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Highlights

- Agent-based model replicated colony behaviour in a mass-recruiting ant
- Individual acceptance thresholds could tune decision speed and accuracy
- Acceptance thresholds could tune decisions to environmental complexity
- Social and private information combined made the best decisions
- Effective decisions could be made with very few discriminating individuals

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An agent-based model of nest-site selection in a mass-recruiting ant

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ABSTRACT

Complex systems are modular entities which can collectively generate sophisticated emergent solutions through interactions based on simple, local rules. In this study, I use an agent-based model to elucidate how numerous individual-level components contribute to the collective decision process during house-hunting in a mass-recruiting ant species. *Myrmecina nipponica* combines the use of pheromone trails with a quorum decision rule in collective decisions among nest sites when searching for a new home. The model employed only individual-level rules but accurately emulated group-level properties observed in empirical studies.

Simulations suggest that in this system i) both social and private information are necessary for effective decision making, ii) decision making was effective even with very low numbers of ‘discriminating’ individuals, iii) individual acceptance thresholds were more influential than quorum thresholds in tuning decisions to emphasise speed or accuracy, and iv) acceptance thresholds could also help tune decisions to suit environmental complexity.

Similar findings in species using one-to-one recruitment suggest that some individual parameters, such as acceptance thresholds, may hold key functions in collective decision making regardless of the form of recruitment.

Keywords: Collective decision-making; quorum sensing; swarm intelligence; emergence.

1. Background

Complex systems are modular entities defined by the actions of, and interactions between, numerous individuals. These systems are typically self-organised, with group-level properties arising as the emergent product of local interactions between individuals, without a global blueprint or top-down direction. Despite this lack of central control, self-organised systems can outperform the additive sum of their component parts in collective tasks such as decision making (Camazine et al., 2001; Canonge et al., 2011; Condorcet, 1785; Dall et al., 2005; Galton, 1907; Hölldobler and Wilson, 2009; Morand-Ferron and Quinn, 2011; Sasaki and Pratt, 2012; Sumpter and Pratt, 2003; Surowieki, 2005). This has clear importance in biological systems as when, where and how individuals or groups decide to act (or not) defines their interactions with other organisms and the environment, and ultimately, their success.

An array of empirical studies of biological systems have in recent years shed light on the importance of various components of collective behaviour, such as how different forms of positive feedback, the use of quorum thresholds, and the weighting of private and social information can allow tuning of speed and accuracy of decision making and/or influence the efficiency of collective processes (Czaczkes et al., 2015b; Franks et al., 2009; Mallon et al., 2001; Pratt, 2005; Seeley and Buhrman, 1999). Nonetheless, elucidating the mechanistic basis of collective behaviour in empirical systems can be hampered by the reliance on observable phenomena, as many components of biological systems (such as the manner in which an ant perceives a chemical trail) are cryptic. For this reason, the study of collective behaviour has long been associated with the use of models (reviewed in Gordon, 2016). In addition to their power as a means to explore parameter space not amenable to empirical

studies, models serve as stepping stones to the development of algorithms of collective behaviour for use in applied roles such as engineering and swarm robotics (Bonabeau and Théraulaz, 2000; Garnier et al., 2007; Gordon, 2016; Trianni et al., 2011). However, models of collective behaviour are often deterministic, and thus unable to incorporate stochastic processes, may use an intentionally narrow focus for analytical tractability or to determine the minimal conditions to explain an observed pattern and, for similar reasons, may not be spatially explicit. While heuristic, such models have limited application in serving as a basis for algorithm development, as individual-level rules cannot easily be extracted for application to artificial entities. To serve as an effective basis for artificial applications, models must replicate the functional mechanisms of natural systems as closely as possible and model functional units (i.e., individuals). In this regard, agent-based models are an ideal platform for emulation of collective biological systems, and have been used to shed light on a range of collective processes (Czaczkes, 2014; Grüter et al., 2013; List et al., 2009; Passino and Seeley, 2006; Robinson et al., 2008). Individual agents are programmed with simple ‘rules-of-thumb’, a mechanism likely to form the basis of many self-organised systems (Camazine et al., 2001). System-level properties are then allowed to arise from interactions between agents in the manner of natural biological systems.

Social insects are particularly amenable to emulation by agent-based models, as individuals are relatively simple and behavioural rules can be parameterised from laboratory studies. It is thus no surprise that they have served as the basis for the development of various artificial systems employing ‘bottom-up’ analytical methods (Brambilla et al., 2013; Dorigo et al., 1999). This form of self-organisation permits social insects to perform remarkable feats, from forming living bridges to the construction of complex physical structures such as termite mounds, despite their individual simplicity (Hölldobler and Wilson, 2009). Study of

the decision-making process in social insects has been one of the most elucidative avenues of research in collective behaviour (Cronin, 2016; Franks et al., 2009; Franks et al., 2013; Pratt et al., 2002; Seeley, 1996), though models have primarily focussed on species which employ direct forms of recruitment, such as the waggle-dance of honey bees (Passino and Seeley, 2006) or tandem running in ants (Marshall et al., 2006; Masuda et al., 2015; Pratt and Sumpter, 2006; Pratt et al., 2005). Social insects use a variety of recruitment systems however, and it remains unclear whether the key parameters in decision making are common to all systems or particular to each case.

Arguably the champions of self-organised behaviour are the ants, and much of their prolific success can be traced back to their ability to dynamically coordinate individuals using an array of communication mechanisms (Hölldobler and Wilson, 1990; Hölldobler and Wilson, 2009). Ants are also able to exploit the decision-making power of groups (Cronin, 2016; Franks et al., 2006; Sasaki and Pratt, 2012; Sasaki et al., 2013), combining imperfect information over many individuals to make more accurate decisions. The ant *Myrmecina nipponica* uses chemical (pheromone) trails during the nest emigration process, a form of indirect mass recruitment. This species exhibits a sophisticated choice mechanism that can adapt to changes in group size (Cronin, 2013b; Cronin, 2014; Cronin and Stumpe, 2014), value of social and private information (Cronin, 2013a), and environmental conditions (Cronin, 2013b; Cronin, 2016). To select among candidate new nests when house hunting, recruitment via pheromone trails is combined with a quorum-based decision process (Cronin, 2012; see Materials and Methods for a description of the emigration process in this species). Pheromone trails are a common and effective mechanism of mass recruitment in ants, as one signal can reach many individuals. However, pheromone trails can also rapidly amplify incorrect information and may lack flexibility in decision-making in dynamic environments,

and thus are likely to work most effectively in combination with other mechanisms of feedback and information exchange (Czaczkes et al., 2015b; Robinson et al., 2005; Seeley et al., 2012). Indeed, a combination of feedback mechanisms in collective biological systems can help imbue them with robustness and flexibility (Czaczkes et al., 2015b; Garnier et al., 2007; List et al., 2009). However, many components of the decision mechanism in this species are cryptic, such as the degree of influence of trails on ant movements and the importance of individual assessment thresholds. The role of these components in avoiding the pit-falls of pheromone trails and in tuning collective decision making to different environmental contexts thus remains unclear.

In this study I develop an ‘ants-eye-view’ model of the nest selection and emigration process in *M. nipponica* using a holistic approach which aims to replicate as many of the natural components of this model system as possible. Agents are programmed using simple threshold rules, as these are thought to underlie behaviour in many solitary and social species (O’Shea-Wheller et al., 2017) and can contribute to self-organisation (Greene and Gordon, 2007; Robinson et al., 2009; Robinson et al., 2011). Individual variability (heterogeneity) and unpredictability (stochasticity) are incorporated into the model as both of these factors can play key roles in collective processes (Gordon, 2016; Masuda et al., 2015; O’Shea-Wheller et al., 2017). The model is also spatially explicit, as spatial relationships are important in organisation of ant colonies (Mersch et al., 2013) and spatial structure of the environment can have an important influence on the ontogeny of collective behaviour (Bles et al., 2018; Forster et al., 2014). I use this model to analyse the importance of different components of the decision-making process, and how these might contribute to the adaptive tuning of decision making in different contexts. The specific aims of the study are to: i) determine if a model relying only on individual rules can replicate the global emigration performance of

mass-recruiting ants; ii) clarify the importance of different individual parameters in the decision-making process in this species, and how this compares to one-to-one recruiting systems; iii) assess the importance of individual heterogeneity; iv) investigate how key parameters can influence speed and accuracy under different levels of decision complexity.

2. Materials and Methods

2.1 Ant model system

An agent-based model is developed to emulate the process of collective decision making during nest-site selection in the ant *Myrmecina nipponica* (Cronin, 2012). This species inhabits broad-leaf forests throughout Japan, and nests in cavities in soil or rotting vegetation where it forms small colonies of 10-70 ants. Colonies can be induced to undertake emigrations in the laboratory to study the collective decision-making process during nest-site selection (Cronin, 2012; Cronin, 2016; Cronin and Stumpe, 2014). As in other collective systems, decisions arise at the system level as emergent properties of interactions among individual ants using simple rules (Sumpter, 2010). Unusually for a small-colony species, *M. nipponica* relies on chemical (pheromone) trails for navigation, which are also employed as a mechanism of recruitment. Combined with the use of quorum-thresholds, this ‘voting’ via pheromone trails forms the primary mechanism for effecting collective decisions (Cronin, 2012; Cronin, 2013b).

2.2 Agent-based model

The model was built in NetLogo version 6.0 (Wilensky, 1999). Agents followed a simple algorithm governed entirely by individual-level parameters, and all group-level properties were emergent products of interactions among these agents. This model differs from previous models of social insect decision making in attempting to replicate as many components of the natural system as possible rather than using a restrictive set of these components. Thus, the model is stochastic and spatially explicit, as well as using a bottom-up approach based on individual agents. While these components have appeared in previous models (Britton et al., 2002; Marshall et al., 2006; Masuda et al., 2015; O'Shea-Wheller et al., 2017; Pratt et al., 2002; Pratt et al., 2005; Robinson et al., 2011), they are not usually integrated into a single model. The model also focusses on a trail-based recruitment system, which is functionally different to that used in previous nest choice models of *Temnothorax* ants and honeybees, though trail-using-ant models have been employed to investigate ant foraging (Czaczkes et al., 2015b; Robinson et al., 2008)

An overview of the model function is provided here, while details of the model and the model code are provided in the Supplementary Material. During nest emigration in *M. nipponica*, ants must find, then move to a new nest site, selecting among available nest sites when necessary. The entire emigration process was modelled from 'destruction' of the original nest to relocation of the final brood item. Following empirical studies, emigrations were defined by phases as follows: the *search* phase defined the period from the initiation of the trial until one ant found any of the candidate nests. The *assessment* phase extended from this point until a quorum decision was achieved at any site. The *transport* phase was from the quorum point until all brood had been relocated to a new site, at which point the emigration was deemed complete.

The parameters investigated in this study are listed in Table 1 (see also Supplementary Material). Ant parameters defined threshold levels of social or environmental signals for determination of behaviour, whereas environmental parameters defined characteristics of the physical environment. Where possible, values for parameters were quantified from empirical data from laboratory emigrations of *M. nipponica* (Cronin, 2012; Cronin, 2014; Cronin and Stumpe, 2014). Several parameters could not be inferred from empirical data because they represented internal ant thresholds without quantifiable external cues (see Supplementary Material). For example, whereas in *Temnothorax* ants the switch from scouting to recruitment is observable by the adoption of tandem-running behaviour, this point is cryptic in *M. nipponica* because it is associated with laying of pheromone trails, which cannot be observed in this context. These cryptic parameters were thus assigned arbitrary values which were then adjusted during pilot simulations until emergent properties of the model (such as total duration of emigrations) approximated empirical data. The influence of varying these parameters was later assessed over a range of values.

Agents assumed one of four different behavioural classes, and could transition between these classes dependent on agent parameters in combination with environmental information, following Figure 1:

1) *Nest ants* remained in the original nest site until they became scouts following a Poisson process with a rate set by the *scout* parameter.

2) *Scout ants* moved about the navigable area until they found candidate new nests.

Movement was random or followed pheromone trails depending on trail strength and individual susceptibility to social information. When a candidate site was found, the quality of this was compared to an internal threshold. Sites with quality scores above the internal threshold were accepted, and ants accepting the site became *decided*.

3) *Decided ants* moved back and forth between the original nest site and their chosen site laying pheromone trails. These ants remained committed (continued recruiting) at rate determined by a parameter *commitment*, with those ‘losing interest’ reverting to *scouts*. This process continued, with accumulation of pheromone trails and increasing numbers of decided ants, until a threshold number of ants (‘quorum’) was attained at any site. Ants detecting a quorum switched behaviour to a *transport* role.

4) *Transport ants* moved between the chosen and original nest sites ferrying brood to the new site until all brood items had been relocated, at which point the emigration was deemed complete (Figure 1).

2.3 Simulation environment and decision metrics

The environment was a 101 x 101-unit square chamber with a ‘source’ nest located at the centre (Supplementary Material). New nests were of ‘good’ (*quality* = 75) or ‘poor’ (*quality* = 50) quality and were located 38 units from the centre of the arena in balanced patterns of 1, 2, 4, 8 or 16 nests (Supplementary Material). The location of the single ‘good’ nest was randomly assigned among the candidate nest sites.

Emigrations had a fixed time limit, set at 15000 steps. This value was approximately five times the average successful emigration time for average sized colonies under simulations with base parameters. For comparison, the maximum duration over 35 experimental emigrations was only double the mean (Cronin 2016). A value five times the mean was deemed a failed emigration, as a colony would suffer high costs from predation and/or environmental effects (desiccation) if a choice had not been reached in this time.

Emigrations were scored as a success if ants emigrated (transported all brood items) to the best available nest. They were recorded as 'split' if brood were transported to more than one new nest (though in general this did not occur, as for empirical studies). Emigrations were deemed a failure if ants moved to the lower quality nest or did not complete the emigration during the experimental period.

2.4 Simulations and data collation

Simulations were run for 100 replicates for each unique set of parameter values, except where being compared with empirical data, in which case a single replicate was performed for each empirical data point. A total of over 90,000 simulated emigrations were performed.

Relocation metrics were summarised from NetLogo output and aggregated over all replicates to obtain mean values, then subject to GAM (generalised additive model) analysis using the key factors in each trial and the *mgcv* package in R (Wood, 2011). Predicted values were then generated from the GAM model for a 100 x100 unit parameter space and used to generate heatmaps in R version 3.4.3 using *ggplot2*.

3. Results

3.1 Emigration dynamics in simulations versus empirical data

The emergent properties of simulations using base parameter values approximated empirical data well (Figure 2): recruitment and transport of brood to the new site followed a similar temporal pattern, decision success and proportionate phase durations were similar, and the

pattern of task allocation (proportion of scouts and transporting ants) tracked that of real colonies (Supplementary Material). Notably, these phenomena were all derived from the behaviour of agents following individual rules. Success in the simulations was higher than empirical colonies, but this is not surprising as it was impossible to *a priori* to quantify individual *accept* thresholds or determine the *quality* of the ‘light’ and ‘dark’ nests used in empirical choice studies.

3.2 Importance of key parameters in decision making

Collective decisions in *M. nipponica* ultimately depend on achievement of a quorum of individuals at one site, which triggers the shift to brood transport. Quorum achievement relies on finding sites and initiating recruitment, and subsequently on the symmetry breaking effect generated by this recruitment. In the model, the *scout* parameter dictated individual propensity to initiate information collection (scouting), while the *accept* parameter determined their propensity to initiate recruitment (trail laying). Once trails were available, their effectiveness as a mechanism of symmetry breaking depended on whether individuals were making use of available social information or relying entirely on private information. In this sense, the *commit* parameter can be thought of as an individual’s ‘confidence’ in its own private information, whereas the *trail* parameter represents the strength of social information. Of these parameters, only *scout* and *quorum* could be estimated from empirical studies. The relative importance of these parameters in influencing the speed and accuracy of decisions during simulated emigrations is summarised below.

3.2.1 Locating and recruiting to sites

The speed at which recruitment begins is dependent on ant scouting activity and acceptance thresholds. The influence of *scout* and *accept* parameters on decision speed and accuracy are summarised in Figure 3a, which indicates that scouting propensity had little influence over decision making speed or accuracy, though very low values of *scout* delayed emigrations. In contrast, variation in *accept* could tune decision making to emphasise decision speed or accuracy, a trade-off common to many decision making systems (Franks et al., 2009).

3.2.2 Information weighting

Figure 3b summarises the influence of varying *trail* and *commitment* parameters and suggests that high values of both parameters are necessary for effective decision making. Values of *trail* below ~90% led to delayed decision making which in many cases resulted in low success because no decision was reached. Higher values of *commit* also improved decision speed and accuracy, but only in conjunction with high values of *trail*. Overall, a high reliance of social information was essential, and use of private information was beneficial, to fast, accurate decision making.

3.2.3 Quorum decision making

The influence of *quorum* in combination with varied levels of *accept* is summarised in Figure 4. This indicates an overwhelming influence of quorum threshold on decision speed and accuracy over the full range of parameter values (Figure 4a). Empirical studies, however, indicate that *quorum* values are typically a consistent percentage of colony size (28%; Cronin, 2016). Interestingly, this value was very near that which could be considered to optimise decision making, by providing for high decision accuracy while also maintaining decision

speed over most of the range of *accept* values. While variation around this value has been observed in different environmental contexts in empirical studies, this deviation is not greater than $\pm 4\%$ (Cronin, 2016). Analyses were thus repeated for this biologically realistic range, and in this case, the relative importance of *quorum* and *accept* was reversed: variation in *quorum* had little or no effect, whereas variation in *accept* again allowed tuning of decisions over the speed-accuracy trade-off.

3.6 Influence of individual heterogeneity

Recent studies have illustrated the importance of group composition in collective processes, and in particular, the importance of variation among individuals in propensity to undertake particular tasks. Previous empirical studies have indicated that contributions to collective decision making are not uniformly distributed among colony members in *M. nipponica* (Cronin and Stumpe, 2014) and that colonies of differing composition can exhibit consistent differences in performance (Cronin, 2015). The potential influence of different levels of heterogeneity among colony individuals on decision making was assessed using two approaches: i) selecting individual *accept* thresholds from a Poisson distribution in comparison to a normal distribution, and ii) by altering the standard deviation of the normal distribution used to generate *accept* thresholds. Generating *accept* values from a Poisson distribution was qualitatively the same as using a normal distribution, with the only difference being delayed decisions at the highest mean values of *accept* in the Poisson case because no individuals accepted any nests (Supplementary Material). Similarly, varying the standard deviation of the normal distribution of *accept* thresholds had little influence on decision making except through delaying decisions when there were too few ants having an *accept* within the range of the available nests (Figure 5a,b). That is, decisions were delayed or

prevented when few or no ants could accept any of the available nests but were otherwise largely consistent regardless of the distribution of *accept* values. This is likely to be an effect of the number of ants present which can make an effective choice by discriminating between ‘good’ and ‘bad’ nests. To assess the influence of the number of discriminating ants, the number of ants with *accept* values above 50 but below 75 (quality of bad and good nests respectively) was calculated for each combination of parameter values in Figure 5a,b. To do so, *z* scores were calculated for each combination of mean and SD for both critical values, and the probability of a given ant being below the critical value predicted using the *pnorm* function in R. Numbers from 75 *accept* were then subtracted from those for 50 *accept* to obtain a number of discriminating ants. The influence of the number of discriminating ants on decision speed and accuracy is summarised in Figures 5c,d which indicate that a very small number of discriminating ants (> 2) were sufficient to make accurate decisions, whereas decision speed increased with increasing numbers of discriminating ants up to 10 (for a colony size of 30 in both cases).

3.7 Efficacy of decision making in different environmental contexts

Optimal parameter values for decision making are likely to depend on environmental context (Cronin, 2016; Czaczkes et al., 2015b; Gordon, 2016). This includes more difficult choices, such as represented by decisions among greater numbers of new nest sites, when a higher amount of information processing is required (Couzin, 2009; Sasaki and Pratt, 2012). The influence of environmental context was investigated using environments containing one, two, four, eight and 16 nests, in each case with a single ‘good’ nest. In simulations with greater numbers of new nests, decision success decreased while the duration of emigrations increased (Figure 6). This was not a result of spatial distribution of nests and thus proximity of different

trails, as varying relative spatial position in a two-nest choice did not influence mean duration or success (Supplementary Material). However, this cost of increased environmental complexity could be mitigated through the use of higher *accept* thresholds. For the highest values of *accept*, speed and accuracy were comparable across all levels of environmental complexity (Figure 6a, b). This effect is likely because higher *accept* values resulted in more accurate and focussed recruitment and thus less competition among candidate sites for achievement of a quorum, giving rise to more rapid decisions and high decision success. As a measure of the efficiency of the recruitment process, the number of ‘votes’ for each candidate nest was quantified as the number of times an ant visited and accepted a given nest (thus becoming a recruiter to that site). The proportion of votes to the single good nest increased with higher values of *accept* (Fig 6c). Thus, higher *accept* values led to less recruitment to bad nests, and a more rapid attainment of the quorum at the good nest because of lower competition among candidate sites for the numbers required to achieve a quorum. Notably, the influence of *accept* was most marked in the most difficult decisions, presumably because the potential for competition was highest here.

4. Discussion

In this study I use an ants-eye-view model of collective decision making in the ant *Myrmecina nipponica* to investigate how different individual-level parameters influence the group-level decision-making process during nest-site selection. Nest selection is a complex and challenging task in which ants must first find possible sites, collectively decide among the available options, and navigate both adults and brood to the new site, as fast, and as accurately as possible. The model was based entirely on individual rules, with all group-level

phenomena arising as emergent properties of interactions between individuals. Nonetheless, it was possible to reproduce group-level outcomes observed in experiments, indicating that this approach is sufficient to implement complex group-level tasks such as the process of nest site selection.

Tuning individual-level parameters can lead to markedly different emergent properties at the group level. For example, the global pattern of swarming fish can shift phases depending on the interaction-distance thresholds used by individuals (Couzin et al., 2002). While various parameters were shown to influence emigration dynamics in the ant model presented here, individual *accept* thresholds were repeatedly identified as a means of tuning decisions in different contexts, and to emphasise the speed or accuracy of decision making. While variation in quorum threshold had a marked effect on decision speed and accuracy over the full parameter range, the influence was marginal over the range of values observed in empirical studies. Although evidence exists from this and other species that ant colonies adjust their quorum thresholds to tune decision making to environment context (Cronin, 2013b; Cronin, 2016; Franks et al., 2009), simulations suggest that the quorum threshold observed in empirical studies of this species (28% of colony size) was close to the optimal possible in terms of both decision speed and accuracy, and thus significant deviation from this value may only lower performance.

The finding that *accept* is an effective decision tuning parameter mirrors the findings of Pratt and Sumpter (2006). In their model of nest emigration behaviour in *Temnothorax* ants, these authors also demonstrate that the propensity for individuals to initiate searching (i.e.: *scout* parameter) can influence decision making in a similar manner to *accept* thresholds, with a higher propensity to scout leading to faster, but less accurate decision making. Pratt

and Sumpter's (2006) model was based on ants employing tandem-running recruitment, a form of individual recruitment yielding linear positive feedback, whereas pheromone trails are a form of mass recruitment producing non-linear positive feedback. The combined findings of these two models suggest that varying individual levels of *accept* is a robust means of tuning decisions to the speed-accuracy trade-off, regardless of the form of recruitment. In contrast to the similarity in the influence of *accept*, *scout* had little effect in the *Myrmecina* model. This may reflect the differences in recruitment mechanisms used by these ants, because even low numbers of scouts can generate effective recruitment in trail-laying species.

The model presented here agrees with models of foraging behaviour in trail-laying species in that high levels of both social information (trail use) and private information (represented by individual 'confidence' in their own private decision) were necessary for fast, accurate decision making (Czaczkes et al., 2015b). Sub-optimal outcomes can arise from the reliance on either social or private information alone (Beckers et al., 1990; Czaczkes et al., 2016) and thus ants may benefit from use of both forms of information. This combination may facilitate the 'independence and interdependence' necessary for effective exploitation of information pooling (Condorcet, 1785; List et al., 2009; Marshall et al., 2006): ants independently assess sites through their own internal *accept* thresholds, but share information via pheromone trails (Cronin, 2013a). While pheromone trails can be effective in decision making during nest emigration or for optimal exploitation of foraging sources (Cronin, 2012; Cronin, 2013b; Czaczkes et al., 2015a), highly non-linear forms of recruitment can lack flexibility and lead to sub-optimal results via information cascades if initial decisions are incorrect (Beckers et al., 1990; Giraldeau et al., 2002). Use of additional mechanisms in decision making, such as vetting social information with private information or employing

quorum responses may help insure against the negative outcomes of highly non-linear positive feedback mechanisms such as pheromone trails (Cronin, 2013a; Czaczkes et al., 2015a; Czaczkes et al., 2015b; Wolf et al., 2013).

While a speed-accuracy trade-off was observed in two-nest and four-nest choices, this trade-off was broken under more complex conditions. Simulations in complex environments indicate that reducing *accept* thresholds with high numbers of candidate nests (8 & 16 nests) could increase decision time while simultaneously reducing accuracy, likely because of greater competition among candidate nests for achievement of a quorum. This effect could be mitigated, however, by the use of higher *accept* values, which counteracted the influence of additional options and normalised decision-making over a range of more complex environments. Groups using quorum decision mechanisms might thus be expected to use *accept* thresholds to tune decisions to emphasise speed or accuracy in simple (few option) environments, but to use higher *accept* thresholds in complex (many option) environments to limit competition costs. This could be tested empirically in species in which acceptance behaviour has an observable indicator, such as ants which recruit via tandem-running.

Recent empirical and modelling studies have indicated that heterogeneous groups can make more effective decision making machines than uniform groups (Czaczkes et al., 2015b; Krause et al., 2011; Masuda et al., 2015; O'Shea-Wheller et al., 2017; Robinson et al., 2014). Simulations here suggest that this is also true for decisions over nest sites in trail-laying ants, but only to the extent that variation among individuals influences the number of individuals capable of discriminating among the available options. Under a simple threshold rule, diversity means that some ants will accept all nests, whereas others will not accept any nest, leaving only percentage of ants which will accept one nest but not the other. An interesting

and unexpected finding of this study is that decision making can be effective with only very small numbers of such discriminating individuals. Simulations indicated that even in cases where only three of four individuals had *accept* values which allowed them to distinguish between good and bad nests, these colonies were able to choose the better nest at a rate comparable to that of colonies with much greater numbers of discriminating ants. Low numbers of key individuals can engineer effective system-level responses in diverse taxa (Beekman et al., 2006; Dyer et al., 2009; Reebs, 2000), raising the question of the relative importance of absolute numbers of leaders and ‘passive’ individuals in generating the advantages of groups over individuals.

5. Conclusions

Social insect colonies can achieve remarkable feats through the combined efforts of simple individuals, from highly structured termite mounds to context-sensitive consensus decision making. In this study I demonstrate that an individual-based algorithm based on mass-recruiting ants can emulate a complex, collective biological process over a range of scenarios. Adjustment of parameters at the individual level was sufficient to tune system-level performance to different environmental conditions. Combined with previous models of nest emigration in species using tandem-running, the findings suggest that some parameters (e.g. individual acceptance thresholds) may be key to collective decision making regardless of the recruitment mechanism, while the importance of others (e.g. propensity to scout) may vary under different forms of recruitment. The same may be true of self-organised systems more generally, and elucidation of such ‘core’ parameters could be achieved through the study of different collective systems using comparable modelling frameworks.

Supplementary information

Supplementary material includes the full model (NetLogo format), a model ODD (Overview, Design concepts and Details), the model code in text format, data from all simulations, and supplementary Methods and Results.

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Tables

Table 1. Model parameters investigated in this study. Base value = default parameter values, based on empirical data where possible. Values tested = values using in simulation models.

Parameter	Description	Base value	Values tested
Ant parameters			
Wait	Time spent in new sites	60	60
Scout	Chance of becoming a scout	0.1%	0.01, 0.1, 1, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100
Accept	Threshold for accepting a site	75	5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 95
Accept SD	Standard deviation for normal distribution for values of Accept	20	0.1, 1, 5, 10, 20, 30
Quorum	Threshold number of ants in a new site to switch to transporting	28% colony size*	5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 95
Accept distribution	Distribution used for generation of accept thresholds	Normal	Normal, Poisson
Commitment	Rate at which committed ants remain committed	99.5%	0, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 95, 100
Trail	Rate at which trails are followed if present	95%	0, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 95, 100
Environmental parameters			
Number of nests	Number of new nests available	1	1, 2, 4, 8, 16

* Ant estimation of quorum thresholds was also subject to measurement error with a Weber fraction of 23% (Cronin, 2014)

Figure captions

Figure 1. Flow diagram of the model for each agent. Decision points are indicated by circles, with black and white nodes representing no and yes responses respectively. Boxes indicate key locations. Agent status is indicated by line colour: black for scouts, blue for decided ants and red for transporters. Blue and red lines are associated with trail laying. Arrows indicate transitions between physical locations (boxes) or decision points (circles).

Figure 1

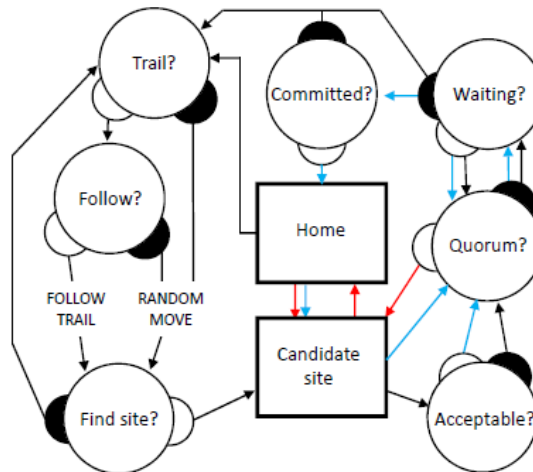


Figure 2. Comparison of emigration dynamics in simulated (Sim) and empirical (Emp) colonies. **A.** Unfolding of the emigration process: cumulative number of entries (grey circles) in a one-nest emigration (colony 25 from Cronin 2012 and simulated colony of the same size and number of brood); blue circles indicate brood transports; time is in steps and seconds respectively. **B.** Decision accuracy in 68 colonies of matched size in a choice between good

(quality 75) and bad (quality 50) nests in simulations and light and dark nests in experiments (from Cronin 2016 experiment 2 control data). **C.** phase durations for 35 colonies of matched size (empirical data from Cronin 2016 experiment 1 and size-matched simulated colonies): red = discovery phase, white = assessment phase; blue = transport phase.

Figure 2

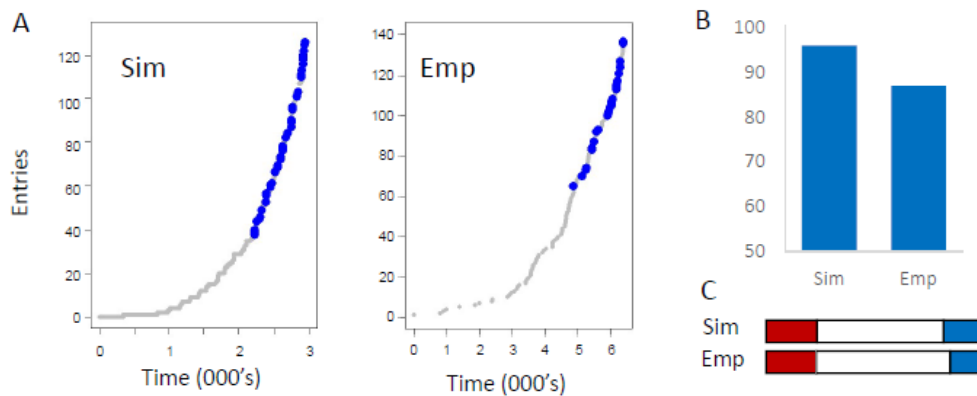


Figure 3. Heatmaps showing the influence of model parameters on decision accuracy (above) and speed (below) in a two-nest choice experiment. **A.** The influence of *scout* and *accept*, **B.** the influence of *trail* and *commit*.

Figure 3

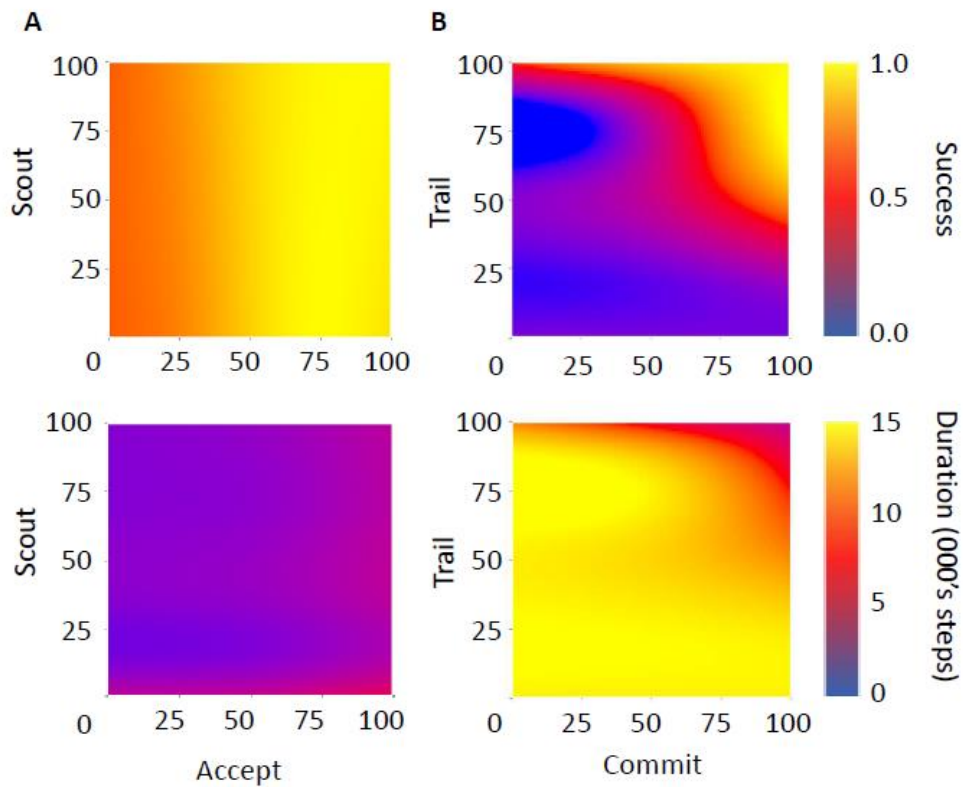


Figure 4. Heatmaps showing the influence of quorum and accept in a two-nest choice experiment. **A.** the full range of possible *quorum* values and **B.** the range observed *quorum* values in empirical studies of nest emigration in *M. nipponica*. The dotted line indicates the mean quorum-threshold percentage used by this species during emigrations under benign laboratory conditions.

Figure 4

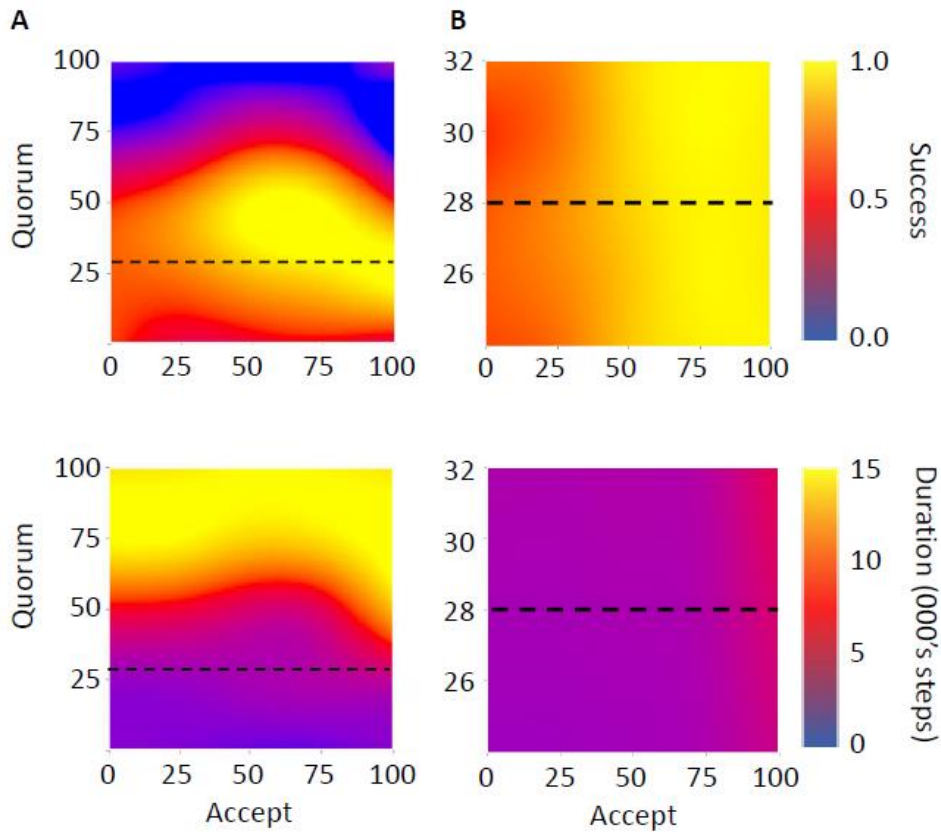


Figure 5. Heatmaps showing the influence of inter-individual variability in decision making. **A & B.** Influence of variation in *accept* on decision accuracy and speed, respectively. **C & D.** Influence of the number of discriminating ants on decision accuracy and speed, respectively.

Figure 5

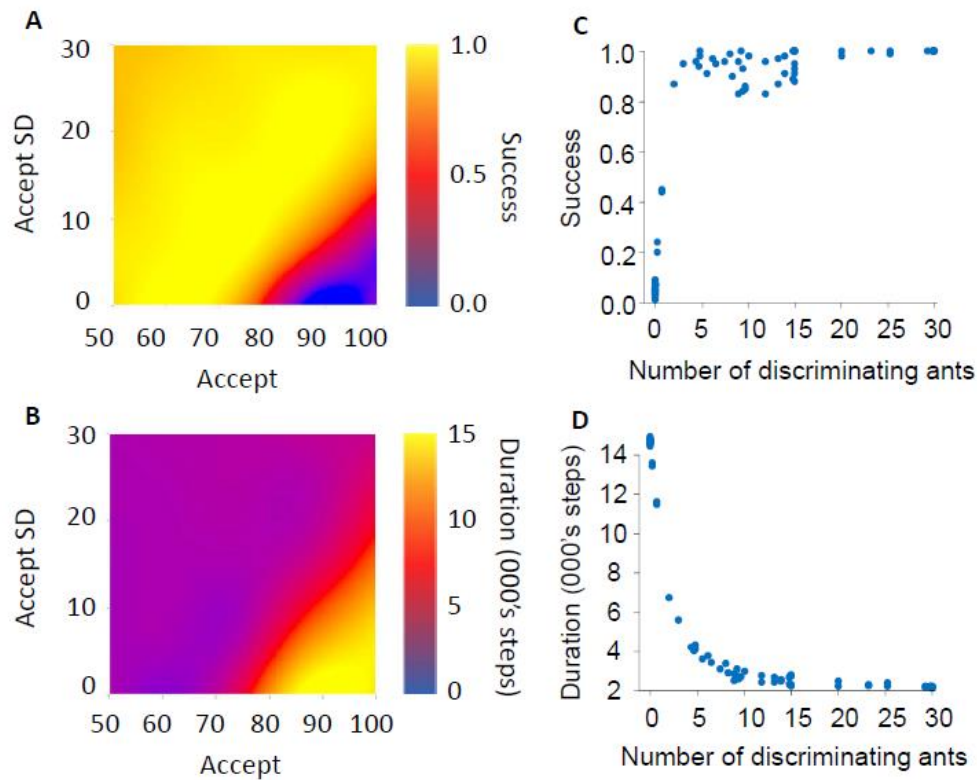


Figure 6. Line graphs showing the influence of environmental complexity (number of new candidate nests) on the emigration process. Simulations performed with a quorum of 28% and base parameters for 1, 2, 4, 8 & 16 nests (darker colours indicate higher numbers of nests), with a single nest of 'good' quality. **A & B.** Influence of number of nests and *accept* on duration and success, respectively. **C.** Proportion of 'votes' for the good nest. Votes were counted as the number of accept decisions (ants switching to *decided*) for each nest.

Figure 6

