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Leader-based and self-organized communication: Modelling group-mass recruitment in ants

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HIGHLIGHTS

- We model a group-mass recruiting ant colony exploiting food.
- Same parameters' values can lead to different exploitation levels.
- Non-linear response to trail pheromone by ants allows saving in signal's emission.
- Group leaders favour the transition from low to high exploitation level.

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ABSTRACT

For collective decisions to be made, the information acquired by experienced individuals about resources' location has to be shared with naïve individuals through recruitment. Here, we investigate the properties of collective responses arising from a leader-based recruitment and a self-organized communication by chemical trails. We develop a generalized model based on biological data drawn from *Tetramorium caespitum* ant species of which collective foraging relies on the coupling of group leading and trail recruitment. We show that for leader-based recruitment, small groups of recruits have to be guided in a very efficient way to allow a collective exploitation of food while large group requires less attention from their leader. In the case of self-organized recruitment through a chemical trail, a critical value of trail amount has to be laid per forager in order to launch collective food exploitation. Thereafter, ants can maintain collective foraging by emitting signal intensity below this threshold. Finally, we demonstrate how the coupling of both recruitment mechanisms may benefit to collectively foraging species. These theoretical results are then compared with experimental data from recruitment by *T. caespitum* ant colonies performing group-mass recruitment towards a single food source. We evidence the key role of leaders as initiators and catalysts of recruitment before this leader-based process is overtaken by self-organised communication through trails. This model brings new insights as well as a theoretical background to empirical studies about cooperative foraging in group-living species.

1. Introduction

Over the last decades, biology has been increasingly connected to the field of complex systems (Goodwin, 1994; Solé and Bascompte, 2006; Goldbeter, 1997; Okubo and Levin, 2001; Ball, 1999; Murray, 2001). Indeed, biological systems –from biochemical to community levels–are characterised by interacting agents –from molecules to populations. In animal societies, collective patterns emerge from information sharing and interactions between individuals. As large groups often lack a global communication system, these patterns frequently rely on self-organized mechanisms: group members respond to local information and follow a set of simple behavioral rules. This decentralized process has been shown to underlie various collective activities in numerous taxa, including humans (Bonabeau et al., 1997; Camazine et al., 2001; Couzin and Krause, 2003; Sumpter, 2006; Moussaïd et al., 2009).

Within eusocial insects, self-organized processes are particularly widespread as shown by studies on collective foraging and nest moving (Bonabeau et al., 1997; Deneubourg and Goss, 1989; Deneubourg and Franks, 1995; Detrain and Deneubourg, 2002, 2006; Theraulaz et al., 2003). In ant societies, the emergence of complex patterns has been reported in the case of collective foraging based on the laying of a chemical trail. Scouts having discovered food lay a trail that stimulates workers to exit the nest and guides them toward the resource. Once fed, those recruits start reinforcing the trail with a snowball effect on the growth dynamics of nestmates that are mobilized towards the food source. This recruitment – called mass recruitment – has been

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deeply investigated and mainly characterizes ant species with large colony sizes exploiting highly profitable food sources (Beckers et al., 1989; Planqué et al., 2010). Theoretical and experimental works provide evidence for emerging properties of mass recruitment such as symmetry breaking (Detrain and Deneubourg, 2006; Beckers et al., 1990, 1993; Nicolis and Deneubourg, 1999) or transition from disordered to ordered patterns (Beekman et al., 2001; Detrain et al., 1991; Edelstein-Keshet, 1994; Fourcassié and Deneubourg, 1994). In these self-organized complex behaviours, communication is based on an "anonymous" chemical trail that can potentially be shared by all the foragers present within the pheromone active space.

But, in some ant species, collective foraging relies on a few leaders sharing their information about food location only with a restricted number of foragers. In this case, a scouting ant that has discovered food, comes back to the nest, stimulates the exit of workers and leads them toward the food source. This leader-based recruitment is called "tandem running" when recruited ants are led one by one (Wilson, 1959; Möglich et al., 1974) or "group recruitment" when the leader concurrently guides several recruited nestmates (Möglich, 1979; Hölldobler, 1971). These leader individuals can have a strong impact on the dynamics of foraging at the collective level since their physical presence is usually required for the guidance of foragers to the food and hence for the success of recruitment. Tandem running is so far the best known leader-based recruitment and has been studied mainly in the context of house-hunting (Langridge et al., 2008; Franks et al., 2009; Pratt and Sumpter, 2006).

Among the numerous ant species living in the world, most of them perform self-organized mass recruitment by chemical trails, some exclusively use leader-based recruitment and only a few ones display a mix of both mechanisms (Hölldobler and Wilson, 1990). In this paper, we focus our study on this latter category of ant species as an ideal model to investigate the coupling of an anonymous and a leader-based communication. Therefore, we perform an in-depth analysis of the impact of leaders on collective food exploitation in a group-mass recruiting ant species, *Tetramorium caespitum*. It is known that group leaders modulate their recruiting behaviour according to food quality and thereby orient collective foraging choices towards the most profitable resources (Collignon and Detrain, 2010). Here, we will investigate in a one-food-source system how a self-organized communication (through the laying of a trail) may combine to a distributed-leadership (group leaders) and may contribute to the emergence of collective food exploitation within a wide range of recruitment parameters. Those predictions are compared with experimental recruitment performed towards different food sources by the *T. caespitum* colonies. By presenting a sucrose solution (0.1 M) or two types of preys (a cut mealworm *Tenebrio molitor* or an entire mealworm), we measured how recruitment parameters of our model are actually tuned by individual foragers and how such a tuning leads to different level of food exploitation.

2. Model

Our modelling of ants' foraging toward a unique food source is based on the behavioural state diagram proposed in (Sumpter and Pratt, 2003) to describe social insect foraging. In our model, foragers can be in one of the three following behavioural states according to their spatial position (nest or food source) and their knowledge about the presence of food (naïve or informed): (i) waiting ants (W): ants waiting inside the nest and naïve about the presence of food; (ii) recruiting ants (R): ants inside the nest informed about the presence of food ant; (iii) exploiting ants (E): ants present at the food source. Fig. 1 illustrates the transitions from one state to another.

A first transition consists in waiting ants (W) that become exploiting ants (E). This can be achieved by different ways. They may discover the food source by spontaneously exiting the nest or by following a chemical trail guiding them to the food source (both are described by the function φ_C). They may also discover food by following a leader ant after having been recruited within the nest (described by the function φ_L). A second transition applies to exploiting ants (E) leaving the food source and becoming recruiting ants (R). It is described by the function (φ_T). This transition $E \to R$ is coupled with the laying of a chemical trail. Transitions also concern recruiting ants (R) that may stop recruiting either because they rejoin the pool of waiting ants (φ_W) or because they leave the nest to exploit the food source (φ_E). Thus, the model is closed and the number of foragers is fixed. For this study, we choose a total population $T=200$ foragers to agree with our experiments (therefore, $W+E+R=200$).

We use the function proposed in Beckers et al. (1993) to account for the spontaneous discovery of a food source and the recruitment of waiting ants (W) by a chemical trail:

$$\varphi_C(C,W) = k(a+C^n)W/(b+C^n) \tag{1.1}$$

In this equation, the ratio ka/b gives the probability for the food source to be spontaneously discovered by an ant (that is in the absence of any chemical trail). We fixed $a=10$, $b=6000$ and $k=0.01$ meaning that at each second, a waiting ant as a constant probability of 1/60,000 to spontaneously exit the nest and discover the food source. Thus, for a total of 200 foragers, a spontaneous food discovery occurs approximately every 5 min on average. During our experiments, we observed a spontaneous discovery every 2 min. However, as they are performed in small sized foraging areas, 5 min is certainly more realistic and closer to open-field natural conditions (personal observation). The exponent n represents the non-linearity of the ants' response to changes in the amount of trail pheromone and C is the concentration of the chemical trail leading to the food source. We choose $n=2$ as experimentally evidenced for several ant species (Deneubourg et al., 1990, Beckers et al., 1992a).

To describe direct recruitment of waiting ants (W) by a leader ant (φ_L), we use the function proposed in Sumpter and Pratt (2003):

$$\varphi_L(R,W) = \mu RWG/(K+W) \tag{1.2}$$

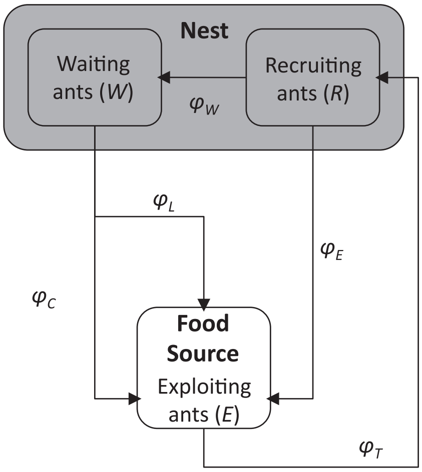

Fig. 1. Flow diagram for behavioural state variables. Ants can be in three different states: waiting inside the nest (W), exploiting the food source (E) or recruiting inside the nest (R). The rates of flow of workers from one state to another are illustrated by arrows and described by φ functions.