50	10 -150
CARRYING_CAPACITY	0.005	0.001 - 0.015
Birth & Death		
P_BIRTH	0.2	0.1 - 0.8
P_DEATH	0.001	0.00025 - 0.002
DEATH_STORM_FACTOR	10	2.5 - 20

Table 2. Parameters governing the behaviour of bee agent by category with their respective default values and value ranges explored through OFAT sensitivity analysis.

Time and space scales

In our model time is discretized, with each agent taking one turn at a single simulation step. Space is a continuous, two-dimensional square grid with side length 300 and fixed boundaries. Implicitly, all agents have a `POSITION` parameter which defines their placement in the grid. Both time and space are unitless and abstract, with no representation in reality. This is because the model focuses on emerging behaviours and their intricacies, rather than a fully realistic representation of a bee colony, for which additional complexity would be required (such as with [21]).

Process overview and scheduling

We use a deterministic scheduler which fixes the order of actions according to the order in which the agents are initialized. Due to implementation decisions, this means that first, the bees in the hive are fed and a new bee agent emerges there stochastically. Then, all the bee agents perform their action based on current activity and the model checks if the foragers reached a resource. Finally, we manage the weather events and gather the relevant data. Algorithm 1 provides the pseudocode for the order of actions within the model. Details of those actions are described in section 3.13

3. Design concepts

3.1. Theoretical and empirical background

3.1.1. Simplifying assumptions

All ABMs simplify the system they study to focus on their core dynamics [8]. The following list contains the key simplifying assumptions and working hypothesis of the model:

1. In-hive activities, such as brood feeding or hive maintenance, are not explicitly modelled, but implicitly captured by the `RESTING` state and passive `NECTAR` depletion in the hive.
2. The reproductive part of colony - queen and drones are captured with passive emergence of new bee agents according to `P_BIRTH`.
3. There is one generalized type of resource, the nectar. Sub-specialization of forager bees to different resources is not treated.
4. Key colony dynamics can be captured with number of bee agents much smaller than realistic number of bees in the colony.
5. `RETURNING` bees perfectly navigate back to the hive.
6. `FOLLOWING` bees perfectly navigate to communicated resource.
7. There are no environmental obstacles in the model space.

3.1.2. Motivation

The main motivation for these modelling decisions was to prevent the overcomplexification of the model, which is also granted given the limited data available on decision making in bees [5]. We decided to focus on key mechanisms validated in previous works [14], such as the division of activities and encoding the location of resource through waggle dance. The aim of this model is to capture key emergent behaviour, not to create a realistic representation of the entire bee colony. In centre of this work are foraging dynamics, which is why the least amount of simplifications were made to this aspect.

Algorithm 1 Determinisic Scheduler

$T \leftarrow$ simulation time steps
$t \leftarrow 0$
while $t < T$ **do**
  Deplete nectar level (feed bees in hive)
  Create new Bee agent according to `P_BIRTH`
  for each bee (in order) **do**
    Perform action based on current activity
    Check for death due to weather, foraging risk, hunger
  end for
  for each resource (in order) **do**
    Distribute nectar to foragers in range
  end for
  Manage storm event (activate/deactivate/maintain)
  Gather related metrics
  $t \leftarrow t + 1$
end while

3.1.3. Empirical data

Our model design was informed by selected studies on Western honey bee foraging and in-hive behaviour and the role that environmental factors play in them [3]. Modelling decisions do fundamentally diverge from existing ABM models for bee colonies (such as in the use of bee states) but further focus and simplify them informed by the literature for our purposes (see section 1.3 for additional details).

3.2. Individual decision-making

Bees are the subjects of decision-making, and change their actions based on a set of predefined rules governing the current activity (state). Figure 1 and Table 1 gives an outline of the state transitions and the overall decision-making process for each state. All states are subject to stochastic effects. The probability of transitioning to a given state or staying in a specific state is determined by agent's environment and predefined stochastic parameters. In the model, this comes down to maintaining sufficient nectar level in the hive. Each bee has an imperfect perception of nectar levels in the hive stock. This perception is updated whenever dormant bee inspect the hive stock levels or obtain information about the hive stock from another dormant bee.

3.2.1. Resting state

Bees residing inside the hive are in the resting state. Resting bees can obtain information about the current hive stock levels in two ways. First, with a fixed probability, the bee can inspect the hive. The resulting perception will depend on true hive stock levels with added uniform error. Second, with a fixed probability, the bee (sender) might communicate its perceived stock level with a nearby bee (receiver). The receiver then obtains the same perception as the sender. Additionally, if there is no rain outside, the resting bee may decide to start exploring based on an exponential distribution with fixed rate and perceived hive stock as the argument. A bee is guaranteed to stay in the resting state for a fixed number of steps after coming back into the hive. In this time it cannot start exploring or be recruited.

3.2.2. Dancing state

The dancing state is a transient state for bees which returned to the hive from a successful foraging trip. It lasts a single simulation step. In that state, a bee performs the waggle dance. Nearby resting bees have a fixed probability to become recruits. After the waggle dance, the bee always starts its resting period.

3.2.3. Exploration state

This state refers to all unrecruited bees looking for resources. Such bees perform a random walk in the space outside the hive with a bias towards resource sites. When explorer finds a resources it switches to carrying state, returns to hive and performs the waggle dance. Otherwise, with a fixed probability, it has a chance to abort the mission and return to hive empty-handed. When the rain occurs, explorer will always choose to abort.

3.2.4. Returning state

Bees coming back empty-handed from a foraging trip are in this state. Returning agents have one task - move to the hive in a straight line. Once they get there, they start resting. Bees transition to the returning state after aborting exploration or recruitment trip.

3.2.5. Following state

The following state represents bees recruited to forage through a waggle dance. Recruits move in the direction of communicated resource in a straight line. Once they reach it, they start carrying the resource back to the hive. Similarly to explorers, recruits have a fixed chance

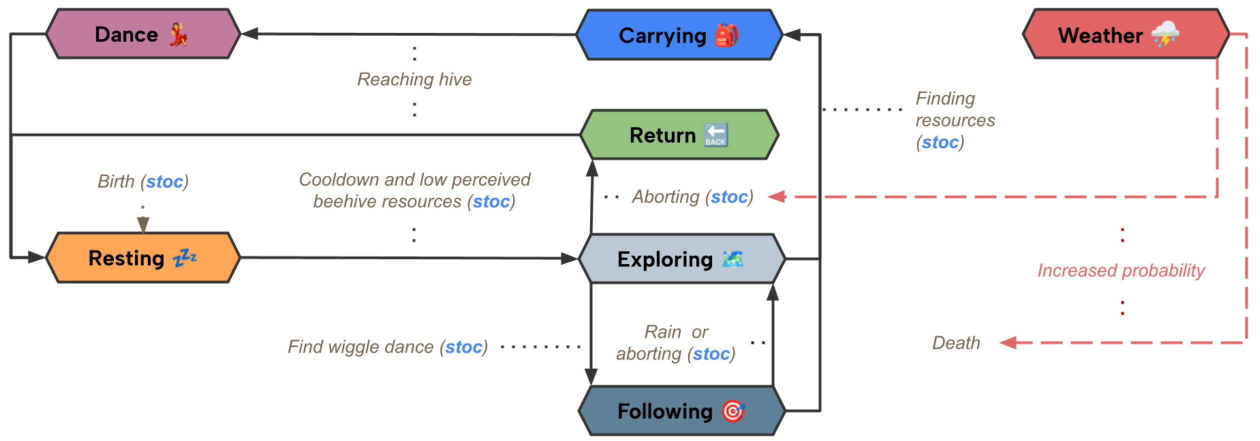

Figure 1. High level diagram overview of bee agent internal states and weather impact in the model (including transition conditions). Internal bee state transitions mediated by stochastic processes emphasized by the *stoc* abbreviation in blue.

to abort the mission and return to hive empty-handed and will always abort when the rain occurs.

3.2.6. Carrying state

This state refers to nectar carrying bees coming from a successful foraging trip. Carriers move back to the hive in a straight line. Once they reach the hive, they deposit their foraged nectar and perform the waggle dance.

3.2.7. Death

Both dormant and forager bees have a probabilistic chance to die and be removed from the simulation. Bees inside the hive can die from hunger based on a scaled exponential PDF as a function of hive nectar stock. Bees outside the hive have a fixed probability to die at each step due to natural risks. This probability is much higher during the raining period.

3.3. Learning

Dormant bees can share their individual perception (see section 3.4) about the hive stock, with other nearby dormant bees. This information spread mechanism allows for collective learning about the

Algorithm 2 Resource scent sensing

POS ← new position of interest
$\epsilon \leftarrow 10^{-24}$
ATTRACTION ← 0
for each resource R (globally) **do**
  $q_{res} \leftarrow$ R.QUANTITY
  $d_{res} \leftarrow$ euclidean distance of R to POS
  ATTRACTION ← ATTRACTION + $\frac{q_{res}}{d_{res}^2+\epsilon}$
end for
return ATTRACTION

Algorithm 3 Metropolis walk of forager bees exploring

CURR_POS ← Bee agent's position
CURR_ATTRACTION ← algorithm 2 using CURR_POS
NEXT_POS ← random point on a circle around CURR_POS with radius equal to SPEED_FORAGING
NEXT_ATTRACTION ← algorithm 2 using NEXT_POS
R ← $\frac{\text{NEXT\_ATTRACTION}}{\text{SCALE\_BIAS}\cdot\text{CURR\_ATTRACTION}}$
$u \leftarrow$ draw from $U(0,1)$
if NEXT_ATTRACTION > CURR_ATTRACTION **or** u < R **then return** NEXT_POS
else return CURR_POS
end if

hive stock levels. The colony is able to capture the overall trend of changes, without perfect information about the actual quantity of nectar in stock (see fig. 2).

3.4. Individual sensing

Dormant (resting) bees can directly inspect the hive to learn about hive stock levels. During the inspection, a random uniform bias is added to hive's NECTAR value, which yield the perceived stock levels of a single agent. Additionally, bees are able to perceive all agents within their field of vision. They can observe the waggle dance of bees and communicate the stock perception (section 3.3) in their field of vision. The sensing and encoding of the waggle dance location is assumed to be noiseless. Bee agents also have a global information about the weather and will cease foraging activity during the rain. Finally, bees can globally sense the scent of resources and will be more likely to move in their direction.

3.5. Individual prediction and interaction

Agents do not make predictions and assess their behaviour based on the current information. Form of interaction depends on the current activity of the bee agent (section 3.6).

3.6. Collectives

Bees form into collectives based on their current activity. Depending on the collective they belong to, agents can engage in different individual interactions. These collectives are a result of preimposed modelling decisions.

3.7. Heterogeneity

No specific parameter heterogeneity between bee agents is considered in this work. The heterogeneity arises in agents' decision making according to the current activity as described in section 3.2 as well as due to heterogeneity of PERCEIVED_NECTAR variable.

3.8. Stochasticity

A number of processes were assumed to be random to reflect the stochasticity in the natural behaviour of individuals. The following processes in the model are stochastic by design:

1. Inspection of hive stock levels occurs with fixed P_NECTAR_INSPECTION chance
2. Communication of perceived stock levels occurs with fixed P_NECTAR_INSPECTION chance
3. Transition from RESTING to EXPLORING occurs based on exponential PDF, taking the perceived stock levels as argument
4. Aborting the foraging trip during SUNNY weather occurs with fixed P_ABORT chance

5. Resting bees will follow the waggle dance with fixed `P_FOLLOW_WAGGLE_DANCE` chance
6. New bee agents emerge with fixed `P_BIRTH` chance
7. Foragers die with fixed `P_DEATH` chance (multiplied by `DEATH_STORM_FACTOR` during rain)

Observation

At each time step key metrics of the model are collected for testing, understanding and analysis, including the distribution of bee activities in the colony, total number of bees and hive nectar stock (see Section 4 for more details). Hive survival emerges as a property of the aggregated behavior of bees interacting with their environment, specially through focused foraging mediated via wiggle dance bee communication.

3.9. Implementation details

We implemented the model defined in Section 2 using Mesa, a widespread open-source Python package for ABM modelling and experimentation [15]. A custom conda environment was created to work with the different packages involved in the project. The most essential package versions used are listed in the following box. The project can be conveniently set up using conda by following the setup instructions on the accompanying GitHub code repository. The implemented model as well as experimental runs and analysis can be found in this repository.

Key environment package versions

python 3.12.4, mesa 2.3.0, numpy 1.26.4, scipy 1.13.1, salib 1.4.7

3.10. Validation

Several validations were first performed before the main experiments to ensure a correct implementation of the model, such as inspecting the model dynamics and creating assert-based tests to ensure appropriate behavior within logical boundaries. Additionally, we made use of the interactive visualization functionality of Mesa, which uses the Solara framework and runs on a browser window [4], which is specially useful for debugging and initial testing[5]. Altogether, these tools helped us iterate the model implementation and debug the code faster. Figure 2 shows an example of one of such validations. For more details on how to reproduce these simulations, see the *README* file of the repository.

3.11. Initialization

As given in table 3, in the default setting hive is initialized with 5.0 nectar in stock and 200 bee agents in the resting state located at the center. Unless otherwise specified, 2 resources are randomly initialized 50.0 distance units away from the hive with `QUANTITY` set to 10. This setting is used for sensitivity analysis and weather effects experiment. Effect of varied number of resources, their spatial distribution and distance to the hive is treated in a separate experimental setup.

3.12. Input data

No input data is required to run the model.

3.13. Submodels

The following section describes the details of actions listed in the section 3.13, in the order of execution given in algorithm 1.

3.13.1. Emergence of new bees (birth)

The birth of new bees occurs as Bernoulli trial. With probability `P_BIRTH` a single new agent will emerge with its `POSITION` variable set to that of the hive.

[4]See https://mesa.readthedocs.io/en/latest/tutorials/visualization_tutorial.html
[5]However, it was unfortunately deprecated on subsequent Mesa versions.

3.13.2. Feeding the bees

First, we check how many bee agents are inside the hive based on their `POSITION` and hive `RADIUS`. Let n define the number of bees inside the hive. The quantity `FOOD_CONSUMPTION` $\cdot n$ is then subtracted from hive's `NECTAR` variable.

3.13.3. Resting bees (`RESTING` state)

First, the bee moves randomly covering `SPEED_IN_HIVE` distance, ensuring it stays within hive bounds. Then, it performs a Bernoulli trial with probability `P_NECTAR_INSPECTION` to determine whether it will inspect the hive. Hive inspection updates its `PERCEIVED_NECTAR` variable with the new value given by:

$$x' = \max\left(0, n + U(-1, 1)\right)$$

where n is the current `NECTAR` value in the hive.

If the bee has not inspected the hive, it performs another Bernoulli trial instead with probability `P_NECTAR_COMMUNICATION` to communicate the information with all nearby bees within its field of vision.

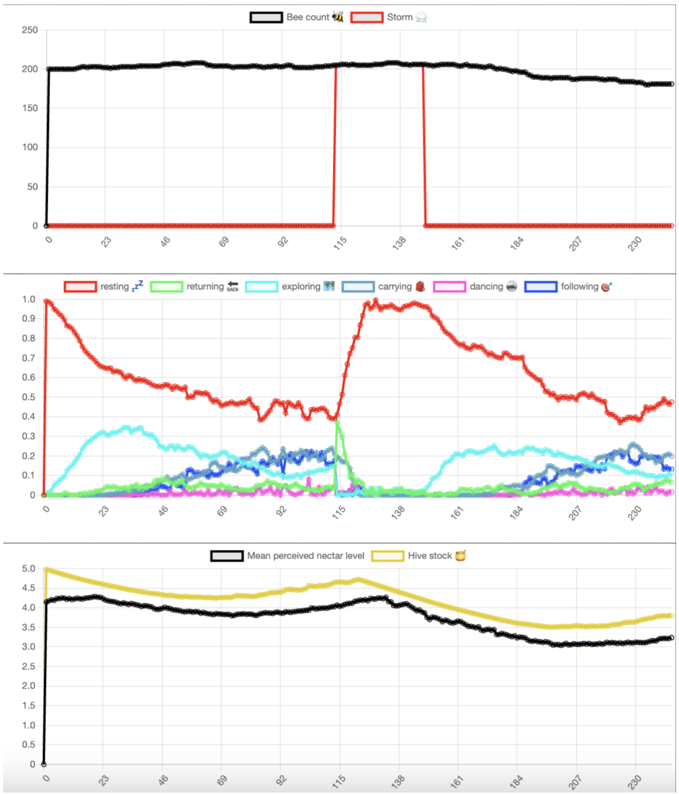

Figure 2. Model validation run of 250 time steps using the Mesa server functionality, including: (first row) bee count (black) and indication of storm event (red), (second row) proportion of forager bees in different states and (bottom row) hive stock and mean perceived nectar level in colony, for 5 flower patches initialized at a distance of 50 units ($P\_STORM = 0.0025$, $STORM\_DURATION = 35$)

Initial condition	Default value	SA Range
Hive		
Bee agents	200	$50 - 400$
Nectar in stock	5.0	$1 - 8$
Resource		
Quantity	10	
Number of resource sites	2	
Resource distance	50	

Table 3. Default initial conditions and local sensitivity analysis value ranges of the model

This results in updating all of the receivers' `PERCEIVED_NECTAR` value to that of the sender.

Independently of whether the bee inspected, communicated or did none of these two actions, it then determines whether it should start exploring based on a scaled exponential PDF and its `RESTING_TIME`. If `RESTING_TIME` = 0 then it switches to `EXPLORING` state with probability

$$p(x) = \lambda \cdot \exp(-\lambda x)$$

with x being agent's `PERCEIVED_NECTAR` value and λ being the `EXPLORING_INCENTIVE` parameter. Otherwise, the `RESTING_TIME` is decremented by 1.

3.13.4. Waggle dancers (DANCING state)

A waggle dancer first gathers all the `RESTING` bees within its `FIELD_OF_VISION`. Then, for each of these bees that have a `RESTING_TIME` = 0 it performs a Bernoulli trial with probability `P_FOLLOW_WAGGLE_DANCE` to determine if the other bee will follow them. On a successful trial, the other bee will change its `RESOURCE_DESTINATION` to the one of the waggle dancer and change its state to `FOLLOWING`. After this process if performed, the waggle dancer switches state to `RESTING`, sets its `RESTING_TIME` variable equivalent to the `RESTING_PERIOD` constant parameter and clears its `RESOURCE_DESTINATION` parameter.

3.13.5. Empty return (RETURNING state)

First, the agent determines whether it has reached the hive based on the hive `RADIUS`. If so, it changes its state to `RESTING` and sets its waiting period to the `RESTING_PERIOD` constant. In all other cases, the bee moves deterministically in an straight line towards its hive.

3.13.6. Exploring foragers (EXPLORING state)

If the model weather is set to `RAIN` it changes its state to `RETURNING`. Otherwise, it performs a Bernoulli trial with probability `P_ABORT` to switch state to `RETURNING`. If it is not raining and the trial was unsuccessful, then the bee will perform a biased random walk according to Metropolis algorithm given in Algorithm 3.

3.13.7. Nectar carrying (CARRYING state)

First, the agent determines whether it has reached the hive based on the hive `RADIUS` and its current position. If the bee has not reached the hive, it will move deterministically in an straight line towards it. If the bee has reached the hive, then the hive's `NECTAR` variable is incremented by the value of `CARRYING_CAPACITY` parameter and the bee switches its state to `DANCING`.

3.13.8. Foraging recruits (FOLLOWING state)

If its raining the agent switches its state to `RETURNING`. Alternatively, it performs a Bernoulli trial with probability `P_ABORT` to switch its state to `RETURNING`. If it was not raining and the trial was unsuccessful, then the bee will move deterministically towards its `RESOURCE_DESTINATION` that was transmitted through the waggle dance.

3.13.9. Agent's death

The death process is performed at each time for each bee in the model. This happens stochastically and depends on agents location. Inside the hive, bees can die of hunger with the probability given by Equation 1, where x is hive's `NECTAR` value:

$$p(x) = 0.1 \cdot \exp(-x) \tag{1}$$

Foragers outside the hive perform a Bernoulli trail to check if they died at each step. This probability is given by `P_DEATH` during `SUNNY` weather and `P_DEATH` · `STORM_DEATH_FACTOR` if the weather is set to `RAIN`. In all cases, whenever a bee agent dies, it is removed from the simulation. Algorithm 4 describes the algorithm for this process.

Algorithm 4 Bee death

```
X ← current level of NECTAR in hive
λ ← EXPLORING_INCENTIVE parameter
BEE ← bee agent of interest
u1, u2 ← random draws from U(0,1)
if BEE not in hive and u1 < P_DEATH then Kill the BEE agent
else
    if in hive and u2 < 0.1 · λ exp(−λX) then Kill the BEE agent
    end if
end if
```

3.13.10. Resource extraction

Resource extraction is computed from the Resource agent's perspective by obtaining the forager bees within its `RADIUS`. This process, detailed in Algorithm 5, is equivalent computationally as doing it from the bee agent perspective but is more optimal computationally, given relatively smaller number of Resource agents. When there is no resource left to take, the bee returns to the hive with empty hands (switches to `RETURNING` state). Otherwise `CARRYING_CAPACITY` amount is subtracted from Resource's `QUANTITY` variable, the bee sets its `RESOURCE_DESTINATION` variable equal to the Resource agent and goes back to the hive.

4. Experimental design

4.1. Baseline colony dynamics

The objective of this experiment was to investigate the role of model stochasticity in survival outcomes given its baseline parameters (table 2, table 3, table 4), which will help uncover basic dynamics in the model and frame interpretation in subsequent experiments. Specifically, it will aim to identify key system trajectory patterns that can distinguish or characterize survival outcomes at the hive-level. 256 simulations of 1000 time-steps were performed. A critical threshold for survival was defined at 100 bees, which was used to cluster the runs into survival and non-survival clusters. All runs were performed with the default parameters, including a single hive with 200 bees and 5 units of nectar. Resources had 10 units of nectar each. The percentage of surviving runs was recorded, as well as the time evolution of key hive-level metrics of colony size, hive nectar level and ratio of forager bees in the population.

Algorithm 5 Resource extraction (r)

```
R := Resource agent
Get nearby foragers within r's RADIUS
for each nearby forager F do
    if R.QUANTITY = 0 then
        F.STATE ← RETURNING
    else
        R.QUANTITY ← max(0, R.QUANTITY - CARRY_CAPACITY)
        F.RESOURCE_DESTINATION ← R.POSITION
        F.STATE ← CARRYING
    end if
end for
```

Parameter	Value
P_STORM	0.005
STORM_DURATION	20
N_RESOURCES_DEFAULT	2
RESOURCE_DISTANCE_DEFAULT	50

Table 4. Default global model parameters used in the experiments

4.2. Weather resiliency

The objective of this experiment was to investigate the role storm probability and storm duration have on key hive-level metrics, thus quantifying hive resiliency to adverse weather conditions. 32 simulations of 1000 time-steps were performed for each input parameter combination. Values of P_STORMS and STORM_DURATIONS used are shown in Table 5. All other parameters were kept at their default values (table 2, table 3, table 4). Final colony size and mean beehive population forager ratio thought the runs, including their standard deviation for each of the 32 simulations of each parameter combination.

4.3. Resource scarcity

The objective of this experiment was to investigate the role that resource number and distance to the hive have on key hive-level metrics, in order to better understand hive resiliency to challenging environments. 32 simulations of 1000 time-steps were performed for each input parameter combination. We kept all model parameters at their default values while changing the number of available resources and their distance to the hive during initialization. All resources were then initialized randomly at a fixed distance. We made the DIST_RESOURCES parameter take values of 30, 40, 50, 60, 70 and 80, while the N_RESOURCES parameter took values of 1, 2, 3, 4, 5 and 6. The Cartesian product of this sets formed the final simulation space for the experiment. Final colony size and mean beehive population forager ratio throughout the runs was recorded, including their standard deviation for each of the 32 simulations of each parameter combination.

4.4. Resource clustering

After studying baseline dynamics, weather resiliency and the impact of resource scarcity, we studied the role of resource distribution. The objective of this experiment was to investigate the role that resource distance together with resource clustering had on key hive-level metrics, in order to better understand its relationship with foraging behavior. 32 simulations of 1000 time-steps were performed for each input parameter combination. We kept all model parameters at their default values while fixing a number of 6 available resources. Their distance and angle spread was then changed during initialization. Figure 3 showcases representative snapshots of this experimental setting with different angle resource separation, which are hypothesized to play a role in the resulting hive-level bee foraging dynamics towards them based on their scent. The model parameter DIST_RESOURCES was varied between 30, 40, 50, 60, 70 and 80 and the parameter MAX_ANGLES took values of $\frac{\pi}{3}, \frac{2\pi}{3}, \pi, \frac{4\pi}{3}, \frac{5\pi}{3}$ and 2π radians. Final colony size and mean beehive population forager ratio thought the runs, including their standard deviation for each of the 32 simulations of each parameter combination.

4.5. Sensitivity Analysis

Finally, we studied how the distribution of output uncertainty could be attributed to the different model parameters. To this aim, we performed local sensitivity analysis (OFAT) with respect to all model parameters defined in table 2 and selected initial conditions in table 3. The parameters space for weather and resource related parameters was treated as separate experiments described in previous sections. Final colony size, hive nectar level and mean beehive population forager ratio thought the runs was recorded including their standard deviation for each of the simulations of each sub-setting were considered. For each parameter we explored 8 equally-spaced samples with 32 iterations of 1000 simulation steps each.

Parameter	Values
P_STORM	[0.0, 0.0025, 0.005, 0.0075, 0.01]
STORM_DURATION	[5, 10, 15, 20, 25, 30, 35]

Table 5. Experiment 2 parameters

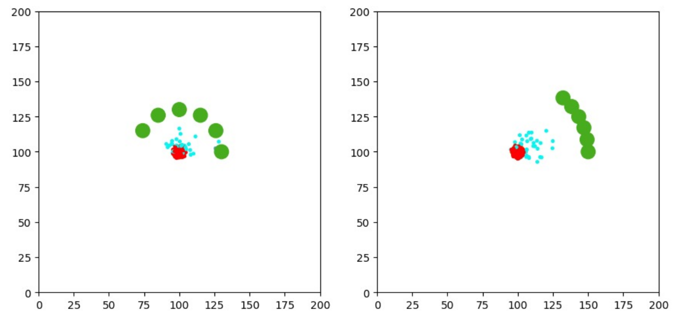

Figure 3. Representative snapshots of the model space showcasing two simulation runs with 6 resources after 10 time-steps with $\pi/2$ and $\pi/6$ angle separation spreads (left and right plots respectively). Red dots are bees clustered within the hive bounds. Light blue dots are foragers outside the hive. Green circles represent the resources.

5. Results

5.1. Experiments

5.1.1. Baseline colony dynamics

Figure 4 showcases the results of our investigation of colony-level dynamics under two qualitatively different scenarios arising out of the baseline conditions: a higher survival regime and a hive extinction regime, defined as a final bee count under 150 bees. In the first case (top row), the bee colony tends to grow in size as it successfully accumulates nectar in the hive. In the second scenario (bottom row), we observe a steady decline of the colony size in almost all runs as time progresses. In a few runs, the colony is able to slightly grow temporarily but without any lasting colony growth. In summary, from the 256 simulated colonies, 69.53% survived in the baseline conditions and 30.47% were considered "deceased" based on their final bee count falling below 150.

5.1.2. Weather resiliency

Figure 5 showcases the main results of the weather resiliency experiment. We observe a clear negative relationship between mean colony size and storm probability and storm duration due to the negative slope of the plane. With storm probability and storm duration at low values, mean colony size is high indicating a survival regime. As storm probability and storm duration increase, the system converges to a regime of low survival for the colony. We observe low variance in our simulations for both high and low mean colony size, indicating

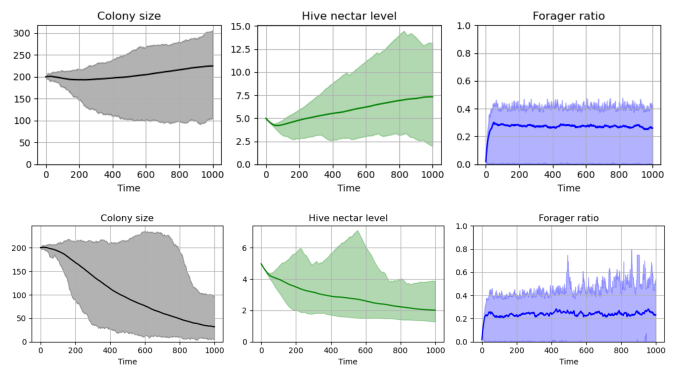

Figure 4. Temporal investigation of colony-level metrics, colony size, hive nectar level and forager ratio showing two different regimes: survival regime (first row) and hive death regime (bottom row). Thicker line for mean value, shaded areas spanning the whole range of values observed (minimum and maximum among all runs). Simulated 256 times for 1000 time steps. Full setting described in section 4.1.

that these regimes are more robust to stochastic effects. Investigating mean forager ratio, we observe negative correlation of the forager ratio with both storm parameters. With increasing storm duration and likelihood, overall storming time increases, inhibiting foraging opportunities as bees shelter for prolonged time in the hive.

5.1.3. Resource scarcity

In Figure 6, we visualize the result of varying selected model parameters after a fixed time of 1000 steps. We can see that resource distance and number play an important role in mean colony size. Distance is especially critical. We observe a high survival & growth regime for scenarios with many resources at low distance to the hive and a low survival regime with low resource availability and increasing distance from the hive. This clearly showcases the vulnerability of the colony to low-resource environments and the importance of hive placement relative to resources. The biggest standard deviation in the colony size output is achieved twofold along both a specific resource distance and resource number. The extinction regime of the colony correlates with low nectar scenarios here, clearly visible in the mean nectar level after the time interval. Interestingly, the standard deviation in this quantity does not correspond perfectly with the uncertainty in hive size and seems to be proportional to the number of resources as well as decreasing from a peak at around a resource distance of 50.

5.1.4. Resource clustering

In figure 7, we inspect the effect of clustering resources at an angle range from the hive, where higher clustering is present for lower angle distribution. We find that angle distribution has little effect on survival outcomes of the colony. We observe a slight increase in variance when increasing angle distribution. We also find a clear positive correlation with resource distance and the ratio of bees foraging, which indicates that our encoded bee behavior enables some adaptation towards colony survival in result to scarce resource environments.

5.2. Sensitivity analysis

In these results, we analyse sensitivity analysis of the model parameters. We commence by interpreting the results in figure 8 where we observe a tipping point influence of the initial hive stock for foraging and colony survival outcomes. We notice a phase transition from low to high survival and growth regimes for initial stock values $\in [2, 5]$.

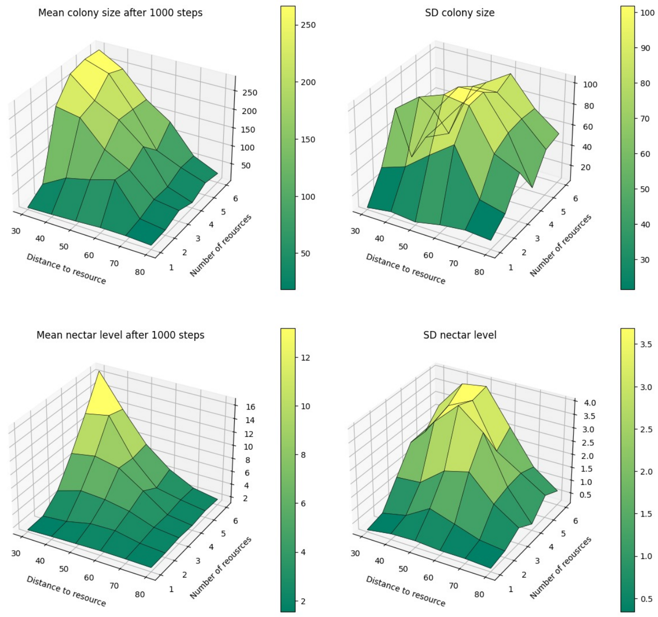

Figure 6. Mean (left) and standard deviation (right) of mean colony size (first row) and mean nectar level (second row) as a function of distance and number of resources during initialization. Simulated 32 times for each parameter pair for 1000 time steps. Full setting described in section 4.3.

We also find that lower initial hive stock increases variance in forager ratios. Another interesting tipping point can be observed in the model response to increasing initial colony size. As the colony size exceeds 200, the available resources are insufficient and we witness a process of decaying nectar, eventually leading to starvation and corresponding reduction in final colony size. Forager ratio increases with colony size at the upper end, likely the result of the low hive stock increasing transitions to foraging.
From our results in figure 9, we notice that the final colony size increases with increasing birth rate up to a threshold value of around 0.5. Further increase results in a rapid drop of final colony size. This

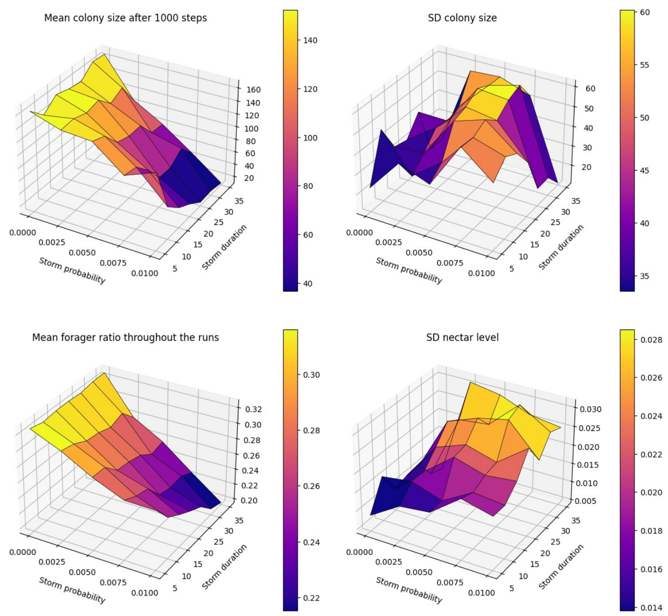

Figure 5. Mean (left column) and standard deviation (right column) of final colony size (first row) and mean forager ratio throughout all steps (second row) as a function of storm probability and duration. Simulated 32 times for each parameter pair for 1000 time steps. Full setting described in section 4.2.

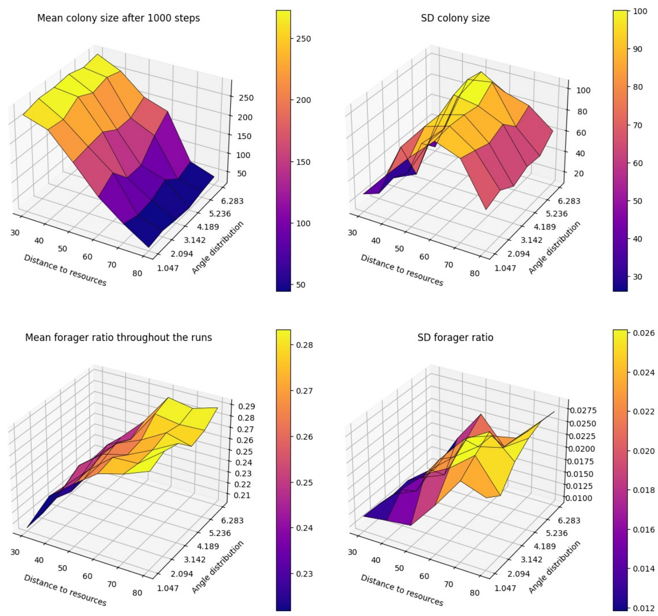

Figure 7. Mean (left) and standard deviation (right) of mean colony size throughout all steps (first row) and mean forager ratio throughout all steps (second row) as a function of distance to resources and their angle distribution during initialization. Simulated 32 times for each parameter pair for 1000 time steps. Full setting described in section 4.4.

can be explained by the increased consumption of nectar with increasing number of honeybees as visible in the figure. The initialized space does not provide sufficient resources to maintain a much larger colony, therefore the colony run out of resources to gather and starves. Inspecting storm death factor, we observe little variation in our model output. We assume this to be the case as storms may not have occurred sufficiently in the simulation to substantially impact the colony.
Inspecting figure 10, we observe a strong emergent phenomenon of the model: collaborative foraging. Increasing the probability to follow the waggle dance quickly optimizes the bee colony's ability to fill up the hive stock and maximises its survival and growth, highlighting the importance of this communication tool. The forager ratio is largely invariant to these changes. We also notice a negative correlation of colony size and hive stock with increasing exploring incentive. This is the result of the parameter modifying the exponential function managing transition from rest to exploration. At low parameter values, honey bees have a higher chance to explore, therefore increasing the probability to find resources.
Inspecting field of view and consumption of the bee swarm agents in figure 11, we discover that the field of view is one of the most essential parameters for colony survival. A tipping point-like behavior as field of view increases from 0.5 to 1.0 can be observed. Below a value of 0.5, the colony is in a clear and robust death regime but rapidly transitions into a survival and growth regime for higher parameter values.
This is likely due to the fact that a low level of perception does not enable effective collaborative as bee swarms will struggle to perceive waggle dances. We also appear to witness super-linear decay of final colony size in response to food consumption, evident from the steady decay from survival to death regime with increasing consumption parameterization.
In figure 12 we note that the resting period has surprisingly little impact on the foraging ratio. Presumably, the increase in resting time is compensated by the decrease in resources which again increases the probability for rest to exploration transitions. We also find that the model is surprisingly invariant to nectar inspection and communication parameter changes. We suspect this to either be a scale issue or the modelled effect is negligible on the colony level.
In our last sensitivity analysis in figure 13, we find rather unsurprisingly, that generally an increase in speed enables more rapid foraging, thus colony survival and growth. We also notice a notable outlier, a very confident death regime for the specific speed value of 13. This is assumed to be an artifact of our initial space and resource configuration where this step size may be causing bees to skip past the resources placed in space, not getting in range to forage them. This repeated movement past resources would then be responsible for their inability to forage nectar.

6. Discussion

6.1. Model dynamics

The model proposed in this work displays many desired properties, such as sensitivity to stochastic events. This was exemplified in our first experiment (Section 5.1.1), in which the same baseline parameters could still give rise to beehive extinction dynamics based on the bees not finding resources in time or a higher frequency of storms happening in some of the runs. Another desired property showcased was a de-facto limited range at which bees are able to forage sufficiently effective to ensure survival (see Section 5.1.2 and Section 5.1.3, we). This biologically established fact has also been empirically validated in a number of works [3], [6] and provides further validity to the model envisioned.
In response to storm events, we also observed how honey bees indeed returned to the hive as storms begin, motivating an increase in unproductive resting activity (as they wait for it to pass). This somewhat trivial result, evident from our validation run in Figures 2 and 5, is also backed by empirical observation of honeybee colonies [4]. Importantly, it exemplifies the desired balance in ABMs between simple rules (aborting foraging during adverse weather conditions) and high-level behavior (colony population staying protected inside the hive, indirectly affording long-term survival). As shown in Figure 6, a clear positive relationship of general resource abundance and its closeness to the hive with colony survival was found. In particular, as resources became scarce, we observed how the survival rate dropped. This is attributed to resource scarcity depleting hive nectar stores and subsequent starvation and lack of growth of the colony, a pattern already studied and verified in real honeybee colonies [19].
Critically, the increase in unproductive resting state was found to not only arise out of external weather and resource conditions but also out of collaborative foraging due to the local communication through the waggle dance. Interestingly, during stable resource retrieval, a baseline of around 40% of exploring population was found, which is also consistent with the literature consulted [2]. This is specially significant given that this model required less parameters than those considered in Section 1.3, which further suggests that this model can provide a good balance between clarity and capabilities

6.2. Conclusions and future work

Bee hive dynamics can be studied with ABMs. The model hereby presented illustrated this previously established fact and suggested that comparable system dynamics with previous models can be achieved using a smaller number of parameters (such as [13], which had more than 60 parameters), including phase transitions and tipping points. Additionally, our local sensitivity analysis suggests that the nectar inspection and communication parameters of our model, together with the resting period could further be discarded, as their impact in output variance is small. Still, global analysis should first be performed beforehand to ensure this.
Despite these promising directions, this model currently has important shortcomings. First, global sensitivity analysis has not been yet performed, which could in turn uncover additional trends towards its interpretation. From a methodological perspective, the lack of age factor in the model is the main drawback towards its validity, given its importance [21]. Similarly, dynamics inside the hive were also ignored, specially regarding bee birth dynamics. Also, the simplification of the weather model, which does not display seasonal effects, further hinders its validity and potential for long-term simulations.

Future work

The identified key role bee communication played deserves further study, as our results suggest that timely communication can have a disproportionate impact on collective beehive survival (such as in the form of threshold phenomena). The same could be said about the field of vision parameter. To sum up, our work suggests the following lines of further research:

1. Perform global sensitivity analysis and large scale simulations, to further test the statistical validity of the experimental results
2. Further research the role of bee communication through waggle dance and field of vision, which could be achieved through bee heterogeneity
3. Implement dynamic resource generation and varying resource types to improve the realism of the model
4. Instantiate the model with multiple hives, to study competing dynamics among them
5. Further calibrate the model parameters, to tailor it for specific ecosystems
6. Migrate the model, to study bee farm dynamics

References

[1] K. von Frisch, *The Dancing Bees: Karl von Frisch and the Discovery of the Honeybee Language*, en. Chicago, IL: University of Chicago Press, Oct. 1927, ISBN: 978-0-226-52650-8. [Online]. Available: https://press.uchicago.edu/ucp/books/book/chicago/D/bo15220404.html.

[2] T. D. Seeley, "Adaptive significance of the age polyethism schedule in honeybee colonies," *Behavioral Ecology and Sociobiology*, vol. 11, no. 4, pp. 287–293, 1982, ISSN: 1432-0762. DOI: 10.1007/BF00299306. [Online]. Available: https://doi.org/10.1007/BF00299306.

[3] T. D. SEELEY, *The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies*. Harvard University Press, 1995, ISBN: 9780674953765. [Online]. Available: http://www.jstor.org/stable/j.ctv1kz4h15 (visited on 07/03/2024).

[4] U. Riessberger and K. Crailsheim, "Short-term effect of different weather conditions upon the behaviour of forager and nurse honey bees (apis mellifera carnica pollmann)," *Apidologie*, vol. 28, no. 6, pp. 411–426, 1997.

[5] Calderone, Nicholas W., "Proximate mechanisms of age polyethism in the honey bee, apis mellifera l.," *Apidologie*, vol. 29, no. 1, pp. 127–158, 1998. DOI: 10.1051/apido:19980108. [Online]. Available: https://doi.org/10.1051/apido:19980108.

[6] M. Beekman and F. Ratnieks, "Long-range foraging by the honey-bee, apis mellifera l.," *Functional Ecology*, vol. 14, no. 4, pp. 490–496, 2000.

[7] S. C. Pratt, D. J. T. Sumpter, E. B. Mallon, and N. R. Franks, "An agent-based model of collective nest choice by the ant *Temnothorax albipennis*," *Animal Behaviour*, vol. 70, no. 5, pp. 1023–1036, Nov. 2005, ISSN: 0003-3472. DOI: 10.1016/j.anbehav.2005.01.022. [Online]. Available: https://www.sciencedirect.com/science/article/pii/S0003347205002332.

[8] I. Politopoulos, "Review and analysis of agent-based models in biology," *University of Liverpool*, 2007.

[9] T. Schmickl and K. Crailsheim, "Hopomo: A model of honeybee intracolonial population dynamics and resource management," *Ecological Modelling*, vol. 204, no. 1, pp. 219–245, 2007, ISSN: 0304-3800. DOI: https://doi.org/10.1016/j.ecolmodel.2007.01.001. [Online]. Available: https://www.sciencedirect.com/science/article/pii/S0304380007000075.

[10] Brodschneider, Robert and Crailsheim, Karl, "Nutrition and health in honey bees*," *Apidologie*, vol. 41, no. 3, pp. 278–294, 2010. DOI: 10.1051/apido/2010012. [Online]. Available: https://doi.org/10.1051/apido/2010012.

[11] B. R. Johnson, "Division of labor in honeybees: Form, function, and proximate mechanisms," *Behavioral Ecology and Sociobiology*, vol. 64, no. 3, pp. 305–316, 2010, ISSN: 1432-0762. DOI: 10.1007/s00265-009-0874-7. [Online]. Available: https://doi.org/10.1007/s00265-009-0874-7.

[12] B. Müller, F. Bohn, G. Dreßler, *et al.*, "Describing human decisions in agent-based models – odd+d, an extension of the odd protocol," *Environmental Modelling & Software*, vol. 48, pp. 37–48, 2013, ISSN: 1364-8152. DOI: https://doi.org/10.1016/j.envsoft.2013.06.003. [Online]. Available: https://www.sciencedirect.com/science/article/pii/S1364815213001394.

[13] M. A. Becher, V. Grimm, P. Thorbek, J. Horn, P. J. Kennedy, and J. L. Osborne, "Beehave: A systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure," *Journal of Applied Ecology*, vol. 51, no. 2, pp. 470–482, 2014. DOI: https://doi.org/10.1111/1365-2664.12222. eprint: https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2664.12222. [Online]. Available: https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12222.

[14] J. Devillers, *In silico bees*. Taylor & Francis, 2014.

[15] D. Masad, J. L. Kazil, *et al.*, "Mesa: An agent-based modeling framework.," in *SciPy*, Citeseer, 2015, pp. 51–58.

[16] N. F. Azmilumur, M. N. Sobri, and W. A. F. W. Othman, "Meerkat foraging behaviour modelling," in *2017 7th IEEE International Conference on Control System, Computing and Engineering (ICCSCE)*, Nov. 2017, pp. 230–235. DOI: 10.1109/ICCSCE.2017.8284410. [Online]. Available: https://ieeexplore.ieee.org/abstract/document/8284410?casa_token=Hax3IXqOSVkAAAAA:FZTAgGlEU_bczlYYgEeogxDY-sdsLd4ybfn4FbGz1dqiAos-f0P6PNnoRJW77H7qQH5jzzph.

[17] M. Betti, J. LeClair, L. M. Wahl, and M. Zamir, "Bee++: An object-oriented, agent-based simulator for honey bee colonies," *Insects*, vol. 8, no. 1, 2017, ISSN: 2075-4450. DOI: 10.3390/insects8010031. [Online]. Available: https://www.mdpi.com/2075-4450/8/1/31.

[18] G. Gall, "Group Coordination and Decision-Making during Foraging in Meerkats (Suricata suricatta)," eng, Publication Title: Gall, Gabriella. Group Coordination and Decision-Making during Foraging in Meerkats (Suricata suricatta). 2017, University of Zurich, Faculty of Science., Dissertation, University of Zurich, Jun. 2017. DOI: 10.5167/uzh-138436. [Online]. Available: https://www.zora.uzh.ch/id/eprint/138436/.

[19] F. Requier, J.-F. Odoux, M. Henry, and V. Bretagnolle, "The carry-over effects of pollen shortage decrease the survival of honeybee colonies in farmlands," *Journal of applied ecology*, vol. 54, no. 4, pp. 1161–1170, 2017.

[20] A. L. Cronin, "An agent-based model of nest-site selection in a mass-recruiting ant," *Journal of Theoretical Biology*, vol. 455, pp. 54–63, Oct. 2018, ISSN: 0022-5193. DOI: 10.1016/j.jtbi.2018.07.004. [Online]. Available: https://www.sciencedirect.com/science/article/pii/S0022519318303175.

[21] J. Rivière, C. Alaux, Y. Le Conte, *et al.*, "Toward a complete agent-based model of a honeybee colony," in *Highlights of Practical Applications of Agents, Multi-Agent Systems, and Complexity: The PAAMS Collection*, J. Bajo, J. M. Corchado, E. M. Navarro Martínez, *et al.*, Eds., Cham: Springer International Publishing, 2018, pp. 493–505, ISBN: 978-3-319-94779-2.

[22] T. Alves, "Visualisation et interactions avec une colonie d'abeilles virtuelle : Simulation, complexité et pédagogie," 2021BRES0101, Ph.D. dissertation, 2021. [Online]. Available: http://www.theses.fr/2021BRES0101/document.

[23] E. Beck, T. Wenseleers, and R. C. Oliveira, "The effect of forager loss on honeybee workers temporal polyethism and social network structure," *Apidologie*, vol. 54, no. 5, p. 51, 2023, ISSN: 1297-9678. DOI: 10.1007/s13592-023-01030-y. [Online]. Available: https://doi.org/10.1007/s13592-023-01030-y.

A. Sensitivity Analysis

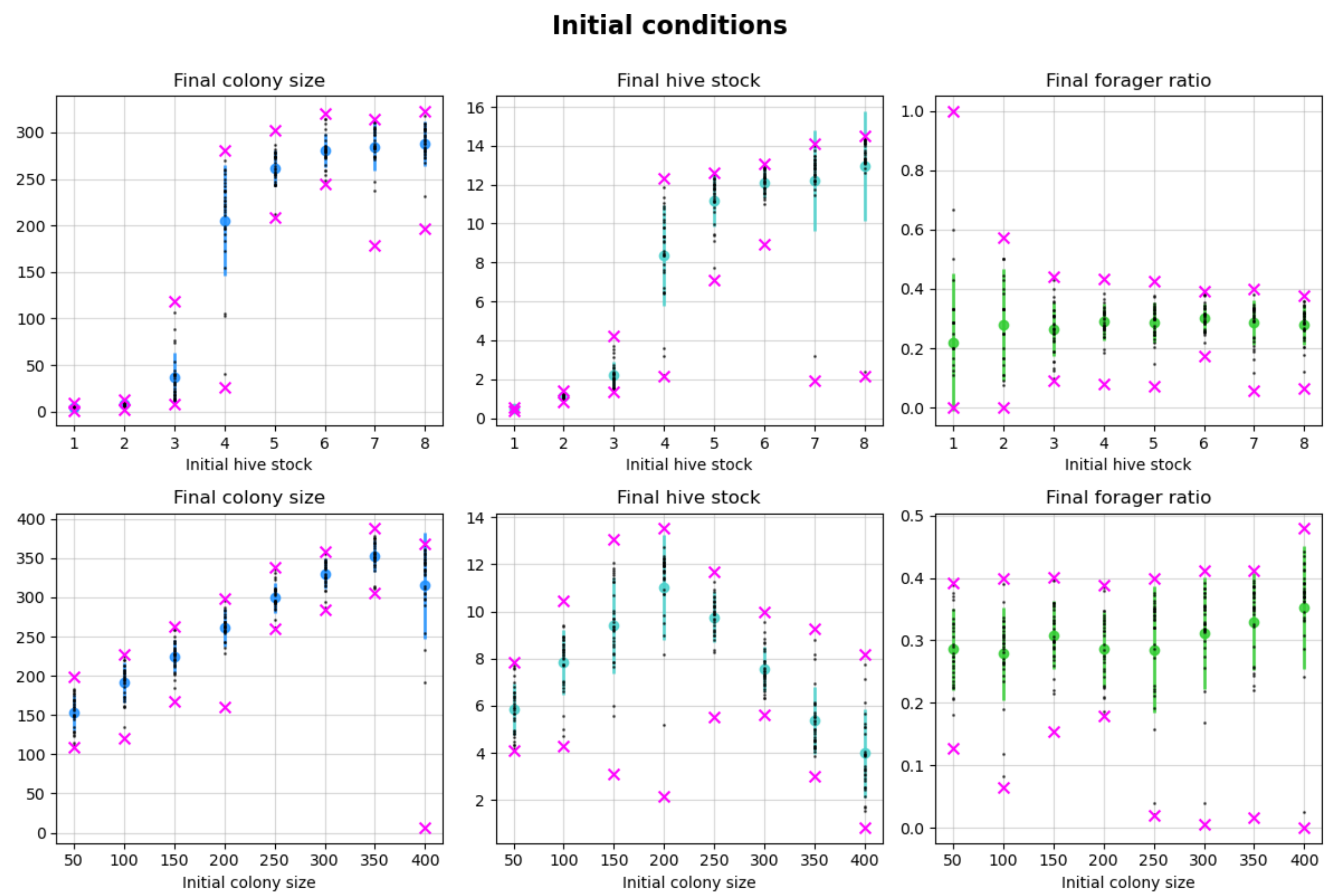

Figure 8. Local sensitivity analysis of initial conditions. Investigated are effects of initial hive stock (first row) and initial colony size (second row) on final colony size (left), hive stock (center) and forager ratio (right).

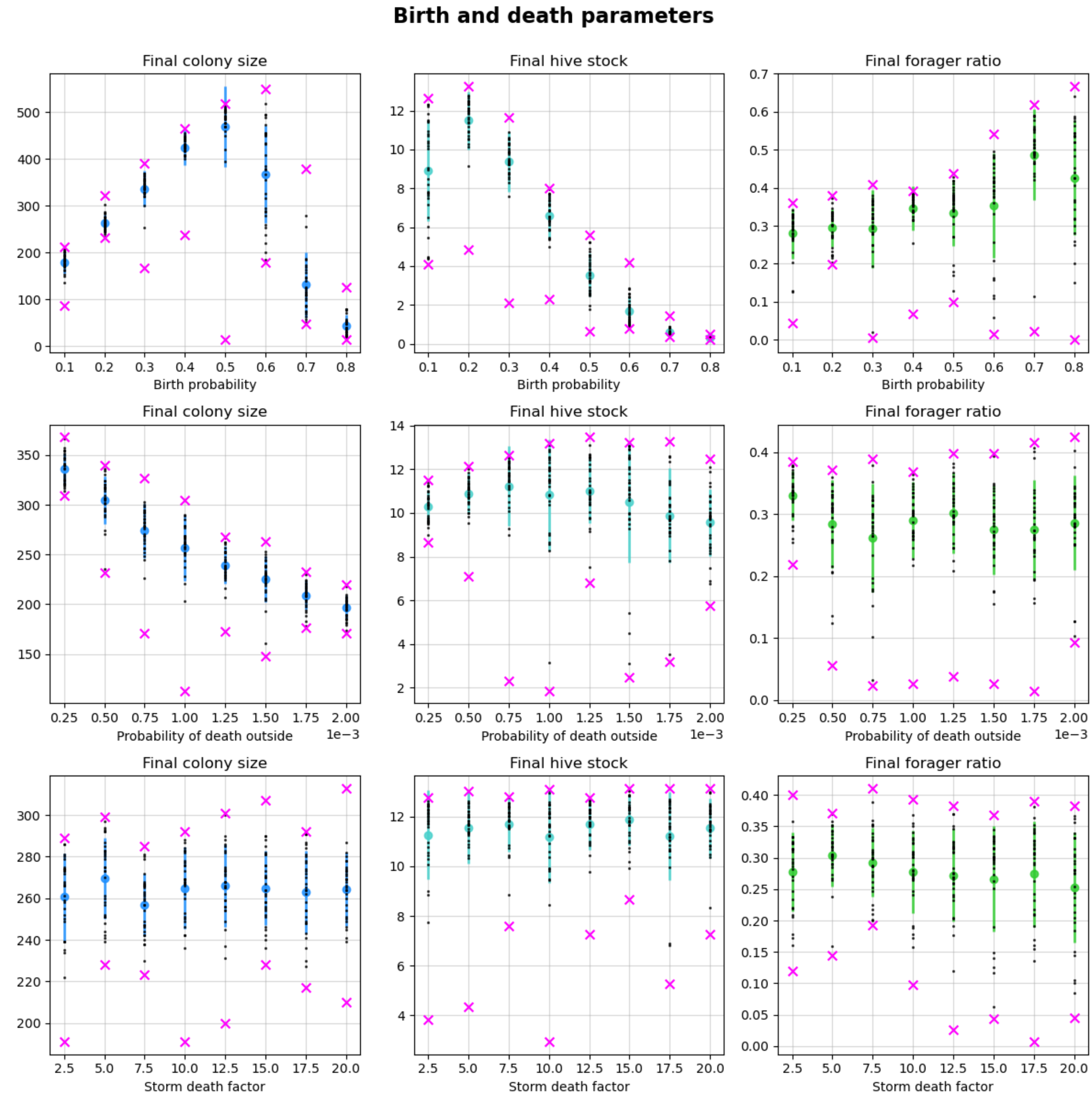

Figure 9. Local sensitivity analysis of birth and death parameters. Investigated are the effects of (p) birth (first row), (p) death (second row) and storm death factor (third row) on final colony size (left), hive stock (center) and forager ratio (right).

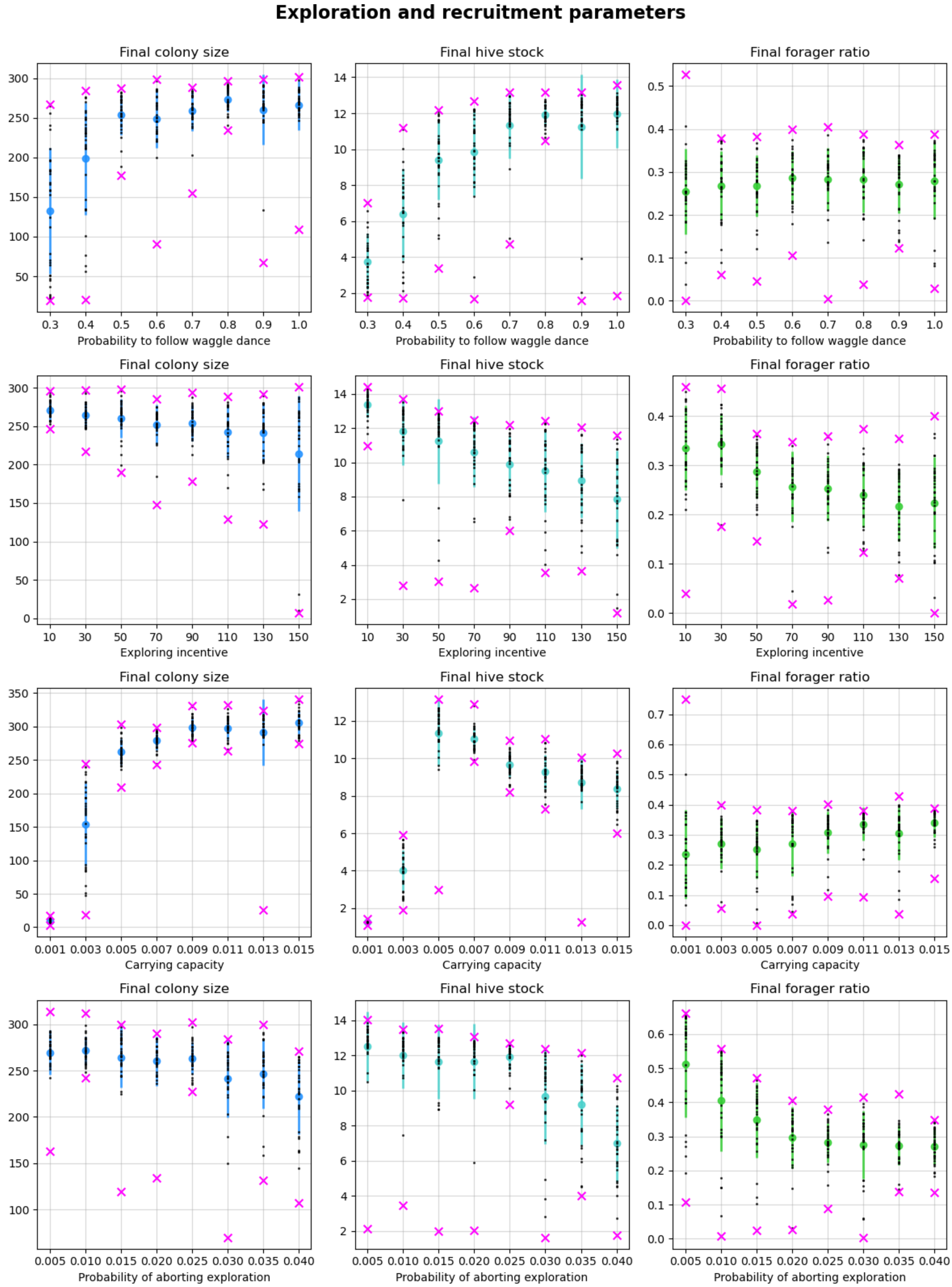

Figure 10. Local sensitivity analysis of exploration and recruitment parameters. Investigated are effects of (p) follow waggle dance (first row), exploring incentive (second row), carrying capacity (third row) and (p) abort (forth row) on final colony size (left), hive stock (center) and forager ratio (right).

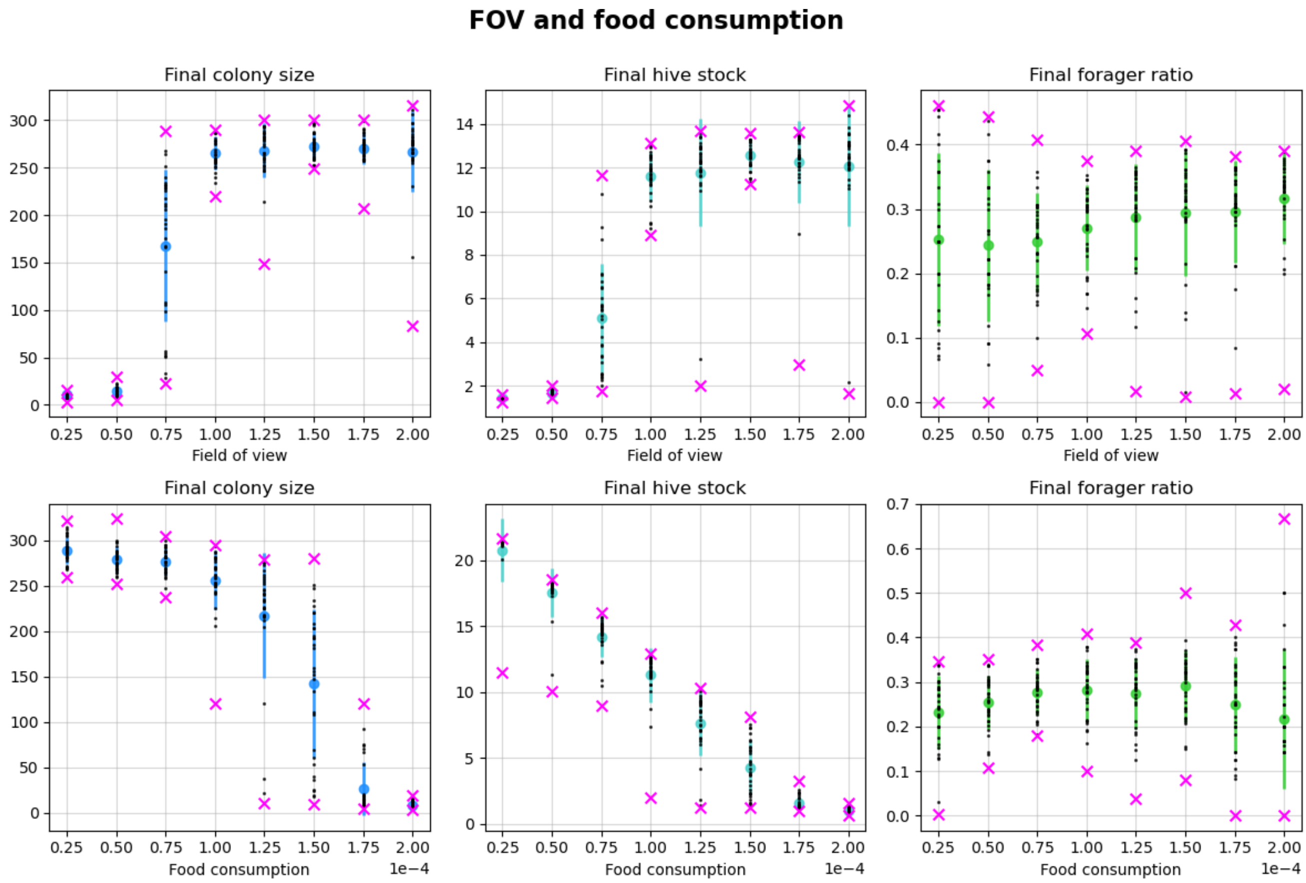

Figure 11. Local sensitivity analysis of agent perception and energy efficiency. Investigated are effects of field of view (first row) and food consumption (second row) on final colony size (left), hive stock (center) and forager ratio (right).

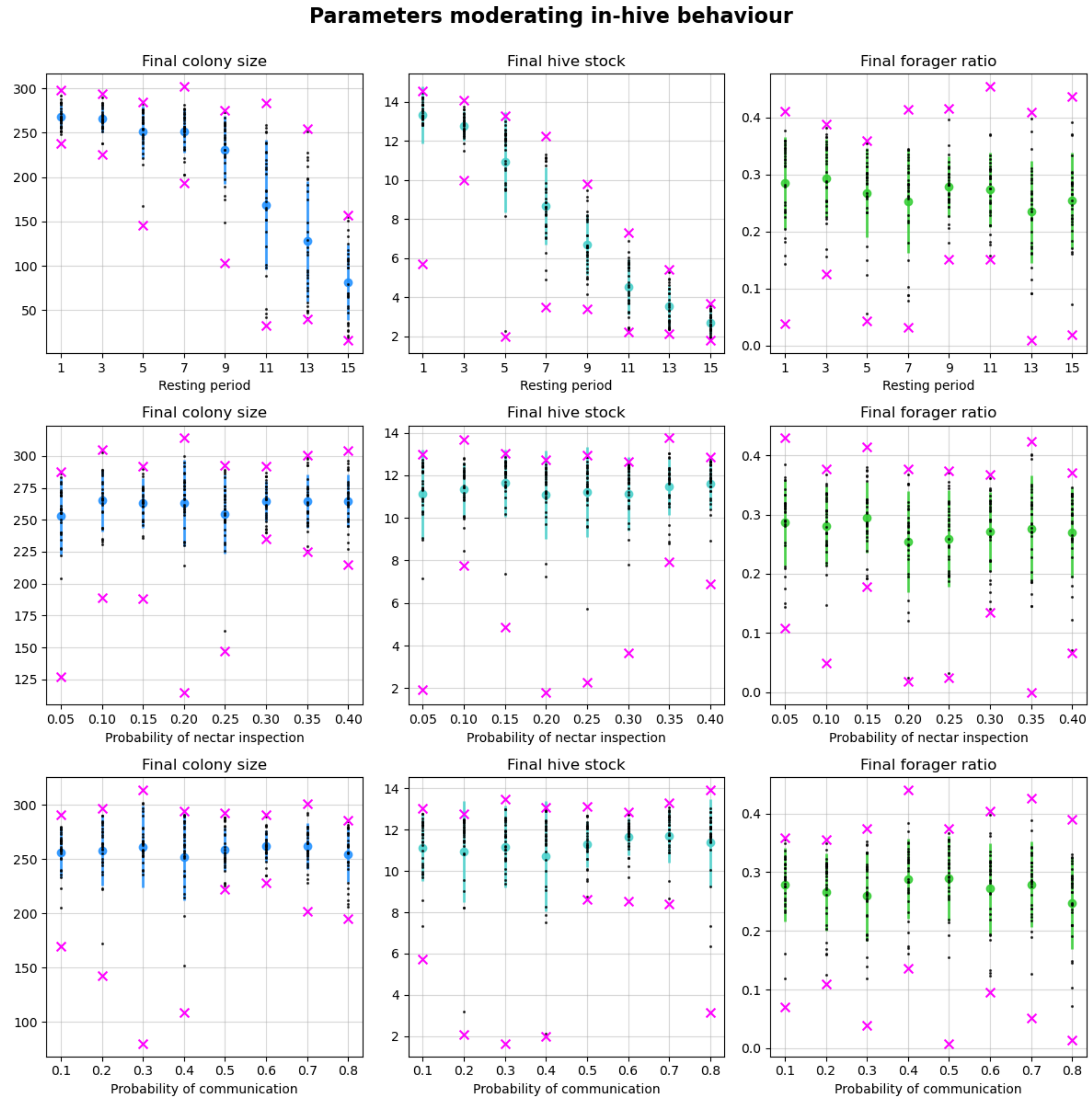

Figure 12. Local sensitivity analysis of in-hive behavior. Investigated are effects of resting period (first row), (p) nectar inspection (second row) and (p) nectar communication (third row) on final colony size (left), hive stock (center) and forager ratio (right).

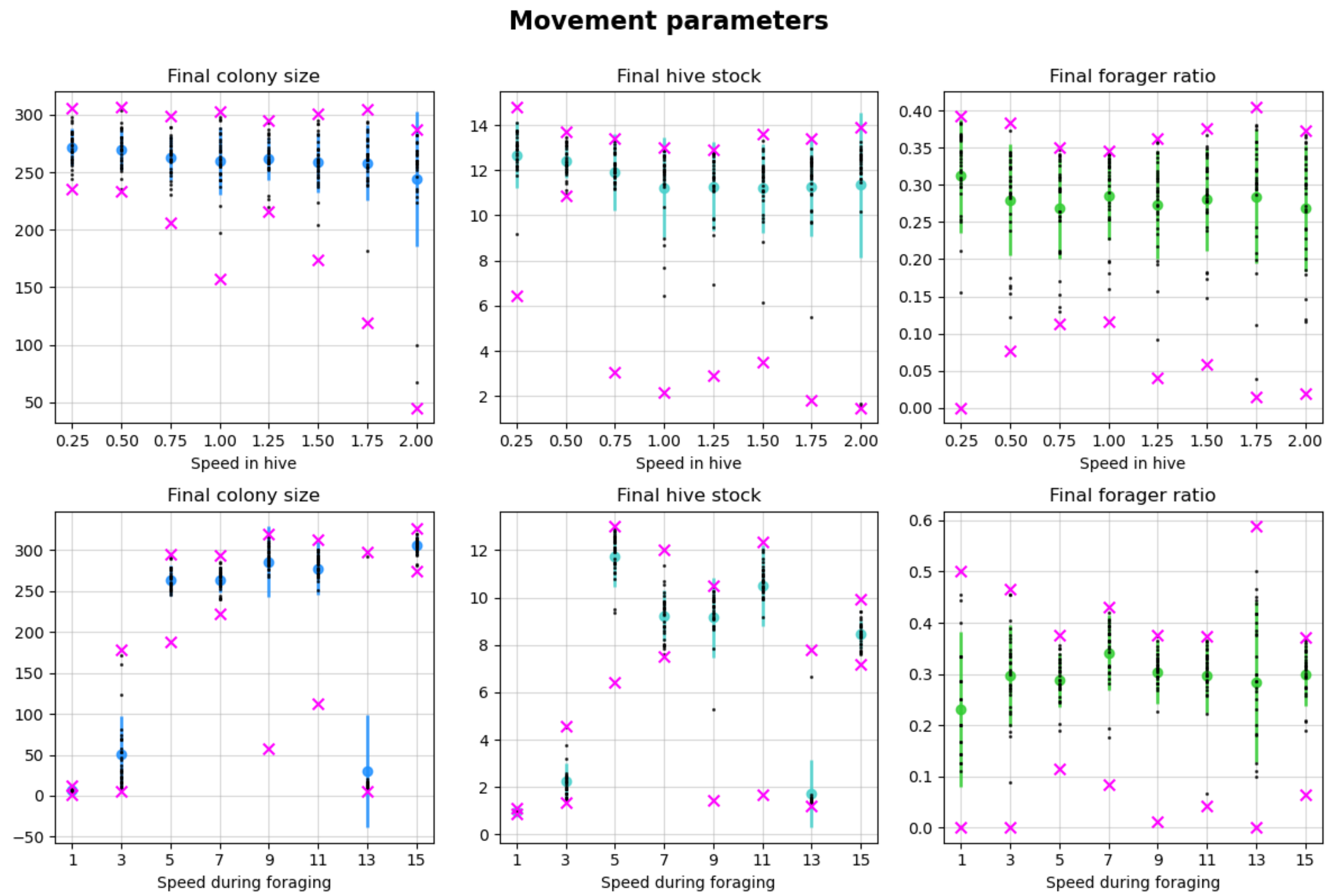

Figure 13. Local sensitivity analysis of bee movement. Investigated are effects of speed in hive (first row) and speed while foraging (second row) on final colony size (left), hive stock (center) and forager ratio (right).