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Research Article

A particle model reproducing the effect of a conflicting flight information on the honeybee swarm guidance

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Abstract

The honeybee swarming process is steered by few scout individuals, which are the unique informed on the location of the target destination. Theoretical and experimental results suggest that bee coordinated flight arises from visual signals. However, how the information is passed within the population is still debated. Moreover, it has been observed that honeybees are highly sensitive to conflicting directional information. In fact, swarms exposed to fast-moving bees headed in the wrong direction show clear signs of disrupted guidance. In this respect, we here present a discrete mathematical model to investigate different hypotheses on the behaviour both of informed and uninformed bees. In this perspective, numerical realizations, specifically designed to mimic selected experiments, reveal that only one combination of the considered assumptions is able to reproduce the empirical outcomes, resulting thereby the most reliable mechanism underlying the swarm dynamics according to the proposed approach. Specifically, this study suggests that (i) leaders indicate the right flight direction by repeatedly streaking at high speed pointing towards the target and then slowly coming back to the trailing edge of the bee cloud; and (ii) uninformed bees, in turn, gather the route information by adapting their movement to all the bees sufficiently close to their position.

Keywords: `Bee swarming; collective dynamics; alignment mechanisms`

AMS subject classification: `92D50, 92D40, 92D25, 93C20`

1. Introduction.

The self-organization and collective dynamics of large groups of animals, such as fishes, birds, insects, is a fascinating phenomenon that in last decades has attracted the interest of different research communities, e.g., ecologists, biologists, sociologists, applied mathematics and physicists, see for instance, [1–5] and reference therein. In this context, an intriguing example to study is the coordinated flight of honeybees when they move with the specific aim of reaching a new nest site. As explained, among others, in [6–9], this phenomenon arises in late spring and early summer when old honeybee colonies that achieve the maximum of their capacity generate new swarms. In more details, a queen and several thousands of worker bees leave the old colony and look for a suitable location for a new hive. Specifically, the selection of the proper location for the new nest is performed by a small fraction of the new colony, i.e., less then 5% [10–12]. These insects, called scout bees, explore the surrounding area, while the rest of the swarm compactly settle on the branch of a tree located few meters away from the original hive to protect the queen [13]. When a scout bee finds a suitable location for the new nest, it returns to the rest of the colony and performs a waggle dance to describe the explored site. Scout bees may initially promote different locations, however, after some hours (or days) a quorum is reached [14]. The entire swarm then finally takes off and compactly flies towards the new nest driven by the few scout/informed bees [9,15,16].

In this respect, biologists have provided different hypotheses to shed light on how the dynamics of thousands of insects constituting a swarm can be dictated by such a small portion of the population. The most reliable assumption on the honeybee guidance mechanism is that the informed bees guide the rest of the insect population via *visual signals*. Specifically, according to the *streaker hypothesis* proposed by M. Lindauer in 1955, see [10], scout bees have been observed to transmit the direction of movement to the other individuals by streaking at high speed through the swarm, pointing towards the target

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destination [8,12,15,17]. However, how the informed bees iteratively carry out these fast flights within the swarm is still among the questions left unanswered. In this regard, T. D. Seeley in [9] suggested two possible behaviours: a scout bee that reach the leading edge of the swarm could either (i) slowly fly back toward the trailing edge of the cloud (*back-and-forth flight* hypothesis), or (ii) wait that the rest of the swarm pass it (*go-and-stop flight* hypothesis). Furthermore, another aspect still unknown is how the non-informed bees gain the flight direction from the informed ones, i.e., if a follower honeybee synchronises its movement to a specific group of individuals (e.g., scouts bees or fast moving insects) or to all groupmates close to it.

In this regard, mathematical models provide useful instruments to investigate the mechanisms underlying collective dynamics of living individuals. In literature, there in fact exists several models that describe the coordinated migration of large groups of animals at different level of details. In particular, the description of the position and/or the state of any single agent and of the environment provides large systems of ordinary or stochastic differential equations (microscopic/stochastic models), see some examples in [18–21]. For huge groups of living individuals, these systems result computationally intensive, so that continuum models consisting of partial differential equations for averaged quantities, as the mean density or mean velocity of the agents, can be preferred, see, for instance, [22–26]. Alternatively, an intermediate approach results in kinetic models, i.e., differential or integro-differential equations for the probabilistic distribution of the living individuals in position and state spaces, as presented, among others, in [27–29].

In this context, we opt for a microscopic/discrete model based on the phenomenological characterization of the behavior of each individual, being therefore suitable to highlight how different assumptions result in the collective dynamics. With the same perspective, several microscopic models for the coordinated flight of honeybees towards a new nest have already been proposed, for instance, in [30–33]. Specifically, the works by S. Janson et al. [30], K. Diwold et al. [31] and R. Fetecau et al. [32] deal with discrete models based on the assumption of a *back-and-forth flight* of scout bees and on selected hypotheses for the behaviour of follower individuals. In particular, uninformed bees are assumed to align to all groupmates in their neighbourhood in [30], and to closest individuals that move two-fold faster in [31,32]. In our previous work [33], both the hypotheses proposed by M. Lindauer (*back-and-forth flight* and *go-and-stop flight*) have been mathematically investigated in combination with distinct assumptions for the set of individuals involved in the synchronisation process of uniformed bees. The numerical results provided in [33] allow us to exclude that follower individuals consider only fast-flying bees and to identify three combinations of the assumptions on scout behaviour and alignment mechanism that result in an efficient and coherent swarming. Specifically, both M. Lindauer hypotheses result in a compact and productive swarm dynamics when we assume that followers align to all groupmates falling within a given neighbourhood; while only the go-and-stop hypothesis results realistic under the assumption that followers do not consider the presence of the scouts in their way back to the rear edge of the swarm.

The goal of this work is to further investigate these three plausible combinations of hypotheses accounting for the empirical evidences provided by T. Latty and coworkers in [34], which studied if and how the migration of real swarms is affected by the presence of a fast-flying traffic line of honeybees pointing towards a different destination. Specifically, they made different artificial swarms, constituted by the queen bee and about 6000 workers per swarm, located in a tree-less field. The swarms were divided in two treatment groups: test swarms and control swarms. To reach the nestbox, test swarms had to fly through a traffic area of fast flying bee foragers headed in a wrong direction, while control swarms were allowed to migrate toward the new nest in absence of bee foragers. To set up the traffic area affecting the dynamics of test swarms, eight honeybee colonies were placed in a row not far from the swarm mount, while a large lucerne field was located on the other side of the minimum path that would lead the swarm to the nest box. As a result, compact and productive navigation of swarms were essentially disrupted whenever they were exposed to a traffic area of fast moving bees headed in a wrong direction. It revealed that the presence of honeybee foragers (whose mean velocity is in the range of streakers mean speed) confuses the transmission of flight information provided by the scout bees and leads to noticeable effects of disrupted guidance, as dispersion of the group and, in most cases, failing to approach the selected nest

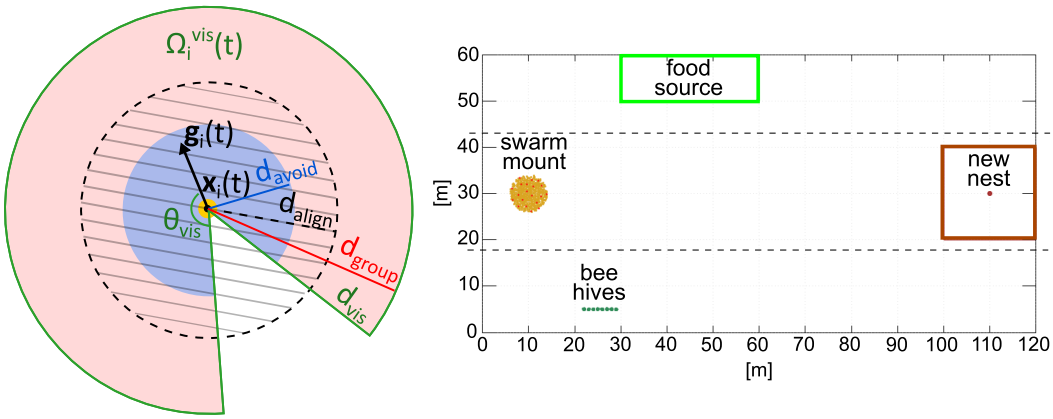

Figure 1. Left panel: Representation of honeybee perception region (green area); the attraction neighbourhood (red area); the repulsion neighbourhood (blue area) and the alignment region (dashed region). Right panel: Representative initial condition reproducing the experimental setting. Yellow and red dots respectively denote the uninformed individuals and the scout bees with a streaker role. Dashed lines define the domain portion represented in Figure 4.

site.

In this respect, in Section 2, we propose an extended version of the model presented in [33] to describe the dynamics of both the informed and non-informed individuals that collectively fly towards a new nest, and of the group of honeybee foragers who individually move to provide food to their hives. In Section 3, we test the above cited hypotheses on honeybee behaviour by performing proper numerical simulations specifically designed to reproduce the experimental scenarios considered in [34]. The possible coherence between the experimental and the modeling outcomes would reveal which are, according to the proposed model, the most reliable assumptions underlying the swarm dynamics, thereby pointing out the consistency of the proposed approach. Finally, some conclusive considerations are reported in Section 4.

2. Mathematical model.

System representation. The dynamics of the migrating swarm and of the group of fast-moving foraging bees is here described in the planar domain $\mathbb{R}^2$: as in [33], we indeed consider a planar section, parallel to the ground, of the system of interest. The nest site selected by scout bees, i.e., the target of the migrating colony, is represented by a dimensionless point $\mathbf{x}_{\text{nest}} \in \mathbb{R}^2$. Moreover, we denote by $\mathbf{x}_h^{\text{hive}} \in \mathbb{R}^2$, with $h = 1, \dots, 8$, and $\Omega^{\text{food}} \subset \mathbb{R}^2$, the centers of the eight hives and the food source, respectively, that have been used by T. Latty and coworkers to produce the highway of fast flying bees.
Each bee is represented by a dimensionless point with concentrated mass located at $\mathbf{x}_i \in \mathbb{R}^2$ and is further characterised by (i) a unit vector $\mathbf{g}_i \in \mathbb{R}^2$ denoting its gazing direction; (ii) a status variable s_i identifying its actual role/behaviour; and (iii) its actual velocity $\mathbf{v}_i \in \mathbb{R}^2$. Entering in more details, the introduction of the gazing direction $\mathbf{g}_i$ allows us to implement the visual hypothesis at the basis of the proposed model by defining a perception region for each bee i:

$$\Omega_i^{\text{vis}}(t) = \left\{ \mathbf{y} \in \mathbb{R}^2 : |\mathbf{y} - \mathbf{x}_i(t)| \le d_{\text{vis}}, \frac{\mathbf{y} - \mathbf{x}_i(t)}{|\mathbf{y} - \mathbf{x}_i(t)|} \cdot \mathbf{g}_i(t) \ge \cos\theta_{\text{vis}} \right\}, \tag{1}$$

being d_{vis} and θ_{vis} the visual depth and the half visual angle, respectively, see Figure 1 (left panel). Despite, in principle, the individual gazing direction can evolve as an independent degree of freedom, we here assume that it is constantly aligned to the actual velocity of honeybee i, i.e., we set

$$\mathbf{g}_i(t) = \frac{\mathbf{v}_i(t)}{|\mathbf{v}_i(t)|}, \quad \text{for all } t \ge 0. \tag{2}$$

In order to model both the migrating swarm and the bee foragers involved in the experiments described

in [34], the set of possible values of the status variable s_i is defined as follows

$$s_i(t) = \begin{cases} \text{“U”, if } i \text{ is a uninformed bee;} \\ \text{“S”, if } i \text{ is a scout with a streaker role;} \\ \text{“P”, if } i \text{ is a scout with a passive role;} \\ \text{“F”, if } i \text{ is a bee forager,} \end{cases} \tag{3}$$

where the first three values characterize the individuals constituting the migrating colony (according to [33]), and the last one denotes honeybee foragers. Both the uninformed bees, i.e., i such that $s_i =$“U”, and the foraging bees, i.e., i such that $s_i =$“F”, never change their role. In fact, according to the biological observations in [9,34], uninformed bees can not acquire the knowledge about the new nest location but just follow the direction indicated by scouts bees; while bee forgers do never join the migrating swarms. Conversely, scout bees repeatedly undergo status transitions: they have a streaker role, i.e., i is such that $s_i =$“S”, when they fly fast through the swarm pointing towards the nest, and a passive role, i.e., i such that $s_i =$“P”, otherwise. Specifically, a streaker bee maintains its status until it reaches the leading edge of the swarm, then as soon as its position satisfies the condition

$$|\mathbf{x}_i(t) - \mathbf{x}_{\text{nest}}| < \min_{\substack{k \neq i \ : \ s_k(t) \neq \text{“F”} \\ \mathbf{x}_k(t) \in \Omega_i^{\text{vis}}(t)}} |\mathbf{x}_k(t) - \mathbf{x}_{\text{nest}}|, \tag{4}$$

it becomes a passive leader. On the other hand, when a passive leader approaches the trailing edge of the bee cloud, i.e., in mathematical terms

$$|\mathbf{x}_i(t) - \mathbf{x}_{\text{nest}}| > \max_{\substack{k \neq i \ : \ s_k(t) \neq \text{“F”} \\ \mathbf{x}_k(t) \in \Omega_i^{\text{vis}}(t)}} |\mathbf{x}_k(t) - \mathbf{x}_{\text{nest}}|, \tag{5}$$

it turns again to have a streaker role.

Honeybee dynamics. Honeybee dynamics are described by a system of first-order ordinary differential equations based on the assumption that the insect velocity is proportional to the acting forces rather than to their acceleration. Such relation, called overdamped force-velocity response (see [35–37] for further comments) is at the basis of several models reproducing the collective behaviour of honeybees (see, for instance, [30,31]), as well as of other living individuals characterised by a complete and intelligent body control, e.g., humans or other animals (see among others, [38–42]). Under this assumption, the equation of motion of the i-th bee reads as

$$\frac{d\mathbf{x}_i(t)}{dt} = \min\left\{ v_{\max}^{s_i(t)}(t), |\mathbf{v}_i(t)| \right\} \frac{\mathbf{v}_i(t)}{|\mathbf{v}_i(t)|}, \tag{6}$$

where $v_{\max}^{s_i(t)}$ denotes the maximal speed of the i-th individual according to its actual status, and avoids unrealistically high speeds. The velocity of each individual is defined by the superposition of different velocity contributions, i.e.,

$$\mathbf{v}_i(t) = \mathbf{v}_i^{s_i(t)}(t) + \mathbf{v}_i^{\text{avoid}}(t) + \mathbf{v}_i^{\text{group}}(t) + \mathbf{v}_i^{\text{rand}}(t). \tag{7}$$

In Equation (7), $\mathbf{v}_i^{s_i}$ denotes the directional migratory mechanism established according to its actual status s_i. $\mathbf{v}_i^{\text{avoid}}$ and $\mathbf{v}_i^{\text{group}}$ respectively implement the natural tendency of each insect to maintain a minimal comfort distance from other bees, and to remain in the neighbourhood of other individuals. Finally, $\mathbf{v}_i^{\text{rand}}$ accounts for fluctuations possibly affecting honeybee dynamics. In order to complete the description of the model, we now discuss each velocity term starting from the directional ones.

Directional velocity component of uniformed individuals, $\mathbf{v}_i^{\text{U}}$. Uniformed bees, being unaware of the position of the new nest, are only able to synchronise their movement with a specific set of groupmates, say

$\mathcal{N}_i^{\text{align}}$. In this respect, the directional velocity component of the i-th uniformed individual is an alignment term that writes

$$\mathbf{v}_i^{\text{U}}(t) = v_{\max}^{U}(t)\,\frac{< \mathbf{v}_j(t) >_{j\in\mathcal{N}_i^{\text{align}}(t)}}{|< \mathbf{v}_j(t) >_{j\in\mathcal{N}_i^{\text{align}}(t)}|}, \tag{8}$$

where

$$< \mathbf{v}_j(t) >_{j\in\mathcal{N}_i^{\text{align}}(t)} = \frac{1}{\#\mathcal{N}_i^{\text{align}}(t)} \sum_{j\in\mathcal{N}_i^{\text{align}}(t)} \mathbf{v}_j(t). \tag{9}$$

Accounting for the empirical suggestions and the numerical results reported in [33] and reference therein, we consider two possible definitions of the alignment set of a given uninformed individual:

HP N1 - the i-th uninformed bee aligns its flight to all insects falling within a given neighbourhood, regardless of their status, i.e.,

$$\mathcal{N}_i^{\text{align}}(t) = \{j \neq i \ : \ \mathbf{x}_j(t) \in \Omega_i^{\text{vis}},\, 0 < |\mathbf{r}_{ij}(t)| \leq d_{\text{align}}\}; \tag{10}$$

HP N2 - the i-th uninformed bee synchronises its flight to all surrounding individuals that fall within a given region, except passive leaders, i.e.,

$$\mathcal{N}_i^{\text{align}}(t) = \{j \neq i \ : \ \mathbf{x}_j(t) \in \Omega_i^{\text{vis}},\, 0 < |\mathbf{r}_{ij}(t)| \leq d_{\text{align}}, \quad s_j(t) \in \{\text{U,S,F}\}\}, \tag{11}$$

being $\mathbf{r}_{ij}(t) := \mathbf{x}_j(t) - \mathbf{x}_i(t)$ and d_{align} the depth of the alignment region. In this respect, we highlight that assumption N2, as well as assumption A4 in [33], translate in mathematical terms the biological hypothesis that scouts in a passive role become almost invisible to the followers, see [8,9].

Directional velocity components of scout bees, $\mathbf{v}_i^{\text{S}}$ *and* $\mathbf{v}_i^{\text{P}}$. The characteristic dynamics of the informed individuals change with their status. Specifically, scout bees with a streaker role are assumed to fly at high speed pointing towards the target nest, i.e., in mathematical terms

$$\mathbf{v}_i^{\text{S}}(t) = v_{\max}^{S}(t)\,\frac{\mathbf{x}_{\text{nest}} - \mathbf{x}_i(t)}{|\mathbf{x}_{\text{nest}} - \mathbf{x}_i(t)|}. \tag{12}$$

On the other hand, for the passive leaders, we consider the two possible behaviours proposed by T.D. Seeley in [9] and already implemented in [33].

HP L1 - Passive leaders slowly fly back towards the rear edge of the swarm, in order to slightly influence the movement of the uninformed swarming bees. In this respect, for the i-th passive leader bee, we define

$$\mathbf{v}_i^{\text{P}}(t) = v_{\max}^{P}(t)\,\frac{\dfrac{\mathbf{x}_{\bar{k}}(t) - \mathbf{x}_i(t)}{|\mathbf{x}_{\bar{k}}(t) - \mathbf{x}_i(t)|} - \dfrac{\mathbf{x}_{\text{nest}}(t) - \mathbf{x}_i(t)}{|\mathbf{x}_{\text{nest}}(t) - \mathbf{x}_i(t)|}}{\left|\dfrac{\mathbf{x}_{\bar{k}}(t) - \mathbf{x}_i(t)}{|\mathbf{x}_{\bar{k}}(t) - \mathbf{x}_i(t)|} - \dfrac{\mathbf{x}_{\text{nest}}(t) - \mathbf{x}_i(t)}{|\mathbf{x}_{\text{nest}}(t) - \mathbf{x}_i(t)|}\right|}, \tag{13}$$

where $\bar{k}$ denotes the uninformed insect farthest from the new nest according to the following relation

$$|\mathbf{x}_{\text{nest}} - \mathbf{x}_{\bar{k}}(t)| = \max_{\substack{k\,:\,s_k(t)=\text{U} \\ \mathbf{x}_k(t)\in\Omega_i^{\text{vis}}(t)}} |\mathbf{x}_{\text{nest}} - \mathbf{x}_k(t)|. \tag{14}$$

HP L2 - Passive leaders stop and wait to be passed by the rest of the groupmates. For the i-th passive leader, we indeed set

$$\mathbf{v}_i^{\text{P}}(t) = \mathbf{0}. \tag{15}$$

Directional velocity components of bee foragers, $\mathbf{v}_i^{\mathrm{F}}$. Bee foragers individually move back and forth between their original hive and a food source. In particular, it has been experimentally observed that bees pointing to a desirable source of food, fly at a speed comparable to that of the fast-flying streakers, so we can assume $v_{\max}^F = v_{\max}^S$. We then state that, at regularly spaced instant times, a bee forager i leaves a randomly selected hive and begins to fly fast towards a point in the lucerne field, said $\mathbf{x}_i^{\mathrm{food}} \in \Omega^{\mathrm{food}}$, which is randomly selected as well. In this respect, $\mathbf{v}_i^{\mathrm{F}}$ is first given by

$$\mathbf{v}_i^{\mathrm{F}}(t) = v_{\max}^F(t)\,\frac{\mathbf{x}_i^{\mathrm{food}} - \mathbf{x}_h^{\mathrm{hive}}}{|\mathbf{x}_i^{\mathrm{food}} - \mathbf{x}_h^{\mathrm{hive}}|}. \tag{16}$$

The frequency of the foragers' liftoff is set according to the experimental amount of bee traffic n_F recorded in [34], i.e., the number of bees leaving the hives over 1 min. Once reached the food source, foragers change their desired travel direction to come back home. Finally, it is worth to stress that we neglect the dynamics of bee foragers within the hives, since it does not affect the behaviour of the migrating swarm.

Interaction velocity contributions, $\mathbf{v}_i^{\mathrm{avoid}}$ *and* $\mathbf{v}_i^{\mathrm{group}}$. These two velocity contributions implement repulsive and attractive inter-individual interactions, respectively. They are both defined as the superposition of binary interactions that result in vectors aligned to the line ideally connecting the couple of interacting insects, and whose moduli depend on their mutual distance. In particular, stating that the coordinated behaviour of honeybees is regulated by visual signals, it is likely to assume that the i-th bee interacts with individual j only if $\mathbf{x}_j \in \Omega_i^{\mathrm{vis}}$. Moreover, the resulting pairwise interaction velocity component is repulsive if their relative distance $|\mathbf{r}_{ij}|$ is lower then the comfort distance d_{avoid} and it is conversely attractive if $|\mathbf{r}_{ij}(t)| < d_{\mathrm{group}}$, where $d_{\mathrm{avoid}} < d_{\mathrm{group}} \leq d_{\mathrm{vis}}$. The interaction repulsive and attractive interaction sets of the i-h individual are thus given by

$$\begin{aligned} \mathcal{N}_i^{\mathrm{avoid}}(t) &= \{j \neq i : \mathbf{x}_j(t) \in \Omega_i^{\mathrm{vis}}, 0 < |\mathbf{r}_{ij}(t)| \leq d_{\mathrm{avoid}}\}; \\ \mathcal{N}_i^{\mathrm{group}}(t) &= \{j \neq i : \mathbf{x}_j(t) \in \Omega_i^{\mathrm{vis}}, d_{\mathrm{avoid}} < |\mathbf{r}_{ij}(t)| \leq d_{\mathrm{group}}\}. \end{aligned} \tag{17}$$

see Figure 1 (left panel). Notice that each bee can simultaneously synchronise and be repelled/attracted to a perceived groupmate, as the alignment region intersect with the ones related to the interactions, i.e., $d_{\mathrm{align}} \in (d_{\mathrm{avoid}}, d_{\mathrm{group}})$, see again Figure 1 (left panel). In agreement with [33,43] and reference therein, the interaction velocity contributions are finally defined by

$$\begin{aligned} \mathbf{v}_i^{\mathrm{avoid}}(t) &= \sum_{j \in \mathcal{N}_i^{\mathrm{avoid}}(t)} f_{\mathrm{avoid}} \left(\frac{1}{d_{\mathrm{avoid}}} - \frac{1}{|\mathbf{r}_{ij}(t)|}\right) \frac{\mathbf{r}_{ij}(t)}{|\mathbf{r}_{ij}(t)|}, \\ \mathbf{v}_i^{\mathrm{group}}(t) &= \sum_{j \in \mathcal{N}_i^{\mathrm{group}}(t)} 4\, f_{\mathrm{group}}\, \frac{(d_{\mathrm{group}} - |\mathbf{r}_{ij}(t)|)(|\mathbf{r}_{ij}(t)| - d_{\mathrm{avoid}})}{(d_{\mathrm{group}} - d_{\mathrm{avoid}})^2}\, \frac{\mathbf{r}_{ij}(t)}{|\mathbf{r}_{ij}(t)|}, \end{aligned} \tag{18}$$

i.e., among the large variety of the possible interaction laws, we opt for a classical Newtonian-type hyperbolic kernel to implement short-range repulsive interactions, and we choose a parabolic shape for the attractive long-range interactions.

Random fluctuations, $\mathbf{v}_i^{\mathrm{rand}}$. The random velocity term $\mathbf{v}_i^{\mathrm{rand}}$ finally accounts for the realistic possibility that fluctuations can affect the behaviour of each individual. The modulus and the direction of this velocity component are here assumed to be random variables which uniformly vary within the ranges of values $[0, v_{\max}^{s_i(t)}/10]$ and $[0, 360°)$, respectively.

3. Numerical results.

The aim of the simulations proposed in this section is to point out the sets of assumptions relative to the behaviour of the passive leaders and the alignment mechanism of the uninformed bees that are able

to reproduce the empirical results presented by T. Latty and coworkers in [34]. In this perspective, we design two simulation settings to reproduce the dynamics either of "control swarms" that fly towards a target nest in the absence of other bees, and of "test swarms" exposed to a flux of fast-moving bees. In both scenarios, we will test the three different combinations of the proposed hypotheses (N1, L1), (N1, L2), and (N2, L2). As a remark, we here discard the set of assumptions (N2, L1), since proper numerical results presented in [33] demonstrated that it is not able to reproduce the coordinated and productive migration of a swarm even in the absence of other bees.

Simulation details. In all simulations, we consider a migrating colony of 500 individuals. As commented above, we are indeed dealing with a planar section of the larger control/test swarm. As shown in Figure 1 (right panel), these bees are initially randomly distributed within a round area of radius 4 m centered at (10 m, 30 m), leading to a realistic density of about 8 bees/m^2 [9]. The initial gazing direction $\mathbf{g}_i(0)$ of each individual is randomly generated. In agreement with the experimental literature [15], we assume that 4% of the migrating individuals are informed of the location of the new nest, while the remaining 480 bees are uninformed. In particular, all scouts initially have a streaker role, i.e., $s_i(0) = S$, then they are able to undergo status transitions according to the evolution of the system, as defined in Equations (4)-(5). We here recall that uninformed bees are conversely not able to become scouts. The nestbox constituting the target of the migrating colony is located 100 m far from the initial position of the swarm, i.e., at $\mathbf{x}_{\text{nest}} = (110\text{ m}, 30\text{ m})$. The eight hives from where bee foragers start flying to provide food for their colony, are respectively located at $\mathbf{x}_1^{\text{hive}} = (22\text{ m}, 5\text{ m})$, $\mathbf{x}_2^{\text{hive}} = (22.5\text{ m}, 5\text{ m})$, $\mathbf{x}_3^{\text{hive}} = (23\text{ m}, 5\text{ m})$, $\mathbf{x}_4^{\text{hive}} = (23.5\text{ m}, 5\text{ m})$, $\mathbf{x}_5^{\text{hive}} = (24\text{ m}, 5\text{ m})$, $\mathbf{x}_6^{\text{hive}} = (24.5\text{ m}, 5\text{ m})$, $\mathbf{x}_7^{\text{hive}} = (25\text{ m}, 5\text{ m})$ and $\mathbf{x}_8^{\text{hive}} = (25.5\text{ m}, 5\text{ m})$, according to the experimental scenario. Finally, the food source is represented by the rectangle area $\Omega^{\text{food}} = [30, 60] \times [50, 60]$ m^2. According to the experimental scenario described in the previous section, the hives and the food site are located on either sides of the straight path connecting the initial position of the swarm and the nest site, see again Figure 1 (right panel).

Table 1. Model parameters.

Par.	Descr.	Val.	Ref.
θ_{vis}	half visual angle	156.5°	[44]
d_{vis}	depth of visual field	20 m	[33]
$v_{\max}^U$	maximal speed of uninformed bees	3 m/s	[34]
$v_{\max}^S$	maximal speed of streakers	9.4 m/s	[9,12,34]
$v_{\max}^P$	maximal speed of passive scouts	3 m/s	[8,9]
$v_{\max}^F$	maximal speed of foragers	9.4 m/s	[34]
n_F	bee traffic	[25, 85] bees/min	[34]
d_{avoid}	extension of the avoidance region	0.3 m	[9]
d_{align}	extension of the alignment region	2 m	[42,45]
d_{group}	extension of the attraction region	20 m	[33]
f_{avoid}	avoidance coefficient	1 m^2/s	[33]
f_{group}	attraction coefficient	10^{-6} m/s	[33]

The entire model parameter setting used in all numerical simulations is summarized in Table 1. These values have been set by taking advantage of the empirical measurements reported in the literature of the field and of the parameter estimation performed in [33]. The bee visual region in Equation (1) is characterised by setting the half visual angle $\theta_{\text{vis}} = 156.5°$ and the visual depth $d_{\text{vis}} = 20$ m. The former is a measure provided in [44]. The latter is an estimate proposed in [33] to allow each insect to potentially see all groupmates (provided that the swarm is not completely dispersed) and it is small enough to avoid that the target destination initially falls within the visual field of uninformed individuals. The maximal flight speeds introduced in Equation (6) are estimated according to the empirical measurements reported in [34] and reference therein. Specifically, the flight of uninformed individuals in the swarm do not exceed $v_{\max}^U = 3$ m/s [34], while scouts in the streaker role are able to fly up to $v_{\max}^S = 9.4$ m/s [9,12,34]. The maximal speed of passive leaders is assumed to be equal to that of uninformed individuals, i.e., $v_{\max}^P = v_{\max}^U$, according to the biological hypothesis that scouts in a passive role become almost invisible to

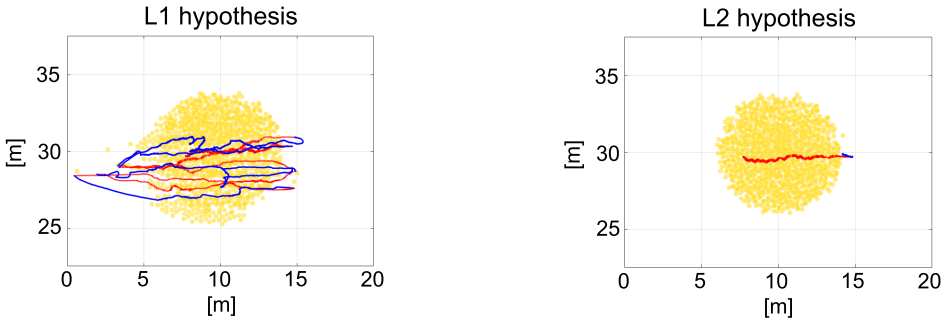

Figure 2. Trajectory of a representative bee scout upon either the back-and-forth hypotheses L1 (left panel) and the go-and-stop hypotheses L2 (right panel). The trajectory is red when the scout has a streaker role, and it is blue when it has a passive role. The yellow shadow represents the entire bee cloud.

the followers, see [8,9]. As a remark, the measurements performed in [34] allow us to estimate the maximal speed of honeybee foragers equal to that of scouts in the streaker role, i.e., $v^F_{\max} = v^S_{\max} = 9.4$ m/s. Plausible values for the outbound bee traffic n_F fall in the range $[25, 85]$ bees/min, so that the resulting ratio between the number of scouts and n_F is consistent with the quantities recorded in [34].
The model parameters that characterize honeybee mutual interactions (affecting all individuals regardless their status) and the alignment mechanism (regulating the behaviour of uniformed insects only) are set exactly as in [33]. The minimal comfort distance between individuals d_{avoid} is fixed at 0.3 m, according to the measurements reported in [9]. The extension of the alignment region d_{align} is assumed to be equal to 2 m, accounting for the values of the ratio $d_{\text{avoid}}/d_{\text{align}}$ tested by Couzin and colleagues in [42,45]. We further set $d_{\text{group}} = d_{\text{vis}}$, assuming that each bee tends to maintain a minimal connection with any other individual it sees. The technical coefficients f_{avoid} and f_{group} are finally settled at 1 m^2/s and 10^{-6} m/s, respectively, following the parametric estimation proposed in [33]. In particular, in [33], we ran a series of numerical realizations looking for pairs of parameters that (i) result in a crystalline equilibrium configuration of the swarm without superposition of individuals, when the evolution of the system is regulated by attractive/repulsive stimuli only; and (ii) allow the specific flight of scouts through the swarm under either hypotheses L1 and L2, when the evolution is regulated by the complete dynamics (see the Appendix of [33] for further details). On one hand, the numerical results reported in [33] show that requirement (i) is satisfied if the parametric relation $f_{\text{avoid}}/f_{\text{group}} > 1.07 \cdot 10^5$, derived by [43,46,47] and reference therein, holds. To account for requirement (ii), we conversely have to verify that the interaction parameter values used in [33] are still admissible even though we here opt for a different value of the maximal speed of uniformed bees. In fact, in order to mathematically reproduce the experiments performed by T. Latty and coworkers, we here set $v^U_{\max}$ equal to the empirically estimated value reported in [34], i.e., 3 m/s, rather than to 6.7 m/s as in [33]. In this respect, we analyse the motion of the scout bees through the cloud of uninformed individuals by running two series of computational tests involving a modified control swarm whose dynamics is regulated only by the repulsive/attractive interactions and the characteristic motion of scouts, L1 and L2, respectively. Specifically, with respect to the complete model in Equations (6)-(7), we neglect the alignment mechanisms and the random contributions. Figure 2 shows the trajectories of a representative informed bee observed in the two cases: under hypothesis L1 (left panel), the informed bee is actually able to streak and fly back repeatedly through the swarm; under hypothesis L2 (right panel), once the scout bee reaches the leading edge of the swarm, it stops waiting the passage of the rest of the colony. However, the cloud of uninformed individuals (and, in turn, the entire swarm) substantially maintains its initial position due to the absence of the alignment process. These numerical results clearly demonstrate that the proposed variation in the model parameters do not disrupt the specific behaviour of informed bees, i.e., the proposed set of parameter satisfies requirement (ii) too.

Control and test swarms. We then turn to test the considered alternative combinations of the hypotheses

on the behaviour of leader scouts, and on the alignment mechanism of uninformed bees, i.e., (N1, L1), (N1, L2), and (N2, L2), looking for those able to reproduce the dynamics of both the control swarms and the test swarms described in [34]. By considering the complete model defined in Equations (6)-(7), we run six series of simulations for each couple of assumptions. First, we deal with the *control case*: by setting $n_F = 0$ bees/min, we show that, in absence of conflicting information, all proposed set of hypotheses reproduce the coordinated and productive flight of honeybees towards their new nest. Then, we look at the evolution of swarms exposed to five different levels of bee traffic (*test cases*): specifically, n_F is respectively set equal to $25; 40; 55; 70; 85$ bees/min.
In order to identify the sets of assumptions able to reproduce the experimental outcomes presented by T. Latty and co-workers, let us recall that in [34] they classify their empirical results accounting for the fraction of the swarm that actually enters the nestbox. The proposed model, however, implements only honeybee navigation toward the new nest, and not the entrance mechanism which conversely involves specific features such as, for instance, the secretion of the Nasonov pheromone [12]. By considering that honeybees begin to coordinate their entrance in the nest at about 10 m from the target [9], we record the number of insects that simultaneously fall within the neighborhood $\Omega^{\text{nest}} := [100, 120] \times [20, 40]$ m^2 around $\mathbf{x}_{\text{nest}}$, see Figure 1 (right panel). The dynamics of the bee population resulting from the considered set of assumptions are then classified according to the following criterion.

Definition 3.1. The coordinated and productive flight of a swarm toward the nest is *disrupted* if

$$N_{\text{nest}} = \max_{t\in[0,T]} \left\{ \# \left\{ j \ : \ s_j(t) \neq \text{“F”}, \ \mathbf{x}_i(t) \in \Omega^{\text{nest}} \right\} \right\} \leq 450, \tag{19}$$

where # denotes the cardinality of a set and T is the period of observation of the realization. Otherwise, the swarm *successfully reaches* the target nest.

All numerical tests are stopped at $T = 1$ min. By noticing that in control cases the time needed by the simulated swarm to cover the straight path to reach the nest is about 35 sec (see Figure 4), it is clear that this choice of T allows to properly classify as *disrupted* the dynamics of swarms that would arrive at the target nest after large deflections from the straight path. Moreover, for each combination of the set of assumptions and for each considered amount of bee traffic (included the control case), we run 10 independent simulations to account for the randomness present both in the initial distribution of the swarm and in honeybee dynamics. The numerical results are then summarized in Figures 3-5.

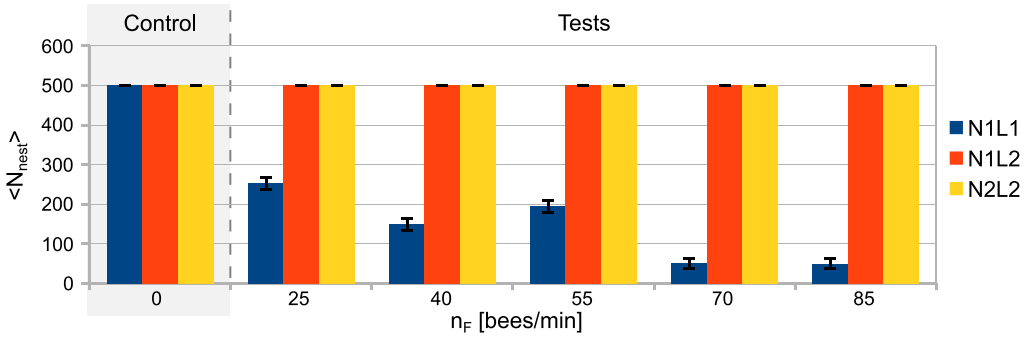

Figure 3. Representation of the mean number of bees that reach the nest, i.e., the mean of N_{nest} defined in Equation (19), arising from 10 independent numerical realizations for each combination of the bee behavioural assumptions and for each level of the traffic bees n_F. The error bars represent the variance obtained for each case.

Figure 3 reports the mean value and the relative variance of N_{nest} characterizing each case. These computational outcomes first highlight that all control cases are characterized by $N_{\text{nest}} = 500$ (i.e., $< N_{\text{nest}} >= 500$, with zero variance), thereby pointing out that the considered set of assumptions on bee behaviour equivalently reflect the empirical outcomes obtained by T. Latty and co-workers in the absence of conflicting directional information. In fact, as shown by the representative snapshots in Figure 4, in all

cases the honeybee swarm remains cohesive during all the dynamics and compactly reach the target nest without large deviations from the straight path. This further confirms that the proposed variation in the speed of uninformed bees w.r.t. [33], does not disrupt the coordinated flight of honeybees, but only gets the swarm migration slightly lower.

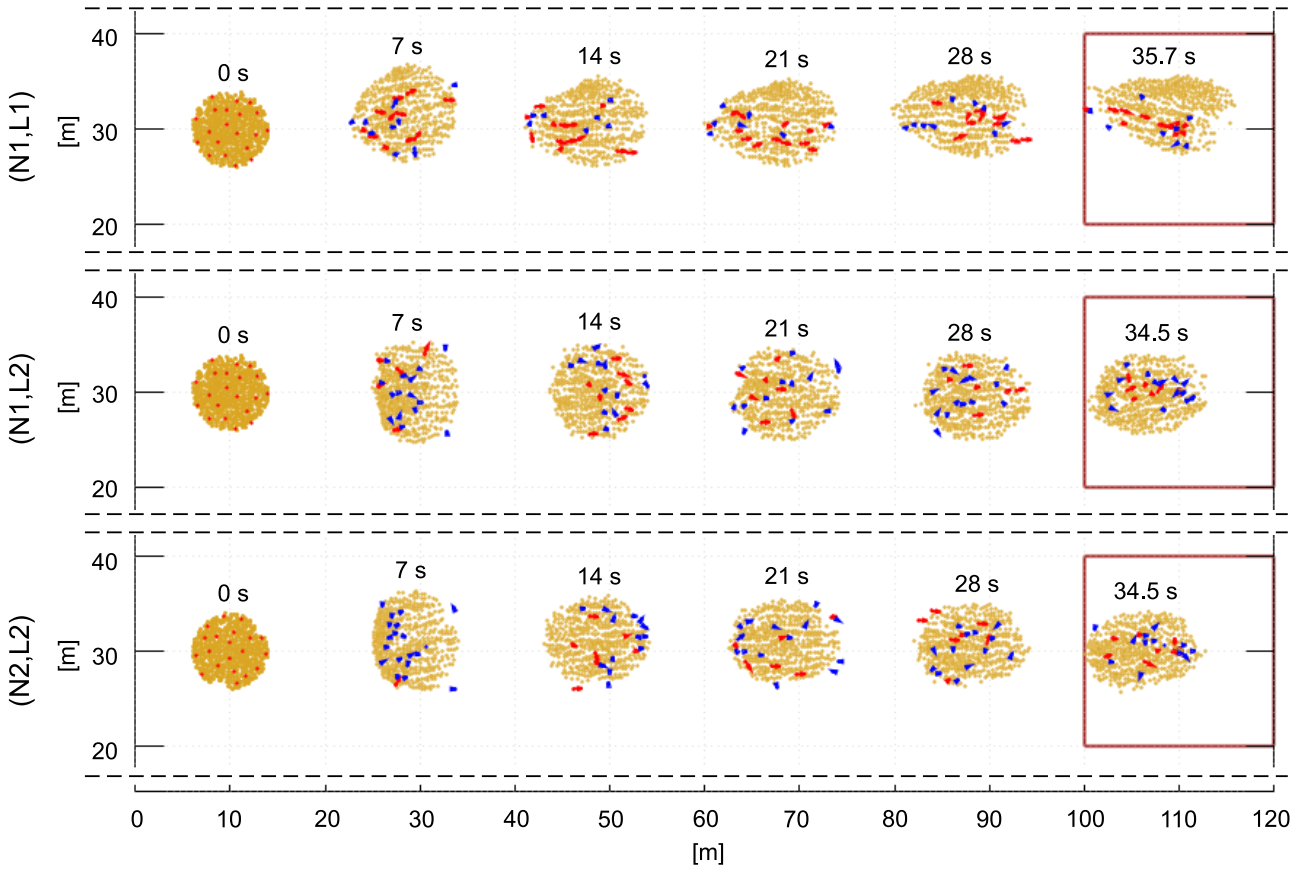

Figure 4. Control cases. Representative evolutions of the bee swarms in the absence of fast-moving bee foragers upon the three hypotheses combinations (N1, L1), (N1, L2) and (N2, L2). For each case, we here show only the portion of interest of the entire empirical scenario represented in Figure 1 (right panel). Yellow dots denote uninformed individuals, red dots scout bees with a streaker role, and blue dots passive leaders.

Figure 3 further highlights that upon the coupled set of assumptions (N1, L2) and (N2, L2), the swarm productive navigation obtained in test cases is never disrupted by the presence of conflicting directional information. In fact, regardless of the level of the traffic bees n_F, the mean number of bees that reach the target upon the coupled set of assumptions (N1, L2) and (N2, L2) is still $< N_{\text{nest}} >= 500$, with zero variance. In other words, the coordinated flight of the bee cloud remains undamaged after crossing the traffic area of fast moving foraging bees and achieves undisturbed the nest exactly as in the control case. This suggests that the presence of passive leaders waiting to be passed by the rest of swarm, i.e. assumption L2, prevents followers from synchronizing their movement to fast moving forager bees and disrupting the coordinated flight of the migrating colony. However, these in silico outcomes do not reflect the experimental findings presented in [34], and therefore lead us to discard both the assumptions (N1, L2) and (N2, L2).

On the contrary, honeybee dynamics obtained under the set of assumptions (N1, L1) are consistent with the empirical outcomes presented in [34], as we have $< N_{\text{nest}} > \ll 450$, with negligible variance, for any tested value of the bee traffic, see again Figure 3. In particular, only 24% of the numerical tests we performed under the set of assumptions (N1,L1) result in a coordinated and productive flight of the swarm. This is consistent with the work of T. Latty and coworkers, which observed that only one of their

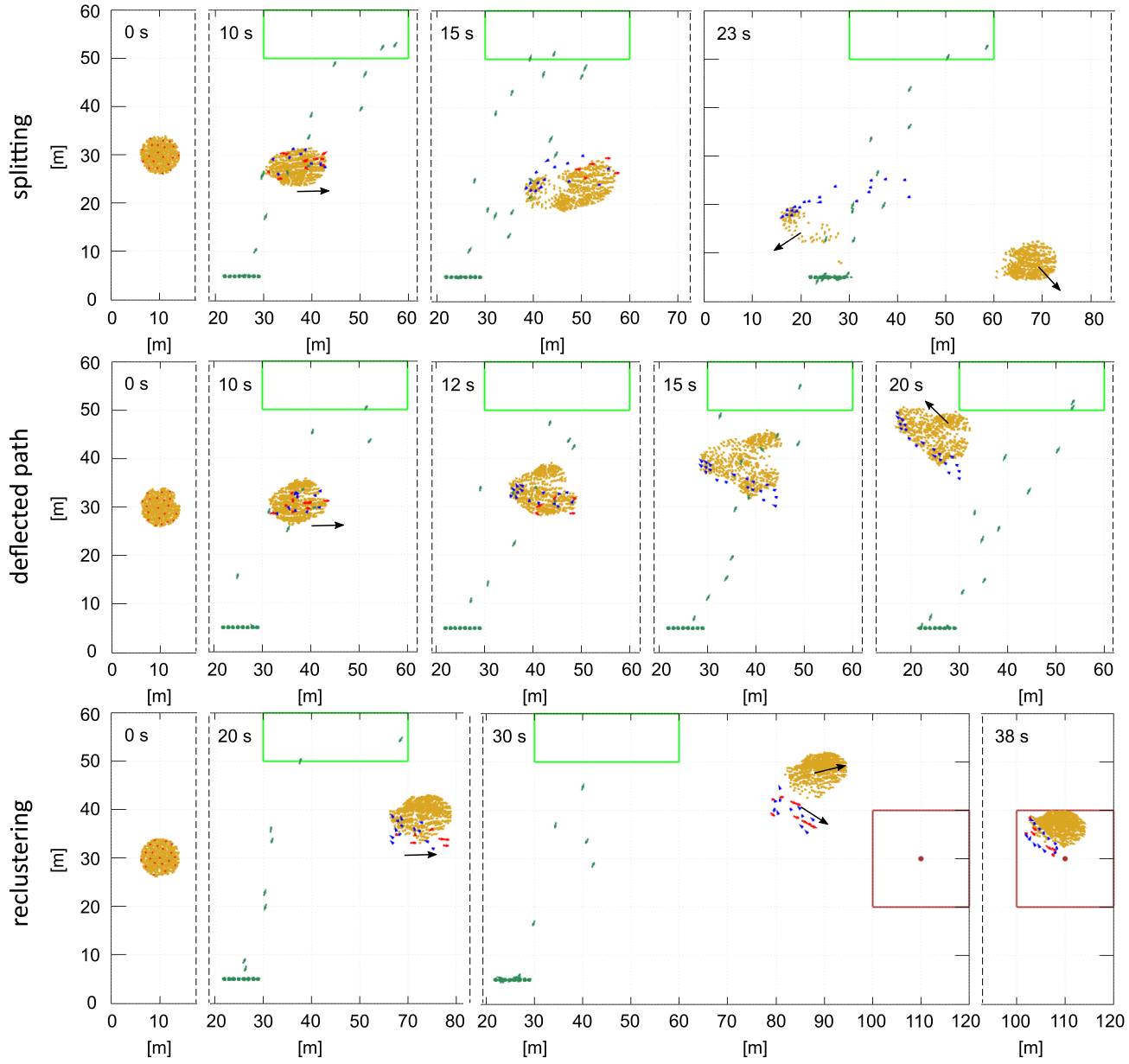

Figure 5. Test cases. Representative realizations of the dynamics of a swarm exposed to conflicting flight information, upon the behavioural set of assumptions (N1, L1). Yellow dots denote uninformed individuals, red dots scout bees with a streaker role, blue dots passive leaders, and greed dots forager bees.

six test swarms (i.e., 16%) reaches the nest. Despite the discrepancy in these values, this is in fact a good starting point with respect to the above discarded set of assumptions.

Furthermore, the swarm dynamics resulting under the coupled assumptions (N1, L1) present clear signs of disturbance of the scout guidance, including splitting, deviated path, and reclustering, in agreement with the experimental outcomes described by T. Latty and coworkers in [34]. In this respect, representative snapshots of three selected in silico experiments are provided in Figure 5. In the first row of Figure 5, once the swarm passes the highway of bee foragers, some uninformed individuals at the rear of the migrating group stop following the scouts and separate from the colony lured by foraging bees. According to hypothesis L1, scouts begin to follow these confused bees trying to recluster the swarm but, at the same time, they leave the rest of the uniformed individuals without a guide. These latter then mutually align and wander in a randomly selected direction. In the second row of Figure 5, as soon as the swarm

bumps into the forager highway, the uniformed bees begin to disperse, clearly confused by the presence of conflicting directional information. In this case, scout bees are able to recluster the colony but not to restore the productive migration of the swarm toward the nest, which therefore undergoes large deviations from the optimal path. Finally, in the bottom row of Figure 5, the migrating bee population initially seems to pass undamaged the traffic area where forager bees go back and forth between their hives and the food source. The effect of the exposition of the swarm to conflicting information in fact arises at about $20 - 30$ sec with the separation of the uninformed bees from the scouts individuals. However, the scout individuals result able both to regroup the entire colony and to re-establish the swarm guidance conducting all migrating bees to the nestbox. This is actually one of the few realizations in which, as observed in a experimental test in [34], the simulated swarm reaches the nest in spite of the interaction with bee foragers headed in a wrong direction.

4. Conclusions.

The biological phenomenon of honeybee swarming represents an interesting example of collective and coordinated motion of animal groups, which has increasingly captured the interest of both the biological and the modeling communities. The aim of this work has been to clarify the mechanisms underlying both the swarming process and the effect of conflicting directional information on the honeybee guidance. In this perspective, we have proposed an extended version of the model presented in [33] to test selected assumptions on bee behaviour, and to find out the rules of motions that reproduce in silico the experiments presented by T. Latty and coworkers in [34].

The numerical realizations described in the previous Section, have shown that both assumptions (N1, L2) and (N2, L2) are not able to successfully reproduce the experimental findings. In these cases, in fact, the bee cloud is able to achieve the nest, by substantially moving along the shortest straight path, even if it has to cross the traffic area of the forager bees to reach the target. Conversely, scenarios comparable to the experimental findings have emerged under the coupled hypotheses (N1, L1). In this case, in fact, the introduction of the conflicting directionality of the fast-flying foragers had a strong impact on the coordinated migration of honeybees and resulted in clear signs of disturbance of the scout guidance, including splitting, deviated path, and reclustering. For these reasons, we have been led to discard both the assumptions (N1, L2) and (N2, L2) in favor of (N1, L1). In other words, this study suggested that the leading plausible assumptions behind the swarming process, according to the proposed model, are the following: the uninformed bees could acquire the travel route synchronising their movement to all the insects sufficiently close to their position regardless of their status, provided that the passive leaders slowly come back from the front to the rear edge of the bee cloud.

In more details, under the behavioural assumptions (N1,L1) none of the simulated swarms presenting signs of disrupted guidance, steered in direction of the lucerne field, nor towards the eight colonies, but they rather seemed to randomly redirect their flight consistently with empirical evidences. This effect could be attributed to the fact that the foragers alternatively moves back and forth, i.e., the bee highway does not include one single preferential movement direction, but two opposite ones (i.e., from the colonies to the field and viceversa). Therefore, it could be interesting to investigate in future works the effect of a one-directional traffic flow on a flying swarm and, in this respect, to address new sets of simulations to the question of how many misleading bees are necessary to completely redirecting the swarm towards a different direction.

In literature, several studies have analysed the mechanisms underlying the decision-making process in presence of multiple conflicting movement information within groups of both humans and animals, see, for instance, [42,48,49]. These studies highlight that individuals generally tend to collectively select the direction adopted by the majority of the informed individuals, thus following the largest group. Furthermore, the quorum rule allows the naive individuals to neglect potentially incorrect information. Conversely, in the experiments by T. Latty and coworkers, as well as in the model outcomes so far presented, a small fraction of forager bees has caused the disruption of the swarm flight. Honeybee swarms therefore appear more sensitive to conflicting information with respect to the other groups studied in

literature. As suggested in [34], this observation could be related to the specific nature of the misleading information. In fact, in this experimental scenario the disturbing traffic line of the foragers represent an external source of flight information for the swarming bees while both in [42] and [48] divergent directional information compete within the same group. Furthermore, we remark that the specific streaker guidance mechanism itself could provide a minimum conflicting information when the leaders come back to the rear edge of the swarm in order to streak again. These considerations could explain the strong effect of the foraging bees on the swarming process.

Finally, a natural and substantial improvement of the model could be its three-dimensional extension. It would allow to enrich the description of the behaviour of all individuals, and in particular, to test the further assumptions that scout bees in a passive role tend to fly in the bottom region or along the external sides of the swarm in order to limit counterproductive interactions with uninformed individuals, as suggested in [8,9].

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