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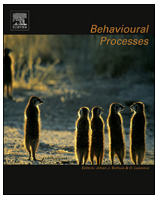

Self-organizing conflicts: Group assessment and the spatio-temporal dynamics of ant territory battles

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ABSTRACT

Territorial battles among ants exhibit temporal and spatial patterns that self-organize, arising spontaneously from distributed decisions by large numbers of individuals. We describe agent-based models of inter-group fights in ants and show that two behavioral mechanisms that are rarely quantified have large effects on the dynamics of intraspecific battles; specifically, the pattern of search by unengaged ants, and assessment of relative numbers. In the absence of assessment, recruitment by both colonies rises to steady averages. Alternatively, if ants tend to lay trails only when they detect that their nestmates outnumber opponents, fights can be rapidly resolved as one colony ceases recruiting. If ants tend to lay trails when their nestmates are locally outnumbered, the position of the battle may oscillate. We show that the collective ability of fighting ants to accurately compare group sizes may be high even if each ant has limited perception and memory. However, amplification of small initial numerical advantages can lead to priority effects favoring the first colony to recruit even if it is the smaller colony.

1. Introduction

Social behaviors in many species are viewed as self-organizing phenomena in which group actions arise spontaneously from repeated, distributed interactions among individuals, rather than from central control (Camazine et al., 2001; Detrain and Deneubourg, 2008). Studies on the self-organization of animal social behavior seek to identify mechanisms that link individual behavior to group behavior (Sumpter, 2006), allowing groups to achieve flexible and favorable outcomes that are beyond the capabilities of any single individual. Well studied examples from the social insects include path selection by trail-following ants (Detrain and Deneubourg, 2008) and nest choice by honey bees (e.g., Passino et al., 2008; Seeley, 2010) and ants (e.g., Pratt, 2005).

While studying territorial battles in ants, we have been struck by strong contrasts among species in the characteristic patterns of battle dynamics. An experienced observer can easily distinguish battles of *Azteca trigona* (Adams, 1990), *Solenopsis invicta* (Adams, 1998; Plowes and Adams, 2005) or *Tetramorium immigrans* (Plowes, 2008; Wagner et al., 2017) from the ways the shape, position, and size of the battle change over the course of the conflict. Studies on other territorial ants reveal further diversity in fight patterns (e.g., Adams, 2016; Hölldobler, 1981; Mabelis, 1979). Because territorial battles between ant colonies often involve large numbers of insects mixing slowly over the region of conflict, each individual has incomplete information, and the main characteristics of battle dynamics are likely to be driven by self-organization.

We develop models of territorial fighting with the aim of discerning individual rules of behavior that generate diversity in battle dynamics and that allow conflict resolution. It immediately becomes clear that such a model must extend beyond the traditional scope of research on self-organizing social behavior, most of which concerns only one social group (e.g., all the examples in Camazine et al., 2001). Territorial battles are self-organizing conflicts between two groups, shaped as much by reactions to opponents as they are by interactions among members of the same colony. Other examples of self-organizing conflicts occur during group predation on social prey (e.g., Benoit-Bird and Au, 2009; Powell and Clark, 2004). It is not currently feasible to produce fully parameterized models of group fighting for particular ant species. Our goals are to bring together into one model individual behaviors and feedback mechanisms that are likely to shape ant battles, to identify important areas for empirical work, and to evaluate the potential for groups to collectively perform mutual assessment.

2. Materials and methods

2.1. Biological background

Although much is known about the territorial behavior of ants

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(Adams, 2016), there have been few efforts to develop models linking individual to collective behavior in this context (e.g., Adler and Gordon, 2003; Adler et al., 2018; Hoover et al., 2016; Lumsden and Hölldobler, 1983) and, to our knowledge, none that address spatial dynamics of mass battles. We propose that the four aspects of behavior having the greatest effects on the spatial and temporal dynamics of battles and their outcomes are the following.

Recruitment is the process by which individuals bring nestmates to particular locations. The mechanisms of recruitment during battles have been well studied in multiple species of ants and are similar in many respects to the mechanisms used to recruit to food (Hölldobler and Wilson, 1990). Trail-laying, the deposition of a pheromone trail from the site of a conflict back to a nest or foraging trail, can allow a single scout to attract large numbers of nestmates over long distances (e.g., Hölldobler and Wilson, 1978). Ants may also use tactile displays and alarm pheromones to enhance recruitment (e.g., Adams, 1994; Hölldobler and Wilson, 1978).

Assessment occurs when ants adjust their aggression and recruitment based on perceptions of the relative fighting abilities of the two groups. There has been much less experimental work on assessment than on recruitment, but some ants alter aggressive behaviors according to the local strength of their own colony or based on comparisons to the opposing colony (Adams, 1990; Hölldobler, 1981; Tanner, 2006).

Fighting consists of actions that impede, immobilize, injure, or kill opponents. Fights among colonies can be lethal to individuals and, in extreme cases, can kill much of the smaller group (e.g., Mabelis, 1979).

Search patterns by unengaged ants as they seek opponents potentially affect the shape and size of the battle, the pattern of mixing of opponents, and the outcome of the fight. Very little information on this aspect of territorial behavior has been published and descriptions of the spatial dynamics of battles are usually verbal or schematic (e.g., Driessen et al., 1984; Hölldobler, 1981).

2.2. Agent-based models

Our model description follows the ODD (Overview, Design concepts, Details) protocol, a standardized format for describing agent-based or individual-based models (Grimm et al., 2010).

2.2.1. Purpose

The model was developed to investigate how species-typical characteristics of ant territory battles emerge from four main elements of individual behavior: recruitment, assessment, fighting, and search. Because the roles of assessment and search are not well studied for territorial ants, we focus especially on the consequences of variation in these two aspects of behavior. We first describe a base-line model lacking assessment: all workers lay trails after fighting regardless of the numbers of nestmates and opponents encountered. To evaluate the effects of search patterns on battle dynamics, we compare variants of this model differing only in the movement rules used by unengaged ants to search for opponents. Next, an assessment process is added, which assumes that the propensity of ants to lay trails depends on the relative number of nestmates and non-nestmates encountered by individual ants. We compare battle dynamics for models that differ in the assessment rules used by the fighting ants.

We also use the model to evaluate the collective ability of opposing colonies to compare their group sizes, given limited memory and perceptual abilities of individual ants. Finally, we test whether assessment can produce priority effects, allowing a smaller colony to win if it has an early advantage in recruitment.

2.2.2. Entities, state variables, and scales

The model simulates a battle between two colonies. For each colony, two types of entities are represented: individual ants and trail segments. The model parameters and state variables are shown in Table 1. Colonies are characterized by the positions of the nest entrance and by two parameters governing the rate at which ants are recruited as a function of the concentration of pheromones on trails reaching the nest. These recruitment parameters are assumed to depend on the size of the colony's worker population. Major characteristics of ants include their position and colony identity, the length of time since the ant left its colony entrance, colony identities of recently encountered ants, and current behavior (whether the ant is moving outward or homeward; whether the ant is moving on or off of its colony's trail system; whether it is fighting, trail-laying, or searching). The number of ants monitored varies as ants come and go from their nest entrances. Each colony's trail system consists of a series of interconnected segments. Each trail segment is straight and is characterized by the positions of the end points, pheromone concentration, an identity number, and the identity numbers of any other segments to which the segment connects at either end. Segments can connect to at most to two other segments at the outward endpoint and to one other segment on the homeward endpoint (Fig. 1).

Space is continuous, two-dimensional, and homogenous except for the pheromone trails, nest entrances, and positions of ants. The modeled region is 2.72 m (x-axis) by 1.28 m (y-axis), sufficient to encompass battles that we have observed in several species of territorial ants (Adams, 1990, 2003; Plowes, 2008) and to give room for the battle to shift in position according to the outcome of local fighting. (The dimensions in mm are evenly divisible by 8, which is helpful in making animations.) Positions are designated in centimeters from the origin, which is at the lower left corner. The colony entrances are 2 m apart at the following x and y coordinates: (35 cm, 65 cm) and (235 cm, 65 cm).

Time is represented in discrete steps of 1 s. The maximum duration of a simulation is 2 h, long enough for most conflicts to resolve and to encompass nearly all battles of several species that we have observed in the field.

2.2.3. Process overview and scheduling

Each second, the following processes are implemented in the indicated order.

(1) New ants are created for each colony, representing recruits that exit the nest entrance.
(2) The status of every ant in the simulation is updated simultaneously.
  (a) The ant detects and stores the colony identities of nearby ants.
  (b) If the ant is fighting, the fight terminates if the duration reaches a fixed limit. The ant then decides whether to lay a trail as it heads homeward.
  (c) If two ants from different colonies that are not fighting and have not previously fought come within distance D of one another, they begin to fight.
  (d) If the ant is not fighting, it moves to a new position. The movement rule depends on whether the ant is on a trail and whether it is headed outward or homeward. Search by unengaged ants is handled here. If the time limit for searching is reached, the search is terminated and the ant heads homeward. When an ant moving on a trail segment reaches the tip, it transfers to a connecting segment if there is one; if there are two connecting segments, it selects one stochastically based on relative pheromone concentrations. Trail-laying ants moving on existing trails increase the pheromone concentration of each segment that they cross. For a trail-laying ant that is not on an existing trail, a new trail segment is created based on the ant's movement in the current time step; if the segment intersects an existing trail segment, the two segments are joined and the branching pattern of the trail system is updated.
(3) The status of each trail segment is updated. Pheromone concentration is reduced by a fixed proportion. If the concentration falls below a critical value, the segment is removed.

A flow chart (Fig. A1) and pseudocode in the Appendix provide more detail about process scheduling and the algorithms used during

Table 1
Parameters and variables in the models.

	Baseline value	Description
Recruitment and trails		
A_1, A_2	1.0, 1.25	Maximum average recruitment rates for colonies 1 and 2
B_i	20	Half-saturation value for recruitment rate of colony *i*
C_j	variable	Pheromone concentration on trail segment *j*
λ_i	Eq. (1)	Poisson mean for recruits per sec exiting colony *i*
P_j	Eq. (2)	Probability of selecting trail segment *j*
Q	1	Trail pheromone increment by trail-laying ants
δ	0.003 per sec	Rate of pheromone decay
Movement and search		
S	2 cm / sec	Movement rate on pheromone trails
W	1 cm / sec	Movement rate by searching ants
d	variable	Distance to target during directed search
V	200 sec	Duration of searching by ants recruited to the battle
Y	1 cm	Distance at which trails are blocked by fighting ants
β	0.04	Dependence of turning correction on distance to stimulus
ε	variable	Random error added to ant's bearing
φ	Eq. (3)	Amount of turn towards target during directed search
φ_{max}	0.2	Turning limit
σ_c	$\pi/2$	Std. dev. of turning angle distribution for undirected search
σ_e	0.5 or 0.01	Std. dev. of turning angle distribution for directed search
σ_h	$\pi/10$	Std. dev. of turning angle distribution for homing ants
Fighting		
D	1.5 cm	Opponents approaching within this distance begin to fight
F	300 seconds	Duration of fights between pairs of ants
Assessment		
M	20	Ant's memory limit
U	2 cm	Distance at which an ant's colony identity can be detected
minR, *maxR*	(1.5, ∞) or (0, 0.5)	Assessing ants lay trails when the ratio of nestmates to opponents in memory is > *minR* and $\leq$ *maxR*.

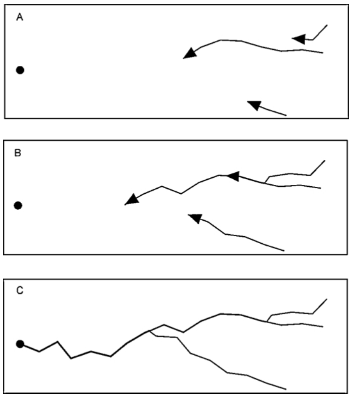

Fig. 1. The sequence of panels illustrates the formation of branching recruitment trails. Three trail-laying ants are indicated by triangles pointing in the direction of movement. The nest entrance is indicated by the solid circle, and pheromone trails by solid lines. Trail-laying ants that encounter an existing trail move onto the trail, producing branching patterns from the point of view of ants subsequently leaving the nest.

battle simulations.

2.2.4. Design concepts

2.2.4.1. Emergence. We directly modeled the behavior of ants (trail-laying and following, fighting, assessment, and search) and the deposition and decay of pheromone trails. From these processes emerged: (1) *temporal patterns* (changes in the numbers of ants moving to and from the nests towards the battle and changes in the numbers of ants fighting); (2) *spatial dynamics* (changes in the extent and position of the zone of fighting and the trail system); (3) *conflict resolution* (how the probability of victory and the severity of fighting depend on the relative sizes of the two colonies and on any head start in recruitment by either colony).

2.2.4.2. Sensing. Ants detect the colony identity of any other ant within distance *U*. Ants can detect pheromone trails, can compare pheromone concentrations on different trail segments when they reach a branching point in the trail network, and can travel along trails and across connections to other trail segments. They do not follow trails of the opposing colony. Unengaged ants can detect opponents with distance *U* and, in some simulations, can detect the closest fight or the closest point on any pheromone trail. Ants headed homeward sense the approximate direction towards their nest and can move to the entrance with certainty when they are close enough to reach it in the current time step.

2.2.4.3. Interaction. Ants interact indirectly with their nestmates by establishing or reinforcing pheromone trails and by following pheromone trails deposited by other members of their own colony. Ants interact with opponents by fighting – grappling for a fixed period of time. If assessment is included, the decision to lay trails back to the nest entrance after a fight depends on the ratio of nestmates to opponents that have been recently encountered.

2.2.4.4. Stochasticity. Stochasticity in collective action arises due to limited numbers of ants, limited information available to each ant, and to spatial variation in the numbers of nestmates and opponents encountered by individual ants. Stochasticity is introduced into (a) the number of new recruits produced at each time step; (b) the distances advanced by new recruits during the time step in which they are created; (c) an ant's choice of branches when it reaches a bifurcation in the trail network; (d) the directions of movement selected by ants that are not on trails. The ants are identical, except for the values of their state variables.

2.2.4.5. Observation. To display fights, the software can show the position of each ant at each time step by a symbol showing the ant's position and bearing. The shading of the symbol indicates colony identity and whether the ant is fighting (e.g., Fig. 2). Trail segments can be displayed with the thickness of segments corresponding to pheromone concentration (Fig. 1). Throughout each simulation, we

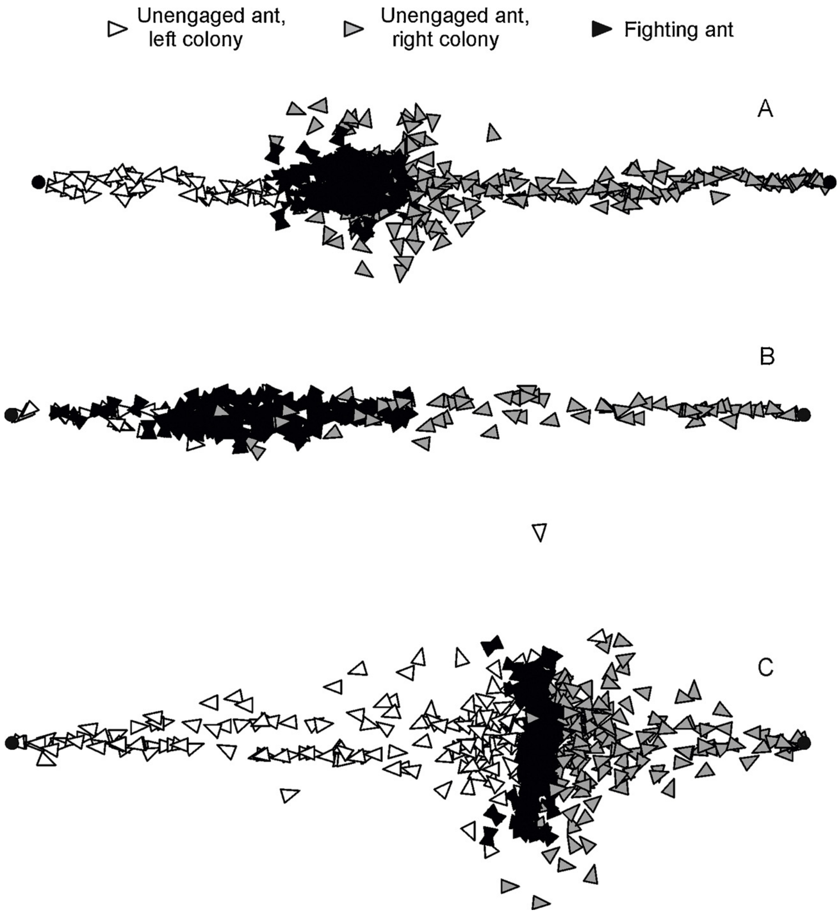

Fig. 2. Battle shapes depend on search tactics. Ants are shown as triangles pointed in the direction of movement. Black: pairs of fighting ants; Open: unengaged ants from the colony on the left; Gray: unengaged ants from the colony on the right. The colony entrances, on the far left and right, are depicted by solid circles. (A) Battle type A: Under the baseline conditions, in which unengaged ants search near other fighting ants, the zone of fighting ants forms a region that is approximately oval. (B) Battle type B: When unengaged ants search near trails, the battle zone is elongated along the trails. (C) Battle type C: When the forward movement of unengaged ants is blocked by fighting ants, the battle forms a front that is roughly perpendicular to the main recruitment trails.

monitored the number of ants exiting from each colony entrance and the number of ants laying trails. We also kept track of the number of fighting ants, their mean position, and the width and breadth of the region within which fighting occurs.

2.2.4.6. *Other design concepts*. The ants do not have explicit objectives, do not learn or adapt, and do not predict consequences of their choices. Assessment and recruitment may allow colonies to adjust their collective fighting in ways that are favorable, e.g. by withdrawing from fights they are not likely to win, but the ants in our models are not assumed to optimize their behavior.

2.2.5. Initialization

In most simulations, battles are asymmetric: the right-hand colony is larger, with a 25% advantage in the maximum rate of recruitment. Battles are initiated by a single pair of ants fighting at a point on the line connecting the two entrances and 50 cm closer to the entrance of the larger colony. This starting position was chosen to give the smaller colony an initial spatial advantage, allowing a greater period of time for the development of the battle before the smaller colony is overwhelmed. At time $t = 0$, the ant from the smaller colony begins to return to its nest, laying a pheromone trail. The ant from the larger colony begins to lay a trail to its nest after a delay of 100 s, a value chosen so that recruits from each side can reach the site of the original fight at the same moment if they leave their nests immediately upon the arrival of the scout.

2.2.6. Input data

There are no inputs from external sources.

2.2.7. Submodels

2.2.7.1. *Creating new ants*. Each second, the number of new ants (recruits) issuing from each colony's nest entrance is drawn at random from a Poisson distribution for which the intensity λ depends on the total pheromone concentration on trails reaching the entrance. The Michaelis-Menten function is used to represent recruitment as a saturating function of pheromone concentration (e.g., Adams and Traniello, 1981). For colony i (i is equal to 1 or 2)

$$\lambda_i = \frac{C_i A_i}{B_i + C_i} \tag{1}$$

where C_i is the current total concentration of pheromone summed across trails reaching the nest entrance of colony i, and A_i and B_i are colony-specific terms governing recruitment rates. A_i is the maximum value of λ: as pheromone concentration rises, the rate at which new recruits exit the colony approaches this value asymptotically. In the baseline model, we selected $A = 1.0$ ant per second for one colony and $A = 1.25$ ant per second for the other colony, giving the larger colony a 25% advantage in maximum recruitment rate. B_i is the half-saturation value, which is the pheromone concentration at which λ reaches half of its maximum possible value. This parameter is inversely related to the sensitivity of recruitment to low concentrations of pheromone. To model battles that are influenced by large numbers of workers, we used $B = 20$, the quantity of pheromone deposited by 20 workers, as the half-saturation value for both colonies. This means that trail-laying by just one or two workers does not bring recruitment close to its maximum level. When a new recruit is created, it is flagged as heading outward (instead of homeward) and the time it exits the nest is recorded. If there is more than one trail connecting to the nest entrance, the recruit's trail is chosen randomly with alternatives weighted by their pheromone concentration.

2.2.7.2. Detecting colony identities of nearby ants. We include an option for ants to assess force ratios. If this option is implemented, each ant detects the colony identity of any other ant that is within distance $U = 2$ cm of its own position at each time step. If the encountered ant is not currently in memory, its ID number and colony identity are stored in the ant's memory. (The ID number is used to prevent counting the same ant multiple times if it stays close to the focal ant for several seconds.) If the memory limit, M, has been reached, the oldest encounter currently held in the ant's memory is removed to make room for the most recently encountered ant. The ant's memory is updated regardless of whether ants are fighting; thus, we assume that ants can monitor local force ratios while fighting, searching, or traveling on trails. We used a default value of $M = 20$, but we also evaluated the effects of changing this parameter.

2.2.7.3. Initiation and termination of fights. Ants are assumed to fight in pairs. New fights are initiated when two unengaged ants (ants that are not fighting and that have not previously fought) from opposing colonies come within distance D (=1.5 cm) of one another. At the start of the fight, the two ants are moved to a shared location midway between their former positions. If either ant was on a trail when the fight began, it is now flagged as being off trail. Fights persist for a fixed period, F. We selected $F = 300$ s for the fight duration, based on observations that fights between pairs of workers in *T. immigrans* typically last several minutes. To prevent ants remaining indefinitely within crowded battles, ants will not engage in a second fight when the first one has terminated. When the fight is over, the ant's direction is flagged as homeward and it may or may not lay a trail, depending on the assessment rules (described below).

We made several simplifying assumptions concerning the effects of fighting. In the species that we have studied, only a small fraction of the colony is killed during a fight (e.g., Adams, 1990). Changes in worker number on the battlefield are driven much more by recruitment and fleeing than by depletion of either colony's population of potential fighters, especially in species that do not readily kill opponents (Hölldobler, 1981; van Wilgenburg et al., 2005). We therefore omit mortality from our models. The main effects of fighting on battle dynamics are that the presence of fighting ants affects other ants' assessment of local force ratios and that fighting removes ants from the pool of workers available for other activities, including recruitment, for as long as the ants grapple. Other complexities are also omitted, including individual variation in propensity to attack (e.g., Sakata and Katayama, 2001) and the dependence of mortality rates on force ratios and motivation (e.g., Adams and Mesterton-Gibbons, 2003; Tanner, 2006). Those assumptions can be changed easily within this modeling framework.

2.2.7.4. Assessment. We include an option for ants to keep track of the numbers of nestmates and enemies encountered (described above) and for trail-laying to depend on the ratio of these numbers. When assessment is included, ants that finish fighting lay trails only if the ratio of nestmates to non-nestmates, among encounters held in the ant's memory, is within specified bounds (*minR* and *maxR*). In alternative models, we assume one of the following rules. All rules are applied when an ant finishes fighting and heads back to its nest. The ant always counts itself (as a nestmate) and the opponent with which it was fighting, so if no other ants were encountered, the ratio of nestmates to opponents was 1:1. Ants that have not fought do not lay trails.

(1) *No assessment.* All ants that have fought lay trails back to their nest entrance.
(2) *Recruit when more numerous.* Ants lay trails when they have encountered opponents and the force ratio, which is equal to (number of nestmates in memory)/(number of opponents in memory), is > 1.5.
(3) *Recruit when outnumbered.* Ants lay trails when the force ratio is less than or equal to 0.5.

For both (2) and (3), we made the critical values more extreme than unity to make the consequences more obvious.

2.2.7.5. Movement on and off trails. Each second, the positions and behavioral states of all ants that are not fighting are updated based on the following rules.

Ants moving homeward on trails. Pheromone trails are represented as a series of interconnected segments (Fig. 1). For each time step, the ant moves in the homeward direction along its current segment, transferring to any connecting segment and continuing along it until the total distance traveled is equal to S. If the ant is trail-laying, whenever it reaches the homeward tip of a trail segment, the pheromone concentration at that tip is increased by Q. Although pheromone is implicitly deposited along the entire segment, it is necessary to monitor concentration only at the homeward tip, because that is where ants make decisions of which segment to follow.

Ants moving outward on trails. Ants move a fixed distance, S, each second along trail segments. If S is greater than the length r of the remaining portion of the current segment, the ant moves distance r to the tip of the segment, then its behavior depends on the number of segments to which its current trail segment is connected:

(i) If the segment is not connected to any other segment, the ant is released from the trail and then travels distance $(S - r)$ following the rules of movement for ants off trails (see below).
(ii) If the segment is connected to a single other segment, the ant moves onto that segment and travels distance $(S - r)$ along it. However, if the connecting segment is shorter than $S - r$, then the ant travels to the tip of the segment and the test for connecting segments is repeated.
(iii) If the segment is connected to two other segments, the ant chooses one of these segments stochastically based on pheromone concentrations. Following Beckers et al. (1993), we assume that the probability P_j that the ant chooses branch j is proportional to the pheromone concentration on the two branches. Beckers et al. (1993) allowed a non-linear response to increasing pheromone concentration, but we use the following formula for simplicity.

$$P_j = \frac{C_j}{C_j + C_k} \tag{2}$$

where C_j and C_k are the pheromone concentrations on the two branches. Similarly, for ants exiting a colony's entrance when there are multiple trails that can be followed, the probability of choosing each trail is equal to the pheromone concentration C_j for that trail divided by the total of pheromone concentrations for all trails reaching the entrance.

Ants heading homeward off trails. Ants of many species can orient towards the colony entrance when they are not on a pheromone trail (e.g., Wehner, 1987). When an ant seeks to return home, its direction of movement is the true direction to the entrance plus an error, which is drawn at random from a Von Mises distribution (essentially a normal distribution wrapped around a circle) with a mean of 0 and a standard deviation equal to σ_h. The error is drawn independently during each time step. We used $\sigma_h = \pi/10$ to give a moderate amount of sinuosity to trails, similar to real ant trails (Fig. 1). If the ant is trail-laying, a new segment is created with concentration Q, connected out its outward tip to the ant's former trail segment (if any) and with the ant's position at the end of the time step determining the coordinates of the other endpoint.

If the ant's path intersects an existing trail segment, it moves onto that segment and travels along it in the homeward direction until it has moved a total distance S for the current time step. If the ant is trail-laying, the intersected parent segment is divided into a basal segment and a distal segment at the point of intersection. The basal and distal segments inherit the pheromone concentration of the parent segment and the basal segment is connected at its distal end to the distal segment and the new segment created by the trail-laying ant up to the point of intersection (Fig. 1). When the ant is within distance S of the entrance, it moves directly to the entrance without error and is removed from memory. When a trail-laying ant reaches the entrance along an existing trail, the pheromone concentration of that trail is increased by Q; if it is depositing a new trail, the proximal endpoint of the trail is given the coordinates of the entrance and the trail segment is added to a list of segments connected to the entrance.

Movement in the battle zone. Recruits that do not immediately encounter an opponent begin to search. Little quantitative information is available on the movement of ants during battles. In some species, battles tend to spread along the recruitment trails (e.g., Driessen et al., 1984), suggesting that search may be biased towards active trails. Alternatively, searching ants may tend to stay near other fighting ants either because they are attracted to short-range alarm pheromones (Adams, 1994; Hölldobler and Wilson, 1978), or because they are attracted to movement, as are some foraging ants (Reznikova, 1982).

All search rules shared the following assumptions. Each second, the ant moves in a straight line for distance W. The rate of movement for searching ants was set to half that of ants following trails because ants tend to move faster when following pheromone trails (e.g., Deneubourg et al., 1989). When the duration of search reaches V, the search is terminated and the ant begins to head homeward.

Two search rules with these attributes were implemented.

(1) Undirected search was represented by correlated random walks. Each second, the bearing of the ant was set to the previous bearing plus an error drawn at random from a von Mises distribution with a mean of 0, and a standard deviation of σ_c. Higher values of σ_c produce more convoluted paths and slower rates of movement from the starting point of the search. We selected $\sigma_c = \pi/2$, so that ants tend to disperse slowly from the point at which they left the pheromone trail.

(2) Directed search. A simple algorithm was adopted to represent ants that concentrate their searches near particular stimuli. Two types of stimuli were considered: recruitment trails and fighting ants. At each time step, the distance (d) and direction to the closest stimulus are determined; i.e., the closest fighting ant, or the closest point on a pheromone trail of either colony. The ant turns towards this stimulus by an amount φ, which depends on the distance to the stimulus:

$$\varphi = \max(\beta d, \varphi_{\max}) \tag{3}$$

Thus, when the ant is at the stimulus ($d = 0$), φ is equal to 0 and the ant does not change its bearing. When the ant is farther from the closest stimulus, it turns more sharply towards it up to a maximum of $\varphi_{\max}$ at distances of $\varphi_{\max}/\beta$ or greater. A small error, ε, is added drawn from a von Mises distribution with mean equal to 0 and σ_e equal to 0.5 when the ants are searching near fighting ants. When the ants are searching near pheromone trails, σ_e is set to a lower value (= 0.01) so that they tend to keep moving forward along the trails. This algorithm leads to stochastic search near selected stimuli. The values of $\varphi_{\max} = 0.2$ and $\beta = 0.04$ were set to produce patterns that appeared reasonable when judged by eye. When the stimulus is a recruitment trail, ants tend to move along the trail while weaving from side to side, approximating the natural behavior of trail-following ants (Calenbuhr and Deneubourg, 1992; Hangartner, 1967).

We included an option for movement on trails to be obstructed by fighting ants, causing traveling ants to move in other directions (see also Deneubourg et al., 1989). When this option was implemented, if a recruit attempts to move outward (away from the nest) on a trail segment, the move is blocked if it brings the ant too close ($< Y$) to any fighting ant. If this happens, the ant is removed from the trail segment and begins searching. While searching, if its proposed movement brings it within distance Y of any fighting ant, the move is not allowed and new movements are proposed for up to five attempts. If none of these attempts yields a position $\geq Y$ from fighting ants, the searching ants remains in place for that time step.

2.2.7.6. Updating trail segments. Trail pheromone concentration declines by a fixed proportion (δ) each second. We used $\delta = 0.003$ for our simulations, producing a half-life of 231 s, or nearly four minutes, similar to estimates from laboratory studies (e.g., Jeanson et al., 2003). When the pheromone concentration on a trail segment drops below 0.1, it is assumed to be undetectable by ants, the trail segment is removed, and any connecting segments are updated to remove the connection.

2.2.8. Implementation

Simulations were programmed and implemented using Lazarus version 1.6.4, an integrated debugging environment for Free Pascal (Lazarus Team, 2017). A compiled freeware program, available from the first author, allows the user to vary the rules governing the ants' behavior and to implement each of the variants described here, as well as many others.

2.3. Simulation experiments

2.3.1. Effects of search patterns on battle shape

We monitored the development of battle shapes arising from three alternative algorithms for search by unengaged ants, described above: (A) directed search concentrated near other fighting ants; (B) directed search along trails; (C) uncorrelated random walks subject to the constraint that movement is blocked by other fighting ants. We conducted 100 replicate simulations for each of the three search rules. The length and breadth of the battle zone were recorded at 10 min intervals. The length of the battle zone is defined as the difference between the maximum and minimum coordinates of fighting ants along the x axis; the breadth is the difference between the maximum and minimum coordinates of fighting ants along the y axis.

2.3.2. Effects of assessment rules on the temporal dynamics of battles

We conducted simulations of the three assessment rules described above: (1) no assessment, (2) recruit when more numerous, and (3) recruit when outnumbered. For each two minute interval, the following values were recorded: the number of ants from each colony laying trails, the number of ants from each colony moving from the nest entrance towards the battle zone, and the number and mean position of fighting ants.

2.3.3. Effects of memory limitations

A series of simulations was conducted to evaluate the effects of limited worker memory on the collective ability of colonies to compare group strengths. In these simulations, fighting ants lays trails only when the ratio of nestmates to opponents in memory is greater than or equal to 1.5. The value of M (the number of encountered ants that can be remembered) was set to 2, 4, 8, 12, 16, or 20. The size (A_2 = maximum rate of recruitment) of the largest colony was either 1.25, 1.5, 1.75, or 2 times that of the smaller colony (A_1). For each combination of memory and size ratio, 100 replicate simulations were run and the fraction of cases in which the larger colony prevailed was recorded as well as the cumulative number of fighting pairs. When the pheromone concentration of trails reaching either colony's entrance dropped below a critical value, so that recruitment essentially stopped, the other colony was judged to have won the contest.

2.3.4. Priority effects

In naturally occurring conflicts, initial recruitment by one colony will be stronger than by the other colony because of chance variation in when scouts begin to lay trails. This gives one colony an initial advantage in numbers that may be amplified by assessment, causing a priority effect. We conducted a series of simulations to evaluate whether the larger colony (the one with the higher potential recruitment) can overcome an initial advantage in recruitment by the smaller colony. For each simulation, the battle was initiated midway between the two colonies by two ants from the smaller colony and a single ant from the larger colony. All three ants began trail-laying at the same moment and both ants from the smaller colony followed the same path. All other simulation rules were identical to those used in the evaluation of memory limitations, with $M = 20$. We conducted 120 replicate simulations recording the winning colony for each fight and, as an index of the intensity of the fight, the maximum number of fighting ants at any point during the battle.

3. Results

3.1. Effects of search patterns on battle shape

Variation in search rules by unengaged ants strongly affected the outcomes of conflicts and the shapes of the regions within which ants fought. Representative examples of three types of battles, differing only in the patterns of movement by recruits, are shown in Fig. 2. The development of battle shapes for these three battle types visualized in Fig. 3 by movement through shape-space defined by the length and width of the zone of fighting. The average rate at which the fighting moves towards the smaller colony is shown in Fig. 4.

In the first type of battle (type A), unengaged ants concentrated their searches near other fighting ants. A dense cluster of fighting ants formed in a region that was approximately oval and slightly elongated along the trails (Fig. 2a). Unengaged ants from the more numerous colony moved in and around the periphery of this cluster, especially on the side closer to their own entrance. The clusters increased in size during the first 20 min, after which the length and width of the battle remained roughly constant (Fig. 3) while the fighting moved gradually towards the smaller colony's entrance (Fig. 4).

In the second type of battle (type B), search by unengaged ants was biased towards pheromone trails. The region of fighting quickly formed a long, narrow zone along the trails (Fig. 2b). The battle moved more rapidly towards the smaller colony than in the previous case (Fig. 4) and the length of the zone of fighting declined as the battle impinged on the smaller colony's entrance (Fig. 3).

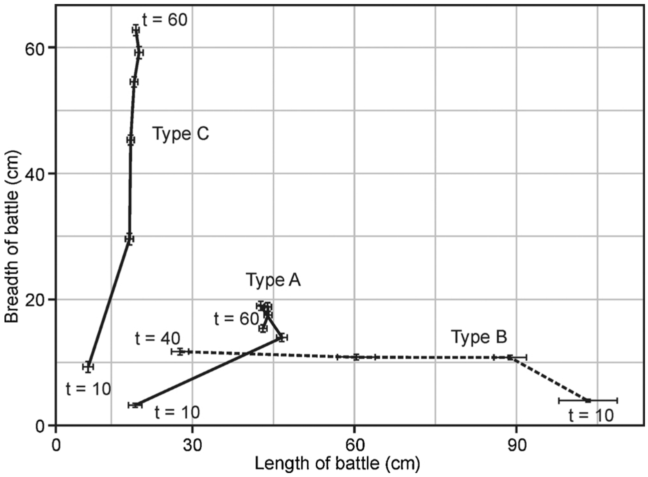

Fig. 3. Changes in the shape of the battle are shown as movement through shape-space defined by the length and breadth of the region of fighting. The means ± 2 standard errors are shown at 10 min intervals for 100 simulations of each of three battles types (A, B, C), beginning at time t = 10 min after the first enemy encounter. The three battle types arise from different search tactics, as described in the legend for Fig. 2. Battles of type B typically reach the opposing entrance within 40 min.

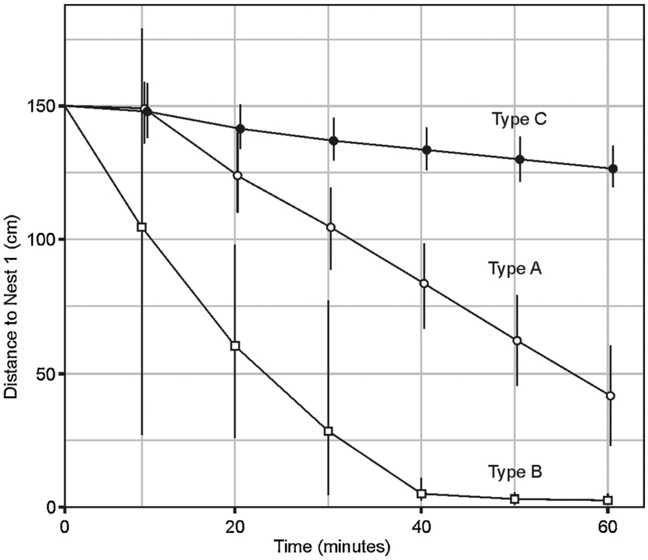

Fig. 4. The rate of movement of the battle zone towards the smaller colony varies with search tactics. The three battle types, which arise from different methods of search, are described in the legend for Fig. 2. The average distance between fighting ants and the entrance of the smaller colony is shown (with 95% confidence intervals) at ten minute intervals for 100 simulations of each battle type.

In the third type of battle (type C), ants fighting on the trails blocked the forward movement of recruits, which then left the trail and searched by correlated random walks. This behavior produced a front that was roughly perpendicular to the axis connecting the two colonies (Fig. 2c). Searching ants tended to accumulate on their own side of the front and to disperse laterally, extending the breadth of the front along its edges (Fig. 3). The zone of fighting ants moved more slowly towards the smaller colony than in the other two battle types (Fig. 4).

3.2. Effects of assessment rules on the temporal dynamics of battles

Variation in assessment rules produced dramatically different temporal patterns of trail-laying and recruitment. Representative examples are shown in Fig. 5, all of which assume directed search near fighting ants. In the baseline case (no assessment), the rate of arrival by each colony rose approximately logistically to a steady average, with a higher rate of arrival by the larger colony (Fig. 5a). The spatial pattern of the same type of battle is shown in Fig. 2a. In the second case, ants laid trails when they perceived their own colony to be locally outnumbered. The two colonies produced alternating bursts of recruitment (Fig. 5b). The position of the battle zone tended to oscillate back and forth, moving closer to the smaller colony during each cycle. In the third case, ants laid trails when they perceived that their colony locally outnumbered the enemy. Typically, a few ants from the smaller colony laid trails early in the encounter, but the larger colony sustained much greater recruitment (Fig. 5c).

3.3. Effects of memory limitations

When individual ants were assumed to assess force ratios, laying trails only when they perceive that their own nestmates locally outnumbered opponents, competing colonies often settled contests without highly escalated fights (Fig. 6). For example, consider the case with the weakest asymmetry in colony size (the worker population of the larger colony is 1.25x that of the smaller colony) and the lowest memory level

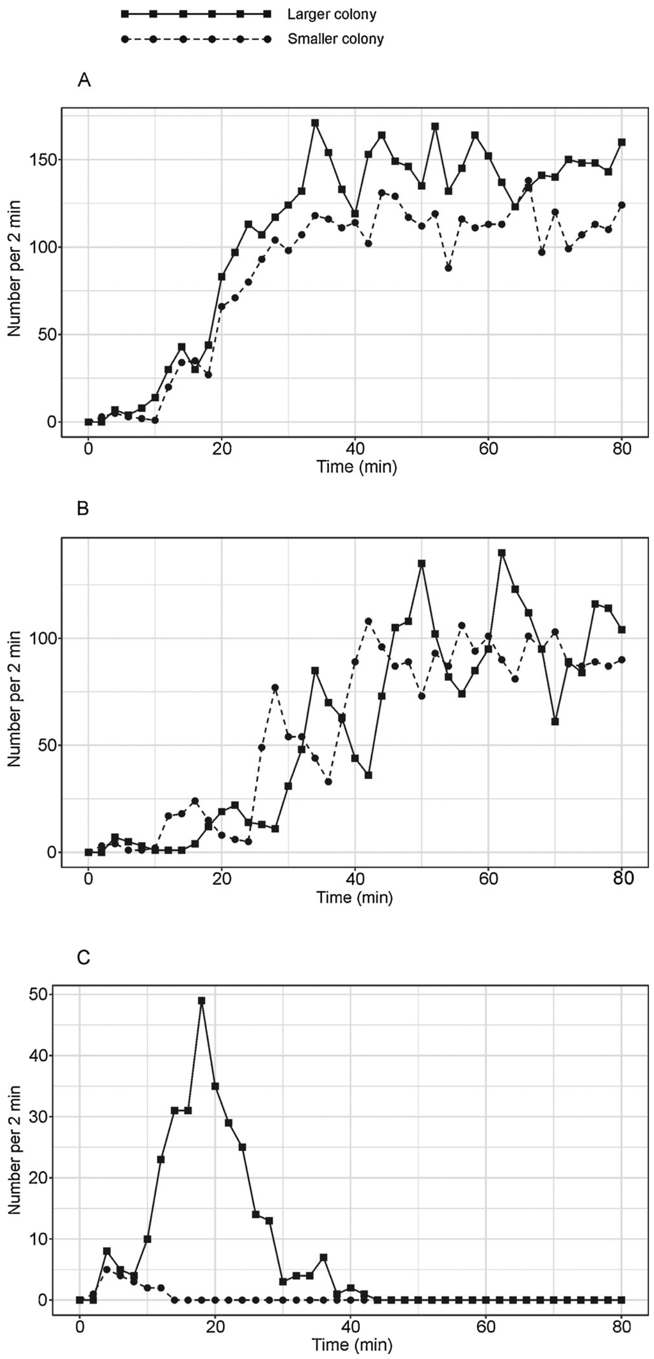

Fig. 5. Rates of recruitment (number of ants exiting the colony per 2 min interval) by the larger colony (solid lines and squares) and the smaller colony (dashed lines and circles) for representative examples of three assessment rules: (A) no assessment; (B) recruit when outnumbered; (C) recruit when more numerous. The larger colony has a maximum recruitment rate that is 25% higher than that of the smaller colony.

(each ant can remember the colony identities of four ants, including itself and the opponent with which it is grappling). In 145 trials (60.4%), the larger colony prevailed because the smaller colony quickly stopped recruiting; the total number of fighting pairs was low (median = 14; range 7–86). In 62 trials (25.8%), the smaller colony prevailed and the larger colony stopped recruiting; the total number of fighting pairs was low (median = 15.5, range 9–85). In the remaining 33 trials (13.8%), both colonies recruited heavily and the contest erupted into a highly escalated battle that was not resolved by the end of the simulation; the median total number of fighting pairs was 3356 (range 2485–4014). Fig. 6 shows these three outcomes using a threshold of 100 fighting pairs as the minimum for an escalated fight. Higher worker memory and greater asymmetries in colony size led to lower probabilities of escalated fights and higher probabilities that the larger colony won without an escalated fight.

3.4. Priority effects

When the smaller colony was given an initial advantage in recruitment, it won 102 of 120 simulated battles (85%), indicating that a head start can considerably increase the probability that a colony prevails. In the 18 battles (15%) won by the larger colony, the maximum number of fighting pairs was 129 ± 25.9 (mean + s.e.), compared to 42.8 ± 4.9 when the smaller colony won.

4. Discussion

Our simulations identify two aspects of behavior – search for opponents and assessment of force ratios – that are likely to underlie much of the variation in battle types across species, pointing to a need for empirical work on these processes. The linkage between individual and collective behavior is the central focus of studies on the self-organization of social behavior (Camazine et al., 2001; Detrain and Deneubourg, 2008; Sumpter, 2010). We discuss here several aspects of battle dynamics that reflect recurring themes in studies on self-organization (Camazine et al., 2001; Couzin, 2009; Sumpter, 2006), including the possibility of collective decision-making that extends the cognitive capacities of individuals. We also discuss how these models can guide empirical work on social insect battles.

4.1. Generation of battle diversity

Analysis of self-organizing social behavior shows that minor alterations to the rules of individual behavior can cause major changes in the macroscopic nature of group behavior. For example, Couzin et al. (2002) found that modifying the range of distances at which pairs of fish tend to align their movement leads to conspicuous shifts in the structures of simulated fish schools. These findings produce testable hypotheses and point to particular aspects of behavior that should be measured or experimentally manipulated.

We found that the rules of movement by unengaged ants as they search for opponents strongly affect the spatial dynamics of battles (Figs. 2 and 3). By changing only that aspect of behavior, we generated three contrasting battle morphologies. In battle type A, short-range attraction to fighting ants tends to produce rounded clusters of fighting ants growing from the original points of conflict (Fig. 2a). In type B, attraction to trails produces elongate battles (Fig. 2b) distributed along the approach routes. In type C, mechanisms inhibiting the forward movement of ants through the battle zone cause battles to spread laterally, with trails fanning from both approach routes to form a front (Fig. 2c). No doubt, other dynamics are possible based on alternative search rules. There are few published diagrams or detailed descriptions of battle shapes, but we have seen battles resembling the first two types in *Tetramorium immigrans* (Plowes, 2008) and *Solenopsis invicta* respectively (unpublished data). Possible examples of the lateral expansion of fronts are seen in territorial battles of the wood ant *Formica polyctena* (see Fig. 37 of Mabelis, 1979).

Variation in battle shapes has several consequences. The spatial development of the battle is likely to affect the mixing of ants from the two colonies and therefore the force ratios experienced by ants in different parts of the battlefield. When ants use assessment strategies, poor mixing, like that seen in Fig. 2c, will increase the probability that some ants from both colonies simultaneously judge their colony to be in the winning role, which can prolong the conflict. Furthermore, battle shapes covary with the rate at which the zone of fighting moves towards the smaller colony. When recruits push rapidly through the

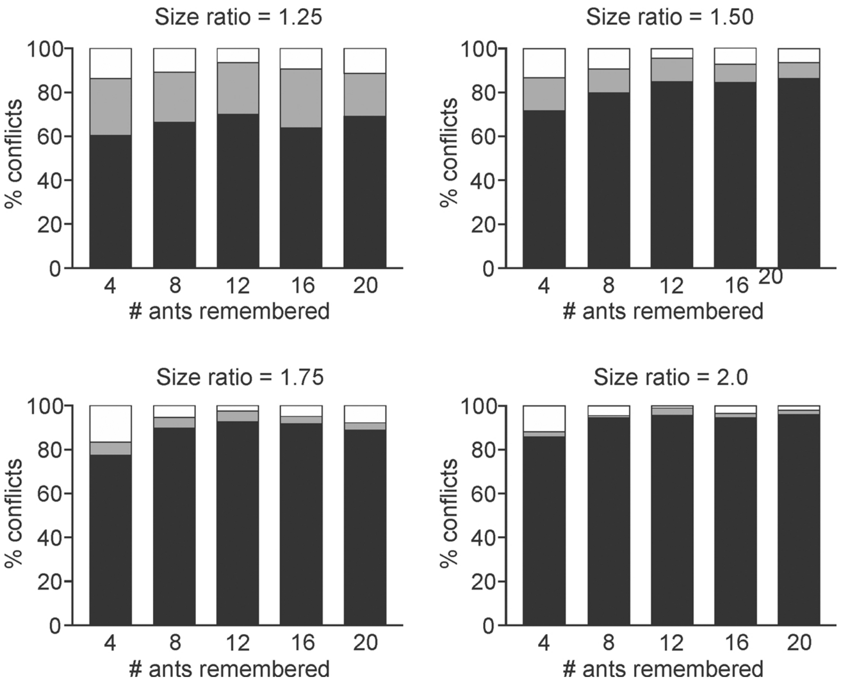

Fig. 6. The percentage of simulated battles resulting in low-cost victory by the larger colony (black shading), low-cost victory by the smaller colony (gray shading), or prolonged escalated contests (no shading) as a function of the size ratio of the opposing colonies (A_2/A_1) and the memory capacity of individual ants. Low-cost contests were those in which fewer than 100 pairs fought. Highly escalated contests involved more than 100 fighting pairs – typically thousands – and were usually not resolved by the end of the simulation.

battle, searching along the opponent's trails (Fig. 2b), the larger colony advances rapidly towards the smaller colony (Fig. 4). At the other extreme, when ants are inhibited from moving through the battle (Fig. 2c), it takes longer for a large colony to acquire territory from a small colony.

The process of assessment, encompassing the sensitivity of behavioral decisions to force ratios, generates diverse temporal patterns. When there is no assessment, the rate of arrival for both colonies rises to an average level that persists until the smaller colony is overwhelmed (Fig. 5a). If ants tend to lay trails only when they perceive that their nestmates are outnumbered, the rates of trail-laying and arrival by both colonies can oscillate out of phase (Fig. 5b) causing the position of the battle to move back and forth. These oscillations are driven by time lags between the initiation of trail-laying by scouts and the arrival of recruits into the battle. Alternatively, if ants tend to lay trails only when they judge their colony to be numerically superior, conflicts can be resolved quickly, with only modest levels of fighting (Fig. 5c). In the latter case, there may be some initial recruitment by the losing colony because, by chance, some individuals encounter more nestmates than enemies, but the rapid increase in numerical domination by one colony suppresses recruitment by its opponent.

To understand how battle dynamics arise, there is a need for data on assessment and search for opponents. Neither of these processes has been well studied. Several studies show that aggression by individual ants is enhanced by the presence of nestmates (Buczkowski and Silverman, 2005; Sakata and Katayama, 2001; Tanner, 2006); however, there has been little experimental work showing how recruitment is shaped by assessment (e.g., Adams, 1990). Search behavior by foraging ants has been quantified for several species (e.g., Fourcassié et al., 2003; Narendra, 2007) but we are aware of no similar investigations for fighting ants.

4.2. Mutual assessment and collective decision-making

Self-organizing groups of social insects can make flexible decisions that solve problems confronted by the colony. For example, ant colonies can find the shortest of several possible routes between the nest and a food source, and both ants and honey bees can select the most favorable of several possible nest sites (reviewed by Detrain and Deneubourg, 2008). These group-level decisions do not depend on workers evaluating each option and deciding individually which is the best; instead, the choices arise automatically from the way workers interact and communicate (Detrain and Deneubourg, 2008; Seeley, 2010).

When social insect colonies fight, they face the problem of deciding when to persist, when to escalate, and when to withdraw. If ants simply attack and recruit whenever they encounter opponents, fights escalate to a maximum level set by the number of workers available (Fig. 5a). Like solitary animals (Arnott and Elwood, 2009; Enquist and Leimar, 1983; Parker, 1974), colonies may be able to reduce the costs of fighting by assessing differences between themselves and their opponents, allowing the probable loser to withdraw without incurring the costs of a fully escalated contest. However, it is unlikely that any single insect is able to perceive the entire battlefield, especially in large contests. Therefore, mutual assessment is likely to self-organize from distributed decision-making by animals with local and incomplete information.

Lumsden and Hölldobler (1983) proposed that ant territorial contests allow competing colonies to compare the sizes of their worker populations. Two of the mechanisms that they explored are particularly relevant to our models. "Head counting" workers keep track of the numbers of nestmates and opponents encountered and use these tallies to estimate the relative strengths of the two colonies. Alternatively, ants that engage in "queue flooding" monitor the presence of unengaged opponents. Each colony recruits to try to match any surplus on the other side; thus, recruitment is enhanced when the ants detect that they are locally outnumbered. Our model of assessment differs by assuming a limit to the ant's memory, rather than a limit to the number of encounters, but both approaches show that accurate comparisons can be made based on modest cognitive abilities, especially when the contrast in colony sizes is large (Fig. 6).

No ant's territorial behavior is known in sufficient detail to produce a fully parameterized model of battle dynamics. However, it is useful to represent search behavior and branching trail systems in a plausible way to understand how collective assessment works. Whereas Lumsden and Hölldobler (1983) assumed that the probability of encountering an opponent instead of a nestmate remains constant, we placed assessment within a spatially explicit model that simulates the pattern of mixing within the battlefield. Force ratios change dynamically throughout the contest and vary from one part of the conflict to another. This allows different individuals to experience different force ratios, rather than assuming that all ants in the battle perceive the same asymmetry (e.g., Adler et al., 2018).

Mutual assessment by fighting groups can fail in two ways. First, the smaller colony may prevail because individual ants do not correctly perceive the asymmetry in colony sizes. This error arises when ants from the smaller colony initially outnumber those from the larger colony due to earlier arrival or stochastic variation in arrival rates. Second, assessment can be said to fail when both colonies recruit heavily, leading to prolonged escalated fights, rather than one colony ceasing to lay trails fairly quickly. Fig. 6 shows that the probability of both types of error is reduced when the asymmetry in colony size is greater or when ants can remember the colony identities of a greater number of other ants encountered in the battlefield.

4.3. Testing and extending the models

The assessment models make several testable predictions. Consider the case in which workers are assumed to recruit only when they judge their nestmates to outnumber opponents. (1) Trail-laying and recruitment are expected to be more pronounced for colonies that outnumber their opponents during early stages of the conflict than for colonies whose workers are outnumbered. (2) The degree of escalation, as measured by the total number of fighting ants from both colonies, is predicted to be lower when the initial asymmetry in numbers present is pronounced. However, the colony that originally has fewer workers present may occasionally overcome that disadvantage by recruitment. The number of fighting ants is predicted to be greater in such cases compared to conflicts in which there is no such reversal. (3) Battle outcomes are subject to priority effects: giving one colony a head start in discovery or recruitment is predicted to increase its probability of victory, even if it is the smaller colony.

All of these predictions match outcomes of experimental studies on territory defense by the ant *Azteca trigona* (Adams, 1990). Groups of *A. trigona* workers adjust their level of aggression according to the relative size of the fighting forces present in the region of the conflict. Rather than attacking and recruiting wherever enemies are discovered, workers tend to withdraw from places where their nestmates are outnumbered and to recruit to places where nestmates outnumber opponents (Adams, 1990). The victorious colony typically undergoes a gradual increase in arrival rate, while the other colony shows occasional smaller bursts of recruitment (compare Fig. 5c to Adams, 1990, Fig. 1). Early numerical advantages suppress recruitment by opponents, creating priority effects that favor the first colony to initiate recruitment. There were occasional reversals during which colonies that were initially outnumbered recruited strongly and gained possession of the disputed area. As in simulated fights, these contests tended to be more highly escalated, with greater numbers of ants fighting (Adams, 1990).

Priority effects occur because assessment leads to amplification of initial conditions, which can prevent the more populous colony from discovering its advantage. This too represents a recurring theme in the study of self-organizing social behavior: positive feedback underlies colony-level decisions, but it also leads to imperfection in the ability to compare alternatives. For example, although ant colonies may be able to find the shortest pathway between their nest site and food, they can become stuck on a comparatively long pathway if it is randomly selected by the first foragers. The progressive reinforcement of trail pheromones, which is essential to the colony's ability to coalesce on a single route, inhibits ants from exploring alternative pathways (Beckers et al., 1992; Camazine et al., 2001).

The modeling framework presented here can be modified or extended in several ways. We explored numerous variations and briefly discuss here how these affect battle dynamics as well as some other possible alterations. Minor changes to the functions governing search and recruitment had few consequences. For example, as an alternative means of causing ants to search near trails, we implemented a procedure in which ants compare the trail pheromone concentration detected on the left and right side of the body, turning towards the side with the greater concentration. Compared to the algorithm described in the paper, the spatial differences at the level of the entire battle were minimal. Similarly, some investigators use Hill functions instead of the Michaelis-Menten function (Eq. (1)) to describe recruitment responses (e.g., Beekman et al., 2001). Hill functions are more flexible, allowing sigmoidal responses to changes in trail pheromone concentration; their use may also affect the proportion of ants choosing each pathway at forks in the trail system. However, we found that while substituting Hill functions for Michaelis-Menten dynamics affected the time-course of recruitment, the effects were too small to alter any of our principal conclusions. We therefore favored simpler algorithms, with fewer parameters.

We simplified the model by assuming that all workers are identical. In reality, competing ants vary in size, fighting ability, and behavior both within and between colonies. For example, not all ants lay trails when returning home after a fight and recruitment may be driven by a minority of individuals. We explored alternative versions in which ants vary in their tendency to recruit nestmates to battles. When only a fraction of the ants are willing to grapple with non-nestmates and to lay trails afterwards, the density of fighting is reduced, but the large-scale spatial dynamics are quite similar to those depicted in the paper. A modest number of trail-laying scouts is sufficient to trigger a self-reinforcing pattern of recruitment that brings the colony close to its maximum possible response.

To simplify the models further, we omitted mortality, but naturally occurring territorial contests can kill many thousands of ants (Adams, 2016). The deaths of fighting ants restrict recruitment and in extreme cases may deplete the fighting force available to one or both colonies (Mabelis, 1979). In an escalated fight, the ability to kill opponents may depend on relative numbers because members of the larger group can "gang up" on their less numerous foes (Adams and Mesterton-Gibbons, 2003; Franks and Partridge, 1993). However, the few studies to experimentally vary numbers of fighting ants have not demonstrated any effect of force ratios on mortality ratios (Batchelor and Briffa, 2010; Plowes and Adams, 2005). When the models were modified to allow fighting ants to kill each other in equal ratios, battles grew more slowly due to reduced trail-laying but otherwise achieved spatial and temporal patterns that were similar to those shown in Figs. 2–5. In many respects, it makes little difference whether ants are considered to die or to return home without laying trails.

We did not include changes in motivation that may arise due to differences in the value placed on contested resources, to chemical marking of territories, or to recent experiences, all of which can affect the outcomes of territorial fighting (Adams, 2016). Furthermore, we did not address other ways that assessment can modify individual behavior, such as through the tendency to flee from concentrations of enemies. When ants flee from concentrations of opponents, territory can be gained more rapidly by the stronger group. Finally, our models are mechanistic and do not consider how selection acts on fighting behavior. An adaptationist extension of the model requires incorporating the costs of fighting and the benefits of resources gained. It will then be possible to determine the optimum rules of behavior at the individual level given outcomes at the group level.

Declarations of competing interests

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2019.01.009.

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