Research

Cite this article: Bles O, Boehly T, Deneubourg J-L, Nicolis SC. 2018 Same length, different shapes: ants collectively choose a straight foraging path over a bent one. *Biol. Lett.* **14**: 20180070.
<http://dx.doi.org/10.1098/rsbl.2018.0070>

Received: 30 January 2018

Accepted: 23 February 2018

Subject Areas:

behaviour

Keywords:

collective decision-making, ant, orientation, exploration, recruitment

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4024462>.

Animal behaviour

Same length, different shapes: ants collectively choose a straight foraging path over a bent one

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In social insects, exploration is fundamental for the discovery of food resources and determines decision-making. We investigated how the interplay between the physical characteristics of the paths leading to food sources and the way it impacts the behaviour of individual ants affects their collective decisions. Colonies of different sizes of *Lasius niger* had access to two equal food sources through two paths of equal length but of different geometries: one was straight between the nest and the food source, and the other involved an abrupt change of direction at the midway point (135°). Both food sources were discovered simultaneously, but the food source at the end of the straight path was preferentially exploited by ants. Based on experimental and theoretical results, we show that a significantly shorter duration of nestbound travel on the straight path, which rapidly leads to a stronger pheromone trail, is at the origin of this preference.

1. Introduction

In the presence of several food sources, many social insects are able to focus their foraging effort towards a particular one [1], especially if they differ in supply [2,3] or if the characteristics of the paths leading to the food sources are different [4,5] (see electronic supplementary material, table S1 for a more exhaustive review). When exploring their environment, ants collect information that will affect their individual behaviour and the collective choice of the colony. Circuitous outbound paths of foraging journeys are integrated into straight inbound vectors, allowing exploring ants to return to their nest along the shortest route. This phenomenon, known as path integration [6], incorporates—and is complemented by—the use of external references, such as light from the sky or objects on the ground. The question arises, therefore, to what extent this system is robust to navigational traps and errors [7,8], particularly how the orientation and the ability to return to the nest are affected by various environmental conditions. It has already been shown that the successful foragers' return rates positively influence the outgoing flow of foragers [9,10] but the link between the nestbound travel durations and the resulting collective decision-making is poorly understood. In this paper, we investigate the collective choice of ants in a binary choice set-up in which individuals could follow two equal length paths leading to two identical food sources (figure 1a). The difference between paths was that one was straight, while the other involved an abrupt change in direction (135° angle) at the midway point. We assumed that this geometrical difference affects individual ant behaviour (foodbound and nestbound trips) and, therefore, the resulting collective choice. Prior hypotheses were that increasing colony size would: (i) lead to a transition from a no choice or a small preference for the straight branch to a systematic collective choice of the straight branch (amplifying the effect of path integration)

Figure 1. (a) Experimental set-up with (1) the nest and (2) two equal quality food sources equidistant from the nest at the end of the (3) straight and (4) bent paths. (b) Time needed for the 1st, 5th and 10th individuals to discover each food source and (c) the duration of travel back to the nest on each path (* $p < 0.001$).

and (ii) decrease the food-discovery time and increase the food-consumption level. Based on our observations, we then build a mathematical model of ants' recruitment to investigate the link between the geometry of the paths to food sources and the behaviour at the colony level.

2. Material and methods

(a) Experimental set-up and procedure

Two large mother colonies of the black garden ant *Lasius niger* (collected in Brussels, Belgium, September 2014) were each divided into queenless and broodless subcolonies of 50, 100, 200 and 500 individuals, for a total of eight experimental groups. Each subcolony was kept in a plastic box ($260 \times 160 \times 50$ mm) containing a square glass nest ($100 \times 100 \times 2$ mm) and ad libitum water and sucrose solution (1 M). After 2 days of starvation, ants had access for 1 h to the binary choice set-up where a 1 M sucrose food source was placed at the end of each path (figure 1a). Each colony was tested three times ($N = 24$), and six experiments were removed from the analysis, as no ants explored the branches. The food-discovery times of the two branches were compared (Mann–Whitney rank) by measuring the time needed for the 1st, 5th and 10th individual to reach each food source. Additionally, in three experiments with colonies of 100 individuals, we recorded the entire duration of all nestbound trips performed over the course of the experiment (101 individuals performing, $N = 132$ trips). We looked at the effect of colony size on the time of food source discovery and compared the mean times of return to the nest for consecutive travels of each tracked individual (Kruskal–Wallis H -test

coupled to a Dunn's post hoc comparison of pairs). The collective choice of food source by the colony was determined by counting the number of ants feeding at each food source during the whole experiment. An individual was considered to be feeding at a food source if its head was positioned above the sucrose for at least 5 s. A one-sided binomial test was used to determine whether the colony allocated significantly more than 50% of its foraging force towards a path.

(b) Model description

The model is described in figure 2a (see also the electronic supplementary material, model section). Here, R is a reservoir containing individuals that may explore the environment with a probability ϕ . Once out, individuals X choose the branch i ($i = 1, 2$) with a probability f_i depending on the concentration of pheromone on each branch (c_1, c_2). Individuals on branch i , X_i , reach the food source i with a probability α . Individuals at the food source Y_i return to branch i and drop a pheromone unit with a probability γ_i (which contributes to increase c_i). The probabilities α and γ_i correspond to the inverse of time needed to reach the source and time to return to the nest, respectively. The pheromone disappears at a rate μ .

3. Results

(a) Exploration activity and travel back to the nest

The comparison of the times needed for the 1st, 5th and 10th individual to reach the food sources showed no significant difference between branches (figure 1b, Mann–Whitney

Figure 2. (a) Scheme of the model. (b) Comparison of experimental and theoretical proportion of ants at the food source at the end of the straight path. (c,d) Probability distributions, mean and standard deviation of the proportion of individuals on the straight branch as a function of (c) the ratio γ_2/γ_1 , where $\gamma_1 = 1/107$, $\phi = 0.058 \text{ s}^{-1}$; (d) ϕ , where $\gamma_1 = 1/107$, $\gamma_2 = 1/260$. Other parameter values are given in electronic supplementary material, figure S5; number of simulations = 10 000 and number of steps of each simulation = 3600. (Online version in colour.)

U-test, 1st: $U = 154.0$, $p = 0.406$; 5th: $U = 144.0$, $p = 0.390$; 10th: $U = 122.0$, $p = 0.157$), and the colony size had no impact on these times, regardless of the branch shape (Kruskal–Wallis H -test, $\chi^2 = 2.9$, $p = 0.407$). The duration of the first nestbound trip from the end of the bent branch was significantly longer than that from the end of the straight branch (figure 1c, $319.83 \pm 219.44 \text{ s}$, $N = 12$ and 130.45 ± 92.98 , $N = 71$, respectively; Mann–Whitney *U*-test: $U = 153.5$, $p = 0.0002$). A similar result was observed for all nestbound trips (figure 1c, $259.82 \pm 207.30 \text{ s}$, $N = 17$ and $107.18 \pm 80.68 \text{ s}$, $N = 115$, respectively; Mann–Whitney *U*-test: $U = 368.0$, $p < 0.00001$).

(b) Relative exploitation of food source and collective choice

No colonial and no colony size effects were observed at the individual or at the collective level (see electronic supplementary material, S1 and figures S1 and S2). A significant food source choice occurred in 16 of 18 experiments in which ants explored their environment (see electronic supplementary material, table S2). The food source at the end of the straight branch was significantly more exploited, with an

average proportion of $75.38 \pm 9.23\%$ of the ants, in 12 of 16 trials (binomial test, $p = 0.038$). The comparison between experimental and theoretical distributions of the proportion of individuals on the straight branch shows no difference (figure 2b, Kolmogorov–Smirnov test, $D = 0.14$, $p = 0.86$). Figure 2c,d displays the theoretical probability distributions of selecting the straight branch as a function of the ratio γ_2/γ_1 and ϕ , respectively. For an increasing γ_2/γ_1 , the simulations predict a transition from a systematic selection of the straight branch to an equal frequency of selection of each branch. When increasing ϕ , the simulations predict a transition from a systematic equal exploitation to an equal frequency of selection of each branch, followed by a transition to a systematic selection of the straight branch.

4. Discussion

Several studies have focused on the effect of the geometrical characteristics of foraging paths on the individual behaviour and collective choices of ants (see electronic supplementary material, table S1). We showed that in a set-up where two food sources are accessible via a straight and a bent branch

of equal length, a colony preferentially exploits the resource at the end of the straight branch. This collective response is not due to any bias in the outgoing movement patterns of ants, as no difference was found in the time needed to reach each food source during exploration. In contrast, the duration of nestbound trips via the bent path was approximately 2.5 times longer than that via the straight path, favouring the rate of pheromone deposition on the straight path.

During their foraging trips, bees and ants keep track of their location using path integration and their memory, allowing them to return directly to the nest [11,12]. In our experiments this phenomenon led the ants to go rapidly from the food source to the nest on the straight branch, independently of the colony size. By contrast, the nestbound durations were longer on the bent branch, resulting from a possible conflict between the direction imposed by the set-up and the one given by path integration and memory. The model that integrates equal foodbound durations and different nestbound durations is in agreement with the experimental results. It supports the hypothesis that the selection of the straight branch is derived from competition between the two trails, which is enhanced by a shorter nestbound travel time via the straight branch. This difference is likely the result of path integration and individual memory [13].

The difference between trip durations plays a similar role in the case where ants are faced with food patches at different distances from the nest [14]. However, in this case, the collective preference results from a different and simple mechanism linking trip duration and distance. Other experiments have shown that the geometrical differences directly

affect the individual preferences. For example, ants preferentially follow the path that deviates less from their original direction [4,5,15], and those returning to the nest are more sensitive to the geometry of the bifurcations [4,16] than naive ants exploring an unmarked environment [17].

The absence of any colony size effect on exploration activity, foodbound flow and choice intensity revealed by our experiments suggests that a pool of foragers is equally effective in small or large colonies. On the other hand, the Monte Carlo simulations allow different exploitation patterns for different flows which, in their turn, are related to the colony size. It would, therefore, be interesting to undertake further experiments with a wider range of colony sizes or a longer starvation period to test the robustness of these predictions. Finally, as far as path integration is concerned, trajectories of returning ants and their relationship with foodbound duration should be analysed.

Data accessibility. All data can be found in the electronic supplementary material. Dryad: <https://dx.doi.org/10.5061/dryad.1f24f> [18].

Authors' contributions. J.-L.D. and O.B. conceived the experiments; T.B. conducted the experiments; O.B. analysed the results and wrote the manuscript; S.C.N. conceived and analysed the model. All the authors contributed to writing the paper. All authors gave final approval for publication and agree to be held accountable for the content herein.

Competing interests. The authors declare no competing interests.

Funding. O.B. was financed by a PhD grant from FRiA (Fonds pour la Recherche dans l'Industrie et dans l'Agriculture).

Acknowledgement. We thank the two referees for their helpful comments on the manuscript.

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