Army ants dynamically adjust living bridges in response to a cost–benefit trade-off

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The ability of individual animals to create functional structures by joining together is rare and confined to the social insects. Army ants (*Eciton*) form collective assemblages out of their own bodies to perform a variety of functions that benefit the entire colony. Here we examine "bridges" of linked individuals that are constructed to span gaps in the colony's foraging trail. How these living structures adjust themselves to varied and changing conditions remains poorly understood. Our field experiments show that the ants continuously modify their bridges, such that these structures lengthen, widen, and change position in response to traffic levels and environmental geometry. Ants initiate bridges where their path deviates from their incoming direction and move the bridges over time to create shortcuts over large gaps. The final position of the structure depended on the intensity of the traffic and the extent of path deviation and was influenced by a cost–benefit trade-off at the colony level, where the benefit of increased foraging trail efficiency was balanced by the cost of removing workers from the foraging pool to form the structure. To examine this trade-off, we quantified the geometric relationship between costs and benefits revealed by our experiments. We then constructed a model to determine the bridge location that maximized foraging rate, which qualitatively matched the observed movement of bridges. Our results highlight how animal self-assemblages can be dynamically modified in response to a group-level cost–benefit trade-off, without any individual unit's having information on global benefits or costs.

collective behavior | self-assembly | swarm intelligence | self-organization | optimization

Scenarios requiring the coordination of many individual units to accomplish higher-level tasks are common to systems at many scales in biology (1). However, we have little understanding of how environmental forces and evolutionary constraints shape the interactions between individuals that produce higher-level order. This remains a fundamental problem for our understanding of systems as diverse as developmental processes, the interactions of neurons in the brain, collective navigation in animal groups, and vehicular traffic (2–4).

The physical joining of discrete units to create composite functional structures at the group level is a subset of these problems that has previously been studied in microscopic systems such as the multicellular "slug" of the cellular slime mold *Dictyostelium discoideum* (5). Larger, more complex self-assemblages of multicellular individuals seem to be confined to the social insects (6), where well-known examples include the floating rafts created by the fire ant *Solenopsis invicta* (7) and the living chains formed by weaver ants of the genus *Oecophylla* (8). For surface-dwelling army ant species of the new world genus *Eciton*, the regular formation of self-assembled structures is fundamental to colony survival, because they are used both for shelter (the bivouac, or temporary nest) and as a means to organize and expedite traffic along the foraging trail.

Eciton army ants are nomadic social predators that hunt primarily other ants and some other arthropods throughout Central and South America (9–11). Raids occur mainly in the leaf litter, where the ants use strength in numbers to overwhelm their prey, and a colony typically harvests around 40 g dry weight of prey per day from an area a few hundred meters across (11). Unsurprisingly, this level of localized raid intensity can have a significant impact on prey populations (11–14), but the army ants avoid local prey depletion by conducting regular colony emigrations to new, potentially prey-rich patches of the forest (11, 12). These ants therefore live an exceptionally time-constrained lifestyle (15), where maximizing prey intake during the day's raid must be followed by high-speed and efficient colony relocation. For both foraging and emigration, high levels of traffic are critical for maximizing overall transport efficiency (16). This high traffic flow is achieved in part by exceptionally fast running speeds of up to 14 cm/s for both prey-burdened and unburdened ants (15), and sustained average speeds of around 8 cm/s (17) along foraging trials that typically range between 100 and 200 m in length (11). However, the leaf litter that blankets the forest floor contains many holes, uneven surfaces, and diversions that can slow traffic (15, 18). *Eciton* workers deal with these obstacles by filling holes and spanning gaps with their bodies, providing a living roadway for their nestmates to run over.

Previous work has shown that individual workers plug small potholes with their bodies, smoothing and widening paths to allow for an increased rate of traffic flow and prey delivery rates. These benefits are likely to more than offset the cost of dedicating a significant proportion of foragers to pothole plugging (18). *Eciton* army ants also build complex "bridges" of multiple linked individuals that span

Significance

Complex systems, from ant colonies to stock markets, share a common property: sophisticated group-level structure emerges from simple individual-level behaviors. Using simple interaction rules, *Eciton* army ants construct complex bridges from their own bodies to span forest-floor gaps. These living bridges are uniquely complex in both their dynamic properties and the number of animals involved and so are of considerable interest for understanding emergent structures in complex systems. In field experiments, we show that construction interacts with traffic rate and environmental geometry, causing bridges to lengthen, widen, and migrate. Bridges provide a shortcut for foraging ants, at the cost of sequestering workers. We show that bridge location represents a cost–benefit trade-off, with potential implications for human engineered self-assembling systems.

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Fig. 1. (*A*) Experimental apparatus from above, with ant bridge cartoon to show relative size. θ indicates the angle of separation between the platforms, in this case set to 20°. Over 30 min, the bridge has moved the distance *d* from its initiation point at the intersection of the platforms to its current location. See *Materials and Methods* for explanations of the empirical measurements *d*, *w*, *b*, and D_{max}, and the cost–benefit model for descriptions of L_A, L_T, L_1, L_0, and L_E. The position of L_T corresponds to the position of the main trail axis, as described in the text. The width (w_A) and length of each movable platform section was 3.3 cm and 24 cm, respectively. (*B*) Apparatus with θ set to 12°. Hinges are shown as circles. (*C*) Apparatus with θ set to 60°. The surface area of a bridge, used to estimate costs, is shown in blue, and the reduction in travel distance is shown with red dashed arrows for the same bridge migration distance (*d*).

larger gaps (19). The ants use these bridges as the leaf-litter terrain demands, such that long stretches of tens of meters over relatively smooth terrain (e.g., large logs and fallen branches) may contain no bridges, whereas areas of particularly rough and broken terrain may contain multiple bridges per meter of trail. The composition of each bridge also varies from just a few individuals spanning a small hole to many hundreds fully suspended across gaps tens of times larger than an individual ant. This variation in the deployment and composition of army-ant bridges further highlights the uniquely dynamic and complex nature of these self-assembled animal structures, but we know very little about them. Previous studies examined the responsiveness of these bridges to traffic flow, demonstrating that they are robust to small perturbations in traffic, yet highly responsive to large interruptions, breaking apart within a few seconds when traffic was stopped (19). What remains unknown is how the presence, shape, and position of bridges are established, and how these may benefit the collective actions of the colony.

Here we use experimental field studies with the army ant *Eciton hamatum* to recreate the natural process of bridge construction and to test how bridges dynamically adjust to the underlying environmental geometry over naturally varying traffic levels. We then examine the cost–benefit trade-offs involved in the construction of these complex structures. Our preliminary observations suggested that large suspended bridges do not form in place, but typically start at the bend of a natural diversion (e.g., the angle of crossed branches that deviate from a straight path) and subsequently build out into the gap, creating a shortcut in the foraging trail. We designed an apparatus that mimicked this natural ecological context and allowed us to test the effect of the angle of path deviation from the main trail (Fig. 1) on the construction dynamics of bridges, focusing on bridge position and shape. To address the net benefit of dynamic bridge structures, we computed the trade-offs between the benefits of bridges in

terms of travel distance saved and traffic flow, and the costs of immobilizing individuals in the structure, unable to engage in prey discovery, capture, and retrieval.

Results

Our results show that army ants dynamically adjusted the location and size of their bridges at the local level to meet a cost–benefit trade-off at the colony level. The bridges formed were not static structures—they were initiated at the apex of the diversion formed by our apparatus and, by a dynamic process of construction and deconstruction, moved toward the main trail axis, lengthening and widening as they did so (shown in Fig. 1*A*; also see Movie S1), and thus shortening the overall path of travel.

The grouped results for bridge movement as a function of experimental time (Fig. 2*A*) clearly show an initial period of rapid bridge migration, which plateaus toward the end of the experiment [generalized linear model (GLM), t_{630} 6.812679, $P < 0.00001$]. Bridges built at smaller angles θ moved further than those at larger angles (GLM, $t_{630} = 2.719549$, $P < 0.01$). For all angles, bridge movement did not continue to its full possible extent where the bridge would have intercepted the main trail axis. Instead, bridge movement plateaued after some distance, with lower angles θ showing a greater movement distance (Fig. 2 *A* and *B*). Traffic intensity also had a strong effect on the distance moved by the bridge, with higher traffic leading to greater movement (Fig. 2*C*; GLM, interaction between time and traffic, $t_{630} = 9.010750$, $P < 0.001$). As bridges moved closer to the main trail axis, they grew longer to maintain the connection between the two platforms. As bridges lengthened, there was a correlated increase in width, as shown in Fig. S1. The slope of the linear regression of length and width decreased with increasing angle θ (12° = 1.25, 20° = 0.96, 40° = 0.59, and 60° = 0.52), indicating that bridge width increased at a faster rate for smaller angles.

Geometric Model of the Cost–Benefit Relationship. The fact that bridge movement stops before creating the maximum shortcut possible suggests the existence of a trade-off between the benefit provided by a shorter path length and the cost of sequestering workers in the living structure, rendering them unable to participate in the capture and retrieval of prey items.

Fig. 2. Bridge movement as a function of (*A*) experimental time, (*B*) angle θ, and (*C*) traffic intensity. Each dot represents the position of a single bridge for each minute of each experiment. These values are partial residuals computed from a GLM as described in the text: they represent the relationship between a given independent variable and the bridge position, given that the other two independent variables are also in the model. The solid line and its semitransparent envelope represent the best fit of the GLM for each independent variable and its 95% confidence interval.

Fig. 3. The relationship between costs and benefits for bridges at certain θ angles. Dashed lines are theoretical cost–benefit relationships as computed from our model (and depicted in Fig. S2). Each circle shows the distance saved and surface area of an individual bridge at any point in time. Solid lines are LOESS curves built from the experimental data for each angle θ that help visualize the general trends in the data.

We adopted a geometric approach to quantify the relationship between the aforementioned cost and benefit. The benefit was computed as the amount of travel distance saved B as a function of the distance d moved by the bridge. It is defined as the difference between the path length in the absence of a bridge and the path length in the presence of a bridge and is given by

$$B = \frac{2d}{\cos(\theta/2)}(1 - \sin(\theta/2)). \quad [1]$$

The cost C of sequestering workers can be approximated by the surface area of the bridge, as a proxy of the number of sequestered workers. Given an angle θ, the distance d moved by the bridge, and the width of the bridge, the cost is

$$C = 4d^2 w_\theta \tan^2(\theta/2)(1 - w_\theta \tan(\theta/2)), \quad [2]$$

where w_θ is the ratio between the width and the length of a bridge, as a function of the angle θ. The value of w_θ corresponds to the slope of the linear regression in Fig. S1.

The theoretical costs (in geometric terms) increase nonlinearly (as d^2) with bridge movement (Fig. S2A), increasing much more rapidly for higher angles θ. The theoretical benefits, in terms of travel distance saved by installing a bridge as a shortcut, increase linearly (as d) for all angles (Fig. S2B). The benefits increase at a faster rate for smaller angles because the longer bridges required at larger angles offset some of the benefits in total path length reduction. To verify our theoretical cost–benefit relationship, we compared the theoretical curves to the cost–benefit relationship of actual bridges (Fig. 3).

Our geometric quantification of the cost–benefit relationship in army ant bridges shows that the cost of sequestering workers increases faster than the benefit gained from reducing travel distance. To demonstrate that this cost–benefit relationship is

responsible for bridge movement ceasing before travel distance along the trail is minimized, we extended the geometric model to the following cost–benefit optimization model of bridge construction. This model assumes that the colony tends to maximize traffic density on their trails as a means to improve traffic output (e.g., increased prey retrieval, shorter migration time). This is compatible with previous studies showing that several army ant behaviors are directly involved in improving traffic conditions on the trails (16, 18).

Cost–Benefit Optimization Model of Bridge Dynamics. We model N ants, which are situated on a section of foraging trail of length L_T in addition to the experimental apparatus, which has an inner edge length L_A and is set at an angle θ (Fig. 1). Owing to the design of the apparatus, L_A is a function of the angle. If L_0 is the length of the arm between the two hinge points and w_A is the width of the apparatus arm (Fig. 1A), then the length L_1 of the apparatus arm that overlaps with the other arm is given by $L_1 = w_A/(2\tan(\theta/2))$. The length of the inner edge of one arm is therefore $L_E = L_0 - L_1$, and the overall inner length of the apparatus is twice this length, so that $L_A = 2L_0 - w_A/\tan(\theta/2)$. In the absence of a bridge, the total (one-way) travel distance for each ant is $L_T + L_A$, and the density of ants on the foraging trail is $N/(L_T + L_A)$.

If a bridge is built across the apparatus at some distance d from the apparatus junction, then the length of the bridge will be $b = 2d\tan(\theta/2)$ (Fig. 1). Consequently, this will decrease the total foraging trail length to $f = L_T + b + (1 - d/D_{max})L_A$, where D_{max} is the maximum distance that the bridge can travel given the constraints of the apparatus and is given by $D_{max} = L_A\cos(\theta/2)/2$. The bridge incurs a cost to the colony by decreasing the number of available foraging ants by an amount $n_b = w_\theta b^2(1 - w_\theta\tan(\theta/2))/(l_n w_n)$, where w_θ is the ratio between the width and the length of the bridge, and l_n and w_n are the length and width, respectively, of an average ant when occupying a position within the bridge structure. The density of ants on the foraging trail in the presence of a bridge becomes

$$\rho = (N - n_b)/f. \quad [3]$$

If we assume that the speed of an ant foraging on the trail is approximately constant within the range of ant densities observed, then maximizing the traffic rate of the colony is equivalent to maximizing the density of ants on the foraging trail (within this range of densities). By differentiating Eq. 3 with respect to bridge distance d, setting the result to 0, and solving for d, we can compute the bridge distance that maximizes colony foraging rate, subject to a maximum value of D_{max}:

$$d^* = \frac{\cos(\theta/2)}{2(1 - \sin(\theta/2))}\left[(L_T + L_A) - \sqrt{(L_T + L_A)^2 - \frac{N l_n w_n[1 - \sin(\theta/2)]^2}{w_\theta[1 - w_\theta\tan(\theta/2)]\sin(\theta/2)^2}}\right]. \quad [4]$$

Finally, we add a free parameter A to adjust the space occupied by an ant on the trail (or equivalently, the length or width of the ants in the bridge). This parameter can be interpreted as differences (i.e., morphological or functional) between the ants that typically contribute to bridge building and those that tend to participate in foraging, which are difficult to measure quantitatively in this experiment (*Discussion*).

$$d^* = \frac{\cos(\theta/2)}{2(1-\sin(\theta/2))}\left[(L_T+L_A) - \sqrt{(L_T+L_A)^2 - \frac{ANl_n w_n[1-\sin(\theta/2)]^2}{w_\theta[1-w_\theta\tan(\theta/2)]\sin(\theta/2)^2}}\right].$$

$$[5]$$

By fitting the resulting Eq. **5** to the data, we find a very good fit to the data for $A = 17.02$ (95% confidence interval [15.22,18.82]) (Fig. 4*B*). The optimal bridge migration distance decreases as the apparatus angle increases and increases as the overall density of ants on the foraging trail increases (Fig. 4*A*), which agrees with the behavior of the ants in our experiment (Fig. 2 *B* and *C*).

Discussion

Our study demonstrates the capacity of army ants to dynamically adjust the properties of their living structures to changing conditions. Although each ant possesses only local information, and does not know the global position or dimensions of the bridge, the structures move, lengthen, and widen in response to traffic levels and environmental geometry. We found that the movement of bridges did not continue to the furthest possible extent over our apparatus, which would have created the shortest path by directly connecting both segments of the main trail. For larger angles, bridge migration ceased sooner, because ants traded off the diminishing returns of shortening the trail to avoid the cost of locking up an increasing number of workers in the structure. Rather than minimizing the length of their trail network with no regard for the cost incurred by larger bridges, army ant colonies modify their bridges according to a cost–benefit trade-off for the given environment.

Our density-based model of bridge dynamics demonstrates that such a trade-off is likely to result from attempts to maximize the foraging rate. The model shows that, given the properties of the traffic along the trail, there exists a bridge position where the cost of sequestering workers in the bridge structure outweighs the benefit gained from reduced travel distance. Our data do not allow us to claim that the positions at which bridges stopped in our experiments are indeed the optimal positions predicted by this idealized model. This is because our model assumes that ants attempt to maximize traffic density. In reality, traffic theory indicates that they should increase traffic only up to a critical density that maximizes traffic flow, and beyond which interactions between individuals would cause slowdowns. Measuring this critical density would be very difficult in field conditions, where it is nearly impossible to control—and in particular to increase—the traffic flow. It is likely that the ants have a number of regulatory mechanisms that naturally keep traffic below the critical density (16, 20–22). Nevertheless, assuming that ant traffic never exceeds this critical density, our model makes two clear predictions: the distance moved by the bridge should decrease with the increasing angle of the apparatus, and for all angles, bridges should move further as traffic increases. Our experimental results match these two predictions very well, supporting the hypothesis that the position and size of army ant bridges result from a cost–benefit trade-off.

There may be several factors contributing to the value of the free parameter A in our cost–benefit model. Although the model treated each individual equally (by simply counting the number of ants on the trail and the number of ants in the bridge), there are substantial differences between bridge-building ants and non-bridge-building ants. The submajor caste of *E. hamatum* rarely participates in bridge building but contributes highly disproportionally to foraging, in terms of the likelihood of carrying a prey item, the size of the prey item carried, and running speed (9, 15). Furthermore, our preliminary observations suggest the

ants contributing to bridge building tend to be younger individuals that are visibly more timid in the raid traffic and lack foraging experience. Together, these factors reduce the cost of ants joining the bridge and account for at least some of the value of the free parameter A.
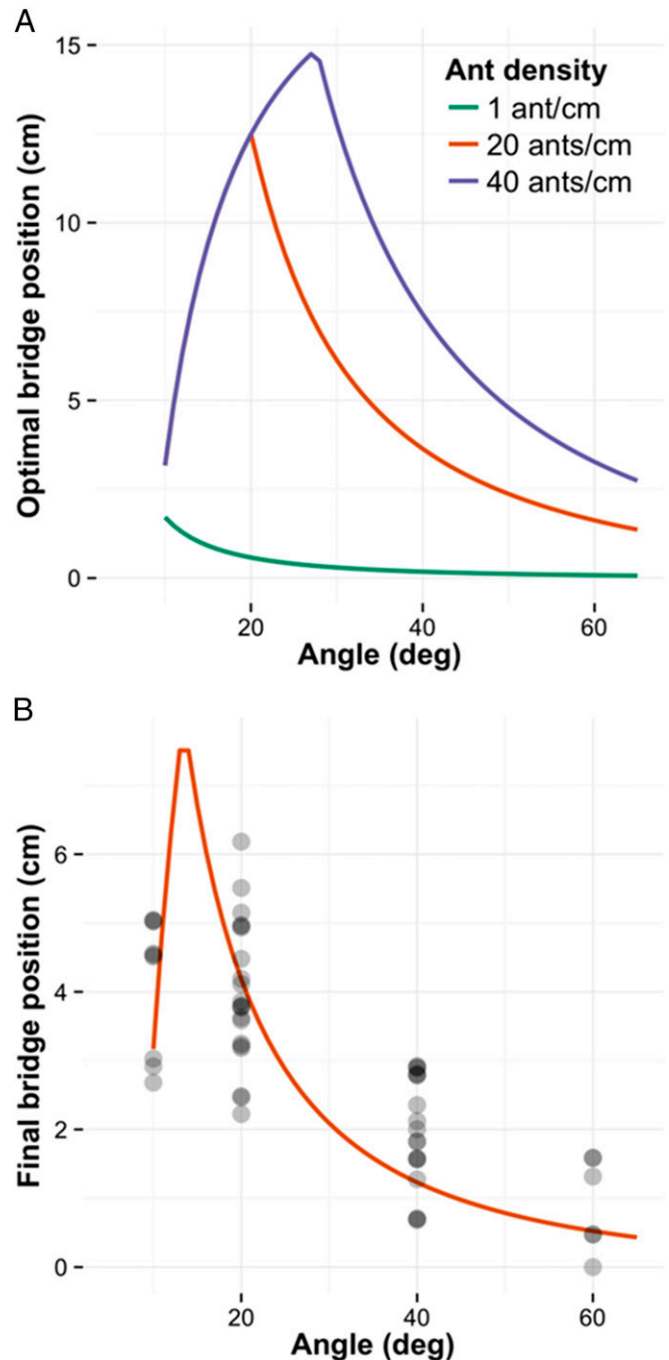
Fig. 4. (*A*) The optimal bridge position *d* as a function of apparatus angle θ for different ant densities. Other model parameters as described in *Materials and Methods*. (*B*) Comparison between the predicted final position of the bridge (solid line) and the experimental observations (dots) as a function of the angle θ. The value of parameter *A* (the only free parameter of the model) was chosen to best fit the experimental observations. Note that changing its value would only affect the numerical outcome of the model, not the general shape of the relationship. The experimental observations reported in this figure are partial residuals computed from a GLM as described in the text.

The most likely mechanism by which army ant bridges adjust to their environment is through individuals modifying their likelihood to join or leave a structure based on interaction rates. Ants in the structure are responsive to changes in traffic, increasing their likelihood to leave when traffic levels drop below a critical threshold (19). When a bridge forms at an angle between two surfaces, as in our experimental apparatus, traffic conditions vary along the bridge's cross-section. Ants seeking the shortest path tend to create a higher traffic flow along the inner side of the bridge (closer to the main trail axis), and lower traffic flows along the outer side, where the path is longer. Passing workers thus experience higher interaction rates on the inner side and are more likely to attach to the structure here (19). Conversely, ants on the outer edge are contacted less, and are more likely to leave the structure. These localized processes of construction and deconstruction in response to a cross-sectional traffic gradient are likely to result in a dynamic structure that steadily moves toward the main trail axis, shortening the overall path of travel.

Our study was necessarily focused on the local dynamics of single bridges occurring on sections of the greater foraging network. To understand the overall colony-level costs and benefits, it would be necessary to quantify both the number of ants per bridge and the number of bridges in an entire foraging network. Powell and Franks (18), using the closely related *Eciton burchellii*, calculated that the cost–benefit trade-off of building plugs vs. contributing to prey retrieval should yield a net gain for the colony under a range of realistic scenarios (pothole plugs can be thought of as ant bridges with one to a few individuals). Nevertheless, under their worst-case estimate, with the loss of one prey item for every plug ant and a total of 20% of total foragers dedicated to plugs, daily intake of prey could drop by as much as 79%. Hence, accurate measures of the proportion of available foragers locked up in bridge structures will be critical for a global, colony-level representation of the cost of bridges to foraging colonies. Similarly, it is clear that the presence of bridges should yield energetic gains at the colony level from increased prey delivery rates, both through minimizing the path length from raid site to bivouac and from the cumulative increase in speed gained by smoothing rough sections of terrain. However, for global, colony-level calculations of the cost–benefit trade-offs of bridge building, it would be necessary to accurately measure the path length of the trail established by the ants, the number and size of bridges along the trail, and the total path shortening that the bridges provide. This is beyond the scope of the present study (although see *Supporting Information* for an estimate of colony-wide bridge investment) but will be critical for extending our results here on the localized net gain of bridges to the collective benefit at the whole-colony level.

Future work should also examine how *E. burchellii* responds to the cost–benefit trade-off induced by bridge-building. The foraging behavior of *E. burchellii* differs from that of *E. hamatum* in that the former species most often uses a single branching trail that is focused in one direction only, and connected to the bivouac by a common, "trunk" trail (23). Colony size is also typically much larger in *E. burchellii* than in *E. hamatum,* further contributing to higher traffic flow and prey delivery rates in *E. burchellii* at the level of individual trails (11, 12, 19, 24), but not necessarily greater colony-level biomass intake when *E. hamatum*'s multiple trail foraging system is considered (11). If all workers are using the same trunk trail [as opposed to the two or three separate radiating trails of *E. hamatum* (11)], then colony-level bridging costs may be lower as less terrain may need to be bridged, and benefits may be higher because the entire prey-laden workforce will benefit from all bridges on the common trail. However, *E. burchellii* bridges may also need to be wider given the higher average traffic flow, and more obstacles may need to be bridged to accommodate the generally wider trail. If *E. burchellii* has also evolved to make a cost–benefit trade-off in bridge building, we might therefore expect

informative differences between species in the distance and rate of bridge migration, further improving our understanding of the cost–benefit trade-offs inherent to collectively solve these problems. Another important area for future work is the role of structural forces in regulating the growth, movement, and stability of bridges. Our experiments demonstrate that a consistent length/width ratio is maintained as bridges increase in size, which suggests that the probability to join or leave a bridge may be influenced by structural forces as well as traffic dynamics. For ants already in a bridge, the decision to remain or leave may be influenced by increasing or decreasing tension forces on the legs, whereas for ants crossing a bridge, the decision to join may be influenced by the relative stability of the structure.

In a previous study, the bridge structure was shown to emerge in a decentralized manner, from simple interactions influenced by local information on the traffic intensity and the presence of gaps along the trail (19). The present study provides quantitative insights into the functional importance of the self-assembly process for the foraging efficiency of the colony. We show that self-assembling bridges can adjust to features of the landscape that are unpredictable from the organism's perspective, and appear to balance construction costs with foraging benefits. As such, these structures demonstrate the adaptive value of biological self-assembly even in complex, multicellular organisms (6, 25, 26) and may inform the design of artificial self-assemblages, at the interface of materials science, robotics and architecture (27–34).

Materials and Methods

The focal species was *E. hamatum* (Fabricius), and all data were collected from Barro Colorado Island, Panama. All experiments were conducted during daylight hours between February and August 2014. *E. hamatum* workers spend the day foraging, establishing a primary trail and several secondary trails by late morning, with bidirectional traffic connecting the bivouac to the raid site. We conducted our experiments along the primary raiding trail, finding a suitable location to set up our apparatus and filming equipment before inserting our experimental apparatus into the existing trail. To accomplish this, we located sticks and small branches along the trail on which ants had been running, which were thus coated in trail pheromone. Removing these, we inserted our apparatus into the interrupted trail, using the pheromone-coated sticks to construct makeshift ramps on either side of our apparatus, which was mounted on tripods ∼40 cm above the forest floor. To encourage the rerouting of traffic, we placed additional leaves from the trail, along with ants, onto the side platforms. After a period of 10–30 min, the trail had fully reestablished over our apparatus.

The apparatus consisted of four 3D-printed platforms attached by adjustable hinges into a V shape (Fig. 1), attached to two larger platforms mounted on tripods. Before each experiment, we set the angle of separation between the platforms (θ) to a randomly designated treatment angle of either 12° ($n = 5$), 20° ($n = 8$), 40° ($n = 7$), or 60° ($n = 3$). In every trial, ants initiated bridges at the intersection point between the platforms, and over time these bridges moved out over the gap in the apparatus toward the main trail. Owing to the hinge mechanism, the absolute distance from the main trail to the junction of the platforms (D_{max}) increased with increasing θ (Fig. 1). However, because bridges were only initiated at this junction, we compared different angles of θ by measuring the absolute distance from the junction to the inner edge (with respect to the main trail) of the bridge (d in Fig. 1).

Data Collection and Analysis. Video data were collected at 60 frames per second using a Panasonic Lumix DMC-GH3 digital camera. The camera was installed on a tripod to film from 30 cm above the deviating platforms. Each experiment was filmed for around 45 min, beginning when a strong trail was visible on the apparatus. All analysis was performed on 30 min of this data, starting when ants first initiated a bridge between the two deviating platforms.

We measured how the collective action of the ants modified various bridge properties over time, performing our analyses for each minute of the experiments by selecting the final frame from each minute of the video data. Fig. 1A shows graphically the properties of the bridge we measured. Using the ImageJ software (v1.46r, imagej.nih.gov/ij/), we measured where the inner and outer edges of the bridge intersected a line drawn through the center of the space between the hinged platforms (D_{max} in Fig. 1A). We measured the absolute distance that the inner edge of the bridge moved from the junction of the two platforms (d). Bridge width (w) was determined by

calculating the distance between the inner and outer edges of the bridge. Knowing the angle θ, and the length of d, we used basic trigonometry to determine the length of the inner edge of the bridge (b in Fig. 1A) and the trapezoidal surface area of the bridge for each minute of the experiments.

In addition to changes over time, we were interested in how the ants modified the structure of their bridges under different traffic conditions. We measured traffic along the trail by counting how many ants passed a point one-quarter of the way along one of the platforms of the apparatus, in both directions, over each minute of the experiments.

The change in position of the bridge over time was analyzed using a GLM with three main effects: time, angle θ, and traffic intensity as measured above. The time variable was transformed using a hyperbolic function to account for the slowing down of the bridge movements with time. The parameters of the hyperbolic function (i.e., the growth speed and the asymptote) were estimated by fitting a hyperbolic curve to the data of each experiment separately and taking the median value for each parameter. Within-group correlation was modeled as an autoregressive process of order 1. Using the Akaike information criterion, a comparison of the different combinations of the three main effects and their interactions showed that the best model included time, angle θ and traffic intensity, and the interactions between time and angle θ, and between time and traffic intensity. Model diagnostics were performed using graphical procedures (Q-Q plot and standardized residuals vs. fitted values).

Model Parameter Estimates. The center of each hinge point is 0.98 cm from the end of each platform. The length of the apparatus arm between the two hinges is thus $L_0 = 24 - 2*0.98$ cm = 22.04 cm, and the width of the apparatus arm is $w_A = 3.3$ cm. Therefore, $L_A = 13.95, 25.36, 35.01$, and 35.36 cm, for apparatus angles θ = 12°, 20°, 40°, or 60°, respectively, and $D_{max} = 6.93, 12.49, 16.45$, and 16.61 cm. From video observations, we estimate the dimensions of an ant to be $l_n = 0.691$ cm and $w_n = 0.107$ cm and the density of ants moving across the apparatus to average 0.42 ants per centimeter, which is compatible with the literature (35). We estimate the ratio between bridge width and length to be ω = $4.799θ^{-0.5014}$. We set L_T, the length of the foraging trail not part of the experimental apparatus, to 100 cm (see bridge spacing estimates in *Supporting Information*), with the total number of ants N determined by ($L_T + L_A$) and the overall density of ants.

1. Camazine S, et al. (2001) *Self-Organization in Biological Systems* (Princeton Univ Press, Princeton).
2. Berdahl A, Torney CJ, Ioannou CC, Faria JJ, Couzin ID (2013) Emergent sensing of complex environments by mobile animal groups. *Science* 339(6119):574–576.
3. Helbing D (2001) Traffic and related self-driven many-particle systems. *Rev Mod Phys* 73.4:1067.
4. Couzin ID (2009) Collective cognition in animal groups. *Trends Cogn Sci* 13(1):36–43.
5. Savill NJ, Hogeweg P (1997) Modelling morphogenesis: From single cells to crawling slugs. *J Theor Biol* 184(3):229–235.
6. Anderson C, Theraulaz G, Deneubourg J-L (2002) Self-assemblages in insect societies. *Insectes Soc* 49(2):99–110.
7. Mlot NJ, Tovey CA, Hu DL (2011) Fire ants self-assemble into waterproof rafts to survive floods. *Proc Natl Acad Sci USA* 108(19):7669–7673.
8. Lioni A, Sauwens C, Theraulaz G, Deneubourg J-L (2001) Chain formation in *Oecophylla longinoda*. *J Insect Behav* 14(5):679–696.
9. Powell S, Franks NR (2006) Ecology and the evolution of worker morphological diversity: A comparative analysis with Eciton army ants. *Funct Ecol* 20(6):1105–1114.
10. Rettenmeyer CW, Chadab Crepet R, Naumann MG, Morales L (1983) Comparative foraging by neotropical army ants. Social Insects in the Tropics, ed Jaisson P (Université Paris-Nord, Paris), Vol 2, pp 59–73.
11. Powell S (2011) How much do army ants eat? on the prey intake of a neotropical top-predator. *Insectes Soc* 58(3):317–324.
12. Franks NR (1982) Ecology and population regulation in the army ant *Eciton burchelli*. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*, eds Leigh EG, Windsor DM, Rand AS (Oxford Univ Press, Oxford).
13. Franks NR, Bossert WH (1983) The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. *Tropical Rain Forest Ecology and Management*, eds Sutton EL, Whitmore TC, Chadwick AC (Blackwell, Oxford), pp 151–163.
14. Kaspari M, Powell S, Lattke J, O'Donnell S (2011) Predation and patchiness in the tropical litter: Do swarm-raiding army ants skim the cream or drain the bottle? *J Anim Ecol* 80(4):818–823.
15. Powell S, Franks NR (2005) Caste evolution and ecology: A special worker for novel prey. *Proc R Soc B Biol Sci* 272(1577):2173–80.
16. Couzin ID, Franks NR (2003) Self-organized lane formation and optimized traffic flow in army ants. *Proc Biol Sci* 270(1511):139–146.
17. Hurlbert AH, Ballantyne IVF, Powell S (2008) Shaking a leg and hot to trot: The effects of body size and temperature on running speed in ants. *Ecol Entomol* 33(1):144–154.
18. Powell S, Franks N (2007) How a few help all: Living pothole plugs speed prey delivery in the army ant *Eciton burchellii*. *Anim Behav* 73(6):1067–1076.
19. Garnier S, et al. (2013) Stability and responsiveness in a self-organized living architecture. *PLOS Comput Biol* 9(3):e1002984.
20. Dussutour A, Fourcassié V, Helbing D, Deneubourg J-L (2004) Optimal traffic organization in ants under crowded conditions. *Nature* 428(6978):70–73.
21. John A, Schadschneider A, Chowdhury D, Nishinari K (2009) Trafficlike collective movement of ants on trails: absence of a jammed phase. *Phys Rev Lett* 102(10):108001.
22. Hönicke C, Bliss P, Moritz RF (2015) Effect of density on traffic and velocity on trunk trails of *Formica pratensis*. *Naturwissenschaften* 102(3–4):17.
23. Schneirla TC (1971) *Army Ants: A Study in Social Organization*, ed Topoff HR (Freeman, San Francisco).
24. Franks N (1985) Reproduction, foraging efficiency and worker polymorphism in army ants. *Experimental Behavioural Ecology and Sociobiology*, eds Hölldobler B, Lindauer M (Sinauer Associates, Sunderland, MA), pp 91–107.
25. Kushner DJ (1969) Self-assembly of biological structures. *Bacteriol Rev* 33(2):302–345.
26. Whitesides GM, Grzybowski B (2002) Self-assembly at all scales. *Science* 295(5564):2418–2421.
27. Soleymani T, Trianni V, Bonani M, Mondada F (2014) An autonomous construction system with deformable pockets. IRIDIA Technical Report Series (January) 2014-002 (IRIDIA, Université Libre de Bruxelles, Brussels).
28. Werfel J, Ingber D, Nagpal R (2007) Collective construction of environmentally-adaptive structures. *Proceedings of the 2007 IEEE/RSJ International Conference on Intelligent Robots and Systems*(IEEE, New York), pp 2345–2352.
29. Stewart RL (2006) A distributed feedback mechanism to regulate wall construction by a robotic swarm. *Adapt Behav* 14(1):21–51.
30. Napp N, Nagpal R (2014) Distributed amorphous ramp construction in unstructured environments. *Robotica* 32(02):279–290.
31. Yoshida E, Murata S, Tomita K, Kurokawa H, Kokaji S (1998) Experiments of self-repairing modular machine. *Distributed Autonomous Robotic Systems* 3:119–128.
32. Hosokawa K, et al. (1998) Self-organizing collective robots with morphogenesis in a vertical plane. Proceedings of the International Conference on Robotics and Automation (IEEE, New York), pp 2858–2863.
33. Gro R, Bonani M, Mondada F, Dorigo M (2006) Autonomous self-assembly in swarm-bots. *IEEE Trans Robot* 22(6):1115–1130.
34. Trianni V, Nolfi S, Dorigo M (2006) Cooperative hole avoidance in a swarm-bot. *Robot Auton Syst* 54(2):97–103.
35. Bartholomew GA, Lighton JRB, Feener DHJ (1988) Energetics of trail running, load carriage, and emigration in the column-raiding army ant *Eciton hamatum*. *Physiol Zool* 61(1):57–68.

Supporting Information

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Estimate of Colony-Wide Bridge Investment

We make some estimates by combining our field observations with those in the literature. A typical *E. hamatum* trail network can extend 200 m from the bivouac (23). Along these trails, bridges are patchily distributed, clustering in areas of particularly rough terrain (18, 23). Based on our observations, we estimate that naturally occurring bridges contain on average 10 individuals. The distribution of bridges along a trail can vary widely, depending on terrain and traffic levels. On the low end, we estimate one bridge per meter of trail. However, in our preliminary observations, it is not uncommon to see lengths of trail with upwards of 10 bridges per meter. Given these figures, as a cursory approximation, we can thus estimate a range for the total number of ants sequestered in bridges at somewhere between 2,000 and 20,000 ants. For a typical colony of 100,000 ants (23), bridges then occupy somewhere between 2–20% of the total population. If we further consider that a large proportion of the colony (perhaps up to half) remain at the bivouac throughout the day and take no part in foraging, these structures certainly segregate a substantial portion of the available foragers.
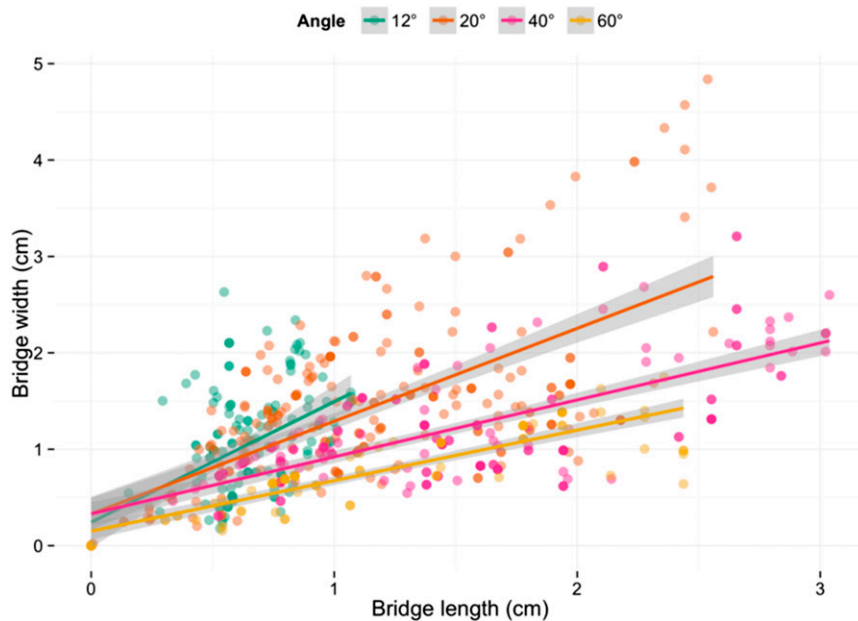

Fig. S1. Bridge width as a function of bridge length for each angle θ. Each circle shows the width and length of a single bridge at any point in time. Solid lines are linear regressions for each angle θ. Shaded areas are the 95% confidence region.
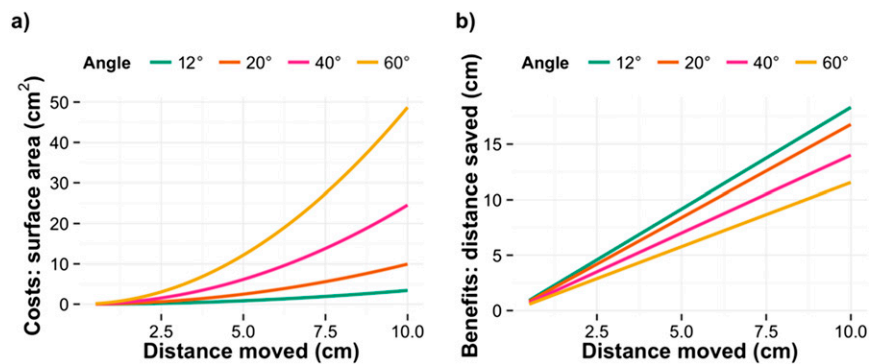

Fig. S2. Theoretical costs (*A*) and benefits (*B*) as a function of distance moved by the bridge toward the main trail axis for different θ angles. In *A*, the cost function takes into account the widening of bridges observed as they move toward the main trail axis (Fig. S1).

Movie S1. Time lapse showing the position of a bridge over time with the apparatus set to an angle θ of 20°. Each frame advances 5 min into the experiment.

Movie S1