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RESEARCH ARTICLE

Argentine ants (*Linepithema humile*) use adaptable transportation networks to track changes in resource quality

Tanya Latty[1],*, Michael J. Holmes[2], James C. Makinson[3] and Madeleine Beekman[2]

ABSTRACT

Transportation networks play a crucial role in human and animal societies. For a transportation network to be efficient, it must have adequate capacity to meet traffic demand. Network design becomes increasingly difficult in situations where traffic demand can change unexpectedly. In humans, network design is often constrained by path dependency because it is difficult to move a road once it is built. A similar issue theoretically faces pheromone-trail-laying social insects; once a trail has been laid, positive feedback makes re-routing difficult because new trails cannot compete with continually reinforced pre-existing trails. In the present study, we examined the response of Argentine ant colonies and their trail networks to variable environments where resources differ in quality and change unexpectedly. We found that Argentine ant colonies effectively tracked changes in food quality such that colonies allocated the highest proportion of foragers to the most rewarding feeder. Ant colonies maximised access to high concentration feeders by building additional trails and routes connecting the nest to the feeder. Trail networks appeared to form via a pruning process in which lower traffic trails were gradually removed from the network. At the same time, we observed several instances where new trails appear to have been built to accommodate a surge in demand. The combination of trail building when traffic demand is high and trail pruning when traffic demand is low results in a demand-driven network formation system that allows ants to monopolise multiple dynamic resources.

KEY WORDS: Path dependency, Trails, Pheromone trail, Dynamic foraging

INTRODUCTION

Transportation networks, whether built by humans, ants or termites, play a crucial role in animal societies by moving individuals, information and resources from one place to another. A major challenge for transportation systems is ensuring that physical infrastructures such as roads (in humans) or trails (in social insects) have adequate capacity to meet traffic demand. When demand exceeds capacity, traffic jams result and individual travel times increase (Varaiya, 2005). In human-built transportation systems, engineers build and modify roadways to accommodate projected levels of demand; this can often be accomplished by ensuring that

high traffic areas are serviced by many roads, or by widening existing roads (Reid et al., 2016).

The problem of designing efficient transportation networks is magnified when traffic demand changes. In human-built road networks, sudden changes in traffic conditions can result from special events (e.g. sporting events), accidents or bad weather (Margiotta and Taylor, 2006). When increased traffic congestion occurs because of a permanent change in user demand (e.g. the construction of a new sporting facility), efficiency can be restored by redesigning the transportation network so that it meets the changed distribution of traffic demand. In humans, however, a rapid response to changes in traffic demand is constrained by the fact that once a road is built, it is costly to move or change. The idea that a network's current shape exists as a result of difficult-to-change decisions made in the past is known as 'path dependency' or 'spatial lock in' (Xie and Levinson, 2009).

Human engineers are not the only organisms to deal with the challenges of designing transportation networks in the face of fluctuating traffic demands and the constraints imposed by path dependencies. Social insects such as ants and termites also use transportation networks to connect their nests to a variety of resources that can appear, change quality or disappear, all of which can lead to changes in the traffic conditions along the trail. Traffic congestion in an ant colony's trail network would reduce foraging efficiency by preventing ants from rapidly moving resources from the food source to the nest. The effect of traffic congestion on travel speed has been documented in leaf cutter ants (*Atta cephalotes*), where researchers observed a negative relationship between density and speed, as would be expected if ants were interfering with one another (Burd et al., 2002). Not only would trail congestion limit foraging efficiency by slowing down resource transportation but it might also put ants at a competitive disadvantage against species capable of rapidly mobilising large numbers of workers. Despite the many differences between human and insect-built transportation networks (e.g. ants can easily leave their trails, while cars cannot), the two kinds of network might be shaped by similar trade-offs and pressures. Using the well-established tools of transportation science could therefore shed light on the dynamics of biological transportations systems.

Most ant transportation systems are based on the use of attractive trail pheromones (Hölldobler and Wilson, 1990). According to a 'classical' view of pheromone trails, worker ants deposit pheromone as they walk, with the attractiveness of a trail increasing with the amount of pheromone laid (reviewed in Czaczkes et al., 2015a,b; von Thienen et al., 2014). In some species, workers only deposit pheromone after feeding on a rewarding food source (e.g. *Solenopsis saevissima*; Wilson, 1962), whereas in others, pheromone deposition occurs continuously (*Linepithema humile*; Aron et al., 1993). In either case, the classical view suggests that pheromone trails may be subject to path dependency as a result of positive feedback loops which make it difficult for new trails to

[1]Faculty of Agriculture and Environment, School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia. [2]Behaviour and Genetics of Social Insects Lab, School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia. [3]Department of Biological and Experimental Psychology, School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK.

*Author for correspondence (tanya.latty@sydney.edu.au)

T.L., 0000-0002-7469-8590

compete with older, continually reinforced trails. For example, when given a choice between feeders offering sugar water of either a high or a low sugar concentration, the trail-laying ants *Lasius niger*, *Iridomyrmex humilis* and *Pheidole pallidula* focused their foraging effort on the higher concentration food if the higher concentration food was discovered before or at the same time as the lower concentration food (Beckers et al., 1990). However, if the lower concentration food was discovered before the higher concentration food, ants preferentially exploited the lower concentration food. This asymmetric and seemingly suboptimal exploitation pattern presumably occurred because the trail to the late-discovered high concentration food could not compete with the established trail leading to the low concentration food. Similarly, Sumpter and Beekman (2003) found that trail laying Pharaoh's ants (*Monomorium pharaonis*) preferentially exploited whichever of two equal-concentration feeders was discovered first.

Not only do the dynamics of pheromone trail evaporation lead to path dependencies but recent research also suggests that 'lock in' effects can be driven by memory alone (Czaczkes et al., 2016). This probably occurs because individuals who remember a rewarding food source tend to return to it exclusively. In social insects, the time it takes for an individual to truly abandon a resource after it has disappeared can be surprisingly long; honey bees, for example, revisit previously rewarding feeders for up to 9 days after the food has been moved (Beekman, 2005). Thus, ant transportation networks face the potential for path dependencies as a result of both the dynamics of pheromone trails and the persistence of their individual memories.

The experiments described above suggest that ant trail networks are subject to path dependency when resources are removed. However, these studies investigated situations where a new resource was discovered after a trail had already been established. What happens when resources remain in the same spatial location, but change in quality, thereby increasing or decreasing demand and traffic? Several lab and field studies have found that trail-laying ants are capable of redistributing their workforce in the face of short-term fluctuations in resource quality. Latty and Beekman (2013), for example, studied the ability of five ant species to refocus their foraging efforts as the quality of food sources changed through time. Two of the ant species studied were known to use pheromone-based trail systems, and, somewhat surprisingly, both trail-laying species rapidly relocated their workforce following a change in food concentration. Similar trail flexibility has been described when trail-laying ants face an obstruction of sections of their trail. Reid et al. (2011) found that Argentine ants (*Linepithema humile*) switched to alternative paths in a maze when their initial route was blocked. *Lasius niger*, another trail-laying ant, used one arm of a two-armed maze when ant densities were low and traffic was free flowing, but switched to using both maze arms when densities increased and trails become congested (Dussutour et al., 2004). While these examples suggest ant trail systems can re-route themselves in response to changes in traffic demand, they give no indication of how the underlying trail network changes to facilitate traffic flow, nor do they examine the extent to which path dependency influences network topology. In the present study, we examined the response of Argentine ant colonies and their trail networks to variable environments where resources differ in quality and change unexpectedly. The challenge for the colony is to track resource concentration by allocating a greater number of foragers to higher concentration resources.

Because we expected greater demand for the higher concentration feeder, our first aim was to determine whether ants increase traffic capacity to high-demand resources by building more and/or wider trails. Second, we determined whether Argentine ants were capable of redistributing their workforce following a change in feeder profitability. Third, we determined whether ants adapted their trail network (by adding or subtracting trails) to reflect the changed traffic situation.

A previous study found that Argentine ant inter-nest trail networks are constructed via a pruning process, where a complex network of trails is gradually pruned down through the removal of superfluous trails until a final network is reached (Latty et al., 2011). Pruning processes have been implicated in the formation of a number of biological transportation systems including slime mould foraging networks (Nakagaki et al., 2004a,b), the mycelial networks of fungi (Bebber et al., 2007) and mammalian vascular networks (Risau, 1997). While such a system provides a simple, decentralised prescription for constructing trail networks, it does not lend itself well to dynamic environments, as trails, once evaporated, generally do not re-appear (but see Jackson et al., 2006, for an example of pathfinding individuals that apparently find and reactivate old trails). Thus, our fourth aim was to determine whether a pruning process is at play in the development of trail networks in dynamic environments.

Lastly, we were interested in determining the impact, if any, of the spatial arrangement of resources in dynamic environments. Animals searching for food often use 'area-restricted search strategies' where search effort is intensified following the consumption of food items (Hassell and Southwood, 1978; Bond, 1980; Kareiva and Odell, 1987; Benhamou, 1992; Benedix, 1993; Nolet and Mooij, 2002; Weimerskirch et al., 2007). We reasoned that an ant encountering a feeder that had declined in quality since its last visit might engage in similar search behaviours in the hope of locating a new, better food resource. Ants using area-restricted search could rapidly discover new food items if they were clumped together, but would have difficulty relocating to widely spaced foods. We therefore predicted that ants would have more difficulty tracking changes in food concentration when food sources were far away from each other (sparse) than when they were clustered together (clustered).

MATERIALS AND METHODS
Study species
Argentine ants, *Linepithema humile* (Mayr 1868), are a trail-laying ant species that builds extensive pheromone-based transportation networks connecting one or more nests to many food resources (Holway, 1999). Argentine ants consume hemipteran secretions and scavenge for animal protein. Originally from South America, Argentine ants have become a major invasive pest in several countries including Australia (Wetterer et al., 2009). Outside their native range, Argentine ants form massive super colonies, the largest of which spreads over 6000 km and contains millions of interconnected nests and billions of workers (Giraud et al., 2002). While individuals within supercolonies do not attack one another, food-sharing interactions between nests are limited to a much smaller spatial scale (~50 m) (Heller et al., 2008).

The Argentine ants used in our experiment came from lab-maintained colony fragments originally collected from a supercolony on the University of Sydney campus (Sydney, NSW, Australia). Ants were housed in large plastic containers containing test tubes half-filled with water and stoppered with cotton wool. Colony fragments were fed artificial ant diet (Dussutour and Simpson, 2008) supplemented with cut meal worms twice a week and had access to water *ad libitum*. Each colony fragment contained

~1000 ants as well as brood and queens. Ants were kept between 20 and 24°C and were exposed to a natural dark–light cycle.

Experimental setup

We assessed the ability of ant colonies to re-allocate foragers by offering each colony a choice between three feeders containing a sucrose solution that periodically changed in concentration. Feeders consisted of wax dishes cut into a six-point star pattern to decrease crowding effects. In the sparse treatment, food sources were 30 cm from the nest and 52 cm from each other; in the clustered treatment, food sources were 30 cm from the nest and 10 cm from each other. At any given time, only one feeder provided high concentration food (1 mol l^{-1} sucrose syrup), while the other two feeders provided lower concentration food (0.5 mol l^{-1} sucrose syrup). At hourly intervals, the concentration of the feeders changed such that the previously high concentration feeder became a low concentration feeder, and vice versa. Every feeder eventually contained high concentration food once during the 3 h experiment. We randomised the order in which each feeder became high concentration. Fifteen and 14 colony fragments were used in the clustered and sparse treatments, respectively.

All experiments were conducted in 75-cm diameter circular arenas. The walls of the arenas were coated with Fluon to prevent ants from escaping. Ants accessed the arena via a stick passing through the centre of the arena and inserted into a nest box beneath the arena.

In order to count the number of ants foraging on each food source, we took photographs of each feeder at 10 min intervals using three Logitech webcams mounted above the feeders (one webcam per feeder). To determine network structure, we videotaped the entire experiment with a Sony Handycam mounted above the arena. We then extracted still images at 30 s intervals from the 10 min preceding a concentration change. These images were used to create composite photographs by overlaying the 20 stills from the 10 min preceding each concentration change using the free, widely used image processing software ImageJ.

Defining trails

One of the difficulties of working with ant transportation networks in an open arena is the bias inherent in defining what qualifies as a trail. Even with composite images, it was sometimes unclear whether a particular 'trail-like' structure should be considered a trail. To deal with the biases of trail identification, we developed an objective image processing-based procedure for classifying and counting trails using ImageJ.

As many of our trails had gaps between groups of travelling ants, we first enhanced images using a 'minimum' filter in ImageJ. The filter works by searching a given number of pixels (search region) around each focal pixel, then finding the minimum value (darkest region) of those pixels. The algorithm then changes all pixels in the region to match the minimum value. We set the 'search radius' to 3, so that all pixels within a 3-pixel radius (~4 mm) of a focal pixel (automatically selected because it had the minimum value) would be brought to a similar level of darkness. The overall effect of this procedure was to exaggerate trails by minimising the white space between ants (Fig. 1).

Next, we used the 'find connected components' function of ImageJ. This function runs an algorithm that identifies 'connected regions', defined as regions where all pixels are touching one another. The resulting output renders all 'connected' regions in a unique colour. For our analysis, we considered any continuous, single-coloured region leading from the nest to a food source as a
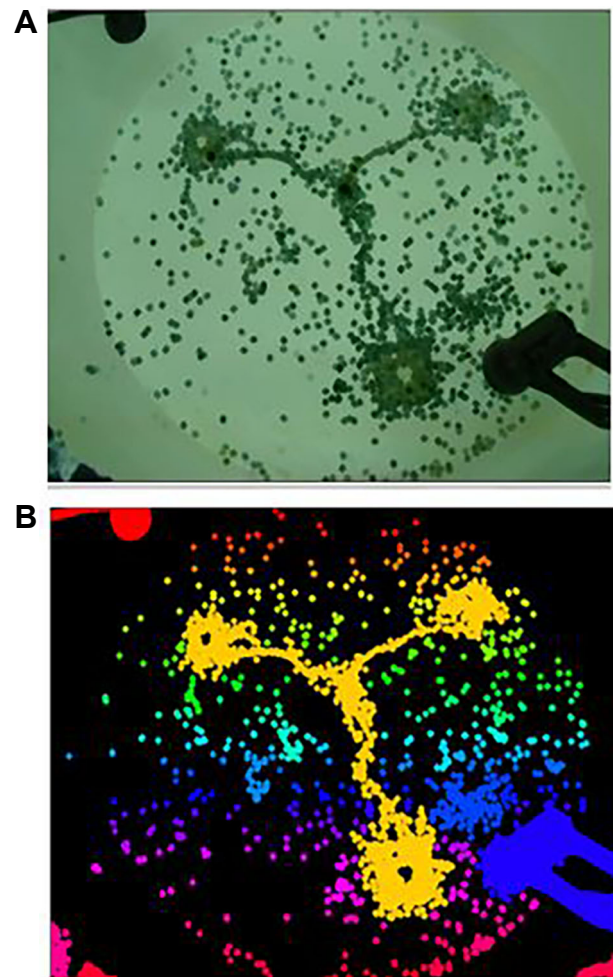

Fig. 1. Example of the method used to quantify trails. The three feeders are arranged in the triangular sparse configuration. (A) Composite image after enhancement with the 'minimum filter'. The dark images in the corners are webcams. (B) Trail network after application of the 'find connected components' algorithm. The yellow represents connected trail components (one trail leading to each feeder).

'complete' trail. If the trail changed colour part way through, indicating a small 'break' between ants, we classified it as a 'partial trail'. Note that to be considered a trail, the connected component needed to start at the nest. All trails that ended at a particular feeder were considered to belong to that feeder. In the case of partial trails, we only considered the connected component proximal to the nest. Unless otherwise noted, our metric 'total trails' includes the total number of both complete and partial trails.

We also counted the total number of 'routes' an ant could take to arrive at a focal feeder. Routes included all the possible paths an ant leaving the nest could take to reach the focal feeder, including paths via other connected feeders. Finally, we recorded the minimum and maximum width of each trail by measuring its width (on the original, unprocessed composite) at the thinnest and thickest point, respectively. All analyses were conducted blind such that the person defining trail networks did not know the quality of each feeder.

Construction of trail networks

We considered three simple ways in which the number of trails in a network could change over the course of the experiment: trail number could decrease, stay the same or increase (Fig. 2).
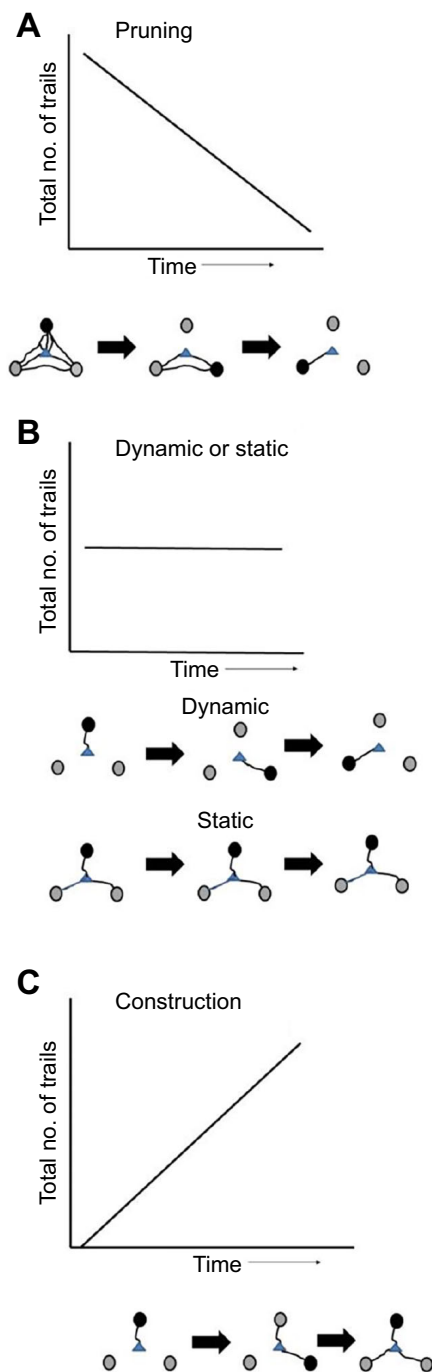
Fig. 2. Possible construction rules for ant trail network. Each panel shows a graph of the expected change in the number of trails over time. The diagram below each graph gives a graphic example of what those mechanisms would look like in our sparse setup. The light circles represent low concentration feeders; the dark circles represent high concentration feeders. The lines show the location of ant trails. (A) A decrease in the number of trails over time would indicate a pruning process whereby the network forms through the progressive deletion of links. The network observed in the time interval here is therefore a subset of the network produced in the first time interval. (B) If trail number remains constant throughout the experiment, a dynamic or static process would be at work. In a dynamic process, old trails are deleted and new trails are added to accommodate flow on high value resources. In a static construction model, the trail network does not change over time. (C) An increase in the number of trails over time would suggest a construction process by which new links are added and old links are not removed.

A decrease in the number of trails would suggest a pruning process whereby trails are successively removed, while an increase in trail number would suggest a construction process whereby new links are continually added to the network while older trails remain in place. Alternatively, the total number of trails could remain constant throughout the experiment. Counter-intuitively, this pattern could result from either a very dynamic or a very static underlying process. In a dynamic process, links to food sources are added and removed to track changes in traffic demand; while this results in no net change in the number of trails, the locations of those trails differ. Conversely, the same trend could emerge if established networks remain the same throughout the experiment (a static network).

We investigated changes in the network by counting the number of trails on our modified composite images for each hour of the experiment. Recall that each composite depicts the trail network in the 10 min preceding the change in feeder concentration. A pruning process would be suggested if the number of trails decreased over time (Fig. 2A), while an increase in the number of trails would indicate a construction process (Fig. 2C). No significant change in the number of trails over time would indicate either a dynamic or a static process (Fig. 2B). To tease these two possibilities apart, we carefully compared each set of three composites (one from each hour of the experiment) and noted whether new trails appeared in later hours.

Statistical analyses
Dynamic allocation of the foraging force
We tested the hypothesis that ants are able to track changes in resource concentration by determining whether there was a greater than expected proportion of ants on the high concentration feeder just before the first (60 min), second (120 min) and third change in concentration (180 min). As there were three feeders, the expected probability of ants allocating themselves to a feeder was 33%. We used a one-sided non-parametric Wilcoxon signed-rank test to test the hypothesis that more than 33% of foragers were allocated to the high concentration feeder. We tested the clustered and sparse configurations separately.

We further investigated the dynamic response of ant colonies using a generalised linear mixed model (GLMM). We used a GLMM to analyse our data because we wanted to account for the possibility that colony fragments differed in their behaviour. The absolute number of ants on each feeder was included as the dependent variable, and configuration and feeder concentration as fixed effects. Colony ID was included as a random effect. We constructed models for each time interval separately.

Response of trail network to changes in food concentration
We were interested in determining whether ants built more trails to high concentration feeders than to low concentration feeders. We tested models with total number of trails, total number of routes, maximum trail width or minimum trail width as the dependent variable; in all cases, we took the average value across all three time intervals. Feeder quality and configuration were included in the model as fixed effects and colony ID was included as a random effect.

Network development
We examined changes in the total number of trails in the arena (the sum of trails to high and low concentration feeders) over time using a GLMM with total number of trails as the dependent variable and time, feeder concentration and configuration as fixed effects. Colony ID was included as a random effect.

RESULTS

Dynamic allocation of the foraging force

Although we were most interested in network remodelling, we first needed to determine whether Argentine ants were even capable of reallocating their foraging force following a change in food concentration. We found that Argentine ant colonies in both the clustered and sparse configurations successfully tracked changes in feeder concentration by allocating significantly more than 33% of their workforce to the highest concentration feeder during all 3 h of the experiment (Figs 3 and 4; clustered: Wilcoxon signed-rank test: first hour: P=0.003, second hour: P=0.009, third hour: P=0.047; sparse: first hour: P=0.008, second hour: P=0.03, third hour: P=0.006).

Ants allocated a greater number of ants to the higher concentration feeder than to the lower concentration feeder (first hour: $F_{1,58.6}$=46.9, P<0.0001; second hour: $F_{1,57.9}$=53.7, P<0.0001; third hour: $F_{1,57.8}$=34.9, P<0.0001). Over the course of the experiment, the total number of ants observed on all feeders declined from a mean 55.3 (±7.6) ants to 39.4 (±5.9) and 36.6 (±6.3) in the second and third intervals, respectively (Fig. 3; $F_{2,232.2}$=11.63, P<0.0001). The number of ants on each feeder was not affected by the time interval or feeder configuration (first hour: $F_{1,29.5}$=0.29, P<0.59; second hour: $F_{1,28.7}$=0.54, P<0.46; third hour: $F_{1,27}$=0, P=0.99).

Response of trail network to changes in food concentration

Ants built more trails and more routes to the high concentration feeder than to the low concentration feeders
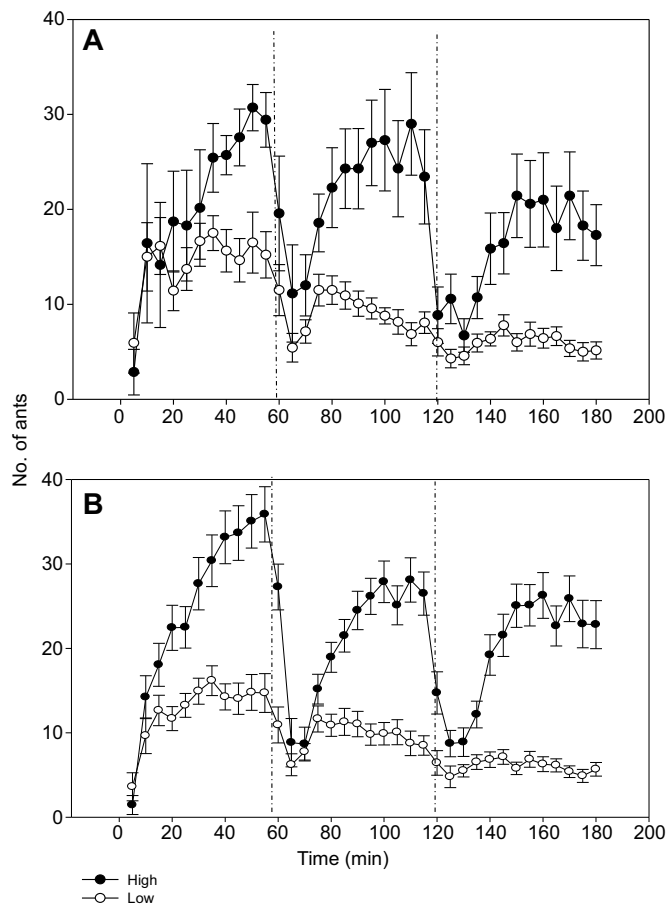

Fig. 3. The number of ants on high and low concentration feeders. (A) Clustered configuration (15 colony fragments). (B) Sparse configuration (14 colony fragments).
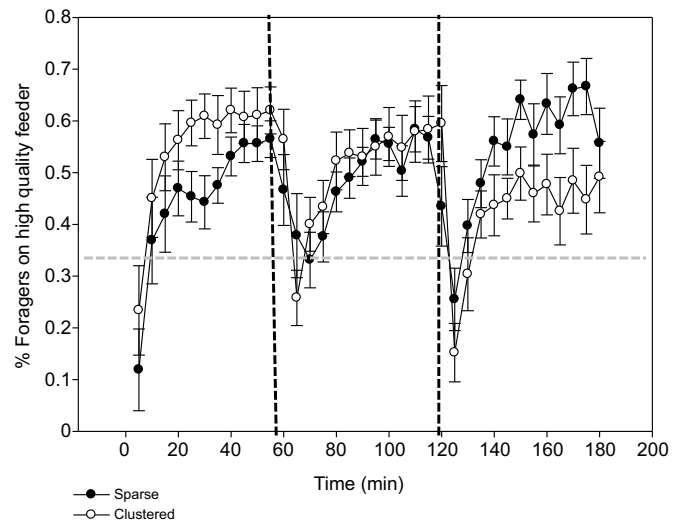

Fig. 4. Change in the mean proportion of foragers feeding on the high concentration feeder over the course of the experiment. Vertical dashed lines show when feeder concentration was changed. Note that at the beginning of each time interval (dashed lines), a new feeder became the 'high concentration' feeder. The horizontal dashed line shows the expected proportion (33%) if ants were distributing themselves randomly across the three feeders. Error bars are s.e.m. Fifteen and 14 colony fragments were used in the clustered and sparse treatments, respectively.

(Fig. 5; trails: $F_{1,24.5}$=13.8, P=0.002, estimate for high concentration feeder=0.25±0.06; routes: $F_{1,24.7}$=19.2, P=0.002, estimate for high concentration feeder=1.2±0.12). Ants built an average of 1.3±0.14 trails to the high quality feeder compared with 0.83±0.12 to the low quality feeder. Similarly, they built an average 1.5±0.16 routes to the high quality feeder compared with 0.9±0.12 routes to the low quality feeder. Feeder configuration had no significant effect on the number of trails or the number of routes built to the feeders (trails: $F_{1,22.9}$=0.6, P=0.44, estimate for clustered configuration=−0.09±0.11; routes: $F_{1,22.9}$=0.45, P=0.50, estimate for clustered configuration=−0.08±0.12).

Ants did not build wider trails to high concentration foods, considered at either maximum or minimum width (maximum width: $F_{1,22.9}$=1.27, P=0.26, estimate for high concentration=0.08±0.07; minimum: $F_{1,23.1}$=2.58, P=0.12, estimate for high concentration=−0.01±0.009). Feeder configuration did not have an effect on the width of trails leading to feeders, in terms of either maximum width or minimum width (maximum: $F_{1,21.9}$=0.03, P=0.85, estimate for clustered configuration=−0.002±0.11; minimum: $F_{1,23.4}$=0.76, P=0.38, estimate for clustered configuration=−0.02±0.02).

Network development

The total number of trails in the arena declined from an average 4.2±0.37 in the first interval to 2.4±0.36 and 1.8±0.36 in the second and third intervals, respectively; this pattern is consistent with a pruning process (Fig. 6; $F_{2,182.1}$=29.59, P<0.001). We visually examined composites from each hour of the experiment and determined whether new trails appeared. In all but four cases, the final network was a subset of the initial network, supporting the existence of a pruning process where trails are successively removed from the network while new trails are rarely added. In all four cases where we did observe new trails, the new trail connected the nest to a high concentration feeder.
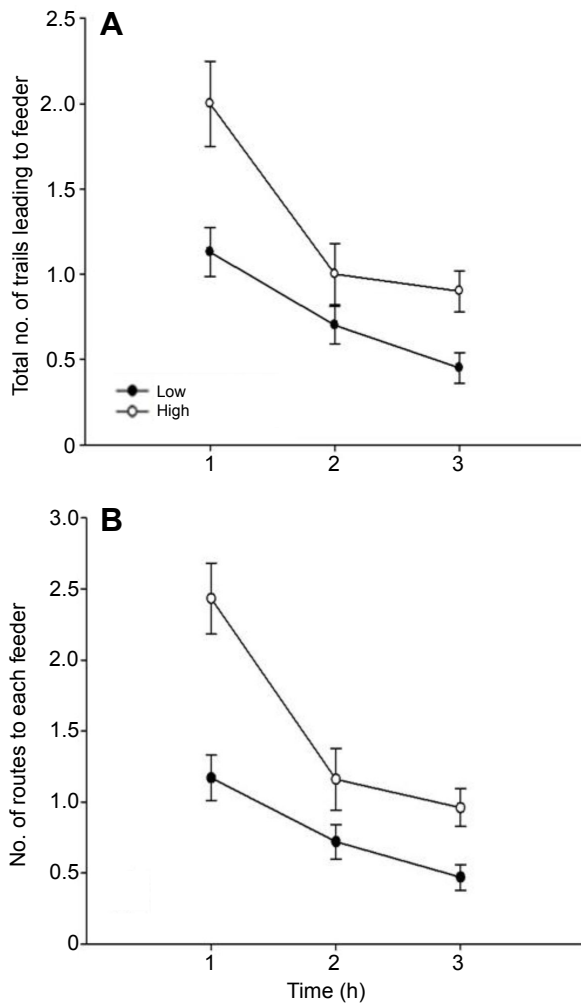
Fig. 5. The number of trails and the number of routes leading to high and low concentration feeders. (A) Mean number of trails leading to high and low concentration feeders. (B) Mean number of routes leading to high and low concentration feeders. Error bars are s.e.m. 'Total' trails included both partial and complete trails, where any continuous, single-coloured region leading from the nest to a food source was a 'complete' trail and any region that changed colour part way through, indicating a small 'break' between ants, was a 'partial' trail. 'Routes' refers to all the possible trails an ant leaving the nest could take to reach the focal feeder, including paths via other connected feeders. Note that results from the clustered and sparse configuration have been pooled as no significant difference was detected between them (N=29).

DISCUSSION

Contrary to theoretical predictions, trail-laying Argentine ants were able to rapidly track changes in their foraging environment so that the majority of foragers were always allocated to the most rewarding feeder. Ant colonies maximised access to high concentration feeders by building additional trails and routes connecting the nest to the feeder. The flexible architecture of the Argentine ant trail network increases access, via additional trails and routes, to high value resources. Interestingly, we saw no evidence that Argentine ants adjust trail width, another potential method for increasing traffic flow. Trail widening in response to heavy traffic has been observed in the leaf cutter ant *Atta colombica* (Shepherd, 1982). In contrast to Argentine ants, leaf cutter ants build physical trail systems by clearing and removing vegetation from trails to create a smoothed surface. In trail-clearing species, where new trails involve labour-intensive work, simply widening a trail by a few centimetres
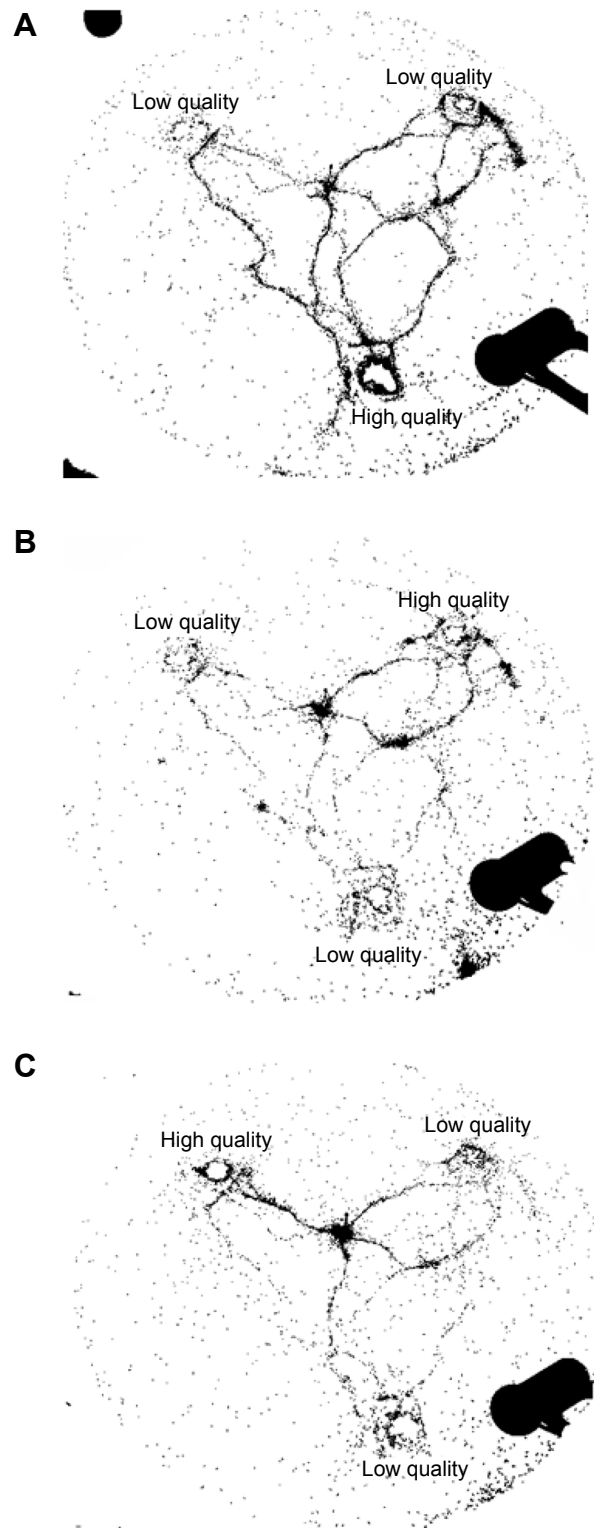

Fig. 6. The development of a trail over the three time intervals. (A) The trail system after 60 min (first interval). (B) The trail system after 120 min (second interval). (C) The network after 180 min (third interval).

might be less costly than building an entirely new trail. In trail-laying species like the Argentine ant, constructing a new trail is likely to be metabolically 'cheap' and has the added benefit of increasing network redundancy. Other ant species decrease traffic congestion by segregating traffic into distinct lanes of travel

(Fourcassié et al., 2010). Army ants, *Eciton burchelli*, split traffic such that nestbound ants carrying loads tend to occupy a central lane, while unladen foodbound ants flow along the edges (Couzin and Franks, 2003). It thus seems that ant species differ considerably in the strategies they employ to reduce or avoid traffic congestion. The exact mechanisms employed are probably heavily influenced by the combination of the species' ecological conditions and the ways in which trails are constructed.

In our experiments, Argentine ants initially built more trails and routes to higher concentration feeders. What are the mechanisms underlying the formation of additional trails and routes to high value resources? Although our study was not explicitly designed to examine individual ant behaviour, previous work by Dussutour et al. (2004) on the black garden ant (*L. niger*) might explain the formation of additional trails in response to high quality resources. Dussutour et al. (2004) found that an increase in collisions between ants on narrow paths 'pushed' individuals onto alternative arms of a diamond-shaped maze, resulting in an alternative route being formed to the food source. Unfortunately, our videos are not of sufficient resolution to allow investigation of collisions between individual ants; nevertheless, we suggest that the same mechanism could explain our results if collisions on crowded trails leading to the high concentration feeder caused ants to deviate from the main trail, ultimately resulting in the formation of new, supplementary trails. Such a simple mechanism would allow for the formation of additional trails when the potential for trail congestion is high. Indeed, ants in Dussutour et al.'s (2004) experiment began using the alternative path before the more crowded path reached capacity; thus, ants were preventing traffic jams before they started (Dussutour et al., 2004). However, Dussutour et al., 2004's experiments used a highly constrained maze-like setup rather than the open arena we used in our experiments; whether a simple pushing mechanism would be sufficient to initiate new trails in a non-constrained environment is unclear. It will be interesting to see how the individual-level behaviours of Argentine ants impact the development and adaptability of their foraging networks.

Alternatively, ants that encounter congestion on a trail could choose to abandon the trail altogether. As Argentine ants constantly deposit pheromone as they walk, an ant that left the trail in search of an alternative route would leave behind a pheromone trail that could conceivably be detected and followed by others. If Argentine ants are capable of navigating to a known food source without a trail, then an ant that abandons the trail could forge a new path to the food item. Unfortunately, not much is known about the ability of Argentine ants to navigate in the absence of a pheromone trail.

The classical view of pheromone trail use suggested that Argentine ants would become trapped by path dependencies, leading to an inflexible network. However, a growing body of research suggests that in many ant species, the use of the trail network is much more complex than simple blind trail following (for a review, see Czaczkes et al., 2015a,b). When ants are faced with the situation in which the pheromone trail leads in a direction different to that which the ant remembers, several species will choose to follow their route memories (Grüter et al., 2011; Aron et al., 1993; Czaczkes et al., 2015a,b). Similarly, *L. niger* workers following a pheromone trail on a rotating table tended to perform a U-turn once the table had rotated 90 deg; this suggests that ants use trails as a guide, and can correct their direction when visual information conflicts with trail information (Minoura et al., 2016). The above experiments all suggest that ants make use of their own route memories when navigating through a trail network; this may

be analogous to an experienced human driver who chooses to ignore seemingly incorrect information from a GPS unit. If Argentine ants can remember the location of alternative food sources, this might allow them to quickly relocate following a change in feeder concentration. Ants that experience a change in quality could elect to navigate toward a different food item within the transportation network, with the trail acting as a navigational aid. The extent to which Argentine ants use route memories of their trail networks is unknown, as is their ability to recall multiple food items. In *L. niger*, foragers can memorise the cues and location associated with at least two items (Czaczkes et al., 2014). However, unlike *L. niger*, Argentine ants appear to prioritise trail information over private information even when the trail is weak and the individual is experienced (Aron et al., 1993; Grüter et al., 2011). Theoretically, the reliance on trail pheromones over memory should make it more difficult for the ants to redirect themselves following a change in food quality, in contrast to our results. Given that few studies have examined the use of memory in Argentine ants, it is entirely possible that Argentine ants combine memory and pheromone trail information in a way that allows for rapid redistribution following a change in food quality.

The use of multiple trail pheromones has also been implicated in allowing trail-laying ants to rapidly respond to changes in food quality (see, for example, Witte et al., 2007). Dussutour et al. (2009) suggest that *Pheidole megacephala* produce two pheromones: a short-acting highly attractive pheromone and a long-lasting, weakly attractive pheromone. The long-acting pheromone trail allows ant colonies to 'remember' the locations of previously rewarding food items, while the short-acting pheromone 'reactivates' trails whose usage had decreased. Whether a similar system exists in Argentine ants is currently unknown, but if found, would partially explain their ability to rapidly reallocate workers following a change in food concentration. Future investigations into Argentine ant transportation networks would do well to consider how ants use different types of route information (memory, visual cues, multiple trail pheromones).

We found no evidence to support our hypothesis that the spatial configuration of resources influences worker re-allocation. Our prediction was based on the idea that an ant whose foraging source had declined in concentration would search for new resources in the vicinity of the previously rewarding resource. Re-allocation would therefore be easier when feeders were close together. In formulating our hypothesis, we underestimated the complexity and flexibility of the trail network. Even in the sparse configurations, we often observed trails connecting feeders directly to one another (Fig. S1), or central trails branching dendritically to multiple resources. In these more complex transportation networks, a disappointed ant could simply choose a new branch of the transportation network and follow it to a new feeder. Complex foraging networks provide resilience by allowing colonies to rapidly relocate foragers in the event that a rewarding feeder declines in quality or disappears altogether. In addition, the construction of multiple trails and routes provides resilience against damage to the trail network as there are usually multiple ways to arrive at a particular resource.

Our study shows that Argentine ant networks are relatively flexible and can adapt when food resources change quality. It is therefore surprising to find that foraging networks apparently formed via a pruning process where the initially complex network was gradually pruned down through the removal of trails. With a few exceptions (4/29), trail networks in later time intervals were a subset of the complex network formed during the first hour of the experiment. The pruning process we observed seems at odds with

our finding that ants build more trails to high concentration resources because a pruning process does not allow for the addition of new trails when traffic flow increases. How then did ants manage to track changes in food concentration? We suggest that our results reflect a general decrease in ant foraging over the course of the experiment. As ants in our experiment were starved, colonies initially responded to the unmarked arena by sending out a large number of foragers, resulting in high traffic and, consequently, the formation of many trails. As ants became satiated and overall traffic decreased, the pruning process selectively removed the less-reinforced trails leading to low concentration feeders. We propose that in later time intervals, the lower traffic levels were adequately served by the existing trail network without need of additional trails. In all four instances in which we observed the genesis of new trails, the new trail led to a high concentration resource, suggesting that a threshold level of traffic is needed in order for a new trail to outcompete an older trail. Thus, while we found some evidence of path dependency (as new trails rarely formed once a network was established), we also observed a degree of flexibility such that trails leading to low concentration feeders were selectively pruned, and new trails could arise if traffic was sufficiently high. This raises an interesting question: how do ant colonies decide which trails to prune and which to reinforce? Czaczkes et al. (2015a,b) found that *L. niger* ants that failed to encounter a dummy nestmate (a glass bead coated with *L. niger* hydrocarbons) made U-turns back to the nest. A similar mechanism, where ants tend to U-turn on or abandon low traffic trails, could result in selective pruning. The combination of trail building when demand is high and trail pruning when demand is low results in a traffic-driven network formation system that allows ants to monopolise multiple resources in a dynamic environment.

We decided to conduct our experiments in a laboratory as this allowed us to control the foraging opportunities of Argentine ants, as well as ensuring equal colony sizes. There are several weaknesses to a lab-based approach. First, our food sources were probably located closer to the nest than would be found in nature. Although there have not been large scale surveys of Argentine ant foraging distance, Argentine ant trails of 3–5 m in length have been observed in our study population (T.L., unpublished data). Second, our large feeding dishes probably represent 'bonanza' food finds as it is unlikely that the honeydew-producing hymenopterans used by Argentine ants would produce such large amounts of food at a time. Third, the temporal scale of our quality changes was relatively short (1 h). Unfortunately, there is a paucity of data about Argentine ant foraging in the wild, so it is difficult to ascertain how realistic our foraging experiments were (Holway and Case, 2000). Nevertheless, we believe our results are robust, and that the mechanisms we observe here would also occur in the wild, albeit on a larger scale. Future research directed at quantifying the natural variability of food resources and mapping wild Argentine ant networks would help to elucidate the transportation system of the Argentine ant.

The transportation networks of Argentine ants show a remarkable capacity to deal with the many problems associated with building an efficient transportation system in a dynamic environment. Amazingly, Argentine ant transportation networks form and change via decentralised processes based on the interplay between individual ant behaviours, the surrounding environment, resource quality and the physical properties of trail pheromones. Understanding the algorithms underlying ant network formation will help clarify how these networks adapt and heal in the absence of centralised control mechanisms.

Data availability
Data are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.t21kq (Latty et al., 2017)

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.144238.supplemental

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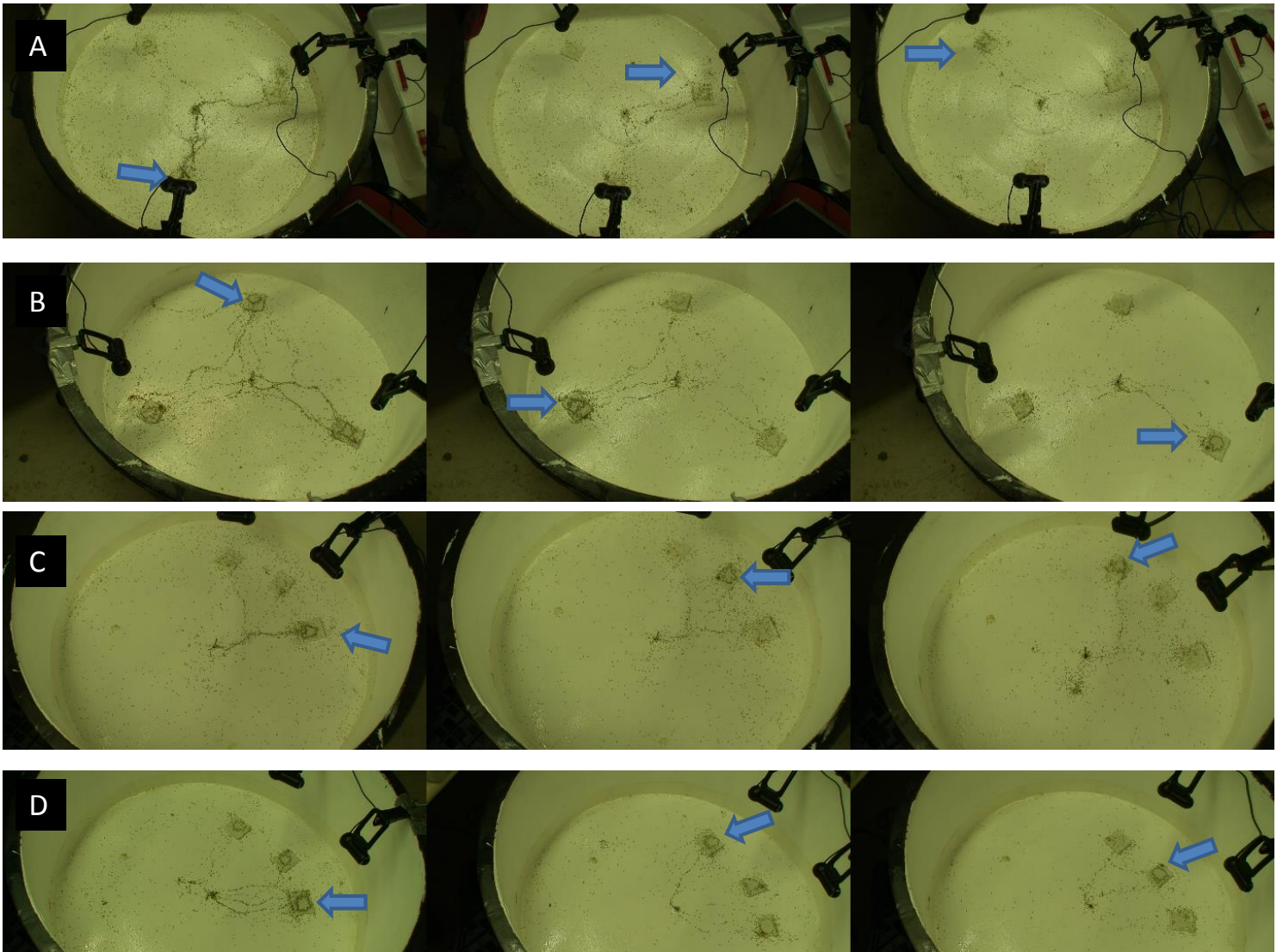
Supplementary information

Figure 1. Selected composite images showing trails at time interval 1, 2, 3 (from the right). The arrows point to the feeder that is currenty filled with the higher concentration feeder. A and B show sparse feeder configuration C and D show clustered feeder configufation.