A model of the best-of-N nest-site selection process in honeybees

Andreagiovanni Reina,\textsuperscript{1,*} James A. R. Marshall,\textsuperscript{1} Vito Trianni,\textsuperscript{2} and Thomas Bose\textsuperscript{1}

\textsuperscript{1}Department of Computer Science, University of Sheffield, UK
\textsuperscript{2}ISTC, Italian National Research Council, Rome, Italy

(Dated: November 24, 2016)

Abstract

The ability of a honeybee swarm to select the best nest site plays a fundamental role in determining the future colony’s fitness. To date, the nest-site selection process has mostly been modelled and theoretically analysed for the case of binary decisions. However, when the number of alternative nests is larger than two, the decision process dynamics qualitatively change. In this work, we extend previous analyses of a value-sensitive decision-making mechanism to a decision process among N nests. First, we present the decision-making dynamics in the symmetric case of N equal-quality nests. Then, we generalise our findings to a best-of-N decision scenario with one superior nest and N – 1 inferior nests, previously studied empirically in bees and ants. Whereas previous binary models highlighted the crucial role of inhibitory stop-signalling, the key parameter in our new analysis is the relative time invested by swarm members in individual discovery and in signalling behaviours. Our new analysis reveals conflicting pressures on this ratio in symmetric and best-of-N decisions, which could be solved through a time-dependent signalling strategy. Additionally, our analysis suggests how ecological factors determining the density of suitable nest sites may have led to selective pressures for an optimal stable signalling ratio.

PACS numbers: 87.23.Cc, 87.10.Ed, 87.23.Ge

\textsuperscript{*}a.reina@sheffield.ac.uk

arXiv:1611.07575v1 [physics.bio-ph] 22 Nov 2016
I. INTRODUCTION

Collective consensus decision-making, in which all members of a group must achieve agreement on which of several options the group will select, is a ubiquitous problem. While groups may be subject to conflicts of interest between members (e.g. [1, 2]), in groups where individuals’ interests align it is possible to look for mechanisms that optimise group-level decisions [3]. In this paper we model collective consensus decision-making by social insect colonies, in the form of house-hunting by honeybee swarms [4, 5], but similar decision-making problems manifest in diverse other situations, from societies of microbes [6] to committees of medical experts [7, 8]. Much attention has been paid to optimisation of speed-accuracy trade-offs in such situations (e.g. [9–13]) but theory shows that where decision makers are rewarded by the value of the option they select, rather than simply whether or not it was the best available, managing speed-accuracy trade-offs may not help to optimise overall decision quality [14]. Here we analyse a value-sensitive decision-mechanism inspired by cross-inhibition in house-hunting honeybee swarms [4, 5]. One instance of value-sensitivity is the ability to make a choice when the option value is sufficiently high—i.e., it exceeds a given threshold. In case no option is available with high-enough value, the decision maker may refrain from commitment to any option, in the expectation that a high-quality option may later become available. As a consequence, value-sensitivity is relevant above all in scenarios in which multiple alternatives exist and possibly become available at different times. Another interesting property of the investigated decision-making mechanism is its ability to break decision deadlocks when the available options have equal quality. Deadlock breaking has been shown to be of interest in a series of scenarios, including collective motion [15, 16], spatial aggregation [17, 18] and collective transport [19]. Previous studies of value-sensitive decision-making have been limited to binary decision problems, although it is known that honeybee swarms and other social insect groups are able to choose from among many more options during the course of a single decision [20–24]. Here, we generalise the model of [5] and examine its ability to exhibit value-sensitive deadlock-breaking when choosing between N equal alternatives, and also to solve the best-of-N decision problem in which one superior option must be selected over N – 1 equal but inferior distractor options.
II. MATHEMATICAL MODEL

A. General N-options case

Our work builds on a previous model that describes the decentralised process of nest-site selection in honeybee swarms [4]. The decentralised decision-making process is modelled as a competition to reach threshold between subpopulations of scout bees committed to an option (i.e., a nest). The model is described as a system of coupled ordinary differential equations (ODEs), with each equation representing the subpopulation committed to one option; an equation describing how the subpopulation of uncommitted scout bees changes over time is implicit, since the total number of bees in the system is constant over the course of a decision. Uncommitted scout bees explore the environment and, when they discover an option $i$, estimate its quality $v_i$, and may commit to that option at a rate $\gamma_i$. The commitment rate to option $i$ for discovery is assumed to be proportional to the option’s quality, that is, more frequent commitments to better quality nests ($\gamma_i \propto v_i$). Committed bees may spontaneously revert, through abandonment, to an uncommitted state at rate $\alpha_i$. Here, the abandonment rate is assumed to be inversely proportional to the option’s quality, that is, poorer options are discarded faster ($\alpha_i \propto v_i^{-1}$). This abandonment process allows bees quickly to discard bad options, and endows the swarm with a degree of flexibility since bees are not locked into their commitment state. In addition to these two individual transitions, which we label as spontaneous, scout bees interact with each other to achieve agreement on one option. In particular, the model proposed in [4] identifies two interaction forms: recruitment and cross-inhibition, which give rise to interaction transitions. Recruitment is a form of positive feedback, by which committed bees actively recruit, through the waggle dance, uncommitted bees [20, 25, 26]. Therefore, the rate by which uncommitted bees are recruited to option $i$ is determined by both the number of bees committed to $i$ and the strength of the recruitment process for $i$, labelled as $\rho_i$. Similarly to discovery, recruitment is assumed to be proportional to the option’s quality ($\rho_i \propto v_i$). The other interaction form that occurs in this decision process is cross-inhibition. Cross-inhibition is a negative feedback interaction between bees committed to different options; when a bee committed to option $i$ encounters another bee committed to another option $j$ (with $j \neq i$), the first may deliver stop signals to the second which reverts to an uncommitted state at a rate $\beta_{ij}$. For binary choices stop-signalling has previously been shown to be a control parameter in a value-sensitive decision-making mechanism, in particular setting a value threshold for deadlock maintenance or
breaking in the case of equal-quality options [4, 5]. In this study, in agreement with the assumptions made above, we assume cross-inhibition proportional to the quality of the option that the bees delivering the stop signal are committed to. In other words, bees committed to better options will more frequently inhibit bees committed to other options ($\beta_{ij} \propto v_j$, see Section II B for more details).

As described above, the set of bees committed to the same option is considered as a sub-population, and the model describes changes in the proportion of bees in each sub-population with respect to the whole bee population. We assume that a decision is reached when one decision sub-population reaches a quorum threshold [27–29]. Precisely, $x_i$ and $x_u$ denote the proportion of bees committed to option $i$ and uncommitted bees, respectively, with $N$ options and $i \in \{1, \ldots, N\}$. A version of the model that we analyse in this study has been originally proposed for the binary decision case (i.e., $N = 2$) in [4] and, later, extended to a more general case of $N$ options in [30]. Analysis of the value-sensitive parameterisation has been presented by Pais et al. in [5]. Here we generalise this model, and extend its analysis to the best-of-$N$ case. The general models is:

$$\left\{ \begin{array}{l}
\frac{dx_i}{dt} = \gamma_i x_u - \alpha_i x_i + \rho_i x_u x_i - \sum_{j=1}^{N} x_j \beta_{ji} x_i, \quad i \in \{1, \ldots, N\}, \\
x_u = 1 - \sum_{i=1}^{N} x_i
\end{array} \right. \quad (1)$$

B. A novel parameterisation for value-sensitive decision-making

Following earlier work [4, 5, 11], we assume a value-sensitive parameterisation by which the transition rates are proportional (or inversely proportional) to the option’s quality $v_i$, as mentioned above. Previous work investigated the dynamics of the system (1) with $v_i = \gamma_i = \rho_i = \alpha_i^{-1}$ and $\beta_{ij} = \beta$ for two options (i.e., $N = 2$) [5]. Such a parameterisation displays properties that are both biologically significant, and of interest for the engineering of artificial swarm systems [30, 31]. One of the main system characteristics is its ability to adaptively break or maintain decision deadlocks when choosing between equal-quality options, as a function of those options’ quality. In fact, it has been shown that when the swarm has to decide between two equally and sufficiently good options, it is able to implement the best strategy: that is, to randomly select any of the two options in a short time. However, in the supplementary material [32] we show that the system’s dynamics qualitatively change for more than two options, i.e., $N > 2$: by adopting the parameter-
isation proposed in [5], the swarm cannot break a decision deadlock for more than two equally good options (see Figure S1 and Section S2 in the supplementary material [32]).

In this study, we extend previous work by introducing a novel parameterisation that features value-sensitivity also for $N > 2$. Unlike [5], we investigate a more general parameterisation in which we decouple the rates of spontaneous transitions (i.e., discovery and abandonment) from the rates of interaction transitions (i.e., recruitment and cross-inhibition), similarly to [30]. The proposed parameterisation is $\gamma_i = k v_i$, $\alpha_i = k / v_i$ and $\rho_i = h v_i$, where $k$ and $h$ modulate the strength of spontaneous and interaction transitions, respectively.

For the cross-inhibition parameter, we consider the general case in which $\beta_{ij}$ is the product of two components: $\beta_{ij} = [A \cdot D]_{ij}$, where $A$ and $D$ are two matrices and $\beta_{ij}$ is the $ij^{th}$ element of their product. The former, $A$, is an adjacency matrix that expresses how subpopulations interact with each other. Therefore, the entries $a_{ij}$ of $A$ are either 1 or 0 depending on whether interactions between subpopulations $i$ and $j$ can occur or not. The introduction of the adjacency matrix allows us to define if inhibitory messages are delivered only between bees committed to different options (i.e., cross-inhibition), or also between bees committed to the same option (i.e., self-inhibition, as self refers to the own subpopulation). In this study, in accordance with behavioural results in the literature [4], we do not include self-inhibitory mechanisms; thus the adjacency matrix contains zeros along its diagonal (i.e., $a_{ii} = 0, \forall i$). On the other hand, we consider that interactions between different subpopulations are equally likely, and this is reflected by having $a_{ij} = 1, \forall i \neq j$. The second component, $D$, is a matrix that quantifies the stop-signal strength, and allows us to define, if needed, different inhibition strengths for each sender/receiver couple. In other words, through $D$ the inhibitory signals can be tuned not only as a function of the option quality of the inhibiting population, but also as a function of the option quality of the inhibited population. In this analysis, we model dependence of cross-inhibition strength solely on the value of the option that inhibiting bees are informed about; thus we investigate the system dynamics for a diagonal cross-inhibition matrix with values $hv_1, \ldots, hv_N$ along its diagonal, where $h$ is a constant interaction term (as for recruitment), and the $v_i, i \in \{1, \ldots, N\}$, are qualities of the options the inhibiting populations are committed to. Hence we parameterise the cross-inhibition term as $\beta_{ij} = A_{ik} D_{kj} = hv_i$, which determines the other parameters of the system as (1)

$$\gamma_i = k v_i, \quad \alpha_i = k v_i^{-1}, \quad \rho_i = h v_i, \quad \beta_{ij} = h v_i.$$ 

(2)

In the following, we introduce the ratio $r = h/k$ between interaction and spontaneous transi-
tions. The ratio $r$ acts as the control parameter for the decision-making system under our new formulation, whereas the strength of cross-inhibition (stop-signalling rate) was the control parameter in the original analysis [5]. This new control parameter has a simple and natural biological interpretation, as the propensity of scout bees to deliver signals to others (here, represented by the interaction term $h$), relative to the rate of spontaneous transitions (here, represented by the term $k$).

We show that the novel parameterisation displays the same value-sensitive decision-making properties of the binary system that are shown in previous studies [5]. In particular, we confirm that, in the symmetric case of two equal-quality options, the ratio of interaction/spontaneous transitions, $r = h/k$, determines when the decision deadlock is maintained or broken (see Figure S2(a) in the supplementary material). Additionally, we show in Figure S2(b) in the supplementary material that the interaction ratio $r$ determines the just-noticeable difference to discriminate between two similar value options, in a manner similar to Weber’s law, as demonstrated for the cross-inhibition rate in [5].

C. The best-of-N decision problem

As well as presenting a general analysis of the system dynamics for small $N$ ($N = 3$), for larger values of $N$ we next analyse the best-of-N decision scenario with one superior and $N - 1$ inferior options. This scenario is consistent with empirical studies undertaken with bees [22], ants [23, 24] and with neuro-psychological studies [33]. Considering such a scenario allows us to investigate the system dynamics as a function of four parameters: (i) the number of options $N$, (ii) the superior option $s$’s quality $v = v_s$, (iii) the ratio between the quality of any of the equal-quality inferior options and of the superior option $\kappa = v_i/v_s$ (with $i \neq s$), and (iv) the ratio between interaction and spontaneous transitions $r = h/k$. The system of Equation (1) with the parameterisation given in (2) can be rewritten in terms of these four parameters as:

\[
\begin{align*}
\frac{dx_1}{d\tau} &= v x_u - \frac{x_1}{v} + r v x_1 \left[ x_u - \sum_{j \neq 1} \kappa x_j \right], \\
\frac{dx_i}{d\tau} &= v \kappa x_i - \frac{x_i}{v \kappa} + r v x_i \left[ \kappa (x_u - \sum_{j \neq 1, i} x_j) - x_1 \right], \quad i = 2, \ldots, N, \\
x_u &= 1 - \sum_{i=1}^{N} x_i
\end{align*}
\] (3)
where $x_1$ is the population committed to the best (superior) option (i.e., $\nu = \nu_1 \geq \nu_i, \forall i \in \{2, \ldots, N\}$) and $\tau = kt$ is the dimensionless time.

The system in (3) is characterised by $N$ coupled differential equations and one algebraic equation. In Equations (S9) in the supplementary material, we reduce this system to a system of two coupled differential equations by aggregating the dynamics of the populations committed to the inferior options. In Section III we show that this system reduction allows us to attain qualitatively correct results for arbitrarily large $N$.

III. RESULTS

We first investigate the system dynamics for the case of $N = 3$ options, then we generalise our findings to arbitrarily large $N$. The reduced system (Equation (S9) of the supplementary material) allows us to investigate the dynamics for arbitrarily large numbers of options $N$ without increasing the complexity of the analysis. In Section III A we show the analysis results for the symmetric case of $N$ equally good options, while in Section III B we report the results for different quality options.

A. Symmetric case

We start by analysing the symmetric case of $N$ equal-quality options (i.e. $\kappa = 1$). The simplicity of the reduced system (Equation (S9)) allows us to determine the existence of two bifurcation points which are determined by the parameters $r$, $\nu$ and $N$, and we show the bifurcation conditions in terms of the control parameter $r$ as:

$$r_1 = f_1(\nu, N), \quad r_2 = f_2(\nu, N).$$

(4)

In the supplementary material, we report the complete equations for (4) as functions of $(\nu, N)$ (see Equation (S17)) or, more generally, of $(\gamma, \alpha, \rho, \beta)$ (see Equation (S15)). In Figure I(a) we show the stability diagram of the system (3) in the parameter space $(r, \nu)$, for $N = 3$. When the pair $(r, \nu)$ is in area I, the system cannot break the decision deadlock but remains in an undecided state with an equal number of bees in each of the three committed populations. This result can be also seen in Figure I(b), where we display the bifurcation diagram for the specific case $\nu = 5$. Here, low values of $r$ correspond to a single stable equilibrium representing the decision deadlock.
FIG. 1. Dynamics of the complete decision system of Equation (3) for the symmetric case $\kappa = 1$ (i.e., $v_1 = v_2 = v_3 = v$). Panel (a) shows the stability diagram as a function of the parameter $r$ and the quality $v$ for $N = 3$ options. The two curves represent the two bifurcations $r_1$ (blue solid) and $r_2$ (red dashed) of Equations (4). There are three possible system phases: (I) decision-deadlock, (II) coexistence of decision deadlock and stable solutions for any option, and (III) decision for any option. Panel (b) shows the bifurcation diagram for $N = 3$ and $v = 5$ as a function of the parameter $r$. This illustrates the three system phases when varying the control parameter $r$. Note that, due to the 2D visualisation, some equilibria overlap and thus the bottom branches in panel (b) correspond to the two overlapping equilibria for the options $x_2$ and $x_3$. Panel (c) shows a stability diagram that visualises the dependence of the bifurcation points $r_1$ (solid lines) and $r_2$ (dashed lines) as a function of $N$ for varying $v \in \{1, 2, 3, 5, 10\}$, and reports the same three system phases.

Increasing the signalling ratio, the system undergoes a saddle node bifurcation when $r = r_1$ in Figure 1(b), at which point a stable solution for each option appears and the selection by the swarm of any of the $N$ equally-best quality options is a feasible solution. However, for $(r, v)$ in area II of Figure 1(a), the decision-deadlock remains a stable solution and only through a sufficient bias towards one of the options the system converges towards a decision. This system phase can be visualised in the bifurcation diagram of Figure 1(b) and in the phase portrait of Figure S3(b) in the supplementary material: The system escapes from the decision-deadlock attraction basin if noise leads the population to jump into a neighbouring basin corresponding to a unique choice.

The system undergoes a second bifurcation at $r = r_2$ in Figure 1(b), that changes the stability of the decision-deadlock from stable ($r < r_2$) to partially unstable (saddle, $r > r_2$). Therefore, for sufficiently high values of the signalling ratio (area III in Figure 1(a)), the unique possible outcome is the decision for any of the equally best quality options. The central solution of indecision remains stable (i.e., attracting) with respect to only one manifold, i.e., the line for equal-size
committed populations, while it is unstable with respect to the other directions (see the phase portraits of Figures S3(c-d) and the video in the supplementary material). Instead, the unstable saddle points that surround the central solution have opposite attraction/repulsion manifolds. For this reason, several unstable equilibria can be near to each other, as in Figure 1(b).

The analysis of the system with three options reveals three system phases as a consequence of the two bifurcations determined by \( f_1 \) and \( f_2 \) (Equation (4)). Increasing the number of options, the number of system phases increases. In particular, for every other \( N \), at odd values (i.e., \( N \in \{5, 7, 9, \ldots \} \)), a new bifurcation point between \( r_1 \) and \( r_2 \) appears. In Figure S6 in the supplementary material, we report the bifurcation diagrams for \( v = 5 \) and \( N \in \{4, 5, 6, 7\} \). Despite the system phase increase, the main dynamics for any \( N > 2 \) can be described by the three macro-phases described above: (I) decision-deadlock only, (II) coexistence of decision-deadlock and decision, and (III) decision only. In fact, the additional equilibria that appear for odd \( N \) are all unstable saddle solutions (with orthogonal attraction/repulsion directions with each other) which do not change the stability of other solutions. Therefore, we focus our study on the bifurcations defined by Equations (4) (i.e., Eq. (S17) in the supplementary material) which determine the main phase transitions.

Figure 1(c) shows the relationship between the bifurcation points \( r_1 \) and \( r_2 \), the options’ quality \( v \) and the number of options \( N \). The effect of \( v \) on \( r_1 \) and \( r_2 \) remains similar to that seen in Figure 1(a), i.e., the bifurcation points vary as a function of \( v \) when \( v \) is low, while they are almost independent of \( v \) when it is large. More precisely, the influence of the quality magnitude \( v \) on the system dynamics decreases quadratically with \( v \) (see Equation (S17) in the supplementary material). The number of options, \( N \), influences differently the two bifurcation points. While \( r_1 \) grows quasi-linearly with \( N \), instead \( r_2 \) grows quadratically with \( N \). Therefore, in the symmetric case, the number of options that the swarm considers plays a fundamental role in the decision dynamics. In fact, too many options preclude the possibility of breaking the decision-deadlock and selecting one of the equally-best options. This result suggests a limit on the maximum number of equal options that can be concurrently evaluated by the modelled decision-maker.

B. Asymmetric case

We next analyse the system dynamics in the asymmetric best-of-N case where option 1 is superior to the other \( N - 1 \) same-quality, inferior options \( i \) (with \( i \in \{2, \ldots, N\} \)). Figure 2 shows the
FIG. 2. Dynamics of the complete decision system of Equations (3) for \( N = 3 \) options for the asymmetric case (\( \kappa < 1 \)) and superior option’s quality \( v = 5 \). The left panel shows the stability diagram as a function of the parameter \( r \) and the ratio between qualities \( \kappa \). The parameter space is divided in five different areas (see Figure S4 in the supplementary material to see a representative 3D phase portrait for each area). In area A, the system has a unique solution corresponding to selection of the best option; in areas B and C, the system may select any of the possible options; in areas D and E the system may end in a decision deadlock. The underlying density map show the population size of the stable solution for the best option. For low values of \( r \) and similar options (top-left corner), this population is relatively small and may be not enough to reach a quorum threshold. The right panels show three bifurcation diagrams as a function of the parameter \( r \) for \( \kappa \in \{0.5, 0.9, 0.97\} \). Note that, due to the 2D visualisation, some equilibria overlap and thus the bottom branches of the bifurcation diagrams correspond to two overlapping equilibria for selection of options \( x_2 \) and \( x_3 \).
stability diagram for $N = 3$ options in the parameter space $r, \kappa$. The results show that low values of $r$ allow the system to have a unique solution, (area A in the left panel of Figure 2). This is especially true when the difference between the options is larger (i.e., low values of $\kappa$). However, such stable solutions may not correspond to a clear-cut decision, as the population fraction committed to the best alternative may be too low to reach a decision threshold, as indicated by the underlying density map in Figure 2 if $r$ is small and $\kappa$ sufficiently high, only about half of the population will be committed to the best option. Hence, a sufficiently high value of $r$ is required for the implementation of a collective decision. For larger values of $r$, the system undergoes various bifurcations leading to $N$ stable solutions corresponding to the selection of each available option (areas B and C of the left panel in Figure 2). Therefore, there is the possibility that an inferior option gets selected. For high values of $\kappa$, two additional areas appear, labelled D and E in Figure 2. These areas correspond to the co-existence of an undecided state together with a decision state for the superior and/or the inferior options, similarly to area II in Figure 1(a). The bifurcation diagrams in the right panels show the effects of $r$ for fixed values of $\kappa$. When the best option has double quality than the inferior options (i.e., $\kappa = 0.5$, see the bottom-right panel), a low value of $r$ guarantees selection of the best option, whereas a sufficiently high $r$ may result in incorrect decisions by selecting any of the inferior options (which are considerably worse than the best one). As the inferior options become comparable to the superior one, the range of values of $r$ in which there exists a single stable equilibrium in favour of the best options gets reduced (see the middle-right panel for $\kappa = 0.9$ in Figure 2), up to the point that there is no value of $r$ in which the choice of the superior option is the unique solution (see the top-right panel for $\kappa = 0.97$ in Figure 2). In this case, however, there is little difference in quality between the superior and inferior options, and the system dynamics are similar to the symmetric case in which it is most valuable to break a decision deadlock, hence to choose a sufficiently high value of $r$.

The dynamics observed for $N = 3$ options are consistent in the case of $N > 3$. Figure 3(a) shows the stability diagram for varying number of options $N \in \{2, \ldots, 7\}$ (see also Figure S5 in the supplementary material). It is possible to note that areas D and E get larger as $N$ increases, leading to a larger range of values in which one or more stable decision states coexist with a stable undecided state, up to the point that area C disappears for $N \geq 5$. This means that, as the number of inferior options increases, the probability of making a wrong decision increases as well, especially for high values of $\kappa$. To minimise the probability of wrong decisions, the value of $r$ should be maintained as small as possible, but still high enough to ensure that a decision is taken (i.e., with
FIG. 3. (a) Stability diagram for best option quality $v = 5$ in the parameter space $r, \kappa$ for varying number of options $N \in \{2, \ldots, 7\}$. For each option, the system has five possible phases that are consistent with the phases described in caption the of Figure 2. Here we label only areas A (monostability) and B (multistability) to facilitate readability. (b) Maximum value of $\kappa$ as a function of $N \in \{2, \ldots, 7\}$ and $r \in (0, 20]$ for which the system has a unique attractor for the selection of the best quality option, defined as the best option attracting commitment from at least 75% of the total decision-making population.

IV. DISCUSSION

We have analysed a model of consensus decision-making which exhibits useful value-sensitive properties that have previously been described for binary decisions [5], but generalises these to decisions over three or more options. In order to preserve these properties the single control parameter in the original model of [5], the rate of cross-inhibition between decision populations, is replaced by a parameter describing the relative frequencies with which individual group mem-
bers engage in independent discovery and abandonment behaviours, compared to positive and negative-feedback signalling behaviours. This new control parameter is biologically meaningful and experimentally measurable, so should be of interest for further empirical studies of house-hunting honeybee swarms.

Previous work has investigated the role of signalling in collective decision making in a somewhat different framework. Galla [34] has analysed a model of house-hunting honeybees [35] where the cross-inhibition mechanism was not included. In this model, increasing signalling (referred to as interdependence) allows the swarm to select the best quality option more reliably. The interdependence parameter modulates the strength of positive feedback; the higher the interdependence is, the more a bee is influenced by other bees’ opinion in determining a change of commitment. There are similarities and differences between the meaning of the interdependence parameter and the signalling ratio $r$ that is introduced in this paper. Similarly to [34, 35], increasing the value of the ratio $r$ corresponds to an increase in the signalling behaviour but, in contrast to previous studies, $r$ is a weighting factor of both positive and the negative feedback. However, note that positive and negative feedback are not necessarily equal in our model, as these mechanisms are also modulated by the option’s quality. In agreement with [34, 35], our results underline the importance of interactions among honeybees in the nest-site selection process. However, given the different meanings of the control parameters, we find that increased signalling behaviour helps to break decision deadlocks (in case of equal alternatives) but too high signalling might reduce the decision accuracy when the decision has to be made among different quality options.

We also note some similarities between our results and the bifurcation analysis of a model of the collective decision making process in foraging ants *Lasius niger* [36]. This model describes the temporal evolution of the pheromone concentration along $N$ alternative trails, each of which leads to a different food source. The bifurcation parameter in the analysis is an aggregate variable composed of the total population size, the options’ qualities and the pheromone evaporation rate. Not all of these components are under the direct control of the decision maker, and thus cannot be varied during the decision process. In contrast, the control parameter in our analysis, the signalling ratio $r$, can be modulated in a decentralised way by the individual bees. Comparing the bifurcation diagrams for deadlock breaking of Fig. 3(a) in [36] with Fig. S6(a) in the supplementary material, the two models present similar dynamics. The authors also present a hysteresis loop as a function of relative food source quality (Fig. 4 in [36]), which is similar to that found as a function of relative nest-site quality in [5] (Fig. 5). Collective foraging over multiple food sources is a fundamentally
different problem to nest-site selection, with exploitation of multiple sources frequently preferred in the former whereas convergence on a single option is required in the latter [11]. Nevertheless it could be interesting to make further comparisons of the dynamics of the model presented here and other nonlinear dynamical models exhibiting qualitatively similar behaviour.

A crucial point in our model is that honeybees need to interact at a rate that is high enough to break decision deadlock in the case of equal options, in addition to the influence of nest-site qualities. This follows from our analysis of the symmetric case (Section III A), where we observed that high signalling ratio $r$ allows the system to break the decision deadlock and to select any of the equally best options. However, the analysis of the asymmetric case (Section III B) revealed that a frequent signalling behaviour may have a negative effect on the decision accuracy, and low $r$ values should be preferred to have a systematic choice of the best available option. These results suggest that a sensible strategy may be to increase $r$ through time. An organism may start the decision process applying a conservative strategy which reduces unnecessary costs of frequent signalling behaviour and that, at the same time, allows quickly and accurately to select the best option if it is uniquely the best. Otherwise, in the case of a decision deadlock (due to multiple options having similar qualities), the system may increase its signalling behaviour in order to break symmetry and converge towards the selection of the option with the highest quality. This strategy is reminiscent of the suggested strategy of increasing cross-inhibition over time to spontaneously break deadlocks in binary decisions [5]. Further theoretical evidence supporting such a strategy comes from the bifurcation diagrams presented in the middle- and top-right panels in Figure 2, corresponding to asymmetric case with $N = 3$ similar options, with $\kappa = 0.9$ and $\kappa = 0.97$, respectively (see also Figure S7 in the supplementary material for further bifurcation diagrams with $N \in \{4, 5, 6, 7\}$). In these cases, an incremental increase in $r$ would allow the system to converge accurately towards the best option. In contrast, immediately starting the decision process with a high value of $r$ might decrease the decision accuracy. For instance, in Figure 2(right-center), starting with low values of $r$ (i.e., $r < 2.1$) would bring the system to the stable attractor (blue line) with less than half of the population committed to the best option. A gradual increase of $r$ lets the process follow the (blue, stable) solution line which leads to the selection of option 1. On the other hand, a process that starts from a totally uncommitted state with a value of $r > 2.1$ may end in the basin of attraction corresponding to selection of an inferior option, as a consequence of stochasticity of the decision process. Such a strategy could easily be implemented in a decentralised manner by individual group members slowly increasing their propensity to engage in signalling behaviours over time;
such a direction of change, from individual discovery to signalling behaviour, is also consistent with the general requirement of a decision-maker to gather information about available options, but then to begin restricting consideration to these rather than investing time and resources in the discovery of further alternatives. Theorists and empiricists have previously concluded that honeybee swarms achieve consensus through the expiration of dissent [37], which occurs as bees apparently exhibit a spontaneous linear decrease in number of waggle runs for a nest over time [26]. However, the discovery of stop-signalling in swarms requires that this hypothesis be re-evaluated, since increasing contact with stop-signalling bees over time will also decrease expected waggle dance duration [4]. Field observations report that recruitment decreases over time in easy decision problems while it increases overall in difficult problems (e.g. five equal-quality nests) [38]. Further theoretical work with our model would reveal whether it is capable of explaining these empirically-observed patterns.

Our analyses also suggest an optimal stable signalling ratio that the decision-making system might converge to. While the level of signalling required to break deadlock between \( N \) equal options increases quadratically with \( N \) (Figure 1(c)), the level of signalling that optimises the discriminatory ability of the swarm in best-of-\( N \) scenarios increases only linearly (Figure 3(b)). Optimising best-of-\( N \) decisions therefore seems at odds with optimising equal alternatives scenarios. However in natural environments the probability of encountering \( N \) (approximately) equal quality nest options will decrease rapidly with \( N \). On the other hand the best-of-\( N \) scenario here, while still less than completely realistic, should still provide a better approximation to the naturalistic decision problems typically encountered by honeybee swarms. Our analysis shows that the level of signalling that swarms converge to may be tuned appropriately by evolution according to typical ecological conditions, namely the number of potentially suitable nest sites that are typically available within flight distance of the swarm. Swarms of the European honeybee \( Apis mellifera \) are able to solve the best-of-\( N \) problem with one superior option and four inferior options [22], presumably reflecting the typical availability of potential nest sites in their ancestral environment.

While our model is inspired by nest-site selection in honeybee swarms, we feel its relevance is potentially much greater. For example, as mentioned in the introduction, decision-making in microbial populations may share similarities with decisions by social insect groups [6]. In addition cross-inhibitory signalling is a typical motif in intra-cellular decisions over, for example, cell fate [39], and single cells can exhibit decision behaviour similar to Weber’s law [40, 41]. Weber’s law describes how the ability to perceive the difference between two stimuli varies with the magnitude
of those stimuli, and may have adaptive benefits [42]. Several authors have also noted similarities between collective decision-making and organisation of neural decision circuits, where inhibitory connections between evidence pathways are also typical [11, 43–46]. Since organisms at all levels of biological complexity must solve very similar statistical decision problems that relate to fitness in very similar ways, we feel there is definite merit in continuing to pursue the analogies between collective decision-making models such as that presented here, and models developed in molecular biology and in neuroscience. Finally, we suggest that the simplicity of the model presented here and its adaptive decision-making characteristics might inform the design of artificial decentralised decision-making systems, particularly in collective robotics (e.g. [30, 31, 47]) and in cognitive radio networks (e.g. [48]).

V. ACKNOWLEDGMENTS

This work was funded by the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation programme (grant agreement number 647704). Vito Trianni acknowledges support by the European Commission through the Marie Skłodowska-Curie Career Integration Grant “DICE, Distributed Cognition Engineering” (Project ID: 631297).

[1] L. Conradt and T. J. Roper, *Trends in Ecology & Evolution*, Trends Ecol. Evol. 20, 449 (2005).
[2] I. D. Couzin, C. C. Ioannou, G. Demirel, T. Gross, C. J. Torney, A. Hartnett, L. Conradt, S. A. Levin, and N. E. Leonard, *Science* 334, 1578 (2011), http://science.sciencemag.org/content/334/6062/1578.full.pdf.
[3] J. A. R. Marshall, AAAI Spring Symposium Series, 12 (2011).
[4] T. D. Seeley, P. K. Visscher, T. Schlegel, P. M. Hogan, N. R. Franks, and J. A. R. Marshall, *Science* 335, 108 (2012), http://www.sciencemag.org/content/335/6064/108.full.pdf.
[5] D. Pais, P. M. Hogan, T. Schlegel, N. R. Franks, N. E. Leonard, and J. A. R. Marshall, *PLoS ONE* 8, e73216 (2013).
[6] A. Ross-Gillespie and R. Kümmerli, Front. Microbiol. 5 (2014), 10.3389/fmicb.2014.00054.
[7] R. Kurvers, J. Krause, G. Argenziano, I. Zalaudek, and M. Wolf, *JAMA Dermatol.* 151, 1346 (2015), /data/Journals/DERM/934706/doi150044.pdf.
[8] M. Wolf, J. Krause, P. A. Carney, A. Bogart, and R. H. J. M. Kurvers, PLoS ONE 10, e0134269 (2015).

[9] N. R. Franks, A. Dornhaus, J. P. Fitzsimmons, and M. Stevens, Proc. R. Soc. B 270, 2457 (2003).

[10] J. A. Marshall, A. Dornhaus, N. R. Franks, and T. Kovacs, Journal of The Royal Society Interface 3, 243 (2006), http://rsif.royalsocietypublishing.org/content/3/7/243.full.pdf.

[11] J. A. R. Marshall, R. Bogacz, A. Dornhaus, R. Planqué, T. Kovacs, and N. R. Franks, Journal of The Royal Society Interface 6, 1065 (2009), http://rsif.royalsocietypublishing.org/content/6/40/1065.full.pdf.

[12] S. C. Pratt and D. J. T. Sumpter, Proc. Natl. Acad. Sci. 103, 15906 (2006), http://www.pnas.org/content/103/43/15906.full.pdf.

[13] R. Golman, D. Hagmann, and J. H. Miller, Sci. Adv. 1 (2015), 10.1126/sciadv.1500253, http://advances.sciencemag.org/content/1/8/e1500253.full.pdf.

[14] A. Pirrone, T. Stafford, and J. A. R. Marshall, Front. Neurosc. 8 (2014), 10.3389/fnins.2014.00073.

[15] W. Li, H.-T. Zhang, M. Z. Chen, and T. Zhou, Phys. Rev. E 77, 021920 (2008).

[16] G. Valentini and H. Hamann, Swarm Intelligence 8, 153 (2015).

[17] J. Halloy, G. Sempo, G. Caprari, C. Rivault, M. Asadpour, F. Tâche, I. Saïd, V. Durier, S. Canonge, J. M. Amé, C. Detrain, N. Correll, A. Martinoli, F. Mondada, R. Siegwart, and J.-L. Deneubourg, Science 318, 1155 (2007), http://science.sciencemag.org/content/318/5853/1155.full.pdf.

[18] H. Hamann, T. Schmickl, H. Wörn, and K. Crailsheim, Neural Computing and Applications 21, 207 (2012).

[19] H. F. McCreery, N. Correll, M. D. Breed, and S. Flaxman, PLOS ONE 11, 1 (2016).

[20] M. Lindauer, Zeitschrift für vergleichende Physiologie 37, 263 (1955).

[21] T. D. Seeley, Honeybee Democracy (Princeton University Press, 2010).

[22] T. D. Seeley and S. C. Buhrman, Behav. Ecol. Sociobiol. 49, 416 (2001).

[23] N. R. Franks, A. Dornhaus, C. S. Best, and E. L. Jones, Animal Behaviour 72, 611 (2006).

[24] E. J. H. Robinson, N. R. Franks, S. Ellis, S. Okuda, and J. A. R. Marshall, PLoS ONE 6, e19981 (2011).

[25] K. von Frisch, The Dance Language and Orientation of Bees (Harvard University Press, 1967).

[26] T. D. Seeley and S. C. Buhrman, Behav. Ecol. Sociobiol. 45, 19 (1999).

[27] S. C. Pratt, E. B. Mallon, D. J. Sumpter, and N. R. Franks, Behav. Ecol. Sociobiol. 52, 117 (2002).

[28] D. J. T. Sumpter and S. C. Pratt, Phil. Trans. R. Soc. B 364, 743 (2008).
[29] T. D. Seeley and P. K. Visscher, Behavior Ecol. Sociobiol. 56, 594 (2004).

[30] A. Reina, G. Valentini, C. Fernández-Oto, M. Dorigo, and V. Trianni, PLoS ONE 10, e0140950 (2015).

[31] A. Reina, R. Miletitch, M. Dorigo, and V. Trianni, Swarm Intelligence 9, 75 (2015).

[32] Supplementary material is available online at http://diode.group.shef.ac.uk/resources/.

[33] J. D. Schall and D. P. Hanes, Nature 366, 467 (1993).

[34] T. Galla, Journal of Theoretical Biology 262, 186 (2010) 0909.1582.

[35] C. List, C. Elsholtz, and T. D. Seeley, Philosophical transactions of the Royal Society of London. Series B, Biological sciences 364, 755 (2009).

[36] S. C. Nicolis and J.-L. Deneubourg, Journal of theoretical biology 198, 575 (1999).

[37] T. D. Seeley, Behavioral Ecology and Sociobiology 53, 417 (2003).

[38] T. D. Seeley, P. K. Visscher, and K. M. Passino, American Scientist 94, 220 (2006).

[39] N. R. Nené, J. Garca-Ojalvo, and A. Zaikin, PLoS ONE 7, e32779 (2012).

[40] J. E. Ferrell, Molecular Cell 36, 724 (2009).

[41] L. Goentoro, O. Shoval, M. W. Kirschner, and U. Alon, Molec. Cell 36, 894 (2009).

[42] K. L. Akre and S. Johnsen, Tr. Ecol. Evol. 29, 291 (2014), arXiv:NIHMS150003.

[43] I. D. Couzin, Nature 445, 715 (2007).

[44] J. A. Marshall and N. R. Franks, Current Biology, Current Biology 19, R395 (2009).

[45] I. D. Couzin, Trends in Cognitive Sciences, Trends in Cognitive Sciences 13, 36 (2009).

[46] K. M. Passino, T. D. Seeley, and P. K. Visscher, Behav. Ecol. Sociobiol. 62, 401 (2007).

[47] N. E. Leonard, Annu. Rev. Contr. 38, 171 (2014).

[48] V. Trianni, A. S. Cacciapuoti, and M. Caleffi, in 2016 IEEE International Conference on Communications (ICC) (IEEE Press, 2016) pp. 1–6.