



# A simple mechanism for collective decision-making in the absence of payoff information

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Animals are often faced with time-critical decisions without prior information about their actions' outcomes. In such scenarios, individuals budget their investment into the task to cut their losses in case of an adverse outcome. In animal groups, this may be challenging because group members can only access local information, and consensus can only be achieved through distributed interactions among individuals. Here, we combined experimental analyses with theoretical modeling to investigate how groups modulate their investment into tasks in uncertain conditions. Workers of the arboreal weaver ant *Oecophylla smaragdina* form three-dimensional chains using their own bodies to bridge vertical gaps between existing trails and new areas to explore. The cost of a chain increases with its length because ants participating in the structure are prevented from performing other tasks. The payoffs of chain formation, however, remain unknown to the ants until the chain is complete and they can explore the new area. We demonstrate that weaver ants cap their investment into chains, and do not form complete chains when the gap is taller than 90 mm. We show that individual ants budget the time they spend in chains depending on their distance to the ground, and propose a distance-based model of chain formation that explains the emergence of this tradeoff without the need to invoke complex cognition. Our study provides insights into the proximate mechanisms that lead individuals to engage (or not) in collective actions and furthers our knowledge of how decentralized groups make adaptive decisions in uncertain conditions.

self-assembly | collective behavior | collective decision-making | uncertainty | swarm intelligence

Making adaptive decisions in the face of the unknown is a difficult task. From capital investment in the stock market to time spent looking for food patches, decision-making almost always involves some degree of uncertainty. Indeed, any choice made without complete knowledge of the possible outcomes may be deemed as uncertain (1–3). Traditional economic and ecological theories predict that individuals make choices that are rational, that is, choices that maximize the payoffs and/or minimize the costs of an action (4, 5). Maximizing the outcomes of a decision, however, implies that individuals possess some knowledge about the quality of available options, or their probability distribution. Individuals may then choose to perform an action only when the predicted probability of success is higher than the probability of failure, or if the quality of the payoffs is worth paying the costs associated with the task.

In real-life contexts, however, individuals are routinely faced with time-critical decisions where both the probability and quality of the possible outcomes are unknown. In such scenarios, individuals can limit their investment (or risk-taking) in order to obtain economic efficiency (6–9). Decision-making under uncertainty could be an even more difficult challenge for animal groups because information about a task's quality is scattered among many individuals and can only be integrated through dispersed interactions between group members (10–13). This challenge is routinely faced by social insect colonies, where sophisticated group-level coordination emerges solely from locally mediated interactions among insects without centralized control (10, 14). Social insects exhibit impressive performance in complex collective tasks such as task allocation (15), cooperative transport (16), and nest construction (17, 18). In particular, social insects represent optimal model systems for studying how self-organized animal groups make optimal decisions under uncertainty. Collective decision-making has been widely studied in social insects, especially in the contexts of colony emigrations (19–21) and foraging (22, 23). These studies have highlighted how optimal decisions can emerge from simple behavioral rules and feedback mechanisms among group members. In most of these studies, however, the insects could access information about the quality of one or more of the available options and modulate their behavior accordingly. It remains unclear how

## Significance

Weaver ants link their bodies together to form chains over gaps and reach unexplored territories. The decision to join or leave a chain is made by individuals, but has cost implications at the colony level, as longer chains sequester more ants, which cannot perform other tasks. Furthermore, the payoff of a chain remains unknown until it is complete and the new area is explored. We demonstrate that individual ants modulate the time they spend in the chain based on their proximity to the ground and that this local behavioral rule caps the colony-level investment into chains. Our theoretical model offers insights into collective decision-making in the absence of payoff information, and could prove useful in the engineering of multiagent systems.

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social insects deal with situations in which the payoffs of their collective decisions are unknown.

Weaver ants of the genus *Oecophylla* routinely modify the surrounding environment by forming complex three-dimensional structures with their own joined bodies (24–27). This behavior, termed “self-assembly,” is rare in multicellular organisms and mostly confined to invertebrates (28–31). Examples of self-assembly behavior include the rafts built by fire ants during inundations (32), swarm clusters formed by honeybees during colony fission (33), and the bridges and scaffolds of foraging army ants (34, 35). Weaver ants form “chains” for bridging vertical gaps along the ground and reaching new territories (27, 36). Chains are usually initiated by one or a few ants spontaneously hanging from a supporting structure, and their growth is promoted by the arrival of nestmates at the structure (27). Feedback mechanisms regulate chain formation: The number of ants in the chain acts as positive feedback by increasing the probability that other individuals will join the structure, but also as negative feedback by reducing the number of ants leaving the chain. Ants will thus prefer to join and remain in larger chains, allowing the colony to concentrate their efforts into a single structure rather than several unsuccessful ones (36).

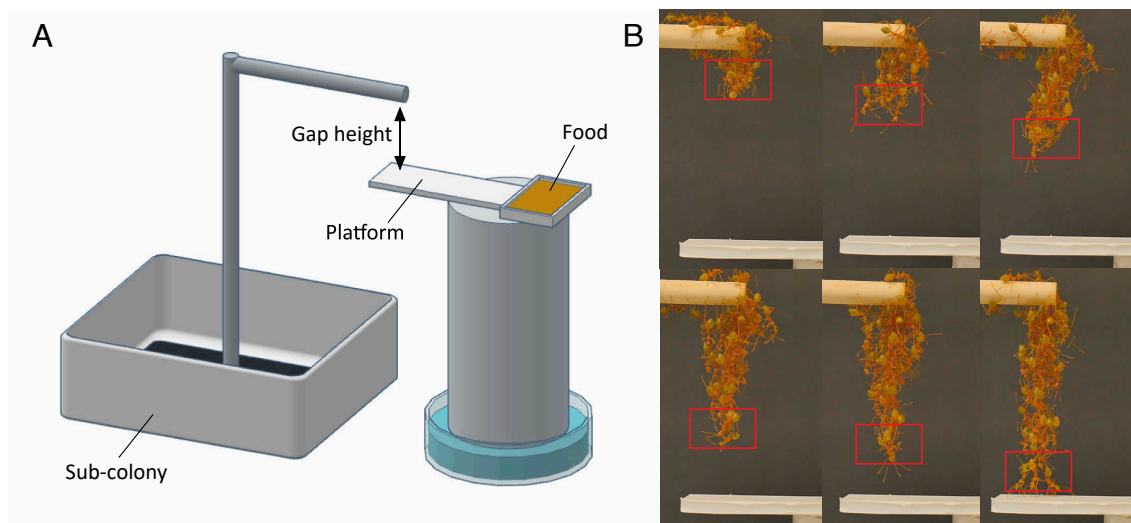
Previous models of hanging chain formation (27, 36) predict that, at large population size, chains should grow indefinitely. Chains do, however, come at a cost to the colony: Ants participating in chain formation cannot contribute to other essential colony tasks such as foraging and territorial defense. The number of ants necessary to build a chain increases with its length, and so does the time needed to reach the target area (27). In addition, the payoff of chain building cannot be discovered until the structure is complete and ants can explore the new area. A chain is beneficial only if the connected area contains profitable resources for the colony. This makes chain formation akin to a gamble: the colony must invest a proportion of its capital (number of ants) to perform a task with unknown outcomes. Since the cost of building a chain increases with the length of the structure, but the payoff remains unknown, we hypothesize that weaver ants may have evolved a behavioral mechanism that prevents them from investing in costly chains. Humans manage the pitfalls of unknown payoffs via “mental budgets,” that is, limits on the amount of resources (e.g., time, money) that an individual is comfortable spending in a given

context (37, 38). This is especially common in gambling (39–41): A poker player may decide to gamble until their total losses amount to a certain sum, or until a given hour, at which point they will stop playing. Similarly, animals at both the individual- and group-level budget the time that they allocate to various activities such as feeding, foraging, traveling, or mating (42). We hypothesize that weaver ants use a similar budgeting strategy to avoid allocating an excessive number of workers to costly chains.

Previous work suggested that ants use visual information when building hanging chains (25, 27, 43). Ants may thus modulate their behavior depending on their visual assessment of the distance from their target. We hypothesize that ants will build chains over a range of vertical gap sizes, but will cease building chains if the gap distance exceeds a certain threshold. We used a combined behavioral and modeling approach to test our hypothesis. In particular, we developed an analytical model in which ants modulate their behavior based on their distance to the ground and parameterized it using data extracted from our experiments (“distance-dependent model”). We also developed an alternative model that did not include active modulation of behavior by the ants (“distance-independent model”). While the distance-dependent model accurately reproduced our experimental results, its performance did not differ from that of the distance-independent model in the parameter space of the experiments. We then used the two models to simulate chain growth over a wide range of traffic conditions and gap heights. Our simulations showed that the two models predict identical chain growth for gap heights lower than 90 mm, but gradually diverged as the distance from the ground was increased. Additional behavioral experiments demonstrated that ants were unable to build complete chains over gap heights of 11 cm as predicted by the distance-dependent model, but still built long chains (>90 mm) when the distance from the visual target was kept constant as the structure grew, validating our understanding of the behavioral rules underlying chain formation.

## Results

Pilot experiments and previous studies (27, 44) demonstrated that ants can successfully build chains over gaps up to 50 mm. Using a simple apparatus (Fig. 1), we analyzed the individual-level behavior of ants joining and leaving chains during their formation



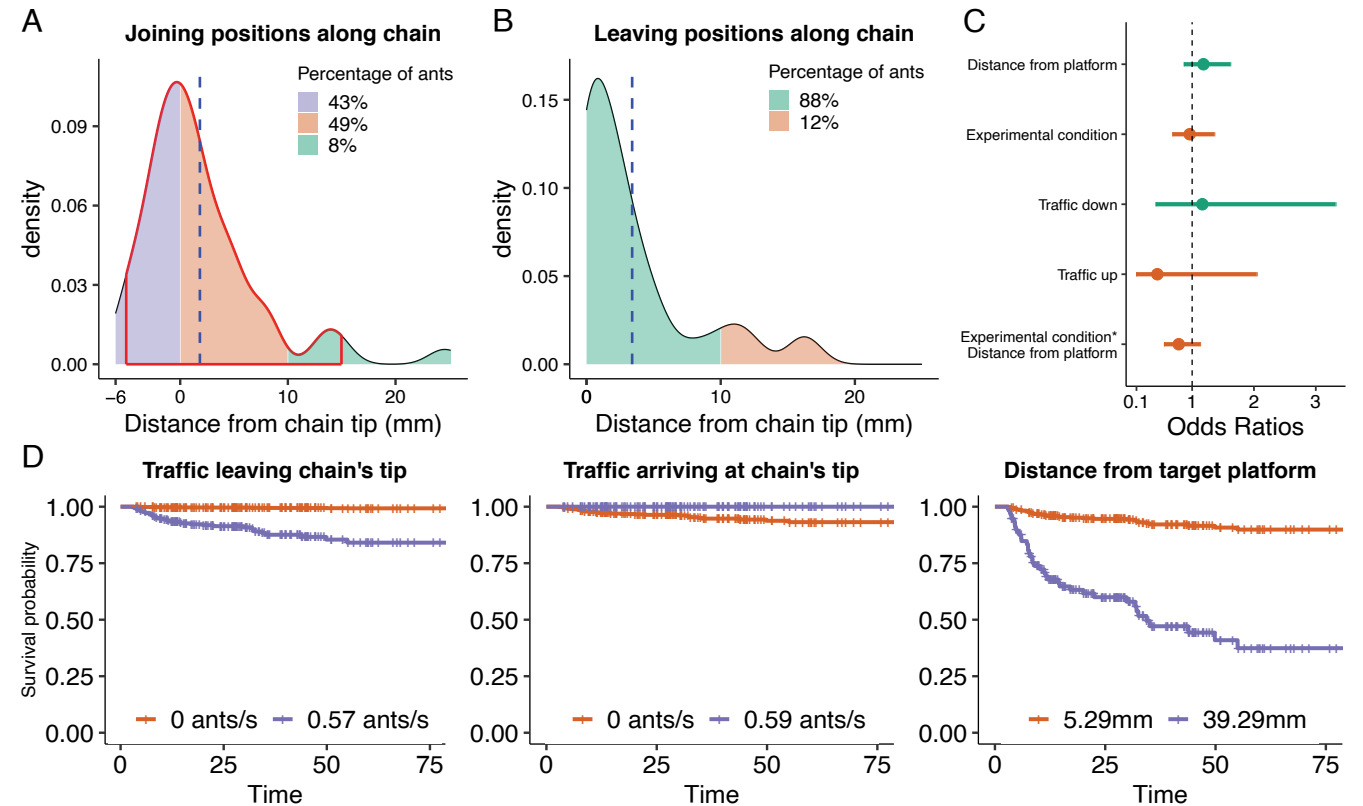
**Fig. 1.** (A) Experimental apparatus. (B) Growth of a chain over a 50-mm gap. The area highlighted in red shows the section of the structure considered for our detailed behavioral analysis (tip of the chain).

over gaps of 25 mm, 35 mm, and 50 mm, to reach a platform with a food source (Movie S1). Ants were thus required to build a complete chain before they could assess and communicate the value of the food source. We conducted a total of 10 trials for each condition, and calculated the average time needed by ants to reach the platform. We then selected 5 replicates for each condition (total = 15) in which ants reached the platform within one SD from the average time for performing the detailed behavioral analyses described below. If more than 5 replicates met this condition, we randomly selected 5 of these replicates for further analyses.

**Joining and Leaving Position of Ants.** We investigated whether ants join the chain at random positions along its length, or preferentially join certain regions. We randomly selected 96 joining individuals across all trials and treatments, manually tracking the location of their mandibles using Fiji (45). We then measured the distance between each ant's mandibles and the lowest point of the chain at the moment of joining. Our analysis revealed that 92% of ants (Fig. 2A and SI Appendix, section 1) chose to join the chain in the bottommost 10 mm of the chain (hereafter called the "tip"). We also observed that 43% of ants protruded over the end of the structure after joining, lengthening the chain, and thereby attaining a negative distance from the chain tip in our analyses (blue area in Fig. 2A). The mean of the distribution is 1.83 mm, indicating a strong preference for joining the chain at or near the tip.

Ants that join the chain at its tip may leave the structure elsewhere along its length, potentially causing structural instabilities or even failure. To investigate the location at which ants leave chains, we tracked  $N = 41$  randomly selected individuals that were observed joining the chain at its tip until they left the chain. Individuals that did not leave the chain were discarded from this analysis. For each leaving event, we measured the distance between the ant's mandibles and the lowest point of the chain at the moment of leaving using Fiji (45). Selected ants remained in the chain from a minimum of 3.3 s to a maximum of 117.8 s (mean = 23.2, s.d. = 26.3). As shown in Fig. 2B, 88% of the leaving events were observed in the bottommost 10 mm of the structure. We also observed that 12% of ants left the chain from regions other than the tip. Ants leaving from the center of the chain may cause structural instabilities, for instance, if the ants remaining in the structure are unable to fully support the weight of the nestmates beneath them. We explored this hypothesis by testing whether leaving events outside of the chain tip cause an instantaneous change in the length of the structure. We averaged measurements of chain length in the 24 frames (1 s) preceding and following each of these leaving events ( $N = 5$ ), and found negligible impact on the length of the structure (average change in chain length = 0.21 mm, s.d. 0.27 mm).

We also documented a behavior that we called "reaching," where ants stretched their body beyond the chain tip and rapidly waved their anterior legs toward the platform. This behavior could be easily distinguished from a joining event,



**Fig. 2.** Experimental results. (A) Probability density function (PDF) of the distance between ants' attachment point and position of chain tip at the moment of joining. Negative values represent instances in which ants joined beyond the tip of the structure, while positive values indicate joining positions along the chain. The area outlined in red indicates 90% of the data, and the dashed line indicates the median of the distribution. (B) Probability density function (PDF) of the distance between ants' leaving position and position of chain tip at the moment of leaving. The blue dashed line indicates the mean of the distribution. (C) Results from the linear mixed-effects model, showing the relative effects of predictors on the probability of observing an ant joining the chain. (D) Survival analysis of the time spent by ants in the structure during chain formation. Survival curves are plotted using predictions extracted from the Cox model for the first (orange) and fifth (purple) quantiles of each predictor.

where ants would become motionless (Movie S2). In line with our hypothesis, a GLMM indicated that ants are more likely to show reaching behavior when the platform is closer ( $N = 327$ ,  $z = -2.626$ ,  $P < 0.01$ ) (SI Appendix, section 2).

Overall, these results suggest that ants may employ the simple behavioral rule of walking down the chain as far as they can before joining. Tactile stimulation provided by nestmates and/or the load of the structure sustained by the ant may then act as inhibitory mechanisms that prevent ants in regions other than the tip to leave the structure, in line with what is observed in other self-assemblages (28, 32, 46).

**Constant Probability of Joining.** Informed by our previous analysis, we focused our behavioral analysis on the ants arriving at the lowest 1 cm of the chain ( $N = 322$ ). We defined a joining event as any event in which the focal ant remained motionless for at least 3 s ( $N = 180$ ). This threshold allowed us to rule out stopping events caused by other factors, such as traffic congestions or difficulty walking on the chain. Ants that joined the chain tip were followed until they either left the chain or until the tip of the chain grew beyond their position, in which case they were censored. Censored ants may have decided to stay in the chain until the end of the replicate or may have left their position after we stopped tracking them. However, censoring is unlikely to impact our results as our behavioral analyses (Fig. 2B) showed that most ants leave the chain at its tip. In addition, ants that leave from other regions of the chain have no impact on the length of the structure. We considered an ant to have left the chain when it resumed walking after a joining event ( $N = 42$ ).

We investigated whether the probability of an ant joining the chain was influenced by the current conditions of the structure using a GLMM with a binomial distribution. The model included the experimental condition (25 mm, 35 mm, and 50 mm), the distance to the platform (mm), and the traffic volume and directionality (ants/s) as fixed effects. The effect of chain length was estimated by including the interaction between the experimental condition and the distance to the platform in the model. All predictors were averaged over the time window starting from the moment in which the focal ant arrived at the tip of the chain until the moment of joining. Trial ID was included as a random effect. We performed residual diagnostics through a simulation-based approach using the *DHARMa* package in R.

Our model shows that the probability of ants to join the chain is not influenced by the traffic conditions (*traffic down*:  $N = 322$ ,  $z = 0.286$ ,  $P = 0.775$ ; *traffic up*:  $N = 322$ ,  $z = -1.05$ ,  $P = 0.293$ ), the length of the chain ( $N = 322$ ,  $z = -1.308$ ,  $P = 0.191$ ), or the distance from the platform ( $N = 322$ ,  $z = 1.051$ ,  $P = 0.293$ ) (Fig. 2C). As expected, the experimental condition did not influence the behavior of the ants ( $N = 322$ ,  $z = -0.226$ ,  $P = 0.821$ ). We also found no significant effect of these predictors on ants' latency to join the chain (SI Appendix, section 3). Overall, our results indicate that ants join chains with a constant probability that is not affected by the current state, position, or utility of the structure.

**Modulated Probability of Leaving.** The time spent by ants as part of the structure was analyzed using a Cox proportional hazard survival model. The model included the distance to the platform (mm), the traffic volume and directionality (ants/s), and the rate of joining of other ants (ants/s) as fixed effects. Chain size was not included in the model because this information is not available to ants once they have attached to the chain tip, and because we found no effect of this predictor on the probability of joining the

chain or on the latency to do so (Discussion). All measurements were averaged over the time period in which the ant was tracked as part of the structure. We stopped measurements when the ant left the chain or when we stopped tracking it because the chain tip grew beyond her position. All ants that joined chains were included in the analysis. The proportional hazard assumptions were checked using the *cox.zph* function in the R *survival* package.

Our model shows that ants spent more time as part of the chain when the platform was closer ( $N = 180$ ,  $z = 3.436$ ,  $P < 0.001$ ). The ants' behavior was also modulated by traffic flow and directionality. Ants remained longer in chains when the traffic flow arriving at the chain tip was high ( $N = 180$ ,  $z = -4.225$ ,  $P < 0.0001$ ). Traffic flow leaving the tip of the chain had the opposite effect, decreasing the amount of time spent by ants as part of the structure ( $N = 180$ ,  $z = 3.772$ ,  $P < 0.001$ ) (Fig. 2D). We found no effect of the joining rate of other individuals on the leaving decision of ants in the structure ( $N = 180$ ,  $z = -0.277$ ,  $P = 0.782$ ).

## Theoretical Model

**Model Description.** Informed by our experimental results, we formulated a theoretical model for the relationship between individual-level behavior and chain formation. The model aims to predict the number of joining and leaving events at the tip of the structure by using parameters extracted from our experimental results. This allows us to validate our hypothesis, and further explore the tradeoffs of chain formation.

We define chain size as the number of ants in the chain at a given time, and calculate it as the cumulative sum of the difference between the number of ants joining the chain at its tip and the number of ants leaving the structure per unit time:

$$\frac{dS}{dt} = N_j - N_l, \quad [1]$$

where  $S$  represents chain size,  $N_j$  represents the number of ants joining the chain at its tip per time unit, and  $N_l$  represents the number of ants that leave the chain at its tip per time unit.

Our experimental results indicate that the probability  $P_j$  that an ant joins the chain at its tip is constant and independent of the current state of the structure (Fig. 2C). We assume that the number of ants joining the chain  $N_j$  per time unit is influenced solely by the traffic rate of ants that can potentially join the chain. The product of these terms therefore describes the total number of ants joining the chain per unit time, or  $N_j$ . We define  $N_j = TP_j$ , where  $T$  is the traffic rate (number of ants that arrive at the chain tip per time unit) and  $P_j$  is the time-independent probability that each ant will join the chain tip. Since traffic flow naturally varies over the time frame of each experiment, our model uses the traffic rate of ants experimentally measured and averaged over 10-s intervals.

Since our survival analyses included not only ants that were observed leaving the chain but also censored ants, the number of ants  $N_l$  that can leave the chain is limited by the current size of the chain  $S$  rather than by the number of ants at the tip of the structure. We denote the proportion of ants leaving the chain per unit time as  $W$ . The product of these terms therefore describes the total number of ants leaving the chain per unit time, or  $N_l$ . We thus define  $N_l = SW$  and reformulate our model as

$$\frac{dS}{dt} = TP_j - SW. \quad [2]$$

Our experimental results indicate that ants adjust their leaving decisions based on their distance from the platform and on the



perceived traffic conditions. Given the relatively small magnitude of the effect of traffic on the ants' behavior (Fig. 2D), and for the sake of model simplicity, we model the leaving decisions of ants as only dependent on the distance  $d$  to the platform, which varies over the duration of the experiment. We model leaving the chain as a memoryless process: Each ant has a constant probability of leaving the chain per unit time, which is independent of the time already spent in the chain. This assumption is validated by the survival curves shown in Fig. 2D as the proportion of ants remaining in the chain per unit time can be reasonably approximated as an exponentially decaying curve (47). The proportion of ants leaving the chain  $W$  per unit time can thus be defined as the decay rate of the exponential curve  $f(t) = e^{-Wt}$ , where  $t = 0$  represents the time at which ants joined a chain. We can obtain the decay rate of the curve by performing a linear regression on the proportion of ants remaining in the structure against time on a log-linear scale (SI Appendix, Fig. S3) (48). To model the change of  $W$  as a function of  $d$ , we calculate the decay rate of survival curves for several values of  $d$  by extracting predictions from our Cox survival model (Fig. 2D). This allows us to represent the relationship between  $W$  and  $d$  (SI Appendix, Fig. S4) as  $W = P_{L0}e^{Rd}$ , where  $P_{L0}$  is the decay rate of ants when the chain is complete ( $d = 0$ ) and  $R$  is a constant that represents the growth or decay of the curve as a function of  $d$ . We lastly need to characterize the relationship between the number of ants in the chain and its length. This allows us to calculate  $d$  from the current size of the chain  $S$ . We use a linear model (*lme4* package in R) to represent this relationship based on our experimental data (SI Appendix, Fig. S5).

Our theoretical model hypothesizes that the leaving decisions of ants are influenced by the distance to the platform. We henceforth refer to our model as the “distance-dependent” model. To validate our understanding of the individual-level behavior of ants, we formulate an alternative model of chain formation which considers the probability of ants leaving the chain to be independent of  $d$ , so that ants have a constant probability of leaving the chain for the duration of the experiment (henceforth the “distance-independent” model). This probability was calculated using the predictions of our Cox survival model for an average chain in the behavioral experiments (SI Appendix, Fig. S4).

In summary, at each time step  $t$ , our model calculates the number of ants joining ( $N_j$ ) and leaving ( $N_l$ ) the chain to find the current size of the chain  $S$ .  $S$  is then used to estimate the distance from the platform  $d$  and its corresponding value of  $W$  from the fit presented in SI Appendix, Fig. S4 for the next time step. This process is then repeated until the chain fully bridges the simulated gap.

The model thus contains three fitting parameters— $P_j$ ,  $P_{L0}$ , and  $R$ —all of which are derived from our experimental data.  $P_j$  is a constant that specifies the time-independent probability that an ant will join the chain, which is estimated from the full range of empirical data on the joining decisions of ants.  $P_{L0}$  and  $R$  are estimated from the survival analysis on the leaving decisions of ants, and describe the relationship between  $W$  and  $d$  as shown in SI Appendix, Fig. S4.

**Model Solution.** In Eq. 2, we have three parameters that vary with time: chain size  $S(t)$ , ants' traffic rate  $T(t)$ , and the proportion of ants leaving the chain per unit time  $W(t)$ . This makes our equation unsolvable analytically. We thus obtain a discrete form of Eq. 2 by using Euler's forward step approximation (49):

$$S_t = S_{t-1} + (P_j T - S_{t-1} W) \Delta t, \quad [3]$$

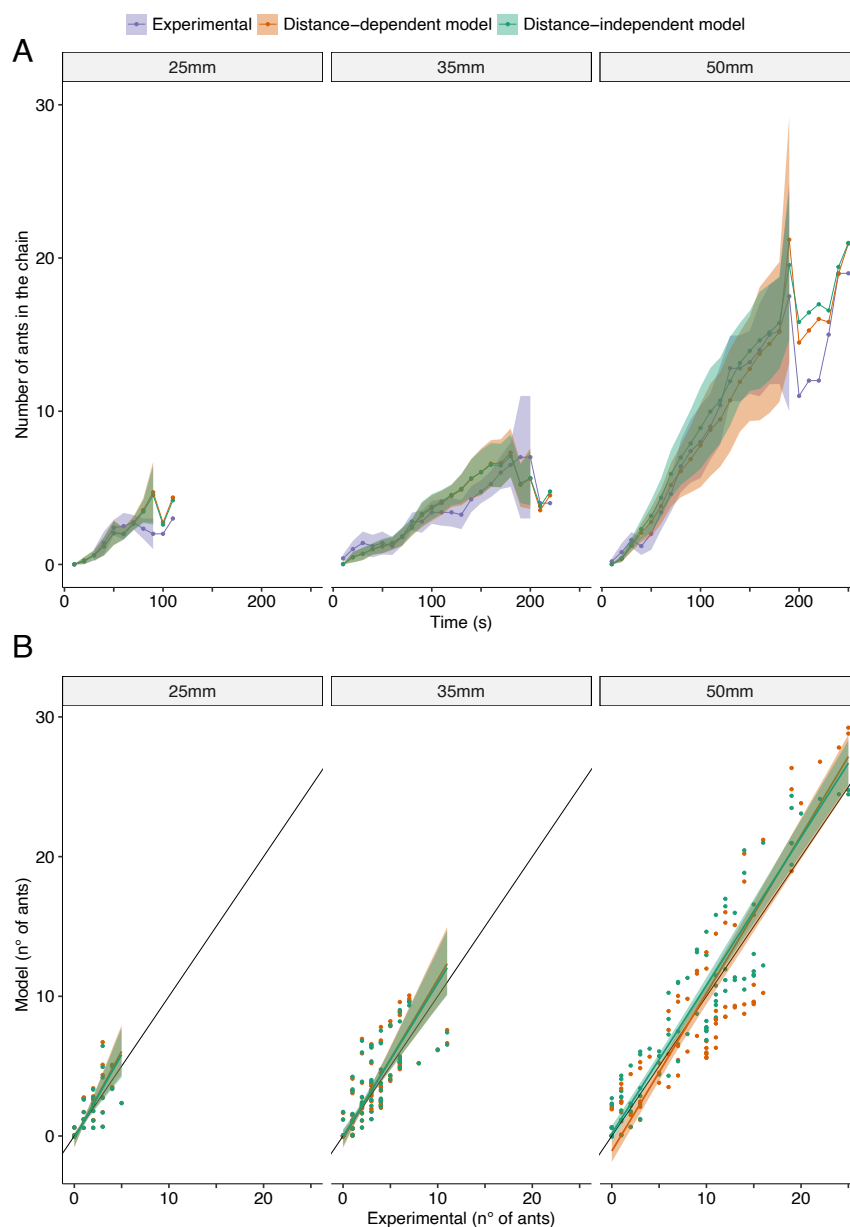
where  $S_{t-1}$  is the chain size at the time step  $t - 1$  and  $\Delta t$  is the difference between any two consecutive time steps  $t$  and  $t + 1$ . This method consists of approximating the solution  $S_t$  for any time step  $t$  by fitting a tangent line to the solution  $S_{t-1}$  at the previous time step. The accuracy of this approximation improves as the distance  $\Delta$  between consecutive time steps decreases.

**Model Simulations.** For each experimental trial ( $N = 15$ ), we ran one simulation with matching duration and traffic rate  $T$  grouped at 10-s intervals. Since the two models do not contain stochastic variables, additional simulations would return exactly the same result. We calculate the proportion of ants leaving per unit time at every time step by estimating the length of the chain at the previous time step. We then extract the estimated number of ants joining or leaving at the tip of the chain at all time steps and compare it to the experimental observations. We find a close agreement between modeling and behavioral data across all experimental conditions (Fig. 3 A and B; SI Appendix, Fig. S6). The plots in Fig. 3 show that both models accurately predict the number of ants participating in chain formation. This suggests that incorporating a local mechanism for ants to adjust their leaving decisions based on the distance to the platform may not be necessary to improve the predictive accuracy of the model within the range of our experimental conditions.

**Extension of Model Simulations.** We thus decided to investigate whether the two models differed in their predictions across a wider range of gap heights and traffic conditions. Indeed, in their natural habitat, weaver ants can build hanging chains much longer than those observed in our experiments ( $>5$  cm). If ants modulate their building decisions depending on the cost of forming a chain, as per our hypothesis, we should find that the likelihood of observing chains decreases with the length of the gap to be bridged. This is because the cost of building a chain (number of ants in the structure) increases with the length of the structure, whereas its benefit remains unknown until the platform is reached.

We simulated chain formation over a wide range of gap heights (from 10 mm to 120 mm, at 2.75-mm increments) and traffic conditions (from 0 to 2 ants/s, at 0.05 increments) using the distance-dependent and distance-independent models. Model parameters were estimated using predictions from our statistical models as described in the “Theoretical model” section. We ran 100 simulations for each combination of traffic and gap height over a time window of 500 s, corresponding to twice the longest duration recorded in our behavioral experiments, or until the chain reached the platform, whichever happened first. To include variability in our simulations, traffic flow  $T$  was randomly drawn from a gamma distribution at every time step. The shape and scale parameters of the distribution were obtained using the selected average traffic value and the experimentally measured traffic variance. For each unique combination of traffic flow and gap height ( $N = 1,681$ ), we averaged the length of the chains from all 100 simulations at every time step and calculated their median growth rate by estimating the change in chain length between every two consecutive time steps.

As expected, the two models differ in their predictions about the growth of chains when a wider range of gap heights and traffic conditions is considered (Fig. 4). Predictions from the distance-dependent and distance-independent models are shown in Fig. 4 A and B, respectively (SI Appendix, Fig. S7). White dots represent our experimental trials and confirm that our behavioral data fall in an area where the predictions of the models do not differ. The distance-dependent model clearly predicts that ants stop investing

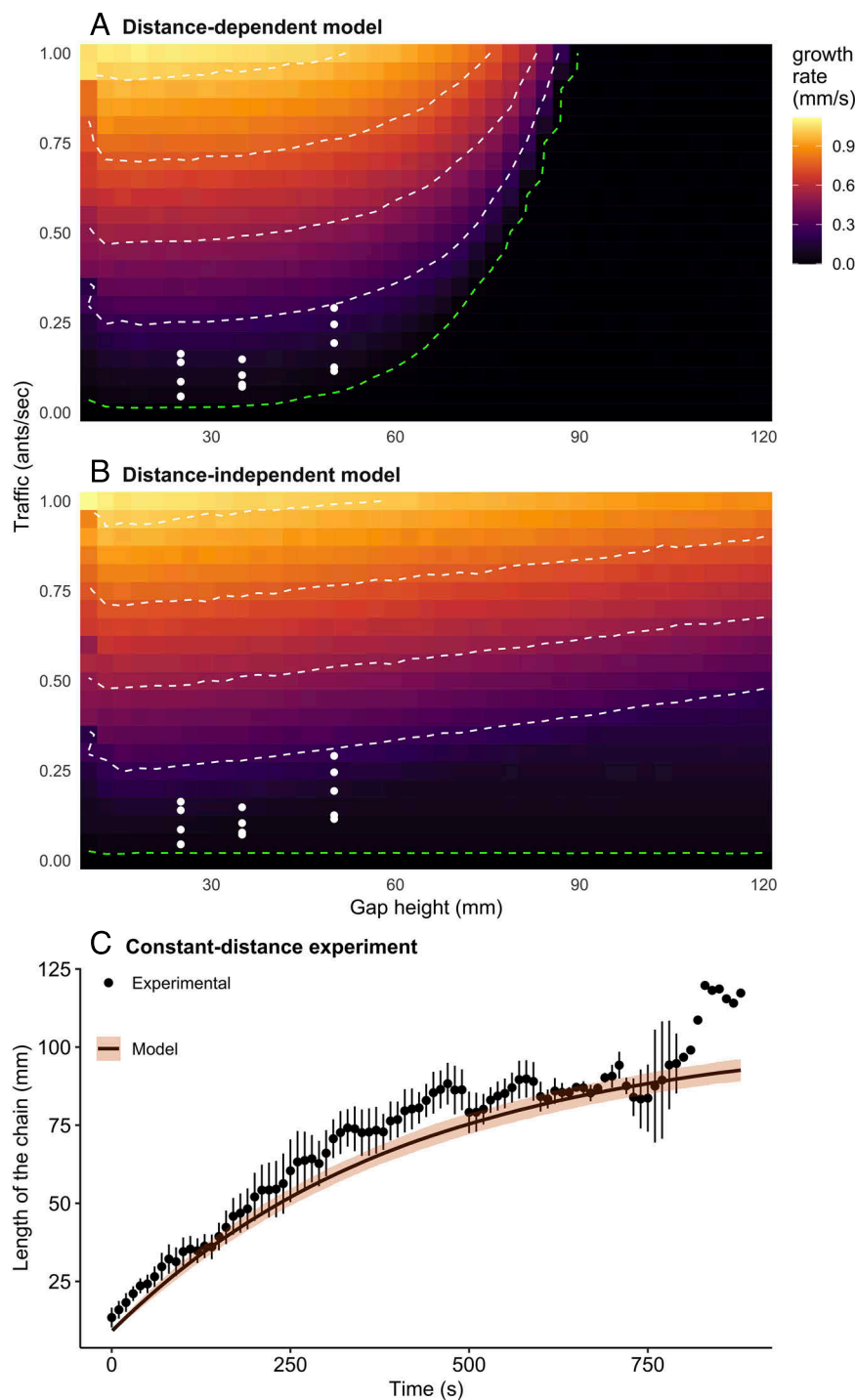


**Fig. 3.** Comparison of modeling predictions and experimental data. (A) Growth in the number of ants participating in chain formation as a function of time for experimental data (purple), distance-dependent model predictions (orange), and distance-independent model predictions (green). The number of ants in the chain is calculated as the difference between the number of ants joining the chain and the number of ants leaving the chain. Measurements are given for each experimental condition: 25 mm, 35 mm, and 50 mm. (B) Number of ants in the chain predicted by the distance-dependent model (orange dots) and the distance-independent model (green dots) as a function of the number of ants measured experimentally. Solid lines and confidence intervals are calculated using a total least square regression. Comparison is given for each experimental condition: 25 mm, 35 mm, and 50 mm.

in chains when the gap is taller than 89 mm (Fig. 4A). To gain insight into the origin of this cap, we extracted the parameters from the distance-dependent model for various values of gap length. This revealed that 89 mm is the distance at which  $W = 1$ , that is, all ants joining the chain quickly leave before the structure can grow. The probability of forming a chain decreases with the length of the gap to be covered, and no complete chains are observed when the platform is farther than 89 mm even at very high levels of traffic. This is in stark contrast with the predictions from the distance-independent model, which indicates that ants always build chains regardless of the distance from the platform (Fig. 4B). In addition, the distance-dependent model predicts that the traffic flow necessary for a chain to grow at some given rate increases nonlinearly with gap height. Indeed, for a given

traffic flow rate, the growth rate of chains rapidly decreases as a function of gap height. This suggests that longer chains may be costlier to build as they require a higher traffic flow to grow at the same rate as smaller chains. A similar prediction is generated by the distance-independent model, although in this case the necessary increase in traffic flow to maintain the same growth rate is linear and lower in magnitude. This effect may, however, arise from the fact that ants have more chances to leave during the formation of longer chains, as they inherently require more time to be built.

**Model Validation.** The most evident difference between the two models is that the distance-dependent model predicts that ants should never build complete chains when the gap distance to



**Fig. 4.** (A and B) Growth rate of chains predicted by modeling simulations for several combinations of gap height (x-axis) and traffic flow (y-axis). The color of each square indicates the median growth rate of chains calculated from 100 simulations. Black regions indicate the absence of chain formation. White regions indicate the presence of chain formation. White dots indicate the position on the graph of our behavioral experiments. Areas of equal growth rate are indicated by white dashed lines. The dashed green line indicates the level of traffic for which chain growth is nil. (A) Growth rate predicted by the distance-dependent model. (B) Growth rate predicted by the distance-independent model. Full range of simulations shown in *SI Appendix, Fig. S7*. (C) Growth in chain length as a function of time for experimental data (points) and model predictions (line) when the distance from the platform is kept constant. The red shaded area shows 95% confidence intervals of the modeling predictions.

be covered exceeds 89 mm (Fig. 4A). To test which of the two models more accurately describes the behavior of the ants, we performed additional behavioral experiments. We prepared ten queenless subcolonies of 200 adult foragers each, selected from four master colonies. For consistency with the previous set of experiments, ants were starved for 24 h and tested the following

day using an identical experimental set-up (Fig. 1A). We set the distance to the platform at 110 mm, a distance at which the two models clearly differ in their predictions (Fig. 4). In our previous behavioral experiments, we measured an average traffic flow rate of 0.12 ants/s. The distance-independent model predicts that at this traffic flow rate, ants should take 32 min to complete the

chain, whereas the distance-dependent model predicts no chain growth. We video recorded the behavior of ants for 30 min after the first individual was observed walking on the horizontal stick. We then returned all ants to their container and let them rest for 30 min. We then allowed the same subcolonies of ants to form chains over a gap of 35 mm to ensure that the lack of chain building in the first experiment was not due to other reasons such as lack of motivation or low colony activity. Four out of ten subcolonies were discarded through this screening procedure.

Only the distance-independent model predicted the formation of complete chains over a gap of 110 mm, and we observed no complete chains in our experimental test ( $N = 6$ ). In 5 out of 6 replicates, ants initiated small chains, with only two replicates containing chains that exceeded 20 mm in length. These quickly disassembled before reaching 50 mm (maximum length = 4.71 cm). These results are clearly in contrast with the predictions of the distance-independent model (Fig. 4B), indicating that the integration of a local mechanism that allows ants to modulate their behavior based on the distance from a platform is necessary to accurately predict chain formation over longer gap heights.

**Tricking Ants into Forming Longer Chains.** The experiments described in the previous section validated the predictions of the distance-dependent model, confirming that weaver ants use visual cues to make decisions when forming chains. If our hypothesized mechanism is correct, we can trick ants into forming long (>9 cm) chains by keeping the distance to the platform constant as the chain grows. This mechanism would deceive ants into thinking that the gap is always easy to fill, causing them to remain in the structure for longer periods of time. We validate this prediction by running additional simulations with our theoretical model where the platform distance is kept constant at 2 cm. As expected, the model predicts chain growth beyond the 9-cm cap for all traffic conditions (SI Appendix, Fig. S8). We therefore tested this prediction using 3 subcolonies of ants extracted from 2 queen-right colonies. We increased colony size to 500 individuals to ensure sufficient traffic levels and starved ants for 24 h prior to experiments to increase foraging motivation. The experimental apparatus was identical to that shown in Fig. 1A, except that the platform was placed on a sliding rail that allowed the experimenter to lower it down using a handle as the chain grew in length. No food was placed on the platform to avoid potential confounding effects and confirm that ants primarily rely on visual cues when forming chains.

We set the distance to the platform at approximately 3.5 cm at the beginning of each experimental trial, and started video recording from the moment in which ants formed a chain of at least 1 cm. As the chain grew, the platform was slid down so that its distance from the chain tip was maintained between 0.5 and 2 cm. Experimental trials were terminated when the chain disassembled or broke down. At the end of each experimental trial, ants were left resting for 30 min before being tested again. Maximum chain length was measured for each replicate ( $N = 8$ ) using the image-processing software Fiji (45). As predicted by our theoretical model, ants formed chains longer than 9 cm in all the experimental trials, with a maximum recorded chain length of 12.5 cm (Movie S3). To further validate our model, we performed additional simulations ( $N = 1,000$ ) keeping the distance from platform  $d$  below 2 cm. We measured the traffic flow of ants arriving at the chain tip in our behavioral experiments and found the average traffic rate to be 0.21 ants/s. We included traffic variability in our simulations by randomly drawing traffic flow  $T$  at each time step from a gamma distribution, with scale

and shape parameters were calculated using the experimentally extracted average traffic rate and variance. The distance from platform  $d$  was randomly drawn at each time step from values between 2 mm and 20 mm. We found a good agreement between the model's predictions and empirical data (Fig. 4C), further demonstrating the accuracy of our model in predicting chain growth. These results indicate that chains can easily exceed 9 cm without being limited by physical limitations, and confirm that ants use visual proximity as a cue for deciding to remain in the chain or leave their position. These experiments also open up the path for exploring which characteristics of visual stimuli are more salient to ants when making these decisions.

## Discussion

In the current study, we used the chain-building behavior of the weaver ant *O. smaragdina* as a model system to investigate how animal groups make adaptive decisions under uncertainty, in particular when no information is available about payoff. We combined detailed behavioral analyses with mathematical modeling to describe the behavioral rules underlying chain formation and showed that weaver ants cap their collective investment into chains when the payoff of building is not known. In our experiments, ants consistently formed chains over vertical gaps up to 50 mm in length, but never formed complete chains when this length was increased to 110 mm. Our results are in contrast with a previous model of chain formation (27, 36), which predicts that chains should grow indefinitely if the initial population of ants is large enough. We here propose a distance-based model for chain formation in weaver ants, which predicts the emergence of a cost–benefit tradeoff from local decisions of ants without requiring global knowledge, complex cognition, or communication among ants.

Informed by our experimental analyses, our model integrates a simple behavioral rule that allows ants to modulate their leaving decisions according to their distance from a platform. We showed that this rule suffices not only to accurately reproduce chain growth within the parameter space of our experiments but also to predict the building decisions of ants when confronted with large gaps. Previous studies on *O. smaragdina* and its sister species *O. longinoda* (27, 36) reported that the individual-level decisions of ants to join or leave a chain were dependent on the number of individuals already in it. In short, the larger the chain the higher the joining probability of ants arriving at the chain and the lower the leaving probability of ants already in it. However, these studies failed to identify the local stimuli that would allow ants to estimate chain size before joining or leaving. A candidate mechanism is that ants estimate chain size by measuring the distance walked over the chain before joining. Both our current results (Fig. 2A) and previous reports (27) showed that ants tend to walk down the entire length of the chain before joining, suggesting that ants may be using the length walked as a cue to join chains. Our results, however, showed no impact of chain length on the probability of joining the chain or on the latency to do so. In contrast, we found that the probability of observing an ant joining a chain was independent of the instantaneous conditions of the structure and/or traffic flow. It is, however, unlikely that ants that are already in the chain can assess chain size using local cues. Our experimental analyses revealed that ants tune their leaving decisions according to their distance from the platform, remaining longer in chains when closer to it. It is important to note here that our analyses were restricted to the leaving dynamics at the tip of the chain. Leaving events in other regions of the chain are rare (Fig. 2B), suggesting the



existence of a behavioral rule that prevents ants from leaving their positions if other individuals are hanging from them. Anderson et al. (28) suggested that ants participating in a chain should join and leave only at its extremity because individuals in the middle may be constrained in the structure and unable to leave. Studies on *Eciton* army ants' bridges demonstrated that the probability of an ant to leave its position decreases with the number of neighboring individuals and that the traffic passing over the ant further increases its probability to remain motionless (50). Our behavioral analyses revealed that weaver ants are more likely to remain in chains when the traffic flow arriving at the chain's tip is high, suggesting that a similar behavioral mechanism may be at play here. This mechanism may also be mediated by the load sustained by ants while in the chain, but further studies are necessary to confirm this hypothesis.

A major assumption of the model is that ants are able to perceive and estimate their distance from the platform. Previous research demonstrated that the presence of visual stimuli is necessary for the initiation of chain formation and that chains are never formed when no stimulus is present (25, 27, 43). It is possible therefore that our results could be explained by perceptual constraints, specifically an inability to detect the platform from a distance. This is unlikely, however, as we observed chain initiation in all our experimental conditions and even when the distance from the target was set at 110 mm. *O. smaragdina* major workers are visual predators and navigators with highly developed eyes that are well-tuned for diurnal light conditions (43, 44, 51–53). Although no comprehensive study on the visual capabilities of *O. smaragdina* workers exists, comparisons of *O. smaragdina* eye anatomy with that of other ants (52–54) suggest that weaver ants should easily detect the platform stimulus in all of our experimental conditions. Our results also show that ants were more likely to lengthen a chain with their bodies when closer to the platform and that the probability of observing “reaching” behavior also increased with the proximity to the target. Taken together, these results indicate that the modulation of chain building is driven by “voluntary” individual-level decisions of ants rather than by perceptual limitations.

Our model also ignores the effect of traffic flow and directionality on the behavior of ants in the chain. This decision is motivated by the relatively small impact of these factors on the leaving decisions of ants (Fig. 2D), and by our effort to maintain model simplicity. Responsiveness to traffic information has been shown to underlie the stability and adaptiveness of the structures built by *Eciton* army ants (35, 46, 50) and *Solenopsis* fire ants (32, 55, 56). In these ant genera, individuals within structures use the tactile cues provided by nestmates walking over them to modulate their behavior. Our experimental results suggest that weaver ants may use a similar mechanism during chain formation. Traffic flow descending chains may promote chain stability by keeping ants within the structure motionless during extended foraging periods. On the other hand, ants walking up the chain may signal the presence of danger at the far end of the structure and trigger ants within the structure to leave their position. This may explain the rapid disassembly of chains when a visual stimulus is removed from below the structure (27). Investigating the impact of traffic cues on chain formation may provide useful insights for comparing the mechanisms governing self-assembly structures in diverse ant genera and shed further light on the local stimuli that regulate decision-making at the individual level.

Similar to observations of individual animals (1, 6, 8, 9, 40, 41), *O. smaragdina* colonies modulate their investment into tasks with unknown payoff. The collective decision of building a chain emerges from the individual-level budgeting

decisions of ants already in the chain, without the need to invoke sophisticated communication or complex cognition. Each ant modulates the time spent within a chain in response to locally available information on target distance, and these decisions lead to a collective-level outcome that limits the overall investment into costly chains. While our work focused on the behavioral mechanisms that ants use in the absence of payoff information, future studies should investigate how access to this knowledge modifies the decision-making of maintaining a chain after exploring the new area (i.e., when payoff information becomes available). Payoff information may be encoded in the traffic flow walking over the structure. The weak effect of traffic flow detected in our behavioral analyses during chain formation (Fig. 2D) may have a major effect on maintaining stability in established chains, as it has been observed in the bridges built by *Eciton* army ants (50).

Our findings also reveal the possibility that noise in the system and/or the motivational state of the ants may regulate chain-building decisions. We observed the initiation of chain formation when the distance from the platform was set at 110 mm, suggesting that some individuals may possess different thresholds for initiating or remaining in chains. Threshold models are common in social insect research (15, 57–59), and interindividual variation in response thresholds has been shown to enhance group performance in various tasks (15, 57, 60–62). Longer than expected chains may also spontaneously emerge in the case of traffic congestions, where ants that are walked over by nestmates may remain locked in position and form small temporary clusters that may seed chain formation.

Research on social insect behavior has led to important advances in our understanding of complex systems (63), and inspired several solutions for the optimization of real-life problems such as traffic formation (64), protein folding (65), and DNA sequencing (66). Our proposed model offers insights for algorithmic solutions to collective decision-making in artificial multiagent systems, especially for cases where information about the outcomes of the decision is unavailable. This is especially relevant for swarm robotics, where scalability, energetic efficiency, and low-cost production are pivotal elements for real-world applications of the swarms (67, 68). The behavioral algorithm presented here requires agents to modulate their behavior depending on their energetic or motivational budget, without the need for active communication or sophisticated cognitive abilities. In scenarios such as search and rescue (69), these behavioral rules may aid robots in navigating unknown environments and make cost-effective decisions without knowledge of the possible outcomes.

The current study improves upon the previous model of chain formation (27) by describing a simple sensory-based mechanism that allows ants to modulate their behavior using only locally available information. The model presented here aligns with the self-organized nature of chain formation, in that a sophisticated group-level behavior can be explained by simple behavioral rules followed by individuals without the need to invoke complex cognition or communication among individuals (10, 14). Our study furthers our knowledge of collective decision-making in animal groups and sheds light on the processes that allow groups to deal with uncertainty in real-life scenarios.

## Materials and Methods

**Biological Material.** Six queenright weaver ant (*O. smaragdina*) colonies were collected from Townsville (QLD, Australia) and maintained in a temperature-controlled room ( $27 \pm 1^\circ\text{C}$ ) under a 12- × 12-h photoperiod at Macquarie

University (Sydney, NSW, Australia). We used a total of 20 queen-less subcolonies of 200 adult workers each, housed in small plastic containers (255 mm × 175 mm × 117 mm) with Fluon-coated walls to prevent ants from escaping. No food was given to ants 24 h prior to the experiments to increase foraging and exploration motivation. A retort stand base was placed in the containers as support for the vertical bar during the experiments. The platform consisted of a white Corflute strip placed on top of a plastic support cylinder (height = 150 mm, diameter = 65 mm) (Fig. 1). We coated the cylinder's walls in talcum powder (70) and immersed its base into a water-filled large petri dish to prevent the ants from escaping.

**Experimental Procedure.** A vertical iron bar (height = 570 mm, diameter = 10 mm) was placed within the subcolony using the retort stand base as support. We attached a 10-cm-long wooden stick perpendicularly to the vertical bar to provide ants with support from which they could form hanging chains. The free end of the stick was positioned directly above the center of the foraging arena. The distance between the wooden stick and the platform was adjusted according to the experimental condition (25 mm, 35 mm, and 50 mm). Preliminary observations and previous studies showed that ants reliably formed chains across this range of heights (27, 36). Generally, ants started forming a chain within 15 min from the beginning of the experiment.

We recorded all trials in FullHD resolution (1,920 × 1,080 pixels) at 24 frames per second using a Panasonic Lumix GH-4 video camera. Filming started when the first ant was observed hanging from the wooden stick and stopped when the first ant left the chain through the platform at the bottom (i.e., before information about the food source could travel back to the colony).

All ants were returned to their container at the end of each experimental trial. We removed chemical traces left by ants by cleaning the vertical bar, the horizontal wooden stick, and the platform with 100% ethanol between trials. Ants were left to rest for at least 1 h before being tested again. After a bout of experiments, the vertical bar was removed from the subcolony, and ants were left to rest overnight in a temperature-controlled room (27 ± 1 °C) before being tested again on the following day. All ants were returned to the main colony after a maximum of 4 d of testing.

**Video Analysis.** We quantified the proportion of chain length walked by ants before joining using the free image processing software Fiji (45). Ants ( $N = 96$ ) were randomly selected using a custom random number generation (RNG) code developed in R using the *randomizr* package (71). For each ant, we noted the coordinates of the ants' mandibles and of the chain tip at the moment of joining. We chose to use the mandibles as the reference point for consistency across ants and to gather information about the joining choices of ants (see *Data manipulation* and *Results* sections).

The individual-level behavior of ants at the chain's tip was analyzed using the open-source event-logging software BORIS (72). We defined the chain's tip as the bottommost 1 cm of the chain (1.5 ant-body lengths). A virtual line was overlaid on the videos to separate the chain's tip from the rest of the chain. For each ant crossing the line in the direction of the tip, we noted the following: 1) time of crossing; 2) time and duration of joining behavior (if any); 3) time of leaving the structure (if the ant joined the chain); 4) time and duration of extension behavior (if any); and 5) time of crossing back over the virtual line (if any). We kept track of all ants joining the chain's tip until they either left the structure (i.e., started walking again after joining) or until the line defining the chain's tip passed beyond them, in which case they were considered as having remained as part of the structure until the end of the replicate. Traffic volume and directionality at the chain's tip were quantified by counting the number of ants that crossed the virtual line in each direction.

The length of the chain was detected using a custom image subtraction algorithm in R (version 4.2.1). The algorithm compared each frame with the subsequent ones to detect only ants that remained stationary for at least 3 s. Measurements were scaled through a known distance recorded in-frame.

**Data Manipulation and Statistical Analyses.** All data manipulation and statistical analyses were performed in R (73) (version 4.2.1) using the packages *glmmTMB* (74) (version 1.1.4), *lme4* (75) (version 1.1-30), *lmerTest* (76) (version 3.1-3), *DHARMA* (77) (version 0.4.5), *ggplot2* (78) (version 3.3.6), *tidyr* (79) (version 1.2.0), *dplyr* (80) (version 1.0.10), *readr* (81) (version 2.1.2), *ggeffects* (82) (version 1.1.3), *survminer* (83) (version 0.4.9), *data.table* (84) (version 1.14.2), *viridis* (85) (version 0.6.2), *scales* (86) (version 1.2.1), and *survival* (87) (version 3.4-0). All data manipulation was performed using the *dplyr*, *tidyr*, *scales*, and *data.table* packages. Statistical models only included predictors that we had an a priori reason for including (88). Residual diagnostics for all GLMMs were performed using the simulation-based approach implemented in *DHARMA* unless otherwise stated.

The probability of an ant joining the chain's tip when it arrives in the area was analyzed with a generalized linear mixed effect model (GLMM) with binomial distribution and "Nelder Mead" optimizer using the *lme4* package. The model tested whether this probability was influenced by traffic volume and directionality, by the length of the chain, or by the distance from the platform. Since the latter two variables inevitably covary, we used the interaction between the experimental condition and the distance from the platform as proxy for the length of the chain in the model. A significant interaction term would thus indicate that the behavior of ants is influenced by the length of the chain. The full model included traffic down, traffic up, experimental condition and distance from the platform as continuous fixed predictors, and the interaction between experimental condition and distance from the platform. We averaged traffic down, traffic up, and distance from the platform over the time window starting when the ant crossed the virtual line at the chain's tip until either the moment of joining (if the ant joined the chain) or until the ant walked away from the chain's tip. Traffic up and traffic down were then divided by the duration of the time window to obtain traffic rates in ants/s. We scaled and centered experimental condition and distance from the platform using the inbuilt R function *scale* for easier data interpretation. Trial ID was included as a random factor.

The time spent by ants as part of the chain was analyzed using a Cox proportional hazards model (CPHM) using the *survival* package. The model tested whether the probability of leaving the chain was influenced by traffic volume and directionality, by the distance from the platform and/or by the number of ants that joined the chain during the time window in which the ant was part of the structure. We averaged traffic up, traffic down, and distance from the platform over the time spent by the focal ant as part of the chain until it either left the chain or was censored. Traffic up and traffic down were then divided by the duration of the time window to obtain traffic rates in ants/s. We found no significant deviations from the proportionality assumption at the local and at the global level using the *cox.zph* function in the *survival* package.

**Ethical Statement.** The Australian code for the care and use of animals for scientific purposes (89) does not specify ethical regulation for the use of invertebrates. Our experiments were conducted minimizing animal stress by reducing manipulation where possible. Only self-motivated ants were tested. No ants were killed during our experiments.

**Data, Materials, and Software Availability.** All code and datasets used for data analyses are available at GitHub: <https://github.com/DanieleCarlesso-Research/WeaverAnts-HangingChains.git> (90).

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