Better tired than lost: turtle ant trail networks favor coherence over shortest paths

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Abstract

Creating a routing backbone is a fundamental problem in both biology and engineering. The routing backbone of arboreal turtle ants (*Cephalotes goniodontus*) connects many nests and food sources using trail pheromone. Unlike species that forage on the ground, arboreal ants are constrained to form trail networks along branches and vines within the vegetation. We examined what objectives the ant networks meet by comparing the observed turtle ant trail networks with alternative networks of random, hypothetical trails in the same surrounding vegetation. We found that turtle ant trail networks favor coherence, keeping the ants together on the trails, rather than minimizing the distance traveled along edges in the graph. The ants' trails minimized the number of nodes traversed, reducing the opportunity for ants to get lost at each node, and favored nodes with 3D configurations most easily reinforced by pheromone, reducing the opportunities for ants to diverge onto different paths. Thus, rather than forming the shortest paths, the ant networks take advantage of natural variation in the environment to promote the maintenance of a coherent trail that ensures that ants stay connected along the routing backbone.

Keywords: Cephalotes, ant trail network, routing networks, foraging, distributed algorithms, search, exploration, shortest path, spanning tree

Introduction

Many engineered systems rely on a backbone routing network, whose goal is to ensure that any two entities or devices on the network can communicate through some path (***Lynch, 1996***; ***Alwan and Agarwal, 2009***; ***Chouikhi et al., 2015***). Some biological systems, such as neural arbors (***Chandrasekhar and Navlakha, 2019***), plant arbors (***Conn et al., 2017***), and slime molds (***Tero et al., 2010***), also use routing networks, to transmit information and nutrients. Effective design of routing networks depends on the physical environment, because variation in the environment can affect the accuracy and rate of communication in both engineered (***Fei et al., 2016***; ***Nguyen and Xu, 2007***; ***Gong et al., 2016***) and evolved natural networks (***Levin, 2016***; ***Wiles et al., 2016***; ***Hein et al., 2016***; ***Couzin et al., 2005***). The environment influences how the system chooses search strategies, prioritizes competing objectives, and coordinates its local decisions. For example, wireless networks operating in difficult to reach environments may use different routing strategies to minimize energy consumption of devices (***Fei et al., 2016***); similarly, in bacterial navigation, chemicals appearing as localized pulses in the environment can affect gradient sensing and movement patterns (***Hein et al., 2016***).

The 14,000 species of ants have evolved diverse distributed routing algorithms to search for, obtain, and distribute resources (***Gordon, 2014***, ***2016***) in diverse environments (***Dussutour et al., 2004***; ***Latty et al., 2011***; ***Middleton and Latty, 2016***; ***Gordon, 2019***; ***Perna and Latty, 2014***). Models of engineered routing networks inspired by ants often emphasize the goal of minimizing the distance traveled. Ant colony optimization (ACO), first proposed in 1991, loosely mimics ant behavior to solve combinatorial optimization problems, such as the traveling salesman problem (***Colorni et al., 1991***; ***Dorigo and Blum, 2005***; ***López-Ibánez et al., 2015***) and other such routing problems (***Di Caro and Dorigo, 1998***). In ACO, individual ants each use a heuristic to construct candidate solutions, and then use pheromone to lead other ants towards better solutions. Recent advances improve ACO through techniques such as local search (***Gambardella et al., 2012***), cunning ants (***Tsutsui, 2007***), and iterated ants (***Wiesemann and Stützle, 2006***).

A fascinating recent area of biological research examines the goals met by the trail networks of ants (***Perna and Latty, 2014***). Studies of species that forage on a continuous 2D surface (***Middleton and Latty, 2016***), including Pharaoh's ants (***Malíčková et al., 2015***), Argentine ants (***Latty et al., 2011***; ***Flanagan et al., 2013***; ***Garnier et al., 2009***), leaf-cutter ants (***Dussutour et al., 2004***), army ants (***Deneubourg et al., 1989***; ***Couzin and Franks, 2003***), red wood ants (***Cherix et al., 1980***), and meat ants (***Cabanes et al., 2014***; ***Bottinelli et al., 2015***), show that ants use local chemical interactions to form trails (***Deneubourg et al., 1986***; ***Franks, 1989***; ***Deneubourg et al., 1989***), regulate traffic flow (***Bouchebti et al., 2019***), search collectively (***Countryman et al., 2015***), and form living bridges (***Garnier et al., 2013***).

There are many objectives that an ant colony's trail network might meet, including minimizing energy costs by reducing the distance traveled, keeping the ants together to form a coherent trail, resilience to rupture, and effective searching (***Cook et al., 2014***). Ant species that forage and build trails on the ground have few constraints on trail geometry because their trails can form nodes and edges anywhere on the 2D plane. Prior work (***Aron et al., 1989***; ***Garnier et al., 2009***; ***Cook et al., 2014***) showed that ground-living ants, such as red wood ants and Argentine ants, may minimize the distance traveled by forming trails with branch points that approximate 2D Steiner trees (***Latty et al., 2011***; ***Buhl et al., 2009***; ***Prömel and Steger, 2012***). However, minimizing distance may not be the only objective that ant trail networks attempt to optimize. Army ants link their bodies to form a bridge across gaps, but may not form the shortest possible bridge if this requires the use of more ants (***Reid et al., 2015***). Meat ants form trail networks that link nests and trees as nodes, and their choices of which nodes are linked, as well as the direction and length of trails, suggest that robustness to the loss of a node is as important as minimizing the distance traveled (***Bottinelli et al., 2015***; ***Cabanes et al., 2014***).

Many ant species operate in 3D environments, such as arboreal ants that nest and forage in trees and bushes. Unlike species that have evolved to create graph structures in continuous space in an unconstrained 2D plane, arboreal ants must solve problems on a natural graph structure. They cannot form trails with nodes and edges at arbitrary locations; instead, they can use only the nodes and edges that are available to them. The arboreal turtle ant (*Cephalotes goniodontus*) nests and forages in the tree canopy of tropical forests (***Powell et al., 2011***). A turtle ant colony creates a trail network in the vegetation that connects several nests, providing a routing backbone that must be maintained to allow resources to be distributed throughout the colony (***Gordon, 2012***, ***2017***). Ants search off the backbone to find and create trails to ephemeral food sources. The colony modifies the trail from day to day, sometimes forming small alternative paths, or loops, of which one is eventually chosen. The colony repairs the backbone in response to frequent changes in the vegetation caused by plant growth and by ruptures made by wind or passing animals (***Gordon, 2017***).

Results

Candidate objectives

Here we mapped trail networks of turtle ants in their natural habitat and computationally tested what objective functions these trails may be optimizing. We compared the observed networks with simulated random networks, to determine how well the observed networks meet three objectives, possibly in combination (***Bottinelli et al., 2015***):

1. Minimizing the distance traveled, which was measured as the average length of the edges in the trail network. This is equivalent to minimizing the total trail length for a fixed number of edges. Minimizing the distance traveled minimizes the energy cost of building the trail network. This distance, however, is not equivalent to the number of nodes traversed, as is often assumed in various optimization algorithms (***Dorigo and Stützle, 2004***; ***Di Caro and Dorigo, 1998***; ***Eberhart et al., 1995***; ***Karaboga, 2005***), including our previous work on turtle ants (***Chandrasekhar et al., 2018***), because in the vegetation, the lengths of edges vary; the distance between one node and another ranges from less than a centimeter to more than a meter (Table 1).

2. Minimizing the total number of nodes, which promotes the maintenance of a coherent trail by reducing opportunities for ants to get lost, but also reduces the opportunities for exploration and thus for finding new resources off the trail. The number of nodes was measured by counting the nodes traversed along edges used in the trail network. We previously studied how ants at a node select which transition through a node to traverse based on the rate at which volatile pheromone is deposited (***Chandrasekhar et al., 2018***). Simulation results were consistent with field observations (***Gordon, 2012***) indicating that ants at a node have a constant probability of exploring, or taking a path that is not the one most strongly reinforced by pheromone, of about 0.2 per node (***Chandrasekhar et al., 2018***). Thus each node presents an opportunity for ants to get lost, and lost ants may lay pheromone trail that could lead other ants astray. Each node is also an opportunity to meet the ants of other colonies that make trails in the same vegetation. We test here the hypothesis, indicated by previous observations (***Gordon, 2017***), that modification and repairs to the backbone tend to reduce the number of nodes over time.

3. Minimizing the difficulty of establishing a pheromone trail by finding trajectories through nodes that are most easily reinforced by pheromone. This objective also contributes to the creation and maintenance of a coherent trail. We hypothesized that the physical configuration of a node influences how likely are successive ants to cross the node in the same way, thus reinforcing it with volatile trail pheromone. The ants have short antennae that detect pheromone only locally, so the transition from one edge through a node to another edge is reinforced only when successive ants take exactly the same trajectory through the node (Figure 1). Nodes are variable 3D structures, ranging from a simple fork created by a branch in a plant, to a cluster of entwined vines and branches from different plants. We used an arbitrary categorical index to estimate how many possible trajectories an ant could take from one edge through a node to another edge, and thus how likely a node is to be reinforced (Figure 1, details below). We tested whether the ants' behavior reflected this estimate. Our previous work (***Gordon, 2017***; ***Chandrasekhar et al., 2018***) did not take into account variation among nodes, and did not examine how trails are selected from among the many available alternative networks.

Preference for nodes more likely to be reinforced was measured as the average *transition index* of all transitions in the trail network. The transition index is a categorical value that ranged from 1, where successive ants are most likely to take and reinforce the same trajectory through the transition, to 4, where successive ants are least likely to take and reinforce the same trajectory through the transition (Figure 1). The value of the transition index was assigned based on a visual estimate of the number of different trajectories available for ants to traverse the node, drawing on

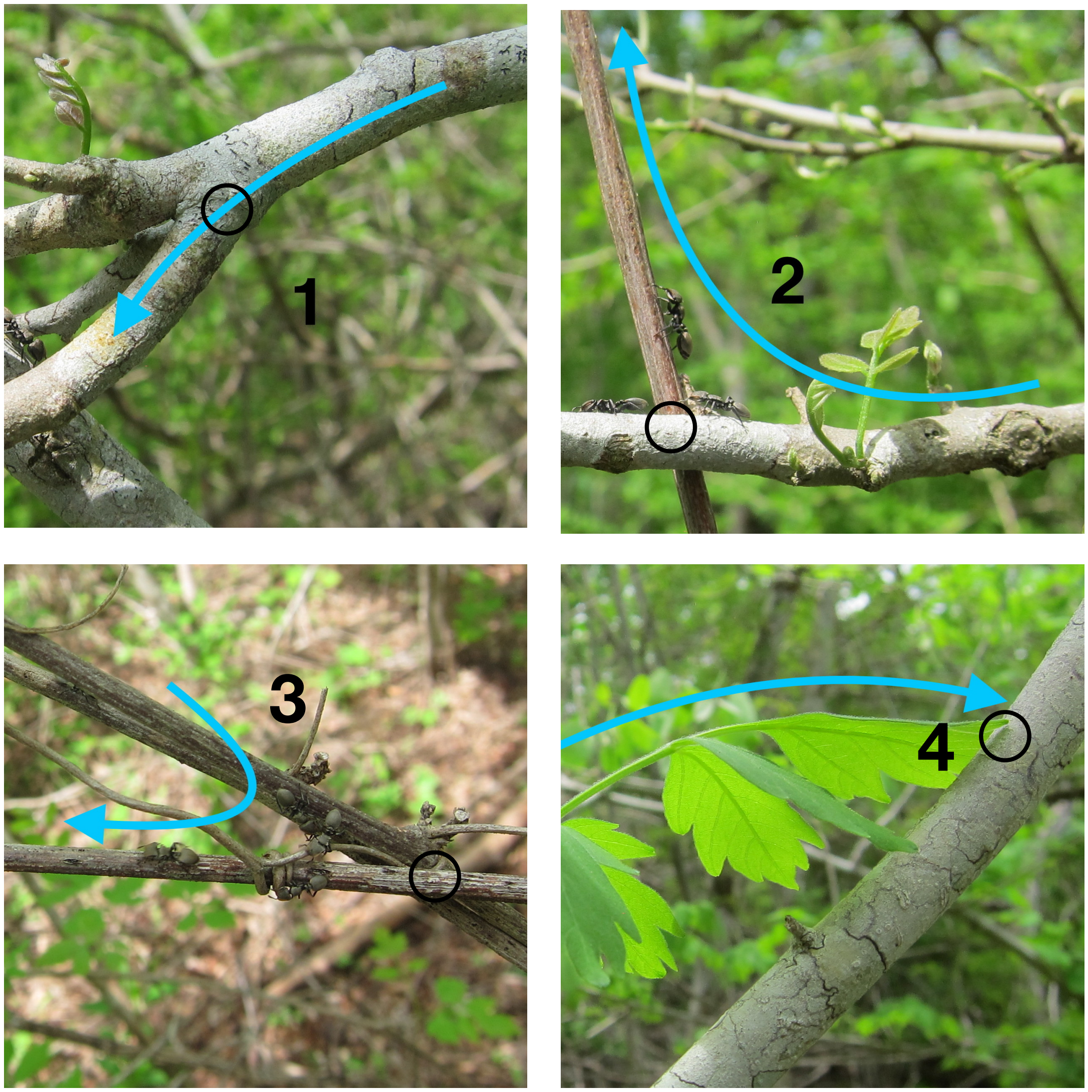

Figure 1. Transition indices. The photos show examples of nodes of each transition index (TI). The open black circle shows the node traversed. The blue arrow shows the transition, leading from the edge along which ants enter the node, through the node, toward the edge along which they exit. Each transition from an edge to a node to another edge was assigned a transition index with a value between 1 and 4. The lower the transition index, the more likely it is to be traversed by successive ants in the same way, and thus more likely to be reinforced. TI–1 (upper left): a node linking two edges on the same plant; in the example shown, all ants are likely to walk the same way across the top of the branch. TI–2 (upper right): a node that links one plant to another along a trajectory through a node that is likely to be the same for successive ants; in the example shown, most ants are likely to climb up the brown vine from the position shown by the ant approaching the junction from the left. TI–3 (lower left): a node that links one plant to another plant with more than one possible trajectory through the node; in the example shown, ants on the upper vine can reach the lower one either directly or by following the smaller vine that ants in the photo are using. TI–4 (lower right): a node that links one plant to another with many possible trajectories that are often changed by conditions; in the example shown, wind can easily move the leaf so that different ants reach the junction between the leaf and branch, at different places.

previous observations of the flow of ants on different edges from a node (e.g., see Fig. 7 in ***Gordon*** (***2017***)). Each transition through a node in the vegetation (e.g., edge $u \rightarrow v$ through node v to edge $v \rightarrow w$; Methods) was assigned a value of the transition index. A particular node v may have more than one transition index if there were many edges connected to that node.

	Tejon 189		Tejon 446		Turtle Hill 460	
	Available	**Used**	**Available**	**Used**	**Available**	**Used**
Edge Length (cm)	10698	20.71 ± 6.21	7615	13.46 ± 0.74	14696	39.97 ± 9.43
Total Nodes	217	43.5 ± 9.43	196	36.09 ± 3.81	202	54.0 ± 17.93
Transition Index	1.60	1.31 ± 0.06	1.70	1.44 ± 0.13	1.48	1.44 ± 0.10
Connectivity	—	3.75 ± 0.23	—	4.00 ± 0.24	—	4.46 ± 0.95

Table 1. Comparison of observed and available networks within the vegetation for the three colonies observed. Values for 'Available' are for all of the vegetation mapped. Values for 'Used' are means, averaged over observation days, for the paths used in each colony's network ($n = 10$ for Tejon 189 and Turtle Hill 460, and $n = 11$ for Tejon 446). Connectivity is a measure of the smallest number of nodes needed to get back to the trail used by the ants from an edge off the trail, averaged over all edges that lead off the trail used by the ants (Methods).

Mapping and modeling turtle ant trail networks

To determine what objectives are optimized by the ants' choice of paths within the vegetation (Figure 2A), we mapped the trail networks that connected the nests and naturally occurring, ephemeral food sources of three colonies (Tejon 189, Tejon 446, Turtle Hill 460), for 10–15 days over the course of 6 weeks, in a tropical dry forest at La Estación Biológica de Chamela in Jalisco, Mexico. We visually tracked the path taken by the ants and identified each node or junction in the vegetation, where an ant had a choice among more than one edge in the direction it is traveling, as well as the edges between nodes. We measured the length of each edge. We assigned a transition index to each each transition from one edge through a node to another edge, to estimate how likely were successive ants to take the same trajectory through the node and thus reinforce it with pheromone. To evaluate how the ants choose nodes and edges from the options provided by the surrounding vegetation, we also mapped all nodes, measured all edges, and assigned transition indices, for all possible paths up to five nodes away from each node used by the ants. A trail network on one day is illustrated in Figure 2B–C.

We modeled the network of vegetation as a directed, weighted graph, $G = (V_G, E_G)$, where each junction forms a node, and edges represent stems or branches that connect one node to another. Edge weights correspond to physical length. Node weights, which are used in some variants of the Steiner tree problem (***Byrka et al., 2016***; ***Bateni et al., 2018***), correspond to transition indices. We modeled transition indices by converting G into its corresponding line graph (Methods). The nodes corresponding to the nests and food sources were designated as terminals. We compared the extent to which each observed network on a given day optimized each of the 3 objectives, relative to a set of 100,000 random networks connecting the same nests and food sources (Methods).

Turtle ant trail networks favor coherent trails over shortest paths

We compared the relation of observed and random networks, testing for differences among objectives, colonies, and for a statistical interaction of objective by colony. We tested the hypothesis that the networks favor coherent trails, and thus minimize the total number of nodes and the average transition index more than they minimize distance traveled.

In all three colonies, the ants' networks optimized the maintenance of coherent trails. There were significant differences among objectives in how well observerd networks were optimized by observed relative to random networks (Scheirer-Ray-Hare two-factor ANOVA df 2, $H = 31.718$, $p < 0.001$). Trail networks minimized the average transition index (Dunn test , $Z = 4.395$, $p < 0.001$) and minimized the total number of nodes (Dunn test, $Z = 5.247$, $p < 0.001$), significantly more than the distance traveled (Figure 3A). There were no significant differences between the extent to which

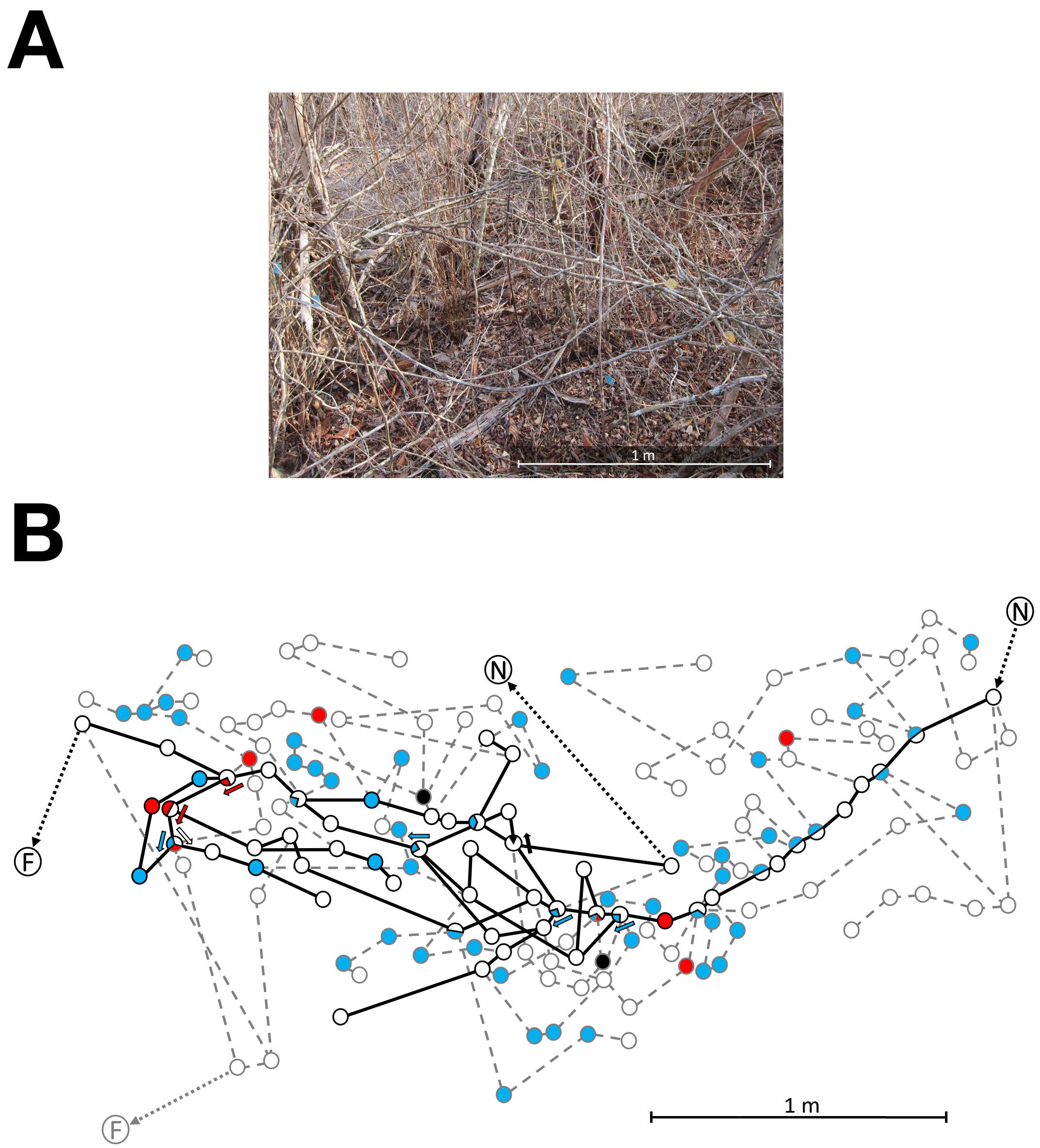

Figure 2. Turtle ant vegetation. A) Vegetation of the network mapped in B, photographed in the dry season before the branches have leaves. B) Illustration of part of the trail network for Tejon 189 on day 9. The figure shows 166 of the 217 nodes mapped in the surrounding vegetation. Edge lengths are scaled to measured distance, but actual location is not represented here. N represents a nest, F represents a food source. Circles represent nodes. Solid lines represent edges used on that day; dashed lines represent edges not used that day (Methods). The color of a node represents the transition index (TI) from the preceding edge to the following one: TI–1, open circles; TI–2, blue; TI–3, red; TI–4, black. At a node where there is a choice of more than one edge in the indicated direction, so that there could be more than one transition taken through a given node, a TI was assigned to each possible transition. For such nodes with more than one transition index, the TI is represented graphically with a pie chart, and arrows show which transition has the TI represented by the arrow's color.

observed networks, compared to random ones, minimized the average transition index and the total number of nodes (Dunn test, $Z = 0.852$, ns).

Colonies did not differ overall in the relation of observed and random networks for the 3 objectives (S-Test, df 2, $H = 2.010$, ns), but there was a significant objective x colony interaction (S-test, df 4, $H = 13.284$, $p < 0.01$). One colony, Turtle Hill 460, differed from the other two colonies in two ways, apparently because of differences in the local vegetation: first, it minimized total nodes, relative to random networks, significantly more than it minimized average transition index (Dunn

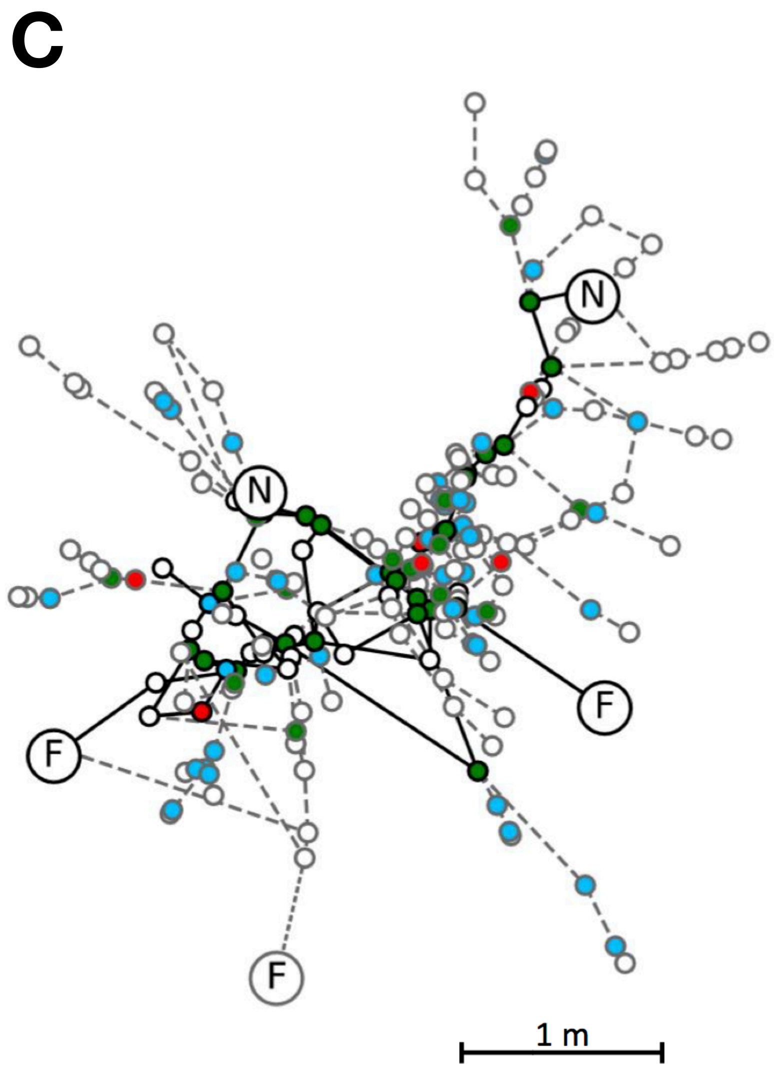

Figure 2. Turtle ant vegetation. C) Map of all 217 nodes for Tejon 189 on day 9. Symbols as in B. The large size of the network makes it difficult to show all TIs per node, so nodes with more than one TI are colored green.

test, $Z = 3.347$, $p < 0.05$), and second, it did not minimize average transition index significantly more than average length, relative to random networks (Dunn test, $Z = 1.012$, ns).

Random networks with the same number of nodes as the observed network did not differ in total length from the observed network. We tested this to control for the confounding of total edge length and total number of nodes because they are correlated ($R = 0.67$), and to test which one is prioritized when the two objectives give different results. We compared total length in observed and random networks by using a percentile measure (Methods). At 50%, the observed network is equal for the objective to the average random network; the lower the percentile, the better the observed network optimized the objective compared to random networks. In all three colonies, the total length of observed networks was similar to that of the random networks with the same number of nodes: the percentiles were $35.49 \pm 39.57\%$ for Tejon 189, $40.59 \pm 27.65\%$ for Tejon 446, and $34.89 \pm 38.84\%$ for Turtle Hill 460). For all three colonies, the percentile was within one standard deviation of 50%.

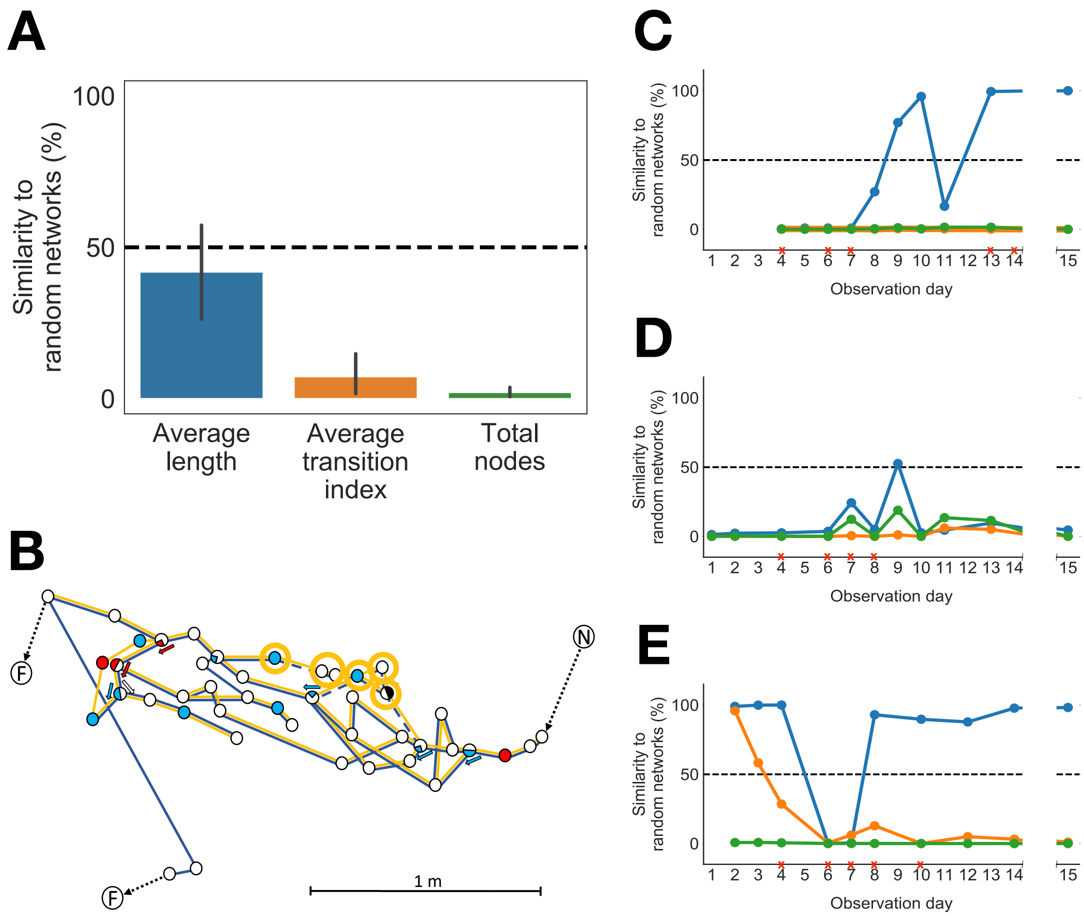

Figure 3. Comparison of random and observed networks. A) Similarity of observed and random networks measured as mean percentile (Methods). A percentile of 50 (dashed line) indicates that the observed network optimized the objective to the same extent as the average random network; the lower the percentile, the better the observed network optimized the objective compared to random networks. Error bars show standard error of the mean. B) Day to day change in trails in Tejon 189, showing a change that decreased both number of nodes and average transition index. Symbols for transition index are the same as in Figure 2B :TI–1, open circles; TI–2, blue; TI–3, red; TI–4, black. Solid yellow lines show trails used on day 9; solid blue lines show trails used on day 10; yellow circles and dashed blue lines show trails linking the six nodes that were used on day 9 but not on day 10. C–E) Day to day changes in mean percentile for each objective. Blue represents average edge length, orange represents average transition index, and green represents total number of nodes. A red 'X' indicates one or more ruptured edges on that day. C, Tejon 189, D, Tejon 446, E, Turtle Hill 460.

Turtle ant trail networks increase coherence over time

From day to day, progressive changes in the trail networks of all three colonies tended to minimize the average transition index and the total number of nodes more than they minimized average length (Figure 3B–E). The extent to which average length was minimized varied greatly from day to day in all three colonies, suggesting that minimizing this objective was not a strong priority. Figure 3B shows an example of a day-to-day change that minimized both the number of nodes and average transition index. From day 9 to day 10, the network changed from the path shown in yellow to the path shown in blue, thus eliminating the 6 nodes circled, including 2 nodes with TI–2 and one node of TI–4, in favor of a path with nodes all of TI–1 (Figure 3B). Overall, trails in Tejon 189 (Figure 3C) consistently minimized the total number of nodes and average transition index but twice increased the average length (days 7 to 10 and 11 to 15). Similarly, in Tejon 446 (Figure 3D), trails progressively decreased the total number of nodes and average transition index, but increased average length from days 6 to 7, 8 to 9, and 11 to 13. In Turtle Hill 460 (Figure 3E), the network consistently minimized the total number of nodes. This trail network shifted nests and food sources, and the change led to lower transition indices (days 2 to 10). There was an initial decrease in average edge length (days 4 to 7), due to a rupture on day 6 of a node leading to a 95 cm edge, one of the longest edges we measured, rather than to a choice of shorter edges, and then the trails increased in average edge length (days 7 to 14). These day-to-day changes indicate that the networks do not consistently minimize the distance traveled.

Turtle ants form loops to promote coherence

Turtle ants form loops in their paths, consisting of small, temporary alternative paths with the same start and end points, and over time, all but one of these paths tends to be pruned away (***Gordon, 2017***). Loops are often considered to decrease the efficiency of routing networks (***Alwan and Agarwal, 2009***; ***Chouikhi et al., 2015***), but may increase robustness by offering alternative paths if links are broken. Here we hypothesize that loops may occur because trails tend to form along easily reinforced nodes, and some sequence of easily reinforced nodes may naturally form a cycle in the graph.

Compared to available loops with the same start and end points (Methods), the observed loops tended to use nodes with low transition indices, and tended to minimize the number of nodes. We compared the centered ranks (Methods) of the average transition index, number of nodes, and average edge length, of paths connecting the same two start and end points on each trail in observed and available loops. A negative value of centered rank indicates that an observed path has a low transition index compared to all of the random paths within the available vegetation with the same start and end points. The mean (SD) of the centered rank in observed loops for average transition index was -1.59 (2.96); for number of nodes was -1.88 (2.91) and for average edge length was 0.44 (2.23); in all cases, significantly different from 0 (T-Test, $|T| > 3$, $p < 0.01$). These results suggest that loop formation in trails may occur as a consequence of selecting trails that have lower transition indices, thus promoting coherence.

Discussion

The trail networks of arboreal ants show how evolution shapes biological distributed algorithms to respond to dynamic environments. Minimizing distance traveled is often considered the main objective in wireless routing algorithms and ant colony optimization (***Di Caro and Dorigo, 1998***; ***Dorigo and Blum, 2005***; ***López-Ibánez et al., 2015***), since rapid communication is often needed between any two nodes in the network. We showed that the trail networks of turtle ants instead optimize the maintenance of a coherent trail by minimizing the total number of nodes, and by minimizing the average transition index; optimizing the latter objective, we show, is NP-complete (Methods). In previous work (***Chandrasekhar et al., 2018***), we proposed a model for the algorithm used to maintain and repair networks. This algorithm did not distinguish between minimizing the number of nodes and the distance traveled, since each edge had equal length. Our results here show that further work is needed to develop an algorithm that captures the role of physical variation in the environment.

Minimizing the transition index and the number of nodes contributes to maintaining the coherence of the trail because both diminish the risk of losing ants from the trail. Like water flowing over a rocky stream bed, turtle ants tend to find trails most conducive to the flow of ants. By avoiding nodes with high transition indices, turtle ants reduce the chances of ants wandering off the path and laying pheromone trail that can lead other ants also to leave the trail. Nodes with transition indices of 1 keep the trail on the same plant (***Gordon, 2017***). The vines and trees of the tropical dry forest tend to have long internode distances to reach the sunlight at the edge of the canopy (***Olson et al., 2009***). By staying on the same plant, ants are also led to resources at the edge of the canopy, such as flowers that provide nectar.

The trail networks must also balance the tradeoff between exploration and coherence. Exploration is necessary for the colony to construct trails (***Sumpter and Beekman, 2003***; ***Garnier et al., 2009***; ***Cook et al., 2014***; ***Latty et al., 2011***; ***Garnier et al., 2013***; ***Bouchebti et al., 2019***), search for new resources (***Emek et al., 2015***; ***Feinerman and Korman, 2017***; ***Stickland et al., 1995***; ***Britton et al., 1998***; ***Monmarché et al., 2000***; ***Countryman et al., 2015***) and repair breaks (***Gordon, 2017***; ***Chandrasekhar et al., 2018***; ***Cabanes et al., 2014***), and the connectivity of the vegetation (Table 1) sets the probability that ants that leave the trail will return to another node on the trail. There appears to be a constant probability of exploration at each node (***Gordon, 2017***; ***Chandrasekhar et al., 2018***), so the probability of leaving the trail accumulates with more nodes traversed. Thus, minimizing the number of nodes traversed reduces opportunities for the ants to get lost.

Our results here suggest that, as in engineered networks (***Byrka et al., 2016***; ***Bateni et al., 2018***), the cost of including a node in the turtle ant network may vary among nodes, because whether other ants follow an exploring ant that leaves the trail at that node depends on the node's physical configuration. The costs of additional nodes include the loss of ants from the trail, and the pursuit of fruitless paths, which may detract from the colony's ability to distribute resources among its many nests, and make fewer ants available to recruit effectively when a new food source is discovered. In addition, each node provides opportunities for encounters with other, competing species traveling in the same vegetation (***Yanoviak and Kaspari, 2000***; ***Vandermeer et al., 2008***; ***Philpott et al., 2008***). Further work is needed to examine variation among colonies (***Jandt and Gordon, 2016***) in how well they minimize the number of nodes, to learn how selection may shape the process that determines how a trail network is constructed and maintained.

Finally, are there useful applications of the principle that variation in the environment provides useful constraints on routing network design? Evolved algorithms operating in the natural world can use structure in the environment to enhance coordination among distributed agents (***Werfel et al., 2014***). In engineering, taking into account the physical structure of the environment may improve the design of routing algorithms (***van Rees et al., 2017***; ***Qi et al., 2019***; ***Bajaj and Agrawal, 2004***; ***Munguia et al., 2012***; ***Pavone et al., 2010***), for example, by reducing the search space of possible routing paths and steering network construction away from parts of the terrain that are difficult to reach. This could be beneficial in applications such as robot swarms, where distributed agents must coordinate in complex environments using a communication backbone to explore new terrain, exploit of temporary resources, and maintain security against intruders (***Duan et al., 2019***).

Materials and Methods

Observation of trail networks

The trail networks of three turtle ant colonies (Turtle Hill 460, Tejon 446, and Tejon 189) were observed between 06/20/18 and 08/03/18 at La Estación Biológica de Chamela in Jalisco, Mexico. Tejon 189 was observed for 10 days from 6/22/208–6/28/2018 and again on 07/01/2018, 7/04/2018 and 8/3/2018. Tejon 446 was observed for 11 days on 6/20/2018–6/28/2018 and again on 07/01/2018, 07/04/2018, and 08/03/2018; and Turtle Hill 460 was observed for 10 days from 06/21/2018–06/28/2018 and again on 07/02/2018, 07/05/2018, and 08/03/2018. Not every network was observed on each day. The colonies appeared to be of about the same size, based on observations in comparison with previous work in which size was estimated with mark-recapture measures (***Gordon, 2012***), but here we did not measure colony size.

The numbers of observation days were 10 for Tejon 189 and Turtle Hill 460, and 11 for Tejon 446, for a total of $93 = (10 + 10 + 11) \times 3$ observed networks.

Networks were mapped using the same methods as in prior work (***Gordon, 2017***), using visual inspection of the paths the ants took through the vegetation. We mapped each node and edge traversed by ants and all possible paths up to 5 nodes away from each node traversed by ants. Each node was assigned a number, and enough nodes were marked, with small labels or stickers on a dead end branch near the node, to identify all same nodes the next day. The initial map of a colony's trail network included all nodes used by the ants, and all nodes up to 5 nodes from each node on the path. The length of each edge was measured with a ruler, including each edge connecting the nodes on the ants path and all nodes up to 5 nodes from each node on the ants' path. A transition index was assigned corresponding to each pair of edges entering and leaving a node. The assignment of a transition index was based on a visual estimate of the number of different trajectories that were available for ants to traverse the node. We were not able to make any direct measurement of the amount of pheromone deposited.

The assignment of the transition index was made using the following criteria:

- TI–1 (Figure 1A): a node linking two edges on the same plant.
- TI–2 (Figure 1B): a node that links one plant to another along a trajectory through a node that is likely to be the same for successive ants.
- TI–3 (Figure 1C): a node that links one plant to another plant with more than one possible trajectory through the node.
- TI–4 (Figure 1D): a node that links one plant to another with many possible trajectories that is often changed by conditions such as the wind.

In each day of observation, we recorded which edges and nodes were used by the ants. As observed previously (illustrated for a different set of 3 colonies (***Gordon, 2017***)), each colony's trail network changed which nodes it used from day to day, although each day's path conserved some parts of the previous day's. In the course of the observations reported here, the path of the ants never went outside the range of the 5 nodes around the trail that were originally mapped. The number of nodes and edges observed in each network is shown in Table 1.

Assigning directionality to edges

Experiments with marked ants show that ants tend to use particular routes from a nest (***Gordon, 2012***), and tend not to turn around on the trail. To account for this, for all edges we defined a direction relative to one terminal; the outbound direction went away from it, and the inbound direction went towards it. We restricted the analysis to paths that proceed in the outbound direction.

Modeling the transition index as a line graph

The transition index of a node describes the probability that successive ants will take the same trajectory from an edge (u, v) through node v to edge (v, w). Thus, a transition index involving node v depends on which incoming edge was used to reach v, and which outgoing edge was used to leave v.

To model the transition index, we used the line graph of G, where $L_G = (V_L, E_L)$. The nodes $V_L = E_G$, and the edges $E_L = \{((x, y), (y, z)) | (x, y), (y, z) \in E_G\}$. The line graph creates a node for each edge in G and connects two nodes if they correspond to two adjacent edges in G. Every edge in the line graph denotes a transition in the original graph; traversing the edge $((u, v), (v, w)) \in L_G$ corresponds to starting at u, going to v, crossing the junction at v, and then going to w. We assigned every edge in L a transition index. Figure 4 illustrates this process. The line graph is used to compare the observed and random networks, as described below.

Generating random trail networks

We compared the observed trail networks to random trail networks based on their average edge length, total number of nodes, and average transition index. The random networks were simulated in the graph made from the map of the paths used by ants and the surrounding vegetation up to five nodes from the nodes used by the ants. The measures of number of nodes, edge length and transition index were those measured in the vegetation. The random trail networks may include loops, as did the observed networks.

We generated random trail networks as follows:

1. **Input:** Graph $G = (V_G, E_G)$, terminals $X \subseteq V_G$.
2. Create an empty graph R; add a random terminal $x \in X$ to R.
3. Choose a random terminal $x' \in X$ that has not already been added to R.
4. Perform a random walk on G that starts at x' and stops when it touches any node in R.

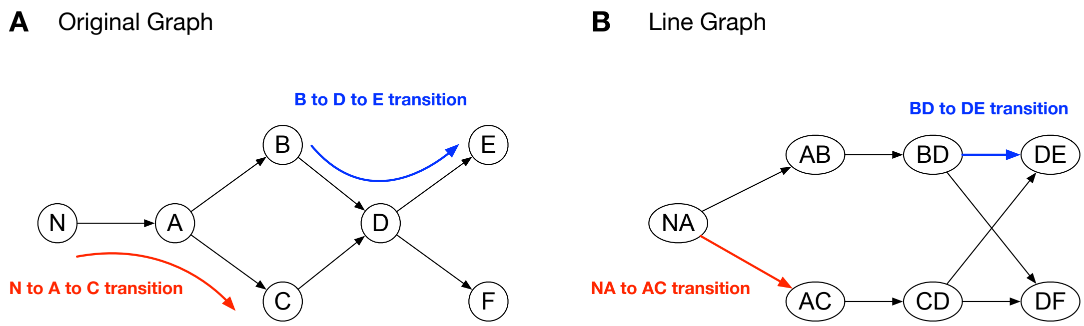

Figure 4. Converting the network to the line graph. A) Original graph. Nodes correspond to junctions in the vegetation, and edges correspond to links, such as a branch or stem, between junctions. B) Line graph. Every edge in the original graph has a corresponding node in the line graph. Two nodes are connected in the line graph if they correspond to two adjacent edges in the original graph. Transitions in the original graph used in this example are highlighted in red and blue.

5. Add all edges and nodes touched by the random walk to R.
6. Repeat steps 3–5 until all terminals have been added to R.

Comparing observed and random networks

To compare the observed and random networks, we computed for each network, using the line graph (Figure 4), the following three objectives: 1) Average edge length: the average length of all edges in the network; 2) Total number of nodes: the total number of nodes in the network; and 3) Average transition index: the average transition index over all transitions in the network.

For each objective, we computed a value of φ_{ants} for the observed network and $\varphi_1, \varphi_2, \ldots, \varphi_n$ for the n random networks. We measured the similarity between the observed network and the random networks for that objective as the percentage of random networks that have a lower value for the objective:

$$100 \times \frac{|\{\varphi_i | \varphi_i \leq \varphi_{\text{ants}}\}|}{n}. \tag{1}$$

An observed network is most similar to a random network when its percentile is 50. The closer the percentile is to 0, the better the observed network optimized the objective, and the closer the percentile is to 100, the better the random network optimized the objective. This percentile-based approach is unit-less, making it possible to compare performance for objectives that differ in the range of values.

We treated each comparison of the observed and simulated paths, drawn from observations on a given day, as independent, because we compared each day's path to a set of randomly generated paths using the same number of nodes. The relation between the randomly generated paths and the observed paths for each day was independent of those on any other day. We did not compare the observed paths from one day to those of another day. The path used by the ants on one day was similar to the one used by the ants on the previous day, perhaps because of the effect of the transition indices which generally remained the same from day to day.

For each colony (Tejon 189, Tejon 446, Turtle Hill 460), and for each objective (average length, total nodes, and average transition index), we computed the similarity of each observed network to 100,000 random networks that connected the same set of terminals, using Equation (1).

Because the total number of nodes and the total edge length are correlated, we did not simultaneously compare total length and total number of nodes between random and observed trail networks. Instead, we tested whether there was a statistically significant difference in total length between observed and random trail networks with the same number of nodes. For each observation of one colony on one day, we found all the randomly generated networks that had the same number of nodes as that observed network (209 for Tejon 189, 1420 for Tejon 446, 221 for Turtle Hill). We then found the total lengths of all of these networks, and used Equation (1) to evaluate how well each observed network optimized total length compared to random networks with the same number of nodes.

Comparision of objectives and colonies

We used the non-parametric Scheirer-Ray-Hare two-factor ANOVA test (***Scheirer et al., 1976***) to test for effects of objective, colony, and the colony x objective interaction on the percentiles of the observed networks compared to random networks. We then applied post hoc Dunn's non-parametric tests (***Ogle et al., 2018***), using a Bonferroni correction for multiple comparisons, with a significance threshold of $p = 0.05$.

Loops

We compared the average transition index and number of nodes in observed loops with loops that were available in the underlying vegetation. A loop was defined as two or more outbound paths that start and end at the same source and target nodes. For each observed loop, we computed all possible paths in the vegetation between the corresponding source and target nodes. We ranked all paths based on the average transition index of the path, and compared this to the rank of the average transition index of the paths used by the ants. We repeated the same measure for total number of nodes and average edge length.

We computed the *centered rank* of each path used by the ants as follows: We ranked n available paths in the vegetation, by the average transition index of nodes in the path, total number of nodes in the path, or average length of edges in the path. The ranks of the paths are $1, 2, 3, \dots n$, and the median rank is $r_m = (n+1)/2$. For each observed path, we computed its centered rank by subtracting the median rank from that path's rank. Using average transition index as an example, the centered rank is 0 when the observed loop had the same average transition index as the median random loop, negative when the observed loop has a lower average transition index, and positive when the observed loop has a higher average transition index. We performed a similar analysis for the total number of nodes and average edge length.

Connectivity

To calculate the connectivity of the vegetation (Table 1), we estimated how many nodes are required for an ant that leaves the trail to return to the trail. For each edge (u, v) connecting a node on the trail to a node off the trail, we found the length, in number of nodes, of the path with fewest nodes from v back to a node on the trail. We measured connectivity as the smallest number of nodes in a path back to the trail, averaged over all edges (u, v) leading off the trail on all days.

Optimizing transition index is NP-complete

Here we show that the problem of constructing the foraging network that connects a given set of terminals while minimizing the average transition index of the network is NP-complete. To do this, we start by showing that finding the minimum average-weight path between two vertices in a graph is NP-complete. In this problem, we are given a graph $G = (V_G, E_G)$ and two vertices $u, v \in V$. The goal is to find a path $\mathcal{P} = [(u, r_1), (r_1, r_2), \dots, (r_k, r_{k+1}), (r_{k+1}, v)]$ that minimizes the average edge length: $\frac{1}{|\mathcal{P}|} \sum_{e \in \mathcal{P}} w(e)$, where $w(e)$ defines the length of edge e. This problem differs from the classic shortest path problem, which seeks a path with minimal total edge length.

The standard method for considering the complexity class of an optimization problem is to consider the equivalent decision version of the problem: given a graph $G = (V_G, E_G)$, two vertices $u, v \in V_G$, and an integer k, we ask: is there a path from u to v whose average weight is $\leq k$?

Lemma 1. *Finding the minimum average-weight path is NP-Complete.*

Proof. First, we show that this problem is in the class NP. If we are given a path from u to v, we can verify that the path is a valid u-v path, and that the average edge weight is $\leq k$. This certificate will clearly be of polynomial length, and we can verify that it is correct in polynomial time.

Next, we show that the problem is NP-hard. We proceed via reduction from the Hamiltonian path problem, which is NP-Complete. Given a directed graph $G = (V_G, E_G)$, the directed Hamiltonian path problem seeks a path that touches every vertex $v \in V_G$ exactly once. We construct a graph G' as follows: G' contains all of the vertices in G along with two additional vertices, s and t. We assign a weight of 1 to all of the original edges in G. We add a directed edge from s to every vertex $v \in V_G$, and we add a directed edge from every vertex $v \in V_G$ to t. We assign a weight of 2 to all edges that include either s or t.

The smallest possible average edge weight for any path from s to t is $\frac{3 + |V_G|}{|V_G| + 1}$, and such a path exists if and only if G has a directed Hamiltonian path.

The reduction requires adding 2 new nodes, and $2|V|$ new edges to G. Thus the reduction clearly takes only polynomial time. □

We now use Lemma 1 to show that optimizing average transition index is NP-Complete. Let $L = (V_L, E_L)$ be a graph whose edge weights correspond to transition indices, which we represent using the line graph (Figure 4). Given a set of terminals $X \subseteq V_L$, we seek to find a subtree $F_X \subseteq L$ that minimizes the average value of all edge weights in F_X. We require that F_X be connected without cycles to represent the fact that cycles in turtle ant trails are typically pruned.

Once again we consider the decision problem: given a line network $L = (V_L, E_L)$, a set of terminals X, and an an integer k, does L contain a subtree F_X whose average weight is $\leq k$?

Lemma 2. *Finding the subtree F_X that optimizes average transition index is NP-Complete.*

Proof. First, we prove that the problem is in NP. Given V_L, X, k, if we are presented with a subgraph F_X as a certificate, we can verify that F_X is a valid solution. We check that F_X is valid subgraph, that F_X is connected, that F_X contains every terminal node X, and that the average weight of the edges in F is $\leq k$. Clearly the size of F_X is polynomially bounded, and we can verify that F_X is a valid solution in polynomial time.

To show that the problem is NP-hard, we proceed via reduction from the minimum average-weight path problem above. Given G and vertices u and v, we simply treat G as the line graph (L), and designate terminals $X = \{u, v\}$; this means F_X is simply a u-v path. We seek the trail that optimizes the average transition index between terminals u and v. By construction, this is the minimum average-weight path from u to v in the line graph, meaning there is a subgraph F_X with average weight of $\leq k$ if and only if the original graph has a u-v path with average edge weight $\leq k$. Further, the reduction clearly takes only polynomial time. □

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Author Contributions

AC: data analysis, computational modeling, manuscript preparation. JARM: computational modeling, manuscript preparation. CA: data collection, manuscript preparation. SN: data analysis, computational modeling, manuscript preparation. DMG: data collection, data analysis, computational modeling, and manuscript preparation.

Competing Interests

None of the authors have competing interests.

Data Availability Statement

All data collected and analyzed will be archived at Stanford Digital Repository at the Stanford Libraries. Python code is available at: https://github.com/DiODeProject/SteinerAnts.

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