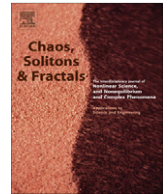


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Flexibility in collective decision-making by ant colonies: Tracking food across space and time

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ABSTRACT

Deciding which of many available resources to exploit is a problem faced by a range of decentralized biological systems. For example, ants are able to choose between food sources that vary in quality using a chemical trail. This communication system characterized by a strong positive feedback allows a rapid transfer of information and the selection of the best food source. This is true in static environment, where a single, unchanging solution exists. In dynamic environments however such recruitment often 'lock' groups into suboptimal decisions, preventing a response to changes in available resources. Here, we investigate decision-making in a dynamic environment for the greenhead ants (*Rhytidoponera metallica*) which use a non-chemical recruitment. To experimentally test our study species' ability to adapt to changes in their foraging environment, we offered three feeders that changed in quality. At any given time, only one feeder provided high quality food, while the others provided low quality food. Every two hours, the quality of the feeders changed such that the previously high quality feeder became a low quality feeder, and vice versa. We showed that ants were able to track changes in food quality across space and time. By coupling behavioral observations to computer simulations, we demonstrate that selection of food sources relies uniquely on a retention effect of feeding individuals on newcomers without comparison between available opportunities. The elegance of these parsimonious foraging systems is that the collective decision arises from the perception of conspecifics without the need for a leader having a synoptic overall view of the situation and knowing all the available options.

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1. Introduction

Many group living animals communicate about the location of food sources. Such communication is especially beneficial when food sources are ephemeral or hard to find [1,2], or when they are too large to be exploited by a single individual [3]. The best-known examples of food recruitment are found in the social insects: ants, termites and some species of bees and wasps which have evolved to acquire a wide range of signaling mechanisms [4]. For example, ants, termites and stingless bees mark the route

between their nest and discovered food sources with a chemical (pheromone), indirectly leading nestmates to the food. Pheromone trails can enable a rapid mass recruitment to food discoveries, but they also impose constraints on the overall foraging efficiency of a species [5].

It is currently agreed upon that many species using pheromone trails are unable to adapt to dynamic environments, such as switching to exploiting a newly discovered high-quality food source when the foraging effort of the colony is already concentrated on a food source of lesser value [6]. The apparent inability of a group of animals to adapt to changing conditions is supported by laboratory experiments [7–9] and mathematical mean field type models or Monte Carlo simulations [7,10–12]. For example, Beckers et al. [13] first provided black garden ants (*Lasius*

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niger) with a poor quality food and after some time introduced a second, high quality food. When the high quality food was added after the ants had established their trail to the poor quality food, the majority of ants continued to forage on the poor quality food. Mathematical models predict that ants will remain on an established trail for periods longer than the evaporation rate of the pheromone because ants continue to reinforce the trail leading the poor quality food [7,10,14]. Pheromone trails can thus result in ants being “trapped” in suboptimal solutions. Such situations have also been observed in other species using pheromones like stingless bees (*Trigona recurva*) [15] or caterpillars choosing balanced foods [16]. Other studies [17,18] reported that the ability to allocate or reallocate most individuals on the best food source is dependent on the strength of the positive feedback. Nicolis et al. [17] argued that a system possessing a high nonlinearity is more susceptible to be trapped in a suboptimal solution because of the possibility of the coexistence between two modes of exploitation while a linear or weakly nonlinear system will always select the best food source but in a weaker proportion.

That being said, there are ways to escape the deadlocks of suboptimal solutions. First, a combination of different pheromones allow ants to remember routes to sites that were previously rewarding and may become rewarding again in the near future, allowing the colony to track changing foraging conditions [19,20]. Second, species using positive feedback loops channeled by direct interactions such as contact instead of pheromones are more flexible and prevent the colonies from locking to poor choice [2,21].

In all these species cited above, individuals that discover a food source convey signals to their congeners and trigger the onset of a recruitment process. The foraging behavior of recruited individuals is then influenced by positive feedbacks enhanced by chemical or tactile signals (e.g. pheromone trail, contacts), leading progressively to the collective exploitation of the food sources [22]. A few studies nevertheless suggest that even in the absence of complex recruitment processes, group decisions could rely on non-linear dynamics based on social amplification [16,23,24]. For example Lihoreau et al. [24] reported a collective foraging decision in the gregarious cockroach *Blattella germanica* and describes a foraging decision-making mechanism based uniquely on a retention effect without requiring active recruitment. Their experiments demonstrate that feeding cockroaches recruit ‘passively’ at the food source without the necessity of active signaling through pheromonal emission or recruitment behavior. All individuals explore their environment randomly and select a resource in relation to the number of conspecifics already on it, thus triggering a positive feedback that leads to collective food selection. In this paper we suggest that these type of decision making process allow more flexibility in changing environment where food source may appear or disappear.

To validate our hypothesis we consider ants that do not use either contacts or pheromone – the greenhead ants *Rhytidoponera metallica*. We study their ability to adapt to dynamically changing foraging conditions. First, we

describe experiments showing that green-headed ants are able to quickly adapt their foraging behavior according to changes in food quality. Then, based on feeding behaviors measured at the individual level (time spent feeding according to presence of neighbors), we propose a model to assess the flexibility of collective decision in a dynamic environment.

2. Method

The ponerine ant genus *Rhytidoponera* also named greenhead ants is distributed throughout Australia and its neighboring islands. Colonies of *R. metallica* are found under rocks, in decaying logs, or in leaf-litter and superficial layers of soil [25,26]. In *R. metallica*, nest founding occurs mainly by budding [25] and is associated with the usual presence of multiple fertilised egg-laying workers (gamergates) in the colony [26]. As with most ponerines, workers are monomorphic [25].

Fifteen colonies of *R. metallica* were collected in March 2008 in Sydney, Australia. We collected 1000 ants per mother colony and housed them in a plastic box (l = 20, w = 15, h = 5 cm) the bottom of which was covered by a layer of cotton. The box was connected to a foraging arena l = 40, w = 25, h = 20). The nests were regularly moistened and the colonies were kept at room temperature (25 ± 1 °C) with a 12:12 L/D photoperiod. We supplied ants with water and a mixed diet of vitamin-enriched food [27], as well as drosophila, two times a week.

Before the experiment, the colonies were starved for five days. The experiment started when the ants were given access to a foraging arena (110 cm diameter) placed over the colony. The ants had access to the center of the arena via a wooden stick. We placed two poor and one high quality feeders in the arena 10 cm from the boarder. We used sugar syrup solidified with agar (high quality = 10%, low quality = 2%) as our feeder to allow a better access to the food. Using liquid food promoted crowding at the feeder.

The experiment consisted of two spatial configurations, each performed with one particular type of feeder



Fig. 1. Focal ant (ants with a white spot) surrounded by four neighbors while feeding.

distribution (Fig. 1). In the sparse arrangement, feeders were placed in a triangular configuration; in the clustered configuration, feeders were 10 cm away from one another. Every two hours we swapped the position of the high quality and one of the two poor feeders (chosen randomly). The experiment lasted for 6 h. We replicated each treatment 15 times using 15 colonies. All experiments were filmed by a video camera placed over the arena. The whole experimental set-up was isolated from any sources of disturbance.

At a collective level, to assess feeder preference we counted the number of ants present on each feeder every five minutes for six hours. Counting began as soon as the first ant entered the arena.

At the individual level, we first measured the time spend feeding for 100 ants for both the high quality feeder and one of the poor feeders, for both spatial configurations (one replicate per treatment) (400 ants followed in total). Ants were considered as feeding when they were in contact with the food for more than 5 s. Brief contacts with the food (less than 5 s) are usually referred as food probing [28]. When an ant started feeding, we counted the number of ants in the close vicinity (5 mm from the focal ants). The maximum number of ants was 4 ants due to crowding around the focal ant (Fig. 1).

Second, we recorded the number of ants that probed the food but did not eat for more than 5 s (210 and 388 ants followed for the high quality feeder and the poor quality feeder, respectively). Finally, we counted the number of ants reaching each feeder per unit of time for 15 min to estimate the flow rate of individuals for each feeder quality.

All the individual behaviors were recorded 15 min after the beginning of the experiment and were done before the first feeder swap.

2.1. Statistics

We used a MANOVA to compare the proportion of ants on each feeder according to spatial configuration. We run a

Factorial Cox-regression analysis testing the effect of neighbors, feeder quality and treatment on time spend feeding.

3. Results

Spatial configuration had no effect on dynamic response (MANOVA: $p = 0.87$, $F_{1,77} = 0.02$). Green-headed ant responded to changes in feeder quality such that, there was a greater proportion of foragers feeding at the high quality feeder (MANOVA: $p < 0.001$, $F_{1,77} = 24.06$, Fig. 2).

In average, ants spent twice more time feeding on the high quality feeder than on the poor feeder no matter the spatial configuration (feeder quality effect: $z = -9.4$, $P < 0.001$, treatment effect $z = -1.3$, $P = 0.1784$, mean \pm SD 255 ± 179 s and 640 ± 249 s for the poor feeder and the high quality feeder respectively). The amount of time individual ants spent feeding on the low quality feeder depended on the number of neighboring ants, such that feeding duration increased with neighbour density (Neighbors effect: $z = -7.6$, $P < 0.001$, Fig. 3). This was not true for the high quality feeder (interaction neighbors \times feeder quality $z = 2.9$, $P = 0.003$). The probability to leave the feeder after probing the food was negligible 0.05 (10 out of 210 ants) on the high quality feeder but considerable 0.48 (188 out of 388 ants) on the poor feeder. This latest results imply that we overestimated the number of ants feeding on the poor feeder when we quantified foraging effort by counting the number of workers allocated to each feeder at set intervals. Hence, on snapshots we were not able to differentiate ants probing the food from ants feeding and we considered all of them as feeding. Spatial configuration and food quality had no effect on the flow rate of individuals reaching each feeder ($F_{1,56} = 0.03$, $P = 0.862$ and $F_{1,56} = 3.25$, $P = 0.077$ for configuration and feeder quality respectively).

4. The model

The model describes the mean number of individuals x at each feeder i through time. It assumes a number N of

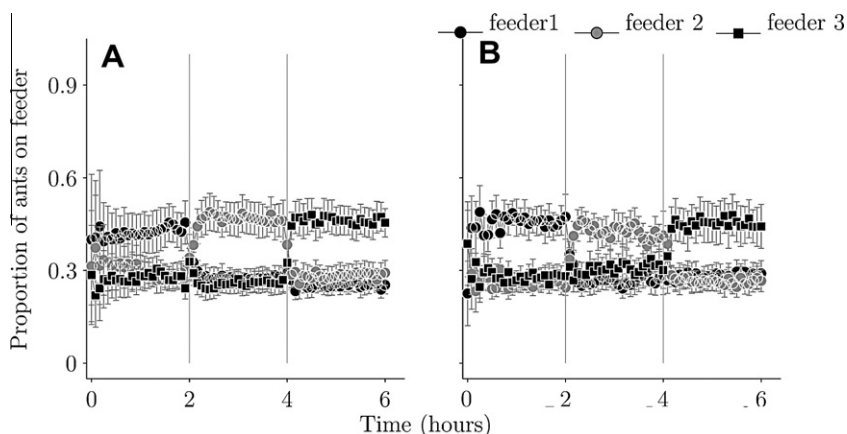


Fig. 2. Time series showing changes in the proportion of foragers on each feeder throughout the experiment for both configuration (A) feeders separated and (B) feeders clustered. Feeders are numbered according to the order in which they became high quality; thus, feeder 1 is the high quality feeder in period 1, feeder 2 is the highest quality feeder in time period 3, and feeder 3 is the highest quality feeder in period 3. The grey line indicates when the feeder changes quality.

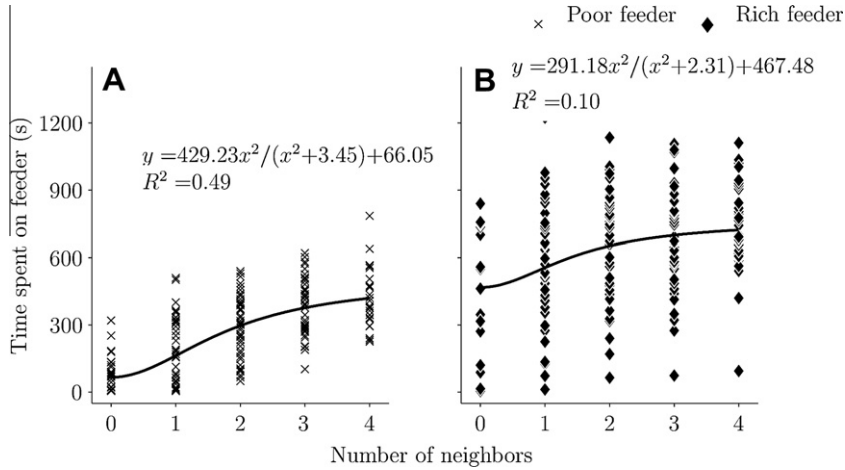


Fig. 3. Time spent feeding as a function of the number of neighbors and the quality of the feeder.

individuals in the arena and a constant flow rates φ_i of individuals on every feeder. Furthermore, ants leave the feeder at a rate λ_i , which is dependent of its quality. This leads to the following rate equations

$$\frac{dx_i}{dt} = \varphi_i \left(N - \sum_{j=1}^3 x_j \right) - \lambda_i x_i \quad i = 1..3 \quad (1)$$

Here λ_i is the inverse at the time spent on a feeder i , as described by Fig. 3. For the poor quality feeders $i = 2,3$ it depends on the neighbors already on these feeders. We account for this dependence through the nonlinear fit on Fig. 3

$$\lambda_{2,3} = \left(\frac{\alpha x_{2,3}^2}{x_{2,3}^2 + \beta} + \gamma \right)^{-1}$$

where γ is the decay rate when no neighbors are present, β is a threshold beyond which the x dependence saturates and α is the saturation value. In the following these parameters will be taken from the values in Fig. 3. As for the high quality feeder $i = 1$, the nonlinear fit displayed in Fig. 3B is not statistically relevant as reflected by its R^2 value. Furthermore the value of γ being large, we can neglect the dependence of the neighbors x . We take thus λ_1 as being constant (and evaluated as the average).

Eqs. (1) can now be explicitly written

$$\begin{aligned} \frac{dx_1}{dt} &= \varphi_0 \left(N - \sum_{j=1}^3 x_j \right) - \lambda_1 x_1 \\ \frac{dx_2}{dt} &= \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_2^2}{x_2^2 + \beta} + \gamma \right)^{-1} x_2 \\ \frac{dx_3}{dt} &= \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_3^2}{x_3^2 + \beta} + \gamma \right)^{-1} x_3 \end{aligned} \quad (2)$$

Eq. (2) admit only one physically acceptable steady state solution (i.e. in a static environment) corresponding to the selection by the majority of individuals of the high quality feeder (given the parameters we extracted from the experiments), the two poor quality feeders being selected equally by a minority of individuals.

Let now study the model in a dynamic environment. We numerically integrate Eq. (2) through time with the parameters belonging to high quality and low quality feeders such that

$$\begin{aligned} 0 < t < T_1 & \begin{cases} \frac{dx_1}{dt} = \varphi_0 \left(N - \sum_{j=1}^3 x_j \right) - \lambda_1 x_1 \\ \frac{dx_2}{dt} = \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_2^2}{x_2^2 + \beta} + \gamma \right)^{-1} x_2 \\ \frac{dx_3}{dt} = \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_3^2}{x_3^2 + \beta} + \gamma \right)^{-1} x_3 \end{cases} \\ T_1 < t < T_2 & \begin{cases} \frac{dx_1}{dt} = \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_1^2}{x_1^2 + \beta} + \gamma \right)^{-1} x_1 \\ \frac{dx_2}{dt} = \varphi_0 \left(N - \sum_{j=1}^3 x_j \right) - \lambda_2 x_2 \\ \frac{dx_3}{dt} = \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_3^2}{x_3^2 + \beta} + \gamma \right)^{-1} x_3 \end{cases} \\ T_2 < t < T_3 & \begin{cases} \frac{dx_1}{dt} = \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_1^2}{x_1^2 + \beta} + \gamma \right)^{-1} x_1 \\ \frac{dx_2}{dt} = \varphi \left(N - \sum_{j=1}^3 x_j \right) - \left(\frac{\alpha x_2^2}{x_2^2 + \beta} + \gamma \right)^{-1} x_2 \\ \frac{dx_3}{dt} = \varphi_0 \left(N - \sum_{j=1}^3 x_j \right) - \lambda_3 x_3 \end{cases} \end{aligned} \quad (3)$$

where T_1, T_2 and T_3 are respectively 2, 4 and 6 h. The results of this numerical integration for all $\varphi_0 = \varphi$ equal are shown in Fig. 5A. Comparing this latter figure with Fig. 2 shows that the very short time needed to switch to the new high quality feeder is very well predicted and that the experimental and theoretical proportions of individuals on each feeder are comparable, the theoretical one underestimating the one on the high quality feeder by 5%. On the other hand, as mentioned before, a non negligible proportion (0.48) of ants on

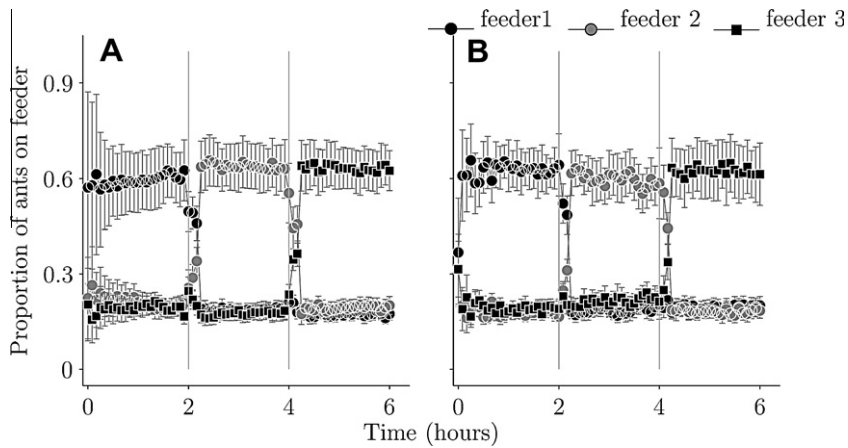


Fig. 4. Time series showing changes in the proportion of foragers on each feeder throughout the experiment for both configurations taking into account the probability of leaving the feeder after probing the food (A) feeders separated and (B) feeders clustered. Feeders are numbered according to the order in which they became high quality; thus, feeder 1 is the high quality feeder in period 1, feeder 2 is the highest quality feeder in time period 3, and feeder 3 is the highest quality feeder in period 3. The grey line indicates when the feeder changes quality.

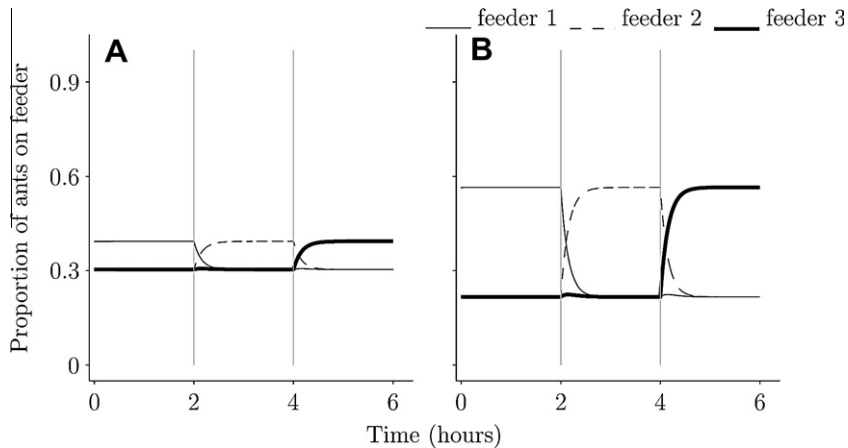


Fig. 5. Time series as obtained by numerical integration of the set of Eq. (3) for parameter values equal to $N = 100$, $\lambda = 1/640 \text{ s}^{-1}$, $\alpha = 429 \text{ s}$, $\beta = 3.5$, $\gamma = 66 \text{ s}$ and (A) $\varphi_0 = \varphi = 0.1 \text{ s}^{-1}$, (B) $\varphi_0 = 0.1 \text{ s}^{-1}$, $\varphi = 0.05 \text{ s}^{-1}$. Initials conditions taken to be at the steady states for the three variables. Feeders are numbered as in Fig. 2, grey lines indicate when the feeder changes quality.

the low quality feeder was only probing the food before leaving, implying the real flow on individuals on the poor feeder was approximately half of the one we measured in Fig. 2 (see Fig. 4). Integrating numerically Eq. (3) to take into account this effect (with $\varphi = \varphi_0/2$) leads to Fig. 5B in which, again, the agreement seems satisfactory, except an underestimation now of 3% of the proportion of ants on the high quality feeder.

On the other hand, taking the most probable value of the time spent (rather than the average one) (see Fig. 6) on the high quality feeder decreases the effective retirement rate by 15% and one obtains the correct proportion (Fig. 7).

5. Discussion

Strong positive feedbacks associated to active recruitment through chemical trails has been shown to lead to

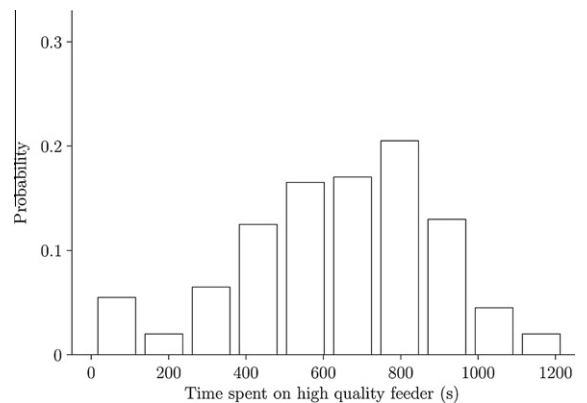


Fig. 6. Probability distribution of the times spent on the high quality feeder.

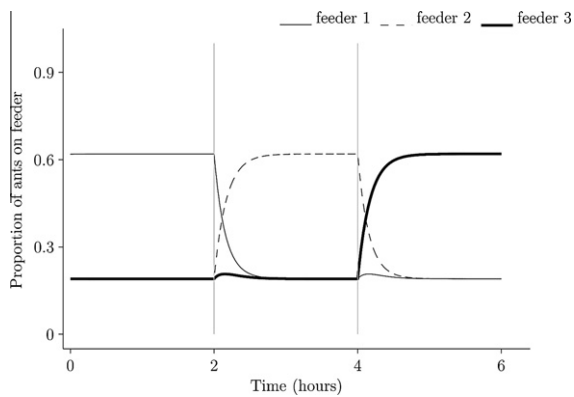


Fig. 7. Time series as obtained by numerical integration of the set of Eq. (3) for parameter values equal to $N = 100$, $\lambda = 1/800 \text{ s}^{-1}$, $\alpha = 429 \text{ s}$, $\beta = 3.5$, $\gamma = 66 \text{ s}$ and $\phi_0 = 0.1 \text{ s}^{-1}$, $\phi = 0.05 \text{ s}^{-1}$. Initials conditions taken to be at the steady states for the three variables. Feeders are numbered as in Fig. 2, grey lines indicate when the feeder changes quality.

an inability of certain species to switch to the best feeder in dynamic environments [7,8,12,16], as they lead to more than one mode of exploitation by the individuals and hence to the possibility to be trapped in a sub-optimal solution.

Species like greenhead ants generally forage alone and active recruitment via chemical trail is never observed [29–31]. Consequently, in our experiment, no such trap was observed and ants were able to track rapidly the best feeder in space and time, showing a great flexibility. Specifically, behavioral observations coupled with a deterministic mean field model showed that colonies of *R. metallica* were able to adjust their foraging activity as a function of environmental changes, in the sense that they were able to choose the best foraging opportunity and adapt their foraging activity rapidly according to change in food quality. We demonstrated that selection of the best food source relies both on a retention effect of feeding individuals and on the individual perception of food quality; without comparison between available opportunities.

In insects, the food quality is detected immediately on contact with the food and may influence both the probability of initiating feeding and the duration of the meal [32]. Indeed, Greenhead ants when confronted to a high quality feeder spent more time feeding than on a poor quality feeder. As a corollary, one notes a high rate of abandon at the poor quality feeder while it was negligible on the high quality feeder.

Moreover, ants being social, we observed that feeding behavior was influenced by the presence of congeners. The time spent feeding on the poor quality feeder increased with the number of neighbors. A similar mechanism was previously shown to be in action in cockroaches [24]. These authors showed that individuals were modulating the time spent at the food source according to the presence of congeners. This retention effect of feeding individuals on newcomers was observed at the richest feeder whereas in our study it was observed only on the poorest feeder. Our model demonstrates that retention effects exerted by conspecifics already present on a resource

combined with feeding behavior are able to trigger group formation without the requirement of sophisticated active recruitments. Greenhead ants were able to assess the quality of resources and to exploit selected sources optimally without global information or explicit comparisons of available opportunities. All individuals explored their environment randomly and select a resource in relation to its quality and to the number of conspecifics already on it. The elegance of these parsimonious foraging systems is that the collective decision emerges from the perception of congeners as well as the individual perception of food quality without the need for a leader having a synoptic overall view of the situation and knowing all the available options.

Undoubtedly, there are many ways for ant colonies to achieve flexibility in their recruitments. Mechanisms like the use of multiple pheromones, involving more complex interactions than just one positive feedback [19] or, on the contrary more elementary mechanisms like a linear recruitment and a linear retirement rate can be at work [33]. The foraging success of social insects is partly due to the sophisticated means of communication they have developed through evolution. The real challenge is now to understand if and how some ways are better adapted than others to particular ecological conditions. We predict that the mechanism we describe in this paper, modulated by quantitative changes due to specific traits, should prove relevant to explore collective foraging strategies in ants and others group-living species with varying levels of social complexity.

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