

Effects of heterogeneity in the consensus decision-making of a honeybee nest-site selection model

Author: Renzo Bruera.

Facultat de Física, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain.

Advisor: M. del Carmen Miguel López

Abstract: We study an agent based model for honeybees' consensual decision-making process. We reduce a previous stochastic model to a low-dimensional discrete dynamical system which permits a more efficient study of the behaviour of the system. We relate the dynamics of the system (namely, relaxation time and oscillation period) to the distribution of the roots of a polynomial on the complex plane and give a complete picture of the transition from no consensus to consensus in the case of two different nest sites.

I. INTRODUCTION

The benefits of collective and consensual decisions has been known for many years (see for example Condorcet's jury theorem). In particular, collective decision making in animals has been a field of study for some years now. In decision making processes, the integrity of the group in social species is often at stake. To preserve the benefits of life in the group, a decision that satisfies all individuals is often needed. That is, consensual decisions [1].

It has been observed that come the end of spring, honeybees colonies split. About two thirds of the bees leave with the queen, and a new queen is left behind. To decide where to build the new nest, several hundreds of scout bees inspect the surroundings. Once they have found a possible site, they come back to the colony and perform a waggle dance to advertise it to the rest of the bees. The duration of the dance depends on the perceived quality of the nest site they have discovered. A process of information exchange and mutual influence begins, in which good sites receive more advertising than bad ones, eventually leading to a consensus amongst the bees. When a particular site receives sufficient support from the colony, the bees move and settle the new nest there [2][3].

Here we study an agent based model for this process first put forward in [2]. We consider a system of N interacting bees in a mean-field-like approach, in which the evolution of each bee is modelled in terms of a discrete-time stochastic process. The aim of this report is to study the dynamics of the model and its "phase space", and give a precise characterisation of the transition from no consensus to consensus in terms of the relevant parameters. Decision making processes are ubiquitous phenomena in nature (be it amongst animals or in humans). Our final goal is to provide new insight to better understand the underlying mechanisms governing these phenomena, which will help us make better models and predictions for the behaviour of this type of systems.

In sec. III we present and validate the reduction of the model to a low-dimensional nonlinear dynamical system. In sec. IV we define consensus, study the transition to consensus, and provide an overview of the characteristic timescales for a system of two possible nesting sites.

II. THE MODEL

We begin by briefly describing the model, as found in [2]. We consider a system of N scout bees and n potential nesting sites, each with an associated quality $q_j \geq 0$. The system evolves at discrete time periods. At each time t , the state of the i -th bee is described by the pair $x_{i,t} = (s_{i,t}, d_{i,t})$, where $s_{i,t} \in \{1, \dots, n\}$ is the site for which the bee is dancing, and $d_{i,t} \geq 0$ is the remaining dancing time of that bee. From now on we will label with $s_{i,t} = 0$ those bees which are "undecided"; i.e., not dancing for any nest site. We will assume that at $t = 0$ all bees are undecided, so $x_{i,0} = (0, 0)$ for all $i \in \{1, \dots, N\}$.

The evolution of the system from time t to $t + 1$ is given in terms of each bee as follows.

(i) **If the bee i is undecided** ($s_{i,t} = 0$).

The bee will fly to one of the sites, j (including $j = 0$), with a certain probability, $p_{j,t}$, which is given by the formula

$$p_{j,t} = (1 - \lambda)\pi_j + \lambda f_{j,t}. \quad (1)$$

Here π_j is the *a priori* probability that site j be discovered, $f_{j,t}$ is the fraction of the total number of bees that were dancing for site j at time t , and λ is a parameter ranging from 0 to 1 that quantifies the interdependence of the bees. That is, $\lambda = 0$ represents the case of completely independent bees: the probability of discovering one of the nest sites depends solely on its *a priori* probability. On the other hand, $\lambda = 1$ should, in principle, represent the case of completely interdependent bees: the probability of discovering one of the sites depends only on the number of bees already dancing for that site. However, as it is seen from the initial conditions, this case is pathological, since no site would ever be discovered. We will therefore restrict ourselves to the cases $\lambda \in [0, 1)$.

Once a nest site is discovered by the bee i , it will start dancing for that site for a time $d_{i,t+1}$ proportional to the site's quality, q_j . For simplicity, we chose both magnitudes to be equal, $d_{j,t+1} = q_j$. Several modifications could be made at this stage, as it is done in [2]: one may consider that there is a certain "error" in the assessment of the site's quality, thereby introducing noise

in the system; or one might also include the possibility of mimicking the behaviour of other bees. In the present paper we restrict ourselves to the first scenario, in which the *waggle time* is exactly equal to the site's quality.

(ii) If the bee i is already dancing for one of the sites ($s_{i,t} \neq 0$).

In this case the bee will continue to dance for that site, and the remaining dancing time will be reduced in one unit, as long as time is not over yet:

$$x_{i,t+1} = \begin{cases} (s_{i,t}, d_{i,t} - 1) & \text{if } d_{i,t} > 1 \\ (0, 0) & \text{otherwise.} \end{cases} \quad (2)$$

III. EQUATIONS OF THE MODEL

Let $N_{j,t}$ be the number of bees dancing for site $j \neq 0$ at time t , and consider a specific nest site, say, j . Since only undecided bees can join one of the sites, the number of bees which will start dancing for site j , $\Delta_{j,t}^+$, is given by a binomial distribution $\Delta_{j,t}^+ \sim B(N_{0,t}, p_{j,t})$.

Similarly, the number of bees which will have run out of time and therefore stop dancing for site j , $\Delta_{j,t}^-$, is exactly the same as the number of bees that started dancing for that site q_j time periods before, $\Delta_{j,t}^- = \Delta_{j,t-q_j}^+$. Hence:

$$N_{j,t+1} = N_{j,t} + \Delta_{j,t}^+ - \Delta_{j,t}^- = N_{j,t} + \Delta_{j,t}^+ - \Delta_{j,t-q_j}^+ \quad (3)$$

The expected and most probable value of a binomially distributed random variable, $X \sim B(n, p)$, is given by $\langle X \rangle = np$. Taking the expected value of eq. 3 and dividing by N on both sides, since both Δ^+ are binomially distributed one gets:

$$f_{j,t+1} = f_{j,t} + f_{0,t}p_{j,t} - f_{0,t-q_j}p_{j,t-q_j}. \quad (4)$$

However, some care needs to be taken in passing from eq. 3 to eq. 4. One must bear in mind that the probabilities, $p_{j,t}$, are random variables themselves, since they depend on the fractions $f_{j,t}$ (see eq. 1) which obviously are random variables. Therefore, strictly speaking, eq. 4 does not correspond to an ‘‘ensemble average’’, so to say (an average over many systems characterised by the same parameters), but rather, it is the average over many systems which are *identical* at time t (both the parameters and the fractions, $f_{j,t}$, are the same at time t). Eq. 4 should then read: $\langle f_{j,t+1} \rangle = f_{j,t} + f_{0,t}p_{j,t} - f_{0,t-q_j}p_{j,t-q_j}$. Still, we will neglect this difference and will take eq. 4 as a good approximation for the evolution of our system, as will later be confirmed by numerical evidence.

The equations governing the evolution of the system will thus be eq. 4 (one for each $j \neq 0$) plus a ‘‘conservation equation’’. One must take into account that no bee will stop dancing for site j sooner than q_j time periods,

so the last term in eq. 4 only appears for $t > q_j$:

$$f_{j,t+1} = f_{j,t} + f_{0,t}p_{j,t} - \theta(t - q_j)f_{0,t-q_j}p_{j,t-q_j} \quad (\forall j \neq 0) \quad (5)$$

$$\sum_{j=0}^n f_{j,t} = 1 \quad \forall t \quad (6)$$

Where $\theta(t - q_j)$ is Heaviside's step function. We have reduced the analysis of the stochastic model described in the previous section to a much simpler discrete dynamical system, with initial conditions $f_{j,0} = 0$ for all $j \neq 0$ and $f_{0,0} = 1$.

Firstly we provide evidence that eq. 5 and 6 are indeed good approximations of the model. We have calculated the relative difference between the fractions obtained through simulations of the model vs. the approximate deterministic model (eq. 5 and 6) for parameter values $q_j = (7, 12, 15)$, $\lambda = 0.3$ and $\pi_j = (0.25, 0.15, 0.1)$, although the particular values are unimportant.

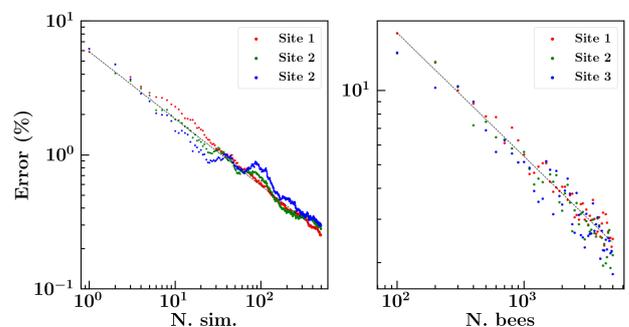


FIG. 1: Average error over 500 time cycles as a function of the number of runs of the simulation (left), and as a function of the number of bees in a single simulation (right). Dashed line indicates a power law $\propto x^{-1/2}$.

It is seen that the error stays well below 10% in most cases. Plus, it is interesting to note that the error decreases as the square root of both the number of runs of the simulation and the number of bees. Therefore, eqs. 5 and 6 are indeed a very good approximation of the model, even when compared to a single run.

IV. RESULTS

The structure of our results is as follows. First we will study in detail the conditions for the achievement of a consensus among the bees. In the second section we will discuss the existence and stability of a stationary state, and the time needed to reach it. All results correspond to the simplified model of eqs. 5 and 6 in the stationary state. It is also assumed that the sites are labeled so that $0 < q_1 \leq q_2 \leq \dots \leq q_n$, and since time cycles are discrete, we can assume $q_j \in \mathbb{N}$.

The existence of a stationary state was already seen in previous work on this model [4]. We provide an example for the sake of familiarity (FIG. 2).

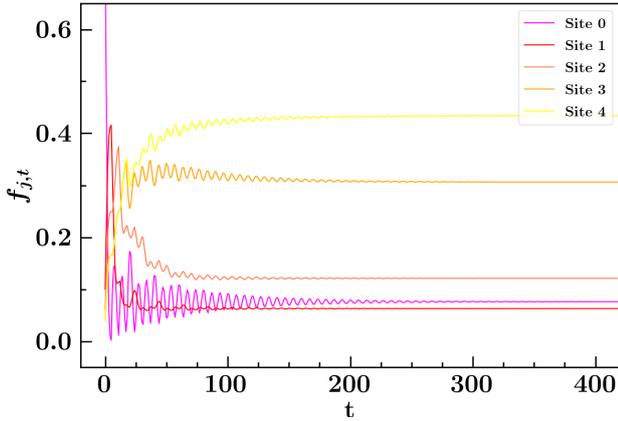


FIG. 2: Evolution of a system with $n = 4$, $\lambda = 0.6$, $q_j = (6, 12, 18, 19)$ and $\pi_j = (0.25, 0.15, 0.1, 0.1)$.

A. Consensus

The first step towards studying the consensus is to define it. As in [2] and [4], we will introduce a restrictive definition and a weak one. We are not only interested in understanding when bees reach consensus, but also when their decision is *correct* (i.e., when they choose the best site). For that purpose, we consider a system of two nest-sites and define a slightly different order parameter

$$Q = \frac{N_2 - 2N_1}{N_2} = 1 - 2\frac{f_1}{f_2} \quad (7)$$

thus, the *restrictive consensus* is achieved either when $f_2 > 2f_1$ or when $f_1 > 2f_2$, which yields $Q > 0$ or $Q < -3$. The first case represents a *correct* decision, while the latter corresponds to a poor choice. *Weak consensus* is achieved either when $f_2 > f_1$ or when $f_1 > f_2$, which yields $Q > -1$ or $Q < -1$. We shall refer to the case $Q > 0$ simply as ‘consensus’.

In [3] it is shown (for a different model) that the behaviour of the bees verifies Weber’s law. Roughly speaking, this law states that for a certain stimulus, the minimum noticeable variation in the stimulus is proportional to the magnitude of the stimulus. Following this idea, we define the parameter Δ ,

$$\Delta = \frac{q_2 - q_1}{q_2 + q_1} \quad (8)$$

It is obvious from the definition and the fact that $0 < q_1 < q_2$ that $0 < \Delta < 1$. This parameter introduces a remarkable simplification. We see that Q is approximately independent of the particular values of q_1 and q_2 and only depends on Δ , so we have $Q \approx Q(\{\pi_i\}, \lambda, \Delta)$ (FIG. 3).

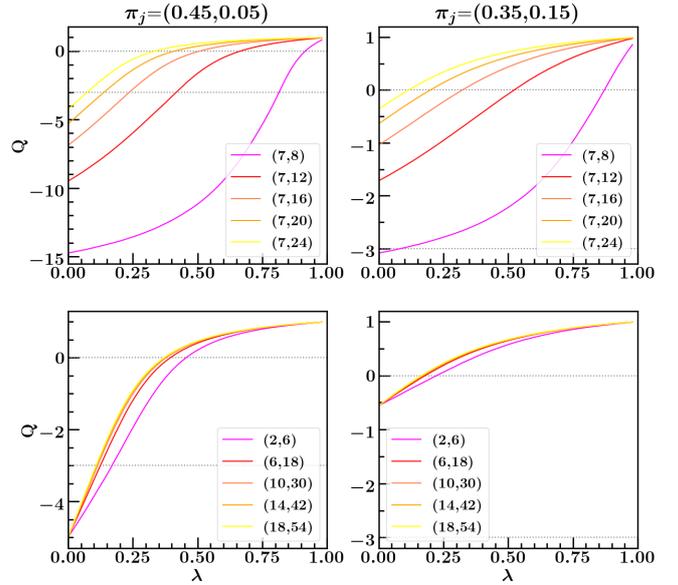


FIG. 3: Consensus parameter Q as a function of λ . Top row corresponds to arbitrary values of (q_1, q_2) , indicated in parentheses; bottom row corresponds to $\Delta = 1/2$.

We are interested in identifying the transition from no consensus to consensus. Therefore we set

$$Q(\{\pi_i\}, \lambda, \Delta) = 0 \implies \lambda = \lambda(\{\pi_i\}, \Delta) \quad (9)$$

We call this function the transition λ , noted λ_t . Since Q is an increasing function of λ , this will give us the minimum value of λ for which consensus is achieved. To compute the values of λ_t we have applied the bisection method to $Q(\{\pi_i\}, \lambda, \Delta)$ for fixed values of $\{\pi_i\}$ and Δ . We observe that for fixed values of $\{\pi_i\}$, λ_t decreases linearly in Δ , $\lambda_t \approx a\Delta + b$. Intuitively, this conveys the idea that if the qualities are different enough, bees will more easily choose the best site.

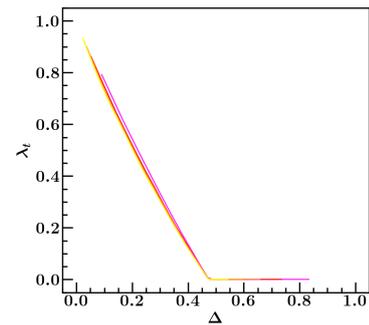


FIG. 4: λ_t as a function of Δ for $\pi_j = (0.35, 0.25)$ for various values of (q_1, q_2) . Notice the (quasi) linear relation $\lambda_t(\Delta)$.

The limit $\Delta \rightarrow 0$ represents the case of (almost) identical nest sites. In that situation bees must rely heavily on each other to choose the best site, hence $\lambda_t \rightarrow 1$. Recall

that b is the value of λ_t for $\Delta = 0$, so b should take values around 1 with little variation. Since $\lambda \geq 0$ we see that $\lambda_t = 0$ for $\Delta \geq \Delta_c$, with $\Delta_c = -b/a$.

Next we analyse the behaviour of the coefficients a and b in terms of the a priori probabilities, $\{\pi_i\}$. We see that the values of a , b and Δ_c are approximately independent of the particular values of π_1 and π_2 and only depend on the ratio $\pi_2/(\pi_1 + \pi_2)$. We observe an abrupt change in the values of a and b at around $\pi_2/(\pi_1 + \pi_2) = 1/2$, that is, when $\pi_1 = \pi_2$. We call this the *equiprobability point*.

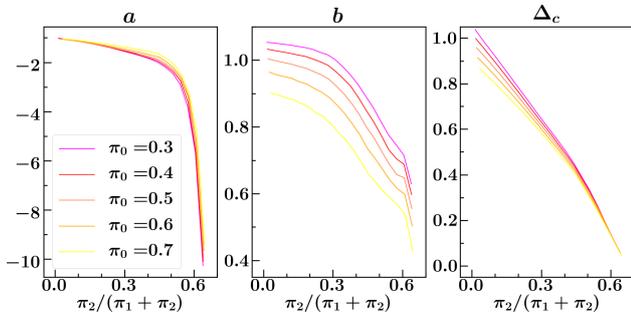


FIG. 5: Values of a , b and Δ_c as a function of $\pi_2/(\pi_1 + \pi_2)$.

Beyond this point, the slope a becomes increasingly negative, $a \rightarrow -\infty$, so $\Delta_c \rightarrow 0$. This means that beyond the equiprobability point, $\lambda_t = 0$ for all Δ : consensus is achieved irrespective of the values of λ and Δ .

B. Dynamics

Simulations have shown that at sufficiently long times, $t \gg \max(\{q_j\})$, the evolution of $f_{j,t}$ is of the form,

$$f_{j,t} \simeq F_j^{eq} - A_j e^{\omega t} \quad (10)$$

where F_j^{eq} are the equilibrium (or stationary) values of f_j , and A_j and ω are constants, which generally take complex values, in agreement with the oscillations observed in simulations like that in FIG. 2. While A_j depends on the site considered, ω does not. Of course, for the system to converge it is necessary that $\text{Re}[\omega] < 0$. Numerical evidence suggests that this is indeed the case, but to further study the matter, we will consider the limiting case $\lambda = 0$. In this limit, eq. 5 becomes “simply” a linear difference equation, which can be solved exactly. Combining eqs. 5, 6 and 1 one gets:

$$f_{j,t+1} = f_{j,t} - \pi_j \sum_{i>0} (f_{i,t} - f_{i,t-q_j}) \quad (11)$$

For simplicity, we will consider the case of two different nest sites, but the procedure is similar for any number of sites. This equation can be written in matrix form as

$$\begin{pmatrix} f_{1,t+1} \\ f_{2,t+1} \end{pmatrix} = \begin{pmatrix} 1 - \pi_1 & -\pi_1 \\ -\pi_2 & 1 - \pi_2 \end{pmatrix} \begin{pmatrix} f_{1,t} \\ f_{2,t} \end{pmatrix} + \begin{pmatrix} \pi_1 & \pi_1 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} f_{1,t-q_1} \\ f_{2,t-q_1} \end{pmatrix} + \begin{pmatrix} 0 & 0 \\ \pi_2 & \pi_2 \end{pmatrix} \begin{pmatrix} f_{1,t-q_2} \\ f_{2,t-q_2} \end{pmatrix} \quad (12)$$

Which we write as $\vec{f}_{t+1} = M_0 \vec{f}_t + M_1 \vec{f}_{t-q_1} + M_2 \vec{f}_{t-q_2}$. The characteristic polynomial of eq. 12 is

$$P(x) = x^{q_2}(x-1)^2 \cdot [x^{q_2} + (\pi_1 + \pi_2)x^{q_2-1} + \dots + (\pi_1 + \pi_2)x^{q_2-q_1} + \pi_2 x^{q_2-q_1-1} + \dots + \pi_2] \quad (13)$$

The solution of eq. 12 is a linear combination of vectors $\nu_k \in \ker(\Delta(a_k) - a_k I)$, where $\Delta(a) = M_0 + a^{-q_1} M_1 + a^{-q_2} M_2$, that evolve exponentially as $(a_k)^t \nu_k$, where a_k are the roots of the characteristic polynomial. If a root a_i has multiplicity $r > 1$ and $\dim \ker(\Delta(a_i) - a_i I) = s < r$, we must consider vectors $\nu_i^{(s+1)}, \dots, \nu_i^{(r)}$ with $\nu_i^{(m)} \in \ker(\Delta(a_i) - a_i I)^m$ ($m \in \{2, \dots, r-s+1\}$) that evolve as $\nu_i^{(s+m-1)}(t) = t^{m-1} (a_i)^t \nu_i^{(s+m-1)}$.

We see that the last factor of eq. 13 is a polynomial, $Q(x)$, of degree q_2 with real, positive, nondecreasing coefficients ($0 < \pi_2 \leq \dots \leq \pi_1 + \pi_2 \leq \dots \leq 1$). By the Eneström-Kakeya theorem we know that the roots of this polynomial, $\{a_k\}$, lie within the unit disk on the complex plane, $|a_k| \leq 1 \forall k$. Plus, it can be shown that for $a = 1$ there are two linearly independent eigenvectors, which therefore remain constant in time.

We can conclude that unless one of the roots of $Q(x)$ lies exactly on the the unit circle, the system will converge to a stationary state. Moreover, the time it will take to converge, τ , will be determined by the root with the greatest absolute value, a_{max} , so in eq. 10 we can substitute $\omega = \ln a_{max}$. Thus, $\tau \sim -1/\ln |a_{max}|$ and the oscillation period, T , is given by $T = 2\pi/\text{Im}[\omega]$. In principle, if for some value of the parameters one of the roots of $Q(x)$ were to lie on the unit circle, the system would undergo a Hopf bifurcation-like transition. However, numerical evidence indicates that this is unlikely to be the case.

Surprisingly, simulations show that τ increases as the values of q_j increase - one would expect that is if the quality of one site is significantly greater than that of the others bees should have no trouble making up their minds, so to say. We have seen that as $q_2 \rightarrow \infty$ the roots of polynomial $Q(x)$ get closer and closer to the unit circle, and thus $-1/\ln |a_{max}| \rightarrow +\infty$.

Even though strictly speaking this results only apply to the case $\lambda = 0$, the behaviour of cases with $\lambda \neq 0$ is qualitatively similar, as we shall see. In [4] it is already pointed out that increasing values of λ result in higher relaxation times. We compare the analytic values of τ , calculated as $\tau_{an} = -1/\ln |a_{max}|$ with the values obtained by regression of the computation of eq. 5.

The first thing one can notice is the appearance of remarkable oscillations in the value of τ as the qualities change, with a tendency to increase as q_2 increases. As already mentioned, increasing the value of λ dramatically increases τ , but the qualitative behaviour (position of maxima and minima and overall tendency) is the same. The second interesting thing is that when considered as a function of Δ , the maxima and minima become aligned. That is, their position only depends on Δ . We have been unable to determine any physical meaning of these

oscillations in the relaxation time, and their existence is quite counterintuitive, as one would rather expect a monotonous behaviour of τ as a function of q_2 . However, this behaviour reveals the existence of particular conditions in which consensus is achieved more efficiently.

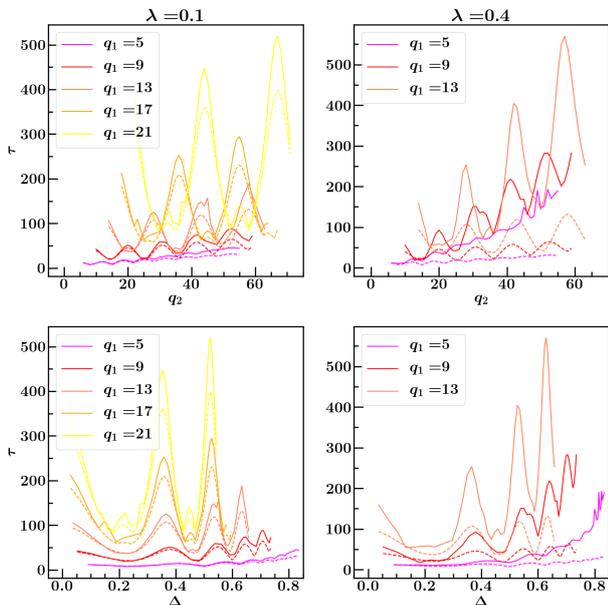


FIG. 6: Relaxation time τ computed analytically (dashed lines) and from linear regression (solid lines) as a function of q_2 (top row) and as a function of Δ , for two values of λ (left and right columns). Different colours correspond to different values of q_1 , with $\pi_j = (0.45, 0.05)$. On the right column higher values of q_1 have been omitted to make the comparison visible.

V. CONCLUSIONS

In this report we have shown how we can obtain equations for the average behaviour of an agent-based model, which allows a much more powerful and efficient analysis of the behaviour of the system, while retaining the relevant traits.

We have defined a parameter to quantify consensus amongst the bees and have performed a thorough study

of the transition from no consensus to consensus in a system of two nest sites, which has been possible thanks to the remarkable observation that the analysis can be simplified enormously by introducing the parameter Δ . This has shown the strong dependence of consensus not only on the qualities of the sites, but on the environmental conditions (here represented by the a priori probabilities, π_j), and has led to a complete and precise characterisation of the phase space in the transition region.

We have shown how mutual influence amongst the bees (here represented by the parameter λ) plays a central role in the reach of consensus when decisions are difficult to make, as had already been pointed out in previous work [2][4]. However, this comes at the cost of greatly increasing the time needed to reach consensus, as already mentioned in [4], thereby reducing the process's efficiency. This is in agreement with observations that bees perform better without the waggle dance in adverse conditions (i.e., when a high interdependence parameter, λ , is needed to reach consensus), as shown in [5].

While the analysis only applies to systems of two nest sites, one may notice in that the definition of Δ corresponds to the quotient between the standard deviation ($|q_2 - q_1|/2$) and the average value $((q_2 + q_1)/2)$ of the qualities. This suggests the possibility that similar studies may be carried out for higher-dimensional systems, by exploring the phase space in terms of a similar parameter (σ/μ , for example) using probabilistic distributions for the qualities.

Secondly, we have provided a way to study qualitatively the dynamics of the system by relating the relaxation time to the distribution of the roots of a polynomial in the complex plane. Even though it has been derived for the case $\lambda = 0$, we have shown that the main traits are maintained for other values of λ . However, we have been unable to give the highly oscillatory, counterintuitive behaviour of the relaxation time any physical meaning.

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