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RESEARCH ARTICLE

Meat ants cut more trail shortcuts when facing long detours

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ABSTRACT

Engineered paths increase efficiency and safety but also incur construction and maintenance costs, leading to a trade-off between investment and gain. Such a trade-off is faced by Australian meat ants, which create and maintain vegetation-free trails between nests and food sources, and thus their trails are expected to be constructed selectively. To test this, we placed an artificial obstacle consisting of 300 paper grass blades between a sucrose feeder and the colony, flanked by walls either 10 cm or 80 cm long. To exploit the feeder, ants could detour around the walls or take a direct route by traversing through the obstacle. We found that, when confronted with a long alternative detour, 76% of colonies removed more grass blades and ants were also 60% more likely to traverse the obstacle instead of detouring, with clearing activity favouring higher ant flow or vice versa. An analysis of cut patterns revealed that ants did not cut randomly, but instead concentrated on creating a trail to the food source. Meat ants were thus able to collectively deploy their trail-clearing efforts in a directed manner when detour costs were high, and rapidly established cleared trails to the food source by focusing on completing a central, vertically aligned trail which was then followed by the ants.

KEY WORDS: *Iridomyrmex purpureus*, Route selection, Trail clearing, Trade-off, Optimisation, Ant foraging

INTRODUCTION

Trails are often an integral part of collective movements. They are broadly deployed, from game trails of herd animals such as elephants (Blake and Inkamba-Nkulu, 2004) or deer (Etzenhouser et al., 1998) up to complex road structures built by human (Lämmer et al., 2006; Buhl et al., 2006) and social insect societies (Latty et al., 2011). The nature of trails depends on their function, be it to reduce energy expenditure (Bochynek et al., 2017; Howard, 2001; Halsey, 2016) or travel time (Ydenberg et al., 1994) or to increase the speed or safety of travel (Loreto et al., 2013; Bochynek et al., 2017). Trails are often used by central place foragers – animals that make multiple trips between fixed destinations – such as ants (Perna and Latty, 2014; McIver, 1991).

In ants, trails last variable amounts of time, ranging from mere minutes in the form of volatile pheromone trails used in some ant species (Czaczkes et al., 2013; Jeanson et al., 2003) or the constantly adapting living bridges built by *Eciton* army ants (Reid et al., 2015), up to months or years in large insect societies (Lanan, 2014; Howard, 2001). Longer usage of trails allows for more sophisticated trail construction, as their costs can be ameliorated by continued energy savings over time (Bochynek et al., 2017). Accordingly, cleared trails are often constructed towards stable food sources or resource-rich regions, where ants can disperse to various end points (Gordon, 1991; Farji-Brener and Sierra, 2016; Hölldobler and Wilson, 1990; Greaves and Hughes, 1974).

Such large trunk trails, which are actively cleared of vegetation to create and maintain highways, are created by many ant species. Removal of vegetation allows for fast travel to stable food sources (Lanan, 2014; Bochynek et al., 2017; Bruce and Burd, 2012; Howard, 2001; Plowes et al., 2013; Greaves and Hughes, 1974; Hölldobler and Lumsden, 1980; Shepherd, 1982; Fowler, 1978) and thus differs from most animal trails, which are created passively by trampling of vegetation (Blake and Inkamba-Nkulu, 2004; Bates, 1950). Trunk trails leave the nest and bifurcate repeatedly, ramifying into the foraging areas (Hölldobler and Wilson, 1990; Salo and Rosengren, 2001; Hölldobler and Lumsden, 1980). They allow expansion to new resources in their vicinity (De Vasconcelos, 1990) and are defended as colony territory (Hölldobler and Lumsden, 1980). Trunk trails allow most foragers to navigate easily and efficiently between nest and foraging sites while also being provided with guidance by trail pheromones (Czaczkes et al., 2015) and the polarity inherent to the trail (Jackson et al., 2004); trails can thus be considered as a form of 'external memory' for the colony (Shepherd, 1982).

Long-term trail networks also connect nests in polydomous colonies, allowing for food and brood transfer between the spatially separated nests (van Wilgenburg and Elgar, 2007; Lanan, 2014; Debout et al., 2007; McIver, 1991). However, trails devoid of vegetation are costly both to create and to maintain. Thus, colonies need to attain a balance between efficient travelling and time and effort expended on trial maintenance (Bouchebti et al., 2018; Shepherd, 1982; Howard, 2001; Bruce and Burd, 2012; Bochynek et al., 2017; Farji-Brener et al., 2015). The importance of efficiency is shown by many ants forming trails along fallen tree trunks that are not aligned with their goal, but allow for easier travel and faster travel speed (Loreto et al., 2013; Farji-Brener et al., 2007; Denny et al., 2001; Frank et al., 2018), while decreasing risks of predation and substrate contacts (Loreto et al., 2013) as well as construction costs. Nonetheless, trails might be optimised to reduce travel time in areas exposed to sun, weather events or high predation risks (Farji-Brener et al., 2015) or when built underground (Mintzer, 1979).

Large trails devoid of vegetation are constructed by the Australian meat ant (*Iridomyrmex purpureus*), which forms trail networks both between nests and to food trees, where workers harvest honeydew from hemiptera (Greaves and Hughes, 1974; van Wilgenburg and Elgar, 2007). The connections between the nests are usually a trade-off between stability (resilience to disruptions) and efficiency (least amount of trails) (Cabanes et al., 2015; Cook et al., 2014). However, vulnerability to obstructions like falling branches is high, and trails without maintenance can quickly become unusable (Evison et al., 2008). The benefits of more efficient travel must surpass costs of

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clearing, and thus trails are expected to be constructed and maintained selectively (Bochynek et al., 2017).

Many studies of trail clearing focus on unfixed obstacles on trails (Bochynek et al., 2019; Howard, 2001; Cevallos Dupuis and Harrison, 2017), which are easily quantifiable and can be dragged off trails quickly. However, grass and other low vegetation can also constitute a significant clearing effort (Farji-Brener et al., 2015), especially in ant species living in open habitats, as is the case for meat ants (Greaves and Hughes, 1974). A recent study found that meat ants prefer shorter routes covered with turf grass to smooth but longer routes, but no preference was found for routes of equal length, indicating that meat ants ignored the surface structure despite slower walking speeds (Luo et al., 2018) but the use of turf grass as an obstacle did not allow clearing outcomes and cutting patterns to be assessed. Another study employed artificial grass obstacles made of 300 hard cardboard or thin paper blades as obstacles to a food source (Middleton et al., 2019). By quantifying clearing effort, the authors showed that meat ants allocated the same number of workers to both obstacle types, irrespective of the longer clearing times for cardboard. These studies thus suggest that trail clearing is not an optimised process.

These findings are surprising, as optimisation is to be expected for such costly behaviours, and can be seen in trail clearing by leaf-cutter ants (Farji-Brener et al., 2015; Bochynek et al., 2017; Howard, 2001; Shepherd, 1982, but see Cevallos Dupuis and Harrison, 2017). In the present study, we used an array of artificial grass blades to directly quantify clearing activity, which is hard to do in natural settings (Bouchebti et al., 2018). We also analysed clearing patterns and their emergence over time. This allowed us to demonstrate, for the first time, cost-dependent deployment of goal-directed trail-clearing behaviour.

MATERIALS AND METHODS

Studied species and field site

Meat ants [*Iridomyrmex purpureus* (Smith 1858)] are a widespread species of Dolichoderinae that are endemic to Australia. They are polydomous, with their large mounds housing tens of thousands of workers (Greaves and Hughes, 1974). Trail networks cleared from vegetation allow the efficient exchange of food and brood between nests and access to trees infested by honeydew-secreting insects (Greaves and Hughes, 1974; van Wilgenburg and Elgar, 2007). All experiments were conducted in a forest area at the Hawkesbury campus of Western Sydney University in Richmond, New South Wales, Australia (33°38′S, 150°46′E) between March and April 2018. The area has a high density of meat ant colonies, which are located along a road through a *Eucalyptus* forest. Only colonies that were on even ground and surrounded by clear ground or little vegetation were used for the experiments, resulting in a total of 17 tested colonies. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Experimental procedure

A 1 mol l^{-1} sucrose feeder was placed 5 cm behind an artificial paper grass obstacle (10 cm×23 cm) (see Fig. 1A). To reach it, ants had to either traverse the obstacle or detour around it. The obstacles were identical to those used in Middleton et al. (2019) (see Fig. 1B) and ants crossing the obstacle were found to be ∼3.5 times slower than ants traversing cleared trails (Middleton et al., 2019). Obstacles contained 15 rows and 20 columns of laser-cut green paper strips (henceforth ‘paper blades’). Each row comprised 20 paper blades each 2 mm wide and 1.5 cm high and placed 2 mm apart, resulting in a total of 300 artificial paper blades. Rows were 1 cm apart. An acetate sheet was placed over the obstacle to protect it from sporadic rain and falling debris. The obstacle was flanked by 10-cm-high Corflute™ walls. Meat ants were found to rarely climb the walls, thus making it a reliable barrier without any chemical treatment. The walls flanking the obstacle were either 10 cm or 80 cm wide, causing a short (∼43 cm) or long (∼183 cm) detour, respectively. At the end of these detour walls, another sham obstacle plate was placed devoid of paper blades to mimic the surface structure of the shortcut (see Fig. 1A). The walls were partially sunk into the soil to prevent the ants from passing underneath. Each colony was tested on both the long and the short detour in a randomised order with a break of at least 5 days (see the data handling protocol, available from Dryad at https://doi.org/10.5061/dryad.7sm50ft) between them during which no setup was present. Half of the colonies started with the short treatment, and the treatment sequence of each colony was included in the analysis to reveal potential sequence effects. Ambient temperature in the shade was recorded directly after the apparatus was installed.

For each detour length, we revisited the setup 24 and 48 h after instalment, resulting in four data points per colony. Each visit, we noted the number of cut paper blades, and recorded the ambient temperature. Incompletely cut paper blades were also counted as ‘cut’ if they lay flat on the ground. A camera mounted on a tripod above the setup recorded all ant activity for 1 min. From these videos we obtained an ant flow rate, i.e. the number of ants passing through the obstacle or sides per minute. The person analysing the video was unaware of the study’s hypotheses and instructed to count

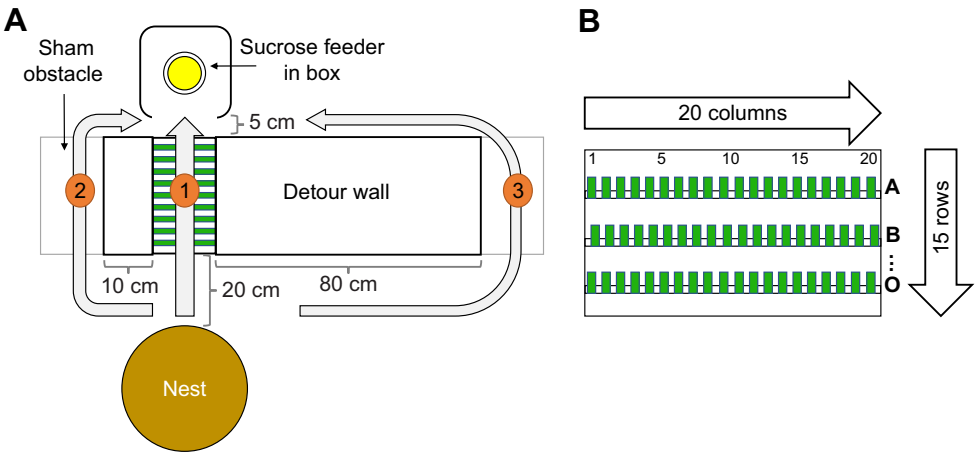

Fig. 1. Schematic illustration of the setup. (A) The direct path (1) to a newly placed feeder was obstructed by an obstacle containing paper blades and flanked by 10 cm high walls. The walls were either 10 cm wide causing a small detour (2) or 80 cm wide causing a long detour (3). Note that both detour routes are shown here, but in the experiment, both sides always had the same length (either 80 cm or 10 cm). To retrieve the food, the ants could either traverse the obstacle (1) or detour around the wall (2,3). (B) The obstacle consisted of 15 rows (A–O) each holding 20 paper blades (1–20). Row A was placed next to the nest.

separately all ants moving through the obstacle and ants moving around it. An ant was counted as soon as it moved onto the obstacle. If it traceably re-entered the obstacle, this did not count as additional visit. Ants that walked through the 5 cm gap between the walls flanking the obstacle and the feeder box (see Fig. 1A) were counted as detouring ants. Each video was analysed twice to ensure reliability of the data.

Statistical analysis

All analyses were conducted in R version 3.5.1 (https://www.r-project.org/) using data.table (https://CRAN.R-project.org/package=data.table), xlsx (https://CRAN.R-project.org/package=xlsx) and knitr (https://yihui.name/knitr/) for data preparation; glmmTMB (Brooks et al., 2017), emmeans (https://CRAN.R-project.org/package=emmeans) and car (https://CRAN.R-project.org/package=car; Fox and Weisberg, 2018) for data analysis; and ggplot 2 (https://ggplot2.tidyverse.org/) and cowplot (https://CRAN.R-project.org/package=cowplot) for data presentation. See ESM1 (Dryad, https://doi.org/10.5061/dryad.7sm50ft) for a protocol leading through all analysis steps. All analyses were conducted using generalised linear mixed models (GLMM; Bolker et al., 2009) and were tested for model fit and overdispersion using the DHARMa (https://CRAN.R-project.org/package=DHARMa) and sjstats (https://CRAN.R-project.org/package=sjstats. https://doi.org/10.5281/zenodo.1284472) packages. *Post hoc* tests were conducted using estimated marginal means of the emmeans package.

Overall clearing activity

To assess the overall difference in clearing activity between the detour treatments, we compared how many of the 300 potential paper blades were cut after 24 and 48 h on each obstacle. The number of cut blades was used as the dependent variable in a negative binomial GLMM with detour length (short or long), duration (24 or 48 h), and the treatment sequence for each colony (first long detour or first short detour) as predictors including their interactions and colony as random intercept. The model formula was:

$$\text{No. of cut blades} \sim \text{Detour length}_{(\text{short/long})} \times \text{Duration}_{(24\text{ h}/48\text{ h})} \times \text{Treatment sequence}_{(\text{short/long detour first})} + \text{Random intercept}_{(\text{colony})}.$$

To test potential temperature effects on clearing activity, we calculated Spearman's rank correlations between the number of cut blades and the average temperature over 24 and 48 h.

Trail cutting

As each paper blade was numbered, we could obtain its exact location and were able to reconstruct the cutting pattern accordingly. If ants cut a trail from the nest to the food, we would expect higher spread of blades along the vertical axis (along rows), as ants cut from the start to the end. By contrast, the width of the trail, i.e. the horizontal spread (along columns) of cut blades, should be narrow.

We used the interquartile range (IQR) as a measure of cutting dispersion. The IQR is non-parametric and provides the range in which 50% of the data are found by subtracting the 25% quartile from the 75% quartile. The IQR was calculated for rows and columns separately. In our case, an IQR_{rows} of 4 would tell us that 50% of all cut paper blades were found within 4 rows. This method makes reasonable assumptions: trails are straight, not diagonal, and only one main trail exists per obstacle.

As the obstacles had 15 rows but 20 columns, we then normalised the IQRs by dividing row IQRs by 15 and column IQRs by 20, to make rows and columns comparable. This resulted in values ranging between 0–1. A value of 0.5 means that the IQR was half of the total rows or columns. To compare the normalised IQR between rows and columns, we modelled a GLMM with a beta distribution ($0<y<1$). The model formula was:

$$IQR_{\text{normalised}} \sim \text{Detour length}_{(\text{short/long})} \times \text{Duration}_{(24\text{ h}/48\text{ h})} \times IQR_{(\text{rows/columns})} + \text{Random intercept}_{(\text{colony})}.$$

Furthermore, to show that meat ants clear trails rather than cut blades randomly, we also created random cut patterns by using a random binomial distribution (see ESM1, Dryad, https://doi.org/10.5061/dryad.7sm50ft). For each treatment of each colony, we created random cut patterns with the exact same number of cut blades. Those patterns underwent the same procedure of calculating IQRs. Then, we again modelled a GLMM with a beta distribution followed by estimated marginal means *post hoc* tests. The model formula was:

$$IQR_{\text{normalised}} \sim \text{Data}_{(\text{empirical/randomly generated})} \times \text{Detour length}_{(\text{short/long})} \times IQR_{(\text{rows/columns})} + \text{Duration}_{(24\text{ h}/48\text{ h})} + \text{Random intercept}_{(\text{colony})}.$$

Ant flow rate

For each treatment, we counted the number of ants traversing the obstacle or detouring around it for 1 min. In order to test for possible effects of detour length, duration and treatment sequence on flow rate, we used a proportional binomial GLMM with colony as random intercept. The model formula was:

$$\text{Ant shortcut/detour} \sim \text{Detour length}_{(\text{short/long})} \times \text{Duration}_{(24\text{ h}/48\text{ h})} \times \text{Treatment sequence}_{(\text{short/long detour first})} + \text{Random intercept}_{(\text{colony})}.$$

In addition, we investigated a potential correlation between flow rate and the number of cut paper blades. We ran separate Spearman's rank correlations for the number of ants traversing the obstacle, and for the number of detouring ants for each treatment.

Ant movement

In order to visualise ant movement trails and compare them to cut patterns, we wrote a motion tracking program using the OpenCV 3.4.1 library (https://opencv.org/) in Python 3.7 (https://www.python.org/) to extract ant movement through the obstacle from the ant flow rate videos. Each ant was detected via background subtraction and its position was tracked frame to frame. As multiple ants were present simultaneously in most videos and ants were not individually marked, each ant's frame-to-frame position was assumed to be that with minimum Euclidian distance to the last position. This method is prone to identity switches when ant paths cross but probable switches do not affect visualisation. We analysed 20 frames per second for the whole duration of the video. The tracking data were then freed from false-positive detections and visualised using R. The tracking program and R code are available from Dryad (ESM5, https://doi.org/10.5061/dryad.7sm50ft)

RESULTS

Altogether, 17 meat ant colonies were tested for both long and short detours. The long detour treatment after 48 h was not available for one colony, and thus only 24 h data points were used.

Overall clearing activity

To see whether colonies allocate more effort towards trail clearing when alternative detours are long, we compared the total amount of cut blades by each colony for each detour. In three colonies, ants managed to rip out parts of the rows without clearing individual paper blades. The corresponding parts were removed in all treatments of those colonies (see ESM1, Dryad, https://doi.org/10.

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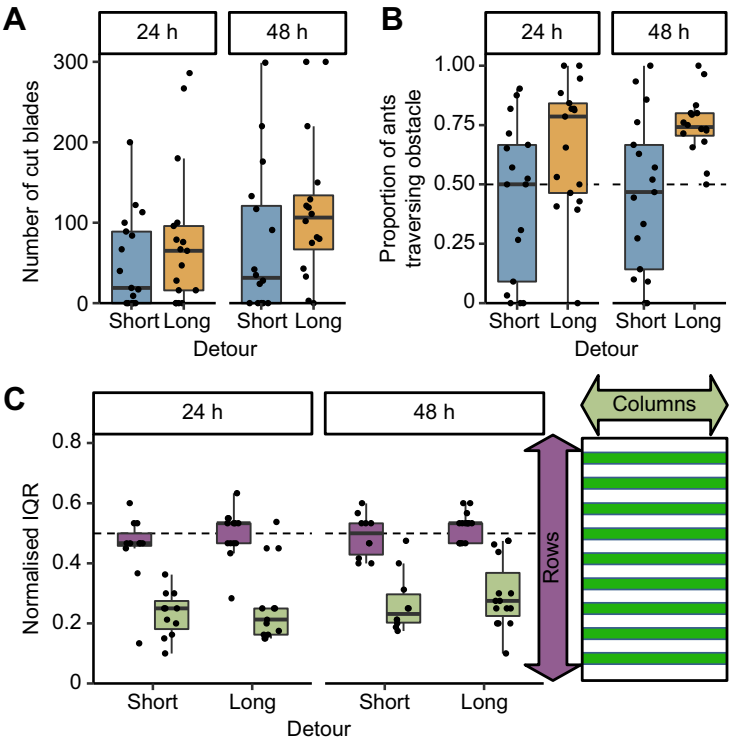

Fig. 2. Trail cutting and obstacle traversal in meat ant colonies after 24 h and 48 h with short and long detours. (A) Colonies cut significantly more paper blades when faced with the long detour (binomial GLMM, χ^2=5.25, P=0.0219) and after 48 h compared with 24 h (χ^2=4.31, P=0.0379). Sample sizes from left to right: n=17, n=17, n=16, n=16. (B) Proportion of ants traversing the obstacle or detouring around it after 24 and 48 h in the short and long detour treatment. 1 corresponds to all ants traversing the obstacle. A higher fraction of ants was found to traverse the obstacle in the long detour treatment (binomial GLMM, χ^2=32.85, P<0.0001), while the proportion was not significantly different after 48 h compared with 24 h (χ^2=2.27, P=0.1315). Sample sizes from left to right: n=17, n=17, n=17, n=16. (C) Normalised interquartile range (IQR) for cutting location of rows (vertical spread of cut blades, see obstacle scheme on right) and columns (horizontal spread) after 24 and 48 h in the short and long detour treatment. A normalised IQR of 0.5 (dotted line) means that 50% of blades were cut in 50% of rows/columns, i.e. were cut randomly. The lower the IQR, the less spread was found. Column IQRs were significantly smaller than row IQRs (beta regression GLMM, χ^2=177, P<0.0001), while IQRs were significantly larger in the long detour treatment and after 48 h (χ^2=4.67, P=0.0307; χ^2=4.78, P=0.0288, respectively). Sample sizes from left to right (note that only colonies that cut blades were used): n=11, n=11, n=13, n=13, n=10, n=10, n=15, n=15. Each colony is represented by a dot. Horizontal lines in boxes are medians, boxes correspond to first and third quartiles and whiskers extend to the largest value within 1.5×IQR.

5061/dryad.7sm50ft). A negative binomial GLMM revealed that significantly more blades were cut in the long detour treatment compared with the short detour (χ^2=5.25, P=0.0219, see Fig. 2A), demonstrating that ants indeed cut blades in a situation-dependent manner. Furthermore, significantly more paper blades were cut after 48 than 24 h (χ^2=4.31, P=0.0379) whereas the treatment sequence did not significantly affect the number of cut blades (χ^2=0.04, P=0.8385). No significant interactions were found (see ESM1, Dryad, https://doi.org/10.5061/dryad.7sm50ft).

Except for one colony, which never cut, all zero-cutters were exclusively found in the short detour treatment after 48 h (6 out of 17) (χ^2=0.94, d.f.=1, P=0.332). Furthermore, 76% (13/17) of the colonies cut more blades in the long detour treatment (χ^2=3.76, d.f.=1, P=0.0523), resulting in overall 703 (60%) more blades cut in the long detour. After 24 h, ants had already removed 62% (1881/3033) of the 3033 blades cut in total after 48 h, excluding one colony which had no data for 48 h. Temperature did not correlate significantly with the number of blades cut (Spearman rho: −0.10, P=0.4321).

Trail cutting

To determine whether ants cut paths through the obstacle, we compared the normalised interquartile ranges (IQRs) of blade removal for rows (spread of vertical cuts from nest to food) and columns (spread of horizontal cuts). We found that column IQRs were significantly smaller than row IQRs (beta GLMM, χ^2=177, P<0.0001, see Fig. 2C). IQRs were altogether higher in the long detour treatment (χ^2=4.67, P=0.0307) and after 48 compared with 24 h (χ^2=4.78, P=0.0288), which are both conditions in which more blades were removed. No interactions were significant (see ESM1, Dryad, https://doi.org/10.5061/dryad.7sm50ft).

When we also added randomly generated IQRs to the model, we found that the empirical IQR was significantly lower than the IQR of randomly distributed cut patterns (beta GLMM, χ^2=65.02, P<0.0001). This was driven by a significant interaction between data type (empirical or randomly generated) and IQR type (rows and columns) (χ^2=85.29, P<0.0001, see Fig. S2). As shown by *post hoc* tests, the horizontal spread (columns) was significantly lower than random spread (ratio=0.41, P<0.0001), while the vertical spread (rows) did not differ significantly from random (ratio=1.02, P=0.7655). As also reported in the above model containing only empirical data, the IQRs of columns were significantly smaller (χ^2=103.9, P<0.0001) and IQRs became larger over time (χ^2=4.15, P=0.0416). No effect of detour length was found in this model (χ^2=3.81, P=0.0509), as the added randomly generated IQRs were very similar between treatments. The IQR data thus demonstrate that the cutting pattern of ants formed vertically oriented, narrow trails from the entrance to the exit of the apparatus. Furthermore, those vertical trails seem to be predominantly constructed in the middle of the obstacle, equidistant from the flanking walls (Fig. S3A). In contrast, both the IQRs of rows and the cutting activity along the vertical axis were evenly distributed (Fig. 2C and Fig. S3B).

Ant flow rate

Overall, significantly more ants traversed the obstacle in the long compared with the short detour treatment (proportional binomial GLMM; χ^2=32.85, P<0.0001, see Fig. 2B). The proportions did not differ significantly between 48 and 24 h (χ^2=2.27, P=0.1315), nor did the treatment sequence have a significant effect (χ^2=0.28, P=0.5941). However, a significant interaction between detour length and treatment sequence (χ^2=6.93, P=0.0084) was found: while the probability of traversing the obstacle was always higher for the long detour, this difference was greater in colonies tested first on the short treatment (see Fig. S1B). No effect of the remaining interactions was found (see ESM1, Dryad, https://doi.org/10.5061/dryad.7sm50ft). Altogether, ants were 60% more likely to traverse the obstacle in the long detour treatment. We found a significant correlation between the number of blades cut and the number of ants traversing the obstacle in both treatments (short detour: Spearman rho=0.67, P<0.0001; long

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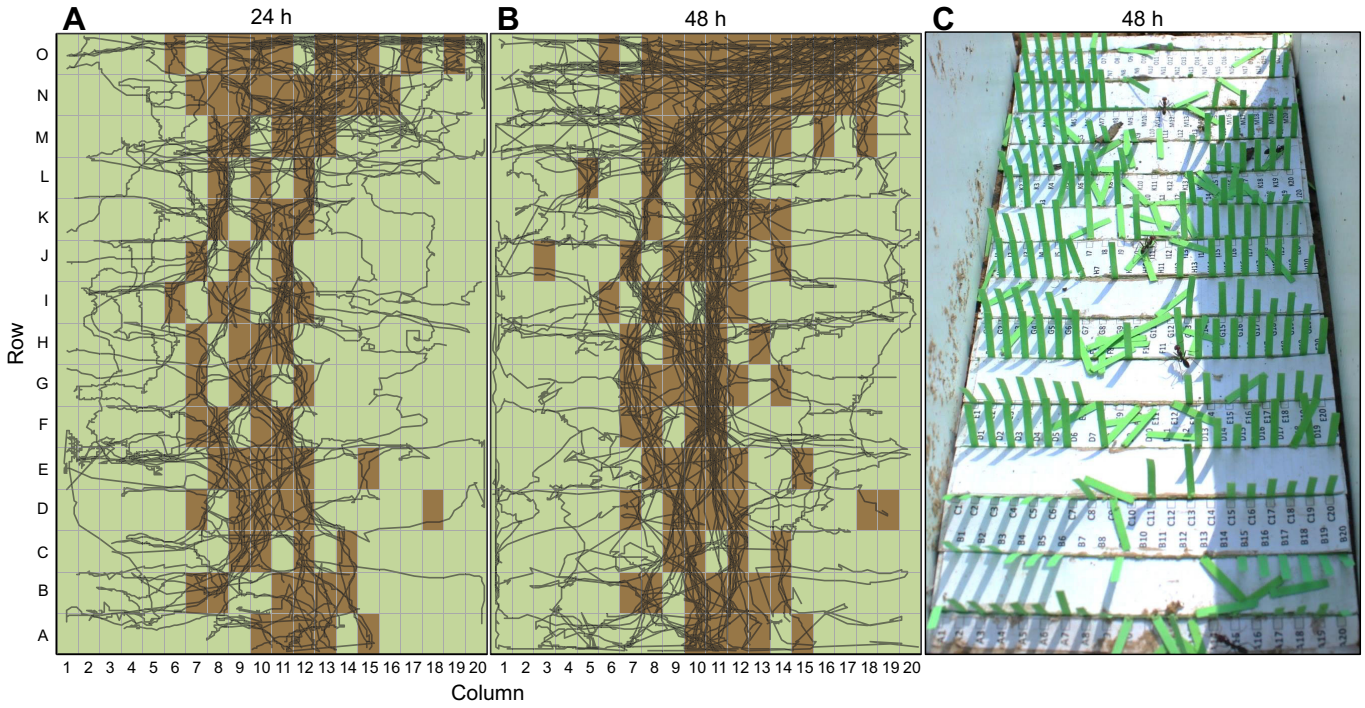

Fig. 3. Cut patterns and tracked ant movement through the obstacle after 24 and 48 h in the long detour setup for one colony. (A,B) Representations of obstacle, green rectangles correspond to uncleared fractions of the obstacle, brown rectangles depict cut blades after 24 h (A) and 48 h (B); nest is at the bottom, food is at the top. Each black line shows the trajectory of an individual ant over time. Note the frequent horizontal movement caused by the blade obstacle rows, and the broadening of the cut trail over time. (C) Photo of the same obstacle after 48 h, with a clearly visible cleared trail through the blades.

detour: Spearman rho=0.42, P=0.0128). The number of ants detouring did not correlate significantly with the number of cut blades (short detour: Spearman rho=−0.14, P=0.4467; long detour: Spearman rho=0.14, P=0.4394).

Ant movement

As can be seen in Fig. 3 (also see ESM4, Dryad, https://doi.org/10.5061/dryad.7sm50ft), ant movement was often very well aligned with the cutting pattern of the colonies. Owing to the noisy nature of the field videos and varying ant flow rates, we could not obtain quantitatively comparable data for each colony. Nonetheless, visual inspection of ant trails and cut patterns clearly demonstrates that ants preferentially travel along cleared trails (see Fig. 3 and ESM4, Dryad, https://doi.org/10.5061/dryad.7sm50ft).

DISCUSSION

Our study demonstrated that meat ants readily cleared artificial obstacles between a food source and their nest, and that 76% of the colonies removed more paper grass blades when they faced longer detours, resulting in 60% more cut blades compared with the short detour treatment after 48 h. This strongly suggests that meat ants can adapt their trail-clearing effort to changing environmental conditions and obstacles. Although the number of cut blades increased significantly over time, we observed a rapid onset of clearing activity. Indeed, 62% of all cut blades were removed within the first 24 h. Such high activity is impressive and may be further facilitated by the close proximity of the setup to the nest. However, colonies varied dramatically in their clearing onset speed: some colonies had removed all 300 paper blades after 48 h while others, mainly in the short detour treatment, removed none. As multiple colonies were tested on the same day, it is unlikely that weather or other environmental factors were the drivers of behavioural variation. Instead, meat ant colonies might display different trail-clearing propensities, with some colonies consistently investing in trails early on. Such colony-level behavioural syndromes are usually consistent across situations and stable over time (Jandt et al., 2014). This is indicated by our finding that some colonies consistently had high or low clearing activity in both treatments (see ESM3, Dryad, https://doi.org/10.5061/dryad.7sm50ft: c29, c31 and c40). However, the data collected in our study are not sufficient to conclude whether meat ant colonies display stable trail-clearing behaviour over time.

Meat ants could reduce both the time costs to foragers traversing the obstacle, and the time spent on clearing, by first establishing a passage through the obstacle to increase forager speed, and then successively widening the trail. Such creation of trails instead of random cutting was demonstrated by the comparisons of the vertical (nest to food) and horizontal (wall to wall) spread of cut paper blades (see ESM3, Dryad, https://doi.org/10.5061/dryad.7sm50ft). While blades were cut evenly on the food–nest axis (see Fig. 2C and Fig. S3), ants focused their horizontal blade removal on fewer columns, resulting in significantly less spread and often well-cleared trails from the food to the nest (see Figs 2 and 3, ESM3 and ESM4, Dryad, https://doi.org/10.5061/dryad.7sm50ft). This was the case in both detour lengths, indicating that ants generally aim to clear trails. The horizontal spread increased over time, suggesting that meat ants focus first on establishing a trail to the food source, which is then successively widened.

Our study found no indications that the ants stopped their clearing activity at a certain stage. Some colonies cleared all or almost all artificial blades, which might be wider than needed for the observed number of ant foragers. This is in accordance with studies in leaf-cutter ants, where trails in the field are often reported as wider than needed by peak traffic (Farji-Brener et al., 2012). It was suggested

that ants are slowed by encroaching vegetation at the trail's edges, and widely cleared trails thus aid efficiency (Farji-Brener et al., 2012). However, a simple behavioural rule such as 'cut encountered paper blade with a certain probability' could also well explain the clearing patterns found in this study, especially the emergence of trails through the obstacles. Ants often moved horizontally along blade rows until they found a missing blade to go through (see Fig. 3 and ESM4, Dryad, https://doi.org/10.5061/dryad.7sm50ft). This favours emergence of trails, as blades situated directly after a removed blade have higher encounter rates. Such an encounter-based mechanism could also explain the different cut rates between long and short detour treatments. The long walls could act as a funnel, causing more ants to walk through the obstacle in the middle. Interestingly, we did not observe a higher cutting activity along the transition of the wall to the obstacle, which might have been favoured by a 'funnel effect'. What we found instead is that most blades were cut in the middle of the obstacle, seemingly equidistant from the walls (Fig. S3A), probably caused by reflection of horizontally moving ants by the walls towards the middle.

Consistent with the differences in clearing activity, ant workers predominantly walked through the obstacle when facing a long detour, while they did not favour the shortcut in the short detour treatment (median ∼50%). This is also reflected by the significant correlation between the number of blades cut and the flow rate of ants through the shortcut. However, it is important to note that causation here may be reversed, as a higher ant flow rate could also be caused by the reduction of hindering paper blades.

As with many collective organisation systems based on positive feedback, initial conditions may strongly influence cutting behaviour. The initial decision to cut strongly influences where the trail forms, and whether it forms at all. This sensitivity to one initial, stochastic choice may explain the high variation in cutting behaviour observed among colonies. A strictly encounter-based cutting strategy would suggest that each ant has a certain threshold to initiate cutting upon contact with a paper blade and continues to do so until it is removed or a certain amount of time has elapsed (Bochynek et al., 2019). This is in accordance with findings by Middleton et al. (2019), who report that ants only cleared for 5.5 s on average before continuing their travel. However, some clearing ants we observed in the field were very persistent, consistently biting the stem of single blades for minutes at a time, and were also found to switch blades (F.B.O., personal observations). Individuals that are more likely to remove obstacles were also reported in leaf-cutter ants (Bochynek et al., 2019; Howard, 2001). This suggests that, while ultimately encounter-based, paper blade removal might be driven by a few persistent ant workers in meat ants. Such 'elite worker' behaviour is widespread in social insects, especially ants (Mersch et al., 2018 preprint; Hölldobler and Wilson, 1990). It is worth noting that cut-initiation behaviour seems to be stereotyped, with most ants first walking up to the tip of the paper blades to then turn around and walk down again until they touch the substrate with their head, after which they initiate cutting at the base of the blade (Middleton et al., 2019; F.B.O., personal observations). A similar behaviour was reported in grass-cutting ants, where it is thought to enable ants to estimate the length of the grass fragment to be cut (Roces and Bollazzi, 2009).

While the highest clearing activity clearly took place in colonies facing long detours, approximately 65% of colonies nevertheless initiated cutting in the short detour treatment. In other words, colonies also began to remove paper blades in situations where they could have easily circumvented them with low energetic or time costs. Such removal of blades irrespective of alternative low-cost detours in meat ants was also reported in Luo et al. (2018). This low threshold to initiate cutting is surprising, but the cost of a clearing workforce consisting of a few persistent workers at a time might be comparably low in colonies comprising thousands of workers (Greaves and Hughes, 1974). Moreover, the provided sucrose might be perceived as a stable resource similar to honeydew, which is a crucial source of energy and water required for meat ant colony survival and often connected to nests via cleared trails (Greaves and Hughes, 1974). Such stable and high-quality resources would favour early trail-clearing onset to maximise gain (Bochynek et al., 2017; Shepherd, 1982) but also to monopolise the resource in the territory (Ettershank and Ettershank, 1982).

Importantly, our results also suggest that prior experience might influence the decision to cut. Colonies that were first confronted with the short detour readily established a way around the obstacle, resulting in fewer ants traversing the obstacle and little cutting activity. However, when colonies first encountered a long detour, they were more likely to traverse the obstacle and to initiate cutting also in the short detour (see Fig. S1), although the setup was not present for at least 5 days. This is very interesting, as it suggests that prior experience is carried over to the new situation. Given the high ambient temperatures and the complete removal and exchange of the setup, it is unlikely that this effect is carried by trail pheromones. Instead, it is possible that individual foragers recalled the previous situation and initiated cutting, irrespective of the possible detour.

Our study demonstrates that meat ant colonies clear trails economically, preferentially cutting when alternative routes are long. Trail clearing is goal-directed and not random, with meat ants tending to first create paths to the food. The low threshold to initiate cutting and the rapid emergence of trails indicates a fast and adaptive system, whose cost might be balanced by employing only a few workers at a time. Taken together, our results demonstrate that trail clearing in meat ants results from a collective decision-making system that allows adaptive and robust collective behaviour.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: F.B.O., T.L., T.J.C.; Methodology: F.B.O., T.L., T.J.C.; Software: F.B.O.; Validation: F.B.O.; Formal analysis: F.B.O.; Investigation: F.B.O., E.J.T.M.; Resources: F.B.O.; Data curation: F.B.O.; Writing - original draft: F.B.O., T.J.C.; Writing - review & editing: F.B.O., E.J.T.M., T.L., T.J.C.; Visualization: F.B.O.; Supervision: T.L., T.J.C.; Project administration: T.L., T.J.C.; Funding acquisition: T.L., T.J.C.

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Data availability
Data are available from the Dryad Digital Repository (Oberhauser et al., 2019): https://doi.org/10.5061/dryad.7sm50ft

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