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

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A B S T R A C T

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.

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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 pro-

cesses (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

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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 *M. 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 was developed to emulate the process of collective decision making during nest-site selection in the ant *M. 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)