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Infrastructure construction without information exchange: the trail clearing mechanism in *Atta* leafcutter ants

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A wide range of group-living animals construct tangible infrastructure networks, often of remarkable size and complexity. In ant colonies, infrastructure construction may require tens of thousands of work hours distributed among many thousand individuals. What are the individual behaviours involved in the construction and what level of complexity in inter-individual interaction is required to organize this effort? We investigate this question in one of the most sophisticated trail builders in the animal world: the leafcutter ants, which remove leaf litter, cut through overhangs and shift soil to level the path of trail networks that may cumulatively extend for kilometres. Based on obstruction experiments in the field and the laboratory, we identify and quantify different individual trail clearing behaviours. Via a computational model, we further investigate the presence of recruitment, which—through direct or indirect information transfer between individuals—is one of the main organizing mechanisms of many collective behaviours in ants. We show that large-scale transport networks can emerge purely from the stochastic process of workers encountering obstructions and subsequently engaging in removal behaviour with a fixed probability. In addition to such incidental removal, we describe a dedicated clearing behaviour in which workers remove additional obstructions independent of chance encounters. We show that to explain the dynamics observed in the experiments, no information exchange (e.g. via recruitment) is required, and propose that large-scale infrastructure construction of this type can be achieved without coordination between individuals.

1. Introduction

The construction and use of paths and highways is not a unique feature of humans, but is known across many different animals including elephants [1], domesticated cattle [2], voles [3], quokkas [4], marine snails [5] and many ants [6]. The function of such trails includes the reduction of movement costs [5,7], the increase of movement speed [7,8], the delineation of colony territory [9,10] and externalization of foraging memory [11,12]. The arrangement of such trails into large-scale networks has been shown to balance and optimize elements of construction cost and network robustness (see [13] for a review).

Among trail constructing animals, the leafcutter ants (*Atta* spp.) show the most intricate trail construction behaviour: workers remove vast amounts of vegetation and undergrowth from prospective trails [14], cut passes through overhanging obstructions [15] and shift soil to level trail surfaces [16]. On average, colonies clear 2730 m of trail per year [14], and individual trails can exceed 200 m [17]. Colonies on average invest 11 000 ant hours annually into construction and

Figure 1. Overview of the obstruction arena (measuring 100 × 50 cm) with central cleared trail and a 10 × 8 cm obstruction zone marked with dotted lines, and folded blue paper strips as obstructions. Inset on bottom left shows magnification of image centre. The obstruction arena was inserted between the nest (to the left of the arena) and the foraging container (to the right).

trail maintenance [14], but the resulting benefits greatly outweigh the cost [7]. Interestingly, not all of their foraging trails are cleared. Foraging occurs on uncleared trails leading to scattered resources [18], and even trails to persistent sites can remain fully or partially uncleared (T. Bochynek 2014, personal observation; [19], figure 3). What, then, governs the clearing of trails, and what role do local obstruction density and energetic considerations [7] play?

Despite the known complexities and dimensions of their behaviour, little is known about the underlying trail construction mechanisms and the corresponding behaviours of individuals. Howard showed that the mean head size of trail clearing ants was 13% larger than the mean size of foragers and that marked clearers and foragers showed fidelity to their previous task after 24 h, although at different rates ([14], cf. figure 1). It would seem most efficient if outbound workers performed trail clearing while incoming workers concerned themselves solely with resource transport: in this way, clearing workers would efficiently reach the obstructions and inbound workers would be freed from performing maintenance tasks, thus maximizing resource flow. The association between a worker's direction of travel and its propensity to engage in trail clearing is unknown. On average, 41% of inbound workers returned from foraging sites without carrying a load, and it is possible that these unladen ants play a role in trail clearing [20,21]. Bouchebti *et al.* [19] found that clearing on a trail branch of 3 m length proceeds at equal rates along the length of the trail (although the distal section of the trail remained less cleared) and suggest that trail clearing is not undertaken by a dedicated 'clearing workfront' moving from the nest to the harvesting site.

Considering the great number of individuals involved in the construction, the question of their coordination arises. Many studied examples of self-organization involve stigmergic processes, in which indirect communication with pheromones organizes the group level behaviour [22–25]. However, recent studies have shown that stigmergy is not necessary to explain concerted construction: Green *et al.* [26] showed that worker aggregation rather than the previously suspected presence of cementation pheromone localized excavation work sites in termites, and Bruce [27] found no behavioural response to freshly excavated soil that would contain a digging pheromone were it an organizing factor in excavation in leafcutter ants. *Eciton* army ants, which self-assemble into bridges to cross trail gaps, gauge the necessity to reinforce or leave these structures based purely on the rate of physical contact with passing workers with no evidence of stigmergic processes [28].

In this work, we investigated two mechanistic questions: (i) are there different individual-level trail clearing behaviours? and (ii) does recruitment (i.e. the engagement in trail clearing behaviour as a result of information transfer) play a role in organizing trail construction? To study these questions, we placed normalized obstructions on foraging trails, observed the individual and colony-level removal dynamics and constructed a computational model based on the observed behavioural rates.

2. Methods and results

(a) Laboratory experiments methods

(i) Experiment set-up

We conducted experiments in the Behavioural Neurobiology laboratory at the University of Konstanz, Germany, in 2014. All experiments were conducted in a temperature control room at 25°C and 40–60% relative humidity, in a 12 L : 12 D cycle with two colonies of *Atta vollenweideri*, collected in 2013 by S. Neupert, L. Kling and C. J. Kleineidam at the Parque Nacional Rio Pilcomayo, Argentina (25° 07′ 37″ S, 58° 10′ 52″ W). The larger of the two colonies was subdivided into two equal-sized subcolonies (one part containing the queen) containing approximately 100 000 workers and equal amounts of fungus in 4–6 connected plastic cylinders of 3.6 l volume each. Each colony was connected to identical experimental set-ups. An obstruction arena of 100 × 50 cm dimensions, in which we conducted removal experiments, was connected on one side with an approximately 30 cm long plastic tube to the interconnected nest chambers, and on the other side with an 8 m long tube to a foraging container. The sides of the arena were coated with mineral oil to prevent escape. In nature, cleared trails are framed by the surrounding leaf litter and vegetation. In order to simulate such trail delineation in the obstruction arena, we framed a designated trail with Seramis® expanded clay pellets (figure 1). The width of the predesigned trail was fixed at 8 cm, approximately twice as wide as the colony's unconstrained traffic flow during peak foraging activity. We designated an obstruction zone halfway along the length of the trail in the arena in which we placed standardized paper obstructions fashioned from a folded paper strip measuring 25 × 5 mm and cut from blue Plano-Color® paper of weight 1.28 mg mm^{-2} (figure 1). They were designed to be obstructive by virtue of their spatial dimensions but to cause no behavioural response based on their chemical properties. To guarantee this, we tested the effect of such paper strips under three different conditions: presented unfolded and flatly placed on the trail, treated with sugar water, marked with Edding® permanent marker pen, and folded in half and standing. In order not to skew the response of a colony via the sugar-treated paper strips, the preliminary tests were conducted on a different laboratory colony of *A. vollenweideri* that was not subsequently used for the experiments. We found that flat paper strips ($n = 20$) did not produce any behavioural response, and workers moved over them without removing a single strip during 2 h of foraging. Strips treated with sugar water were picked up and carried into the colony where they were shredded and integrated into the fungus. Standing strips folded into half generated the desired removing behaviour and were picked up and deposited at (or beyond) the trail delimiter. Marker-treated paper strips were likewise removed, but much more rapidly than those folded in half, possibly representing an antipathetic response to the marker solvent.

Colonies were fed *Rubus* sp. leaves every morning at approximately 10.00. All experiments occurred within a 10 h window following the feeding. One hour after providing leaves, intense and stable foraging activity was established, and experiments were conducted. On days on which foraging activity was low or inconsistent, we did not perform experiments. All experiments were recorded with a GoPro 4 camera suspended centrally above the arena and capturing its entire expanse at 1920 × 1080 pixels resolution and at 24 frames per second. Each experiment lasted for 1 h and whenever possible two replicates, separated by 1 h, were recorded during one foraging bout.

(ii) Experimental procedure

At the start of the experiment, 20 paper obstructions were placed equidistant to each other in the obstruction zone which spanned the entire 8 cm width of the trail. To test the influence of obstruction density on the removal behaviour, we varied the length of the obstruction zone but not the number of obstructions: in set high density (HD), the zone measured 5 × 8 cm with 0.5 obstructions cm^{-2}; in set low density (LD), it measured 10 × 8 cm with 0.25 obstructions cm^{-2}. We performed 19 and 16 replicates in sets HD and LD, respectively.

We recorded the time at which a worker removed obstructions. A removal action was defined as grasping the obstacle with the mandibles and moving it for at least 5 mm. Rarely ($n = 7$), carried obstructions were subsequently dropped back on the trail and abandoned; these were excluded from further analysis.

Foraging traffic did not occupy the entire width of the provided trail outline. In all experiments undertaken within a colony fragment, the path of foraging traffic was adjacent to one of the trail borders, and its location did not change between subsequent experiments. While movement of some workers not obviously associated with foraging occurred in the remaining trail width, the main traffic flow in all experiments covered less than half of the available trail width. We hence recorded only removals of the 10 obstructions placed on the used half of the trail.

To investigate individual removal behaviour, we tracked the point of entry into the obstruction arena of all removing workers and labelled them as in- or outbound relative to the nest. For some workers, we could not assign directions because they did not move consistently with the foraging flow, but instead moved along or beyond the perimeter of the trail. We labelled those workers as 'meandering'.

(iii) Automated flow quantification

We quantified flow rate via an automated method to track worker movement in a trail segment of approximately 10 cm length, adjacent to the obstruction zone. In each frame, individual ants were identified using an image classifier, which extracted ant locations and associated them in consecutive frames via a nearest-neighbour algorithm. The directional flow was quantified by counting crossings of a virtual line. Counts were conducted on 30 s video segments at 2, 20 and 40 min into the experiments, and the results averaged for each experiment. We verified a subset of eight automated data counts against counts made by humans watching videos at half speed.

(iv) Automated encounter quantification

We hypothesized that the number of encounters between workers and a given obstruction influences the speed of its removal. To investigate these dynamics, we quantified encounters throughout the experiment duration in consecutive video segments of 30 s length. In each video segment, we measured the traffic flow in each area of the trail by comparing pixel intensity values z ($z \in \mathbb{Z} : 0 \leq z \leq 255$) in consecutive, greyscale converted frames using a Python script and the OpenCV library. We used a pixel value difference threshold of $\Delta z = 30$ (where $\Delta z = z^{t}_{x,y} - z^{t-1}_{x,y}$ for each pixel at index (x,y) in a frame taken at time t) to differentiate between unoccupied and occupied pixels in consecutive frames. At the beginning of each 30 s video segment t, we manually recorded obstruction locations and placed a circular mask with a radius $r = 1$ cm around it. The diameter was chosen to be large enough to capture any ant that came within an antenna's length of the obstruction and can, therefore, be considered to have encountered it. We used the number of changes in occupancy count v^{t}_{i} in each mask around a given obstruction i during video segment t as a measure of encounter quantity. For each video segment t, the number of encounters relative to the number of obstructions $relEnc_t$ was then $\text{relEnc}_t = (\Sigma^{i_t}_{i=1} v^{t}_{i})/i_t$, where i_t is the number of remaining obstructions at that time. We averaged all measurements of $relEnc_t$ for the same number of i_t.

(b) Laboratory experiment results

The data gathered during the laboratory experiment provided the overall clearing dynamics, the quantification of removals by workers moving in either direction, and—in preparation for the construction of a mechanistic model—the quantification of worker flow, and the change in encounter numbers per obstruction present as removals progressed.

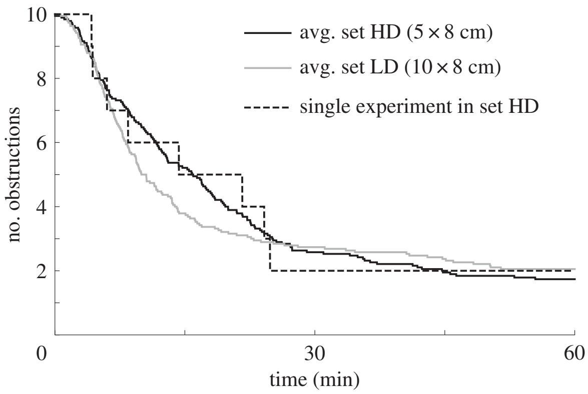

Figure 2. Plot of colony-level removal dynamics, averaged over all experiments in both experimental sets (solid lines), and in a representative replicate of set HD (dashed line).

Figure 2 shows the averaged obstruction removal dynamics over all experiments in sets HD and LD.

Overall, removal occurred most frequently at the beginning of the experiments and progressed slightly faster in set LD (at obstruction density of 0.25 cm^{-2}) than in set HD (0.5 obstructions cm^{-2}). At the end of the experiment, the average number of obstructions remaining on the trail was 1.7 in set HD and 2 in set LD.

(i) Individual clearing behaviours

We manually tracked all clearing workers back to the time when they entered the obstruction arena and followed their path until their departure from it. Of 282 workers engaging in clearing across both sets, we successfully identified the movement direction of 113 (i.e. 53%) clearing workers as either in- or outbound (table 1). Workers were classified as outbound if they traversed the whole obstruction arena from the nest entrance side to the foraging container side, and vice versa for inbound workers. Possible U-turns during the traversal were ignored for this classification. Inbound ($n = 51$, 34.46% of tracked clearers) and outbound clearers ($n = 60$, 40.54% of tracked clearers) did not continuously move in a given direction—they were meandering workers that performed U-turns along the trail and were never observed entering and leaving the arena. The path of the remaining clearers could in repeated manual viewings not reliably be resolved owing to loss of identity during passage over the trail delineation or during collisions.

We observed that individual workers may engage in one of two different trail clearing behaviours: the majority of clearing workers continued their progress along the trail in the original direction after dropping the removed obstruction. However, a portion of the clearing workers returned to the obstruction zone and continued clearing. We term these workers ‘repeaters’ because they remove more than one obstruction in sequence before re-joining the trail traffic. Although the number of repeaters was relatively small, they accounted for a significant portion of the trail clearing: About one-third, 116 of a total of 356 removed obstructions in both obstruction density conditions, were attributed to only 42 repeaters (table 2). Each repeater was responsible on average for 2.72 and 2.79 removed obstructions in sets HD and LD, respectively. The probability of first-time clearers becoming repeaters p_{WR} (i.e. the number of repeaters divided by the sum of both one-off and repeater clearers) was 0.13 and 0.16 in the respective experiment sets. On average, repeaters continued clearing for 113.2 (s.d. = 68.7) and 222.5 s (s.d. = 183.6). The mean rate at which they removed obstructions k_{RR} (i.e. the inverse of inter-removal interval times calculated for individual repeaters) was 0.0184 and 0.0128 s^{-1}, and their mean rate of returning to trail-following behaviour k_{R0} (i.e. the inverse of repeater bout duration calculated for individual repeaters) was 0.0126 and 0.009 s^{-1}, respectively (table 3).

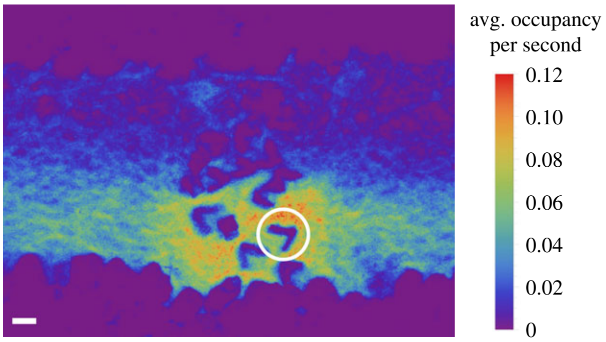

Figure 3. Visualization of ant movement over a 30 s period in (and adjacent to) the 5 × 8 cm obstruction zone, early in an experiment. For visualization, the original greyscale image has been linearly re-scaled to maximum pixel values of 255 and colour-mapped. Purple pixels indicate the absence of movement and show the folded paper obstructions and the expanded clay pellets delineating the trail. Brighter colours indicate ant movement. White scale bar measures 1 cm; white circle shows diameter of the summing mask applied to all obstructions (see text). Traffic flows horizontally. (Online version in colour.)

(ii) Automated flow quantification results

Comparing the automated flow count method against human counts, we found that the automated counts were on average 5.9% lower (mean signed difference; s.d. = 0.09%). We considered this an acceptable deviation given the increase in our capacity to gather data. Worker flow rate per second in set HD (mean = 3.95, s.d. = 1.47) was about a quarter higher than in set LD (mean = 2.82, s.d. = 1.05). Since we conducted experiments at the peak foraging time, we assume balanced in- and outflow of workers.

(iii) Automated encounter quantification

Figure 3 shows a colour-mapped example of the output of the encounter quantification. The relative rate of encounters per obstruction measured for set HD dropped sublinearly as clearing progressed (figure 4).

(c) Field experiments methods

The laboratory experiments aimed to observe the progress of trail clearing from the occurrence of obstruction until the establishment of a cleared trail. In the field experiments, we focused on the investigation of recruitment dynamics in a natural environment only. We conducted experiments at the La Selva Biological Station in Costa Rica during October and November 2017. During the time of experiments, leafcutter ants foraged during the night (from approx. 8.00–6.00). We conducted all experiments only after a consistent foraging flow had been established, and recorded the entire experiment duration with a Canon EOS600 with 50 mm f/1.8 lens at 1920 × 1080 pixels resolution and 30 frames s^{-1}. To minimize the irritation

Table 1. Movement direction of tracked clearing workers. (For repeaters, only the initial clearing event was counted.)

movement direction	set HD ($N = 113$)	set LD ($N = 34$)	sum ($n = 147$)	percentage of total tracked removers
outbound	48	12	60	41%
inbound	38	12	51	34%
meandering	27	10	37	25%

Table 2. Number of trail obstructions removed by different clearing behaviours.

	set HD ($N = 167$)	set LD ($N = 189$)	total ($n = 356$)	percentage of total removals
removals by one-off clearers	118	122	240	67.4%
total removals by repeaters	49	67	116	32.6%

Table 3. Metrics of repeater behaviour.

	symbol	set HD	set LD
number of repeaters		18	24
probability to become repeater after a removal	p_{WR}	0.13	0.16
mean number of removals per repeater		2.72 (s.d. = 1.07)	2.79 (s.d. = 1.32)
mean repeater bout duration (seconds)		113.2 (s.d. = 68.7)	222.5 (s.d. = 183.6)
mean interval length between repeater removals (s)		66 (s.d. = 31)	124 (s.d. = 118)
rate of removals by repeaters (s^{-1})	k_{RR}	0.0184	0.0128
rate of stopping repeater behaviour (s^{-1})	k_{RO}	0.0126	0.009

to the foraging workers we illuminated the trail with mounted LED lights generating only the minimum light needed to allow video recording. In a total of 14 *A. cephalotes* colonies, we selected an accessible segment of an active foraging trail at least 5 m distant from either nest and foraging site. We measured the width of the trail, and for a 5 cm long trail segment placed paper obstructions (identical to those used in the laboratory experiments) to achieve the previously used density of 0.5 obstructions cm^{-2}. In contrast to the laboratory experiments, we continuously replaced all removed obstructions to maintain a fixed obstruction number. Experiments were conducted for a duration of 30 min.

(d) Field experiment results

The average width of the 14 observed trails was 7.9 cm (s.d. 1.7). Figure 5 shows the proportion of removed obstructions over time. A Kolmogorov–Smirnov test shows no significant difference of the averaged removal progress over time from the distribution resulting from a uniform rate (KS statistic = 0.0699779, $p = 1$).

(e) Simulation methods

Using simulations, we investigated if the experimental results can be explained by a fixed probability that a worker will remove an obstruction upon encountering it, or if a provision for recruitment to obstructions (via an increase in the removal probability as the experiment progresses) is required. We further tested if the difference in obstruction density in the two sets of laboratory experiments had an influence on the individual removal probability. In the simulation, we replicated the conditions of the laboratory experiments in which 10 obstructions were present on a trail. Starting from the most parsimonious hypothesis, we assumed that obstruction removal was not regulated via recruitment, but based on fixed behavioural probabilities p: on encountering an obstruction workers either removed or ignored it (with probabilities p_R and $1 - p_R$, respectively); after a removal, they either rejoined the traffic flow (with $1 - p_{WR}$) or, as repeat clearers,

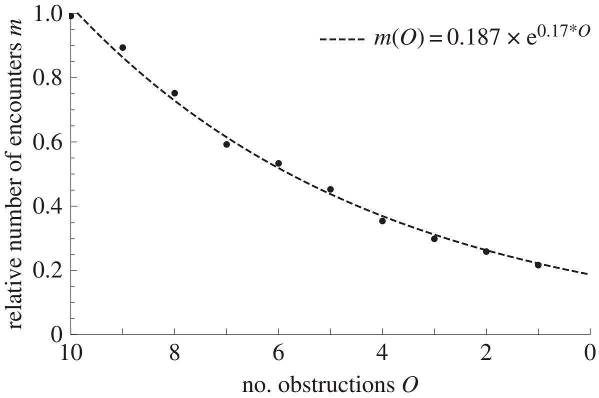

Figure 4. Change of relative encounter numbers per obstruction, plotted against the number of remaining obstructions. Dashed line is the fitted exponential function $m(O) = 0.187 \times e^{0.17*O}$, $R^2 = 0.9986$, where O is the number of obstructions on the trail. The fit function was obtained using the *NonlinearModelFit* function in Wolfram Mathematica 11.3.

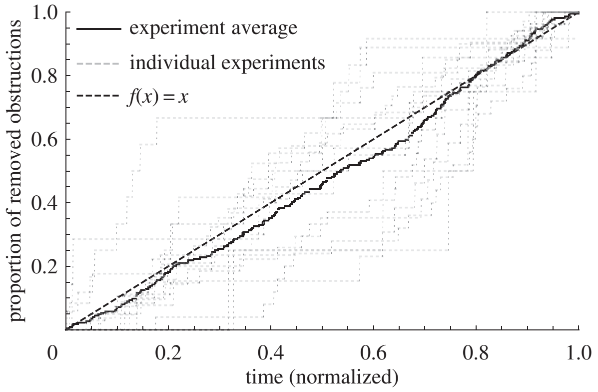

Figure 5. Proportion of removed obstructions over experiment time. Solid line shows the average of all experiments, and the dotted lines gives individual experiment trajectories. The dashed line corresponds to a hypothetical constant removal rate.

switched to repeater behaviour (with probability p_{WR}). In the latter case, they continue removing additional obstructions with p_{RR} or re-join the traffic stream with $p_{R0} = 1 - p_{RR}$. Figure 6 shows a diagram of the conceptual individual behavioural model with associated behavioural probabilities.

We simulated the system-level trail clearing process using the Gillespie algorithm (Gillespie, 1977) which gives stochastic trajectories of the occurrence of the different clearing behaviours based on the above-calculated behavioural rates and encounter dynamics. As we noted above, in the laboratory experiments not all obstructions were removed from the trail. We ascribe that to the formation of a cleared channel through the obstruction zone that accommodated the majority of the traffic. The spatial location of a given obstruction in regard to the main traffic channel hence determines the probability of its encounter and subsequent removal, and as the formation of the channel progresses, the rate of worker-obstruction encounters is reduced. In the model, we encompass these dynamics by modulating the rate of encounters with a dynamic exponential function of the shape $m(O) = a \times e^{b^*O}$ (where O is the number of obstructions remaining on the trail; cf. figure 4). The modulated encounter ratio k_E between workers W passing an obstruction at any given time, and obstructions O, was then given via the law of mass action: $k_E = W \times O \times m(O)$. As a proxy for worker number W, we used the empirically measured flow rate.

We formulated each removal behaviour as a reaction equation taking as reagents obstruction numbers and worker numbers in different behavioural states (workers W and repeating clearers R) and a corresponding reaction rate k, and returning changes in reagent numbers. In table 4, we give the reaction notation for each removal behaviour and the system propensity α for this reaction. We empirically recorded behavioural probability p_{WR} and reaction rates k_{RR} and k_{R0} (table 3), and that encounter probability k_E was a function of the system state. We determined parameters a and b of encounter function $m(O)$ and rate of one-off removals k_{WO} by fitting the simulation output to the experimental data using parametric search (5000 simulations per parameter set) to minimize the least square error. k_{WR} was calculated as the product of the empirically derived p_{WR} and the simulation parameter k_{WO}. The details of the algorithm are given in the electronic supplementary material.

We then calculated the probability for individual ants to remove an obstruction upon encountering it, p_R, by fitting the simulation with the derived encounter function parameters a and b to individual experiment trajectories, and divided the resulting experiment-based removal rate k_{WO} by the experiment flow rate.

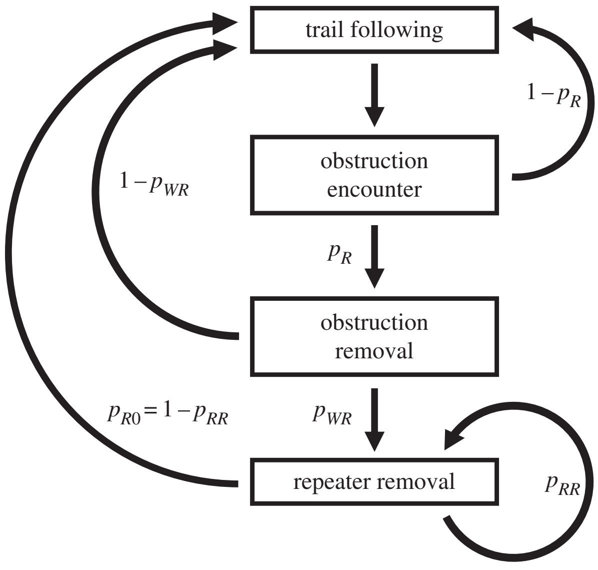

Figure 6. Diagram of the conceptual individual behavioural model underlying the trail clearing behaviour: upon encountering an obstruction, workers have a probability of p_R to remove it (and probability $1 - p_R$ to return to the trail following behaviour). After a removal, they either return to trail following (with probability $1 - p_{WR}$) or switch to repeater behaviour (with p_{WR}). In the latter case, they continue removing additional obstructions with p_{RR} or rejoin the traffic stream with $p_{R0} = 1 - p_{RR}$. Refer to the text for details on the variable terms.

(f) Simulation results

The best fit was obtained by the parameters $k_{WO} = 0.0003$, $a = 0.18$, $b = 0.13$, least-squares error $= 510$ for experiment set HD and for $k_{WO} = 0.0003$, $a = 0.17$, $b = 0.22$, least-squares error $= 764$ for set LD (figure 7).

The fitted individual removal probability p_R was on average 0.0002 (s.d. = 0.00026) in set HD, and 0.00033 (s.d. = 0.00038) in set LD. Applying the assumption of a fixed removal probability and the absence of recruitment dynamics to a scenario where removed obstructions are replaced (as implemented in the field experiments), the simulation replicated the linear dynamics shown in figure 5 for any arbitrarily chosen values for flow rate and p_R.

3. Discussion

We set out to describe the individual trail clearing behaviours and underlying probabilities, to examine the possibility of different trail clearing behaviours and to investigate possible recruitment dynamics organizing trail construction.

(a) Individual removal behaviours and dedicated clearing workforce

We identified two clearing behaviours: one-off removals based on probabilistic encounters between workers and obstructions, and repeater removals. We quantified the probability of obstruction removal based on worker traffic and probabilistic encounters. We then separated the probabilities

Table 4. Possible removal behaviours formulated as reactions and mass-action-based reaction propensities. (Workers, repeaters and obstructions are given as W, R and O; k is the corresponding reaction rate in s^{-1}, and probability p is unitless.)

removal reaction	symbol	reaction equation	reaction propensity
one-off obstruction removal	w_1	$W + O \xrightarrow{k_{WO}} W$	$\alpha_1 = k_E \times k_{WO}$
one-off removal and switch to repeater behaviour	w_2	$W + O \xrightarrow{k_{WR}} R$	$\alpha_2 = \alpha_1 \times p_{WR}$
repeater removal	w_3	$R + O \xrightarrow{k_{RR}} R$	$\alpha_3 = R \times k_{RR}$
repeater stopping	w_4	$R \xrightarrow{k_{RO}} W$	$\alpha_4 = R \times k_{RO}$

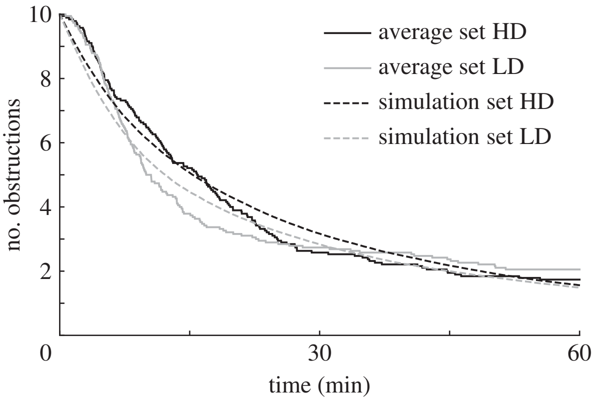

Figure 7. Fit of removal simulations (dashed lines; average of 20 000 replicates) to averaged empirical data from both experimental sets (solid lines). Squared error values were 510 for set HD and 764 for set LD.

for one-off removals and repeater removals and found that repeater removals occur much more frequently than expected by chance.

Workers appeared to have a fixed base probability to remove obstructions on encounter, and we found no differences in the probability in relation to obstruction densities. We showed that clearing occurred at equal frequency in both inbound and outbound traffic, based on observations of clearing workers for more than 1 m as they traversed the arena. We acknowledge that observations over such a short distance might be insufficient to capture the dependence of clearing on travel direction, owing to behaviours such as U-turns, and that further study of clearing dynamics over broader spatial scales may be needed. Likewise, we note that while 75% of removals came from within the traffic flow, 25% were undertaken by workers that could not be associated with any movement direction and that appeared to meander along the trail perimeter. Furthermore, recent work found that *A. colombica* foraging traffic shows a degree of lane-separation, with about two-thirds of outbound traffic moving in the central 50% of the trail, while inbound traffic along the trail margins was much more likely to be composed of unladen than laden workers [29]. Such traffic structure could affect the encounter rate of inbound and outbound workers with obstructions, and raises the question of how lane location might be influenced by local obstacles. Although we recorded data on only half the delineated trail, essentially all traffic occurred on the monitored half, and any lane segregation in our traffic would have been incorporated in our measured removal rates. If all on-trail workers had the same probability to engage in trail clearing, the number of removed obstructions should be lower for the inbound than the outbound traffic flow, because a fraction of the inbound workers (on average 58%, see [7]) carried leaf fragments. Leaf-carriers were never observed dropping their fragments and engaging in trail clearing and were hence unavailable as clearers. A possible explanation for these findings would be that clearers are behaviourally different from foragers and have an intrinsically increased probability to remove obstructions coupled with a decreased probability to contribute to foraging, which would agree with Howard's findings of short-term task fidelity in these two groups [14]. Under these circumstances, the inbound unladen workers would be more likely to be potential clearers than potential foragers, which would explain the observed clearing rates. To verify if clearing is undertaken by a behaviourally different subgroup of workers, a more exhaustive tracking of foraging and clearing workers will be necessary.

We showed that some workers, after removing an obstruction, continued clearing at a greatly increased probability: the binomial probability that repeated removals were a result of subsequent chance encounters with mean removal probability $p_R = 0.0003$, even under the upper-bound assumption that workers encountered 10 obstructions at each pass through the obstruction zone, was $P(X \geq 2) = 4.04 \times 10^{-6}$. The binomial probability that, as in our experiments, 42 of 282 clearers would show such repeater behaviour was $P(X = 42) = 7.08 \times 10^{-177}$. These findings suggest that repeater clearers actively searched out obstructions on the trail and that repeater clearing represents a dedicated trail clearing behaviour that complements one–off removals. This raises the question of whether all workers have the ability to probabilistically switch to repeat behaviour, albeit for a limited period of time only, or whether there is a behaviourally different sub-group of workers that systematically exhibits time-limited repeat behaviour. This cannot be distinguished in the data. As above, detailed individual tracking is required to investigate this question.

(b) Absence of recruitment

Trail clearing represents an effort of many thousand individual ants distributed across kilometres of trails. In many cases, such large-scale collective effort is coordinated via recruitment dynamics. Overall, we found no evidence for recruitment: the simple assumption of flow-regulated probability of an individual that encounters an obstacle to engage in removal is sufficient to explain both the laboratory results and those obtained under natural conditions in field experiments. On the contrary, the near-linear increase of removed obstruction numbers over time observed in the field (figure 5) would be inexplicable in the presence of either recruitment or inhibition of other workers to the removal behaviour. This suggests that there might be no recruitment dynamics involved in the trail clearing process, and that the stochastic process of worker-obstruction encounters, a fixed removal probability, and the provision for occurrence of repeater behaviour were sufficient assumptions to describe the emergence of large-scale trail network construction.

We note that trail clearing did not continue once obstructions had been removed from the immediate trail area, and that some obstructions remained in the obstruction zone in some laboratory trials. This suggests that trail width emerged as a function of local traffic volume. The dynamics for this remain unclear: workers leaving the trail might be too few to, via the described stochastic process, clear off-trail areas, or the clearing behaviour is only displayed in the presence of trail pheromone or foraging traffic. Investigation of occurrence of off-trail obstruction removal might be a venue for future research.

In addition to those key findings, our experiments showed that physical properties play an important role in the definition of an obstruction: flat paper strips on the trail surface were ignored, and upright, folded ones removed. This offers another perspective on the persistent foraging on apparently uncleared trails and the presence of uncleared parts on otherwise cleared trails, on which fallen and compressed leaf litter might not actually interfere significantly with the foraging workflow.

Saverschek *et al*. [30] showed that leaf-disks placed on trails are foraged upon or removed from the trail depending on their palpability; we likewise showed that sensory cues influence the classification of on-trail objects: sugar-treated paper strips were taken into the nest, while permanent marker treated ones were removed from the trail. The role of inorganic and organic volatiles on trail clearing probabilities requires further investigation.

In summary, while cleared trails in leafcutter ant colonies are one of the most striking cases of collective behaviour and large-scale infrastructure construction, our behavioural model based on our empirical data is consistent with the assumption that there are neither inter-individual feedback mechanisms nor active recruitment mechanisms specifically for removal activities regulating the trail clearing process. In the absence of a need for it, this lack of information transfer might be the most economic, and by virtue of parsimony the most resilient, the solution to achieving a collectively cleared foraging trail. Our findings suggest that direct or indirect information transfer between individuals is not a prerequisite for collective large-scale behaviours like infrastructure construction. Thus, such behaviours can also evolve in group living animals if intragroup communication is limited by behaviour, the inhabited environment, or individual capacities.

Data accessibility. Empirical data and MATHEMATICA notebooks containing the analysis and simulation are available as part of the electronic supplementary material.

Competing interests. We declare we have no competing interests.

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