Incidental interactions among Neotropical army-ant colonies are met with self-organized walls of ants (Hymenoptera: Formicidae)

Kaitlin M. BAUDIER & Theodore P. PAVLIC

Abstract

Warfare between social groups has long been a popular topic of study among ethologists, but less well studied are the mechanisms by which interacting groups maintain peace. We report on the use of transient living walls as a mechanism by which avoidance is established between army-ant mass raids and non-prey ant species commonly encountered in the environment (other army ants and leafcutter ants). These transient walls are composed of a series of individuals performing stereotyped posturing displays at the border between interacting colonies. Unlike preemptive column guarding by soldiers, these walls are composed of a variety of worker sub-castes and can arise and disappear rapidly in response to the presence of local threats. Quantified videos of in-field artificial introductions revealed that walking ants switch to the task of posturing within a wall following multiple contacts with non-nestmates and that posturing ants return to walking as contacts with intruders decline and contacts with nestmates increase. The rapid shift of army ants to the task of forming transient walls at the instant when they are needed for traffic management provides a highly observable system in which to study the rules of individual-based living constructions, providing potential insight into similar processes across levels of biological organization.

Key words: *Eciton*, emergent structures, *Labidus*, *Nomamyrmex*, self-assembly, walling.

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Introduction

From cellular membranes to skin, one of the most basic hallmarks of life is a physical partition between external and internal environments. Such partitions both facilitate internal homeostasis and protect from intrusion. However, similar pressures exist at higher levels of biological organization, as in cases of large interacting groups of social-insect colonies. To mitigate the costs of aggressive interactions, many ant species that engage social defense to maintain their own territory also avoid foraging close to the territories of others, leading to regions of decreased interaction akin to intercellular space (HÖLLDOBLER 1976a, PLOWES & al. 2013). However, nomadic species often forage in novel environments with unknown distributions of competitors and with a decreased predicted benefit of territoriality because their home ranges are transient (WILLSON & al. 2011). In these cases where there is no territory to be lost or gained, coordinated movement away from regions of potential conflict may be more advantageous than costly aggression. Gaining information on how such species maintain social cohesion while moving to avoid costly interaction with foreign threats potentially informs how transient barriers between internal and external environments function across levels of biological organization.

Nomadic army ants in the subfamily Dorylinae are top predators with large colony sizes enabling mass raids (GOTWALD 1995). Army ants are distributed densely in Neotropical lowland forests (O'DONNELL & al. 2007), making inter-colonial raid and emigration collisions a high probability (FRANKS & BOSSERT 1983, KRONAUER 2020). Anecdotes and models suggest that inter-colony raid encounters typically result in avoidance due to the high cost of combat with a robust competitor and low benefit of defending a transient territory (FRANKS & BOSSERT 1983, SWARTZ 1997, WILLSON & al. 2011). However, little information exists on

fine mechanisms of how this complex truce is achieved between two such immense groups. By investigating the progression of individuals and groups through stages of detection, recognition, decision making, and behavioral response, we gain insight into how small subsets of social groups can self-organize in a local area to avoid escalation to large-scale conflict with an encountered threat.

Army ants do not appear to be repulsed by volatile trail pheromones of other colonies (WILLSON & al. 2011). Instead, opposing groups of army ants appear to shift to avoidance following physical contact (SWARTZ 1997, WILLSON & al. 2011), suggesting that local tactile interactions or close-range olfactory cues are a major part of adaptive inter-colony avoidance in these species. In this note, we investigate the rules of these local interactions among several common army ants in the Neotropics – *Eciton burchellii foreli* MAYR, 1886, *Eciton hamatum* (FABRICIUS, 1782), *Labidus praedator* (SMITH, 1858), and *Nomamyrmex esenbeckii* (WESTWOOD, 1842). We report high incidence of a collective behavior in which, upon encountering ants of another colony, multiple posturing ants begin to stand side-by-side in living walls, a low-aggression group behavior establishing a transient boundary that facilitates avoidance of further inter-colony interactions. These temporary wall formations are distinct from previously described pre-emptive and static wall fortifications (MIURA & MATSUMOTO 1998, ANDERSON & al. 2002) in that they arise only in proximity to a sensed threat. We also present anecdotes of army ants using temporary walls to delineate foraging and emigration routes from those of other social insects, including the conspicuous trunk trails of the leaf-cutting ant *Atta cephalotes* (LINNAEUS, 1758).

Although there are accounts of raid avoidance in *Eciton burchellii* (see SWARTZ 1997, WILLSON & al. 2011) and in the Old World army ant *Dorylus molestus* (see SCHÖNING & al. 2005), it is poorly known whether and to what degree other species have similar behavioral responses. Army ants differ substantially in the degree to which they forage above ground, a factor that can shape social and physiological dynamics of their foraging ecology (KUMAR & O'DONNELL 2009, BAUDIER & al. 2015). Differences in inter-colony avoidance behaviors among species can help inform the generalizability of these collective behavioral strategies and highlight important correlates of life history and ecology. To this end, we report the outcome of pairings of different species that may encounter each other in natural scenarios.

Methods

Inter-colony introductions: Artificial cross introductions between different colonies were used to elucidate local mechanisms by which army-ant raids avoid one another. Work was conducted on Barro Colorado Island (Panama Province, Panama, 9° 09' N, 79° 51' W) from 29 January to 2 February 2018. Army-ant colonies were located by using trail-encounter methods (KUMAR & O'DONNELL 2009). Conspecific raids found at least 300 m apart within 24 hours were assumed to be different
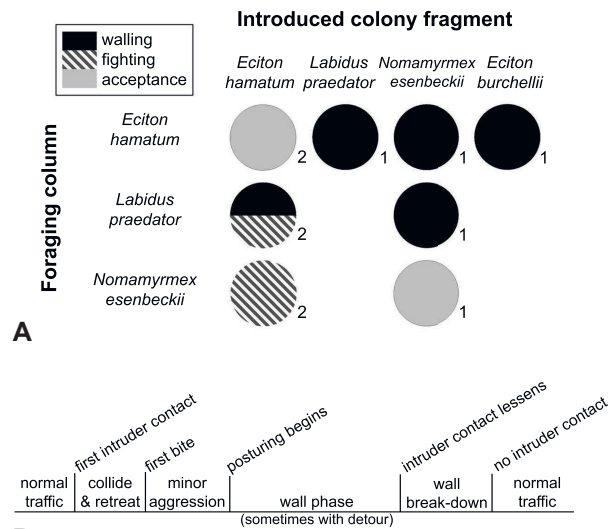

Fig. 1: (A) Occurrence of different behaviors across army-ant colonies artificially brought into contact by introduction of colony fragments (*n* = 100 ants) from the raid column of one colony to that of another colony in different species combinations. Behavior reported here was of the defending foraging column, though in most cases the response from the introduced colony fragment was reciprocal. Numbers in the bottom right of each circle represent the number of times each scenario was repeated using unique colony combinations. Each encountered raid column was used for only one introduction. (B) Observed timeline of transitions to and from emergent collective walling behavior. Depicted length of phases is not proportional to time spent within each behavioral phase.

colonies, as this exceeds the typical length of raids for the species in this study (RETTENMEYER 1963, TELES DA SILVA 1982). One hundred army-ant workers were collected from the first raid column encountered and then carried to the next encountered raid of a different colony, where they were deposited on top of a naturally occurring raid column. Each encountered raid column was used for only one introduction. Paint markings distinguished conspecific colonies. Sharpie® oil-based paint pen was applied to the dorsal surface of the alitrunk, a standard method (HOLBROOK 2009). Preliminary work showed no apparent differences in behavior or treatment of painted ants when placed within groups of unpainted nestmates. Following introduction of colony fragments, the resultant behavior of both parties of ants was filmed for a maximum of 20 minutes or until the interactions between the two groups dwindled (more than 60 s elapsed without non-nestmates coming within one body length of one another). Once this was complete, the process was repeated. Number of introductions (equal to number of raids) is shown in Figure 1A. Colony fragments were provided water *ad libitum* during transport. Length of time between collecting and introducing fragments did not exceed three hours. A dichotomous key by WATKINS (1976) was used to confirm species identities.

If two or more ants were observed posturing side-by-side during the observation window, this was considered to be an outcome of "walling", although in practice all observations of walling involved more than three ants. Cases where no walling was observed and there were instances of biting, pinning, stinging, or dismemberment were categorized as "fighting". Cases where no walling was observed and there were no cases of biting, pinning, stinging, or dismemberment were considered "acceptance".

Testing hypothesized cues of walling: Next, the potential cues that trigger individuals to transition into and out of walling behavior were investigated by studying, a single filmed raid introduction which displayed the highest number of visible posturing individuals (an introduction of *Labidus praedator* to a column of *Eciton hamatum*). Army ants use a suite of local tactile and olfactory cues to orient along raid columns (Topoff & Lawson 1979, Billen & Gobin 1996). As such, we hypothesized that higher non-nestmate contact could stimulate previously walking ants to assume and maintain a stationary defensive posture over time (leading to the collective formation of a wall in areas dense in non-nestmates). It was also hypothesized that ants would grow more likely to abandon defensive posturing if the front lines of non-nestmate encounter and high nearby nestmate traffic moved away from them, causing a local decrease in non-nestmate encounters.

To test whether walking ants were more likely to initiate motionless posturing based on recent nestmate or non-nestmate collisions, encounters of 25 randomly selected *Eciton hamatum* walking in a raid column were counted over the field of view (~15 cm length of trail column), and were compared between those that ended up posturing and those that continued walking out of the frame using exact Wilcoxon rank-sum tests (α = 0.05) performed in R version 4.0.0 (R Core Team 2020). These 25 ants were chosen at random as they entered the field of view (without knowledge of which ants would begin posturing) from the first 4 minutes immediately following introduction of a *Labidus praedator* fragment to an *E. hamatum* column and included 13 ants walking towards the bivouac (temporary nest) and 12 outbound ants within the raid column. Each *E. hamatum* worker was observed from the time it entered the field of view until it either exited the field of view (in the case of walking) or until it began to posture. An ant was considered to be posturing if it stopped walking and extended its mandibles and antennae while facing the general direction of one or more non-nestmates for a minimum of 3 seconds.

To test whether and which encounters were associated with the decision of ants within walls to resume walking, nestmate and non-nestmate contacts for 22 observed posturing *Eciton hamatum* were counted. These 22 posturing ants were chosen at random (without knowledge of whether subjects would continue posturing or resume walking) from two central timepoints in the same video when maximum walling could be seen. Each posturing ant was observed starting at the maximal wall timepoint.

The number of nestmate and non-nestmate contacts that occurred over the next 30 s was recorded, as was whether each ant continued posturing or stopped posturing during observation. If an ant ceased posturing during the 30 s observation window, observations were backtracked to before the starting timepoint to ensure that number of collisions over 30 s were counted in each case, regardless of outcome. Ants that began fighting (biting, pinning, stinging) or shifted and disappeared from view were excluded from consideration in both sets of comparisons (beginning and stopping posturing). As described for initiating walling behavior, nestmate and non-nestmate encounters were compared between ants that remained posturing and those that resumed walking using exact Wilcoxon rank-sum tests.

Results and discussion

Inter-colony introductions: We observed workers of various sub-castes within the raid column corralling introduced non-nestmate ants by engaging in a stereotyped side-by-side posturing ("walling") where they stood motionless with their mandibles open and antennae extended, with body either straightened or in c-posture as described by Jeanson & al. (2005). Posturing ants paused from walking in apparent response to encountering non-nestmates, subsequently forming an outward-facing line at the border between the two groups (Fig. 2A; Video S1 as digital supplementary material to this article, at the journal's web pages). Walls were often formed by both parties of ants facing each other in formations similar to picket lines or American football linemen. Opposing postured ants periodically thrusted forward at one another, contacting each other briefly on the legs or antennae but typically returning to static postures afterwards. These threat displays between individuals of different colonies created transient borders between the two groups of ants. Walling emerged following initial stages of retreat and light aggression, which included intense antennation and often some biting between non-nestmates (Fig. 1B). However, all observed instances of walling were initiated within 55 seconds from first contact between groups. The duration of walling varied substantially, but incidence of posturing decreased as non-nestmates dispersed.

Collective use of this walling behavior is apparently context specific (Fig. 1A). Although walling against heterospecific introductions was observed in multiple army-ant species, it was not observed in *Nomamyrmex esenbeckii* workers (Fig. 1A). Instead, defending *N. esenbeckii* showed a tendency to defend raid columns from heterospecific threat by engaging in outright fighting (biting, pinning, stinging, dismemberment; Fig. 2D). This high level of aggression appears to be only in the context of the raid column and was not observed when *N. esenbeckii* workers were introduced as fragments to the raid columns of other species. As the most subterranean species in the study, *N. esenbeckii* colonies frequently traverse landscapes to raid other ant nests using confined underground tunnels (Schneirla 1971, Swartz 1998). Avoidance via walling

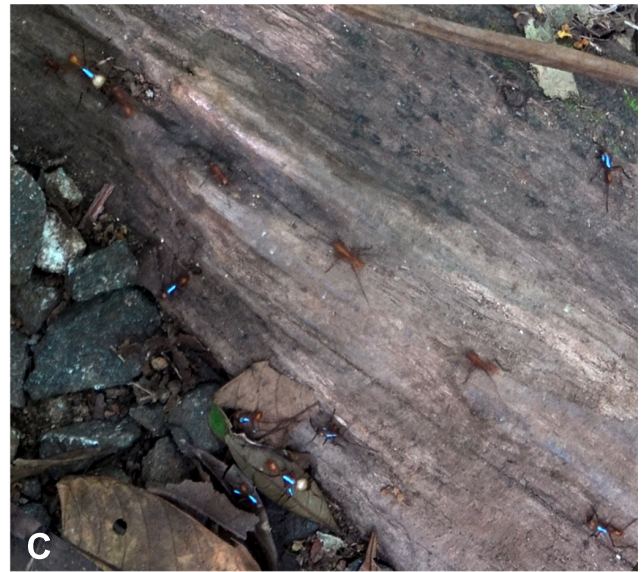| walling	no walling

Fig. 2: Different responses to cross introduction of army-ant colonies to one another: (A) A foraging column of *Eciton hamatum* using walling behavior to corral an artificially introduced colony fragment of *Labidus praedator* (background lightened for visibility); (B) in some cases, posturing ants surrounded an individual intruder, or small pocket of intruders, forming a cyst-like shape; here, *L. praedator* use walling to prevent an isolated *Nomamyrmex esenbeckii* worker from interacting with a raid column; (C) *E. hamatum* workers in a column ignore introduced *E. hamatum* from another colony (marked with blue), allowing several to roam freely within the raid column; (D) *N. esenbeckii* defend their column from introduced *E. hamatum* (marked with white) using direct engagement (biting, stinging, dismembering) rather than walling behavior.

may be a less effective strategy in such confined environments.

Both in the case of *Eciton hamatum* and *Nomamyrmex esenbeckii*, conspecific colony fragments were accepted without aggression or walling following rigorous antennation (Fig. 2C), and this is in spite of the observation that *E. hamatum* did form walls in the case of heterospecific introductions. Our artificial (albeit brief) separation of worker fragments from queens may have altered worker cuticular hydrocarbon (CHC) profiles sufficiently to make non-nestmates unidentifiable within species where these differences are presumably the most subtle. Similar mechanistic factors have been suggested to explain observations of colony fusion, wherein colonies of army ants that have lost queens combine worker forces with other encountered queened colonies, an effect presumably resulting from loss of CHCs among queen-less workers (Schneirla 1949, Schneirla & Brown 1950, Kronauer & al. 2009). Alternatively, acceptance may have been high among selected conspecific colonies due to inadvertent introduction between colonies with high relatedness. Regardless of speculated mechanism, our observations of manipulated
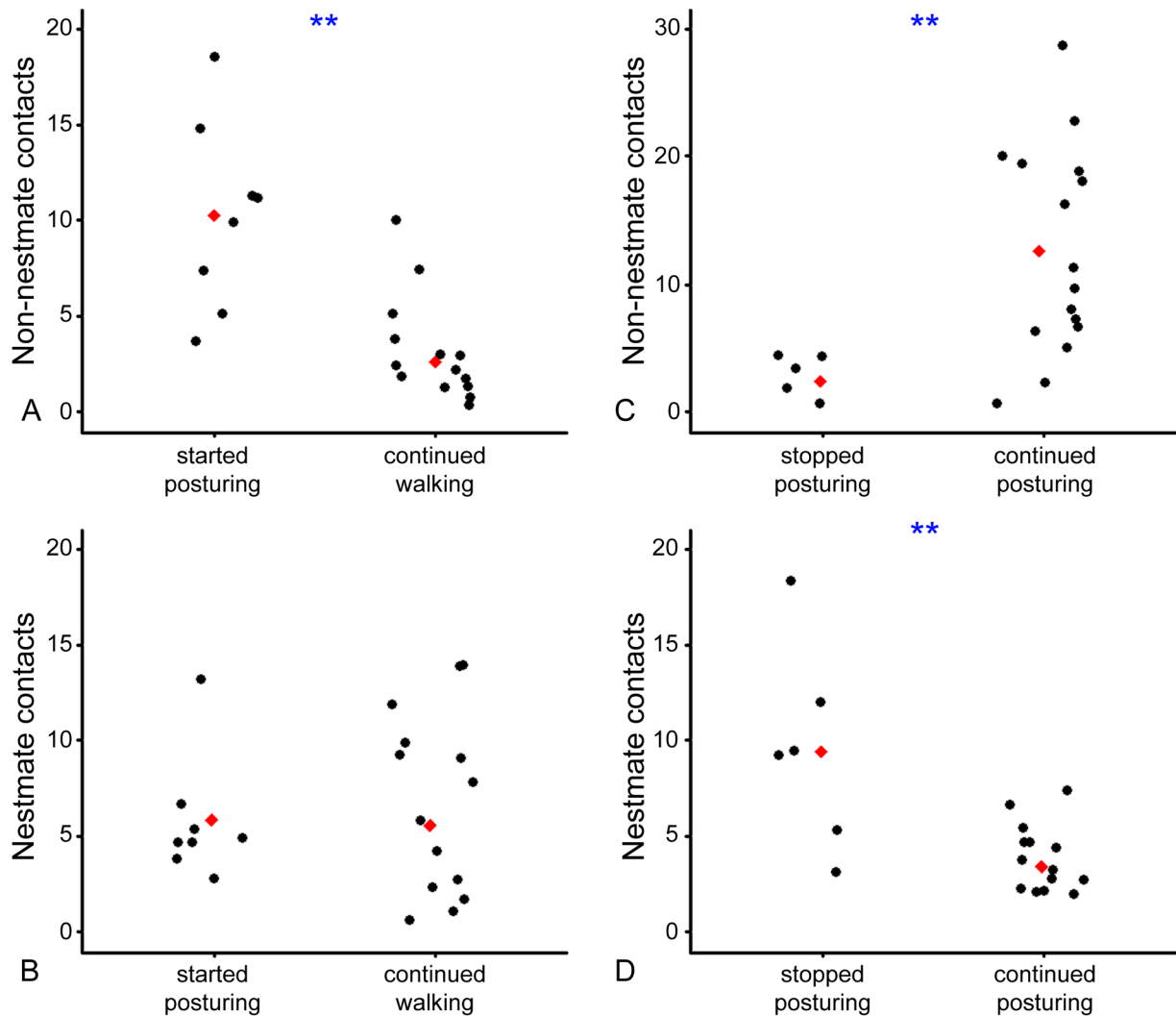
Fig. 3: Immediately previous nestmate and non-nestmate encounters as potential predictors of likelihood for an individual ant (*Eciton hamatum*) to begin and stop stationary open-mandibled posturing behavior (building blocks for collective "walling") when encountering other army ants (*Labidus praedator*); * $p < 0.05$, ** $p < 0.01$. Red diamonds represent means. Data are graphed using random jitter to improve visualization of overlaying points, however the x-axis is categorical. (A) Ants that started posturing during our observation window (from entrance into the video frame until ants either walked out of view or began posturing for at least 3 s) had significantly more recent non-nestmate contacts. (B) Ants that started posturing and those that continued walking during our observation window had no significant difference in numbers of recent nestmate contacts. (C) Ants that persisted in wall postures during the observation window (30 s) had significantly more non-nestmate encounters. (D) Ants that abandoned the task of posturing during the observation window had significantly more recent nestmate encounters.

conspecific non-nestmates being accepted without walling stands in contrast to anecdotes which suggest that walling does occur between naturally colliding colonies of the same species (RETTENMEYER 1963).

Emergent rules of walling: We detected no difference in likelihood of ants to begin posturing based on whether they were walking towards the bivouac versus walking towards the raid front (Fisher's exact test: $p = 0.411$; Tab. 1). Ants that stopped walking and began posturing had significantly more recent non-nestmate encounters (exact Wilcoxon rank-sum test: $W = 128$, $p < 0.001$) but similar numbers of recent nestmate encounters (exact Wilcoxon rank-sum test: $W = 77$, $p = 0.616$) to those that did not begin posturing. Ants that gave up the

Tab. 1: Frequency table used to test the effects of walking directionality on likelihood to begin posturing (walling) behavior.

Walking direction	Began posturing	Continued walking
Bivouac	3	10
Raid front	5	7

task of posturing within a wall had fewer recent non-nestmate encounters (exact Wilcoxon rank-sum test: $W = 8$, $p = 0.002$) and more recent nestmate encounters (exact Wilcoxon rank-sum test: $W = 84$, $p = 0.005$) than those that continued posturing (Fig. 3). Together, this suggests

that, although non-nestmate encounters primarily drive the initiation of posturing and wall formation, both nest-mate and non-nestmate encounters may be factors in determining when posturing and walling ends. The role of this asymmetry in the spontaneous emergence and persistence of self-organized walling behavior could be a target for further theoretical investigation. Data used in these analyses can be found in digital supplementary material to this article (Data S1 & S2) at the journal's web pages.

Observations of walling against leaf-cutting ants: Walling behavior may also be of use beyond dealing with other army ants. Where both species occur, raid columns of *Eciton burchellii* commonly use the cleared trunk trails of the leaf-cutting ant *Atta cephalotes* to navigate between the bivouac and raid front (Rettenmeyer 1963; K.M. Baudier, unpubl.; S. Granados Martínez, pers. comm.). Although some army ants are specialized predators of leaf-cutting ants, *E. burchellii* is not (Watkins 1971, Hoenle & al. 2019). Large colonies of *A. cephalotes* are therefore unlikely to become aggressive with *E. burchellii* colonies as the potential costs of such conflict could be mutually high with little benefit. Consistent with this notion, we observed co-trailing *E. burchellii* and *A. cephalotes* passing one another within centimeters without conflict or even apparent need for defensive walls (K.M. Baudier, unpubl.). However, we have also witnessed two instances of army ants using walling to corral encountered leaf-cutting ants: once when the army-ant colony was emigrating (*E. burchellii foreli* at La Selva Biological Station, Costa Rica), and once when the army-ant column fully bisected a leafcutter column (*E. burchellii parvispinum* in Monteverde, Costa Rica).

On 27 June 2014 at approximately 21:00, a colony of *Eciton burchellii foreli* formed a living wall separating their emigration column from an adjacent foraging column of *A. cephalotes*. The two columns followed one another closely and ran side-by-side for more than nine meters. Workers in the emigration column carried prepupae. Where the two columns abutted one another, unburdened *E. burchellii foreli* workers collectively engaged in walling behavior similar to what we observed in inter-colony army-ant interactions, with the exception that walling was not reciprocal. Workers of *E. burchellii foreli* faced outwards and spaced at antennal length from one another with mandibles open, with the occasional *A. cephalotes* worker colliding with an aggressively postured army ant before returning to the main column.

We observed an additional instance of army ants using walling behavior to corral *A. cephalotes* while both parties foraged in Monteverde on 22 July 2013 at 15:53. In this case, a raid column of *Eciton burchellii parvispinum* entirely bisected a column of *A. cephalotes* en route to a paper-wasp nest (*Polybia raui* Bequard, 1933) approximately three meters away in a mud bank. The two colonies interacted atop a fallen tree branch that leaned across the mud bank and was partly connected to the trunk of the tree from which it had fallen. The *A. cephalotes* appeared to have used this branch to access the canopy prior to bisec-

tion. Canopy-bound *A. cephalotes* encountering the wall of *E. burchellii parvispinum* immediately retreated, while nest-bound *A. cephalotes* bearing leaves accumulated densely but did not engage in reciprocal walling behavior.

In both cases, the living-wall behaviors between army ants and leaf-cutting ants were identical to those observed between army ants with the exception of reciprocity; leaf-cutting ants did not engage in posturing, but they instead bumped into and avoided posturing army ants within the barrier before retreating. Leaf-cutting ants in the genus *Atta* have been previously observed forming lines of stationary ants at nest entrances in defense against the attine-specialized predator *Nomamyrmex esenbeckii* (see Swartz 1998, Powell & Clark 2004). However, this behavior did not appear to be used in response to encounter with *Eciton burchellii* away from the nest in our observations. As before, army ants facing leaf-cutting ants only formed living walls in the immediate vicinity of the encounter, and walls were composed of various worker sub-castes.

Interpretations and implications: Temporary living walls are a strategy used by multiple epigeic army-ant species to organize collective avoidance of high-cost interactions with other social insects that might otherwise compete for access to space while raiding and emigrating. These living walls help to coordinate the otherwise arbitrary assignment of ants to surface area to ensure minimal interactions and maximal flow of the two groups. This transient walling behavior emerges from multiple posturing ants in close proximity. At the individual level, posturing appears to initiate after a rise in non-nestmate encounters, and a return to walking behavior occurs when those non-nestmate encounters decline and nestmate encounters increase. This strategy of creating living walls only in the presence of an adversary is notably distinct from preemptively positioning defense-specialized individuals to flank foraging routes, a strategy commonly observed in multiple species of New and Old World army ants (Gotwald 1995, Sendova-Franks & Franks 1999, Weissflog & al. 2000, Kronauer 2020) and in some termites (Miura & Matsumoto 1998). By contrast, we observed these walls arising from a mix of worker sub-castes (predominantly non-soldier). Also, by only creating walls as needed, colonies can reduce numerical investment in unnecessary defense tasks. For example, in our reports of contact between army ants and leaf-cutting ants living walls were constructed only on the side of the trail which came into contact with non-nestmates. To our knowledge, there are only two previously published reports of ephemeral living walls as a mechanism of inter-colony avoidance in army ants. The first is a brief anecdote by Rettenmeyer (1963), who described "picket lines" with "little conflict" between sides. This observation of natural raid collisions is consistent with our observations of manipulated introductions. Second is a recently published account of collision between emigration columns of *Eciton burchellii* and *Neivamyrmex gibbatus* (see Kronauer 2020). This account showed intriguing evidence of age polyethism in

this walling behavior, with visibly darker and less callow workers predominantly performing defensive posturing within contact-dependent walls.

Living walls are one case in the vast repertoire of living structures (e.g., self-assembled structures) performed by army ants, as reviewed by ANDERSON & al. (2002). Other striking examples (which similarly implicate contact rate with nestmates) include the formation of traffic-easing living bridges (REID & al. 2015), pothole filling by small ants (POWELL & FRANKS 2007), and the formation of massive living "bivouac" nests composed of interlocking worker bodies that shelter and dynamically thermoregulate the queen and brood (SCHNEIRLA & al. 1954, RETTENMEYER 1963, FRANKS 1989, BAUDIER & al. 2019). One challenge to studying how army ants individually function in most of these complex structures is that not all ants are continuously visible. By contrast, army-ant walls present an easily observable system for assessing individual interactions in the context of a complex collective behavior.

Transient avoidance walling in army ants has elements that appear convergent among a wide variety of cursorial social insects and may represent a broadly applicable mechanism by which social agents establish temporary borders. Colonies of the Southeast Asian termite *Longipeditermes longipes* forage on leaflitter in the open air and commonly defend their foraging columns using living walls of outward facing soldiers in advance of contact with potential threats (MIURA & MATSUMOTO 1998). Workers of the honey-pot ant *Myrmecocystus mimicus* also use paired and stereotyped posturing in "territorial tournaments" to collectively establish transient borders with nearby colonies, and may use a comparison between nestmate and non-nestmates contacts to trigger recruitment of recruit raiding parties (HÖLLDOBLER 1976b, HÖLLDOBLER & LUMSDEN 1980, LUMSDEN & HÖLLDOBLER 1983). Although less stereotyped and more directly aggressive, nearby colonies of pavement ants (*Tetramorium immigrans*) similarly establish individually pairwise and transient battlefronts that move towards the nest of the weaker colony when establishing territory (PLOWES 2008). Army-ant walls also bear a striking, though less self-sacrificial, resemblance to the manner in which social gall aphids (*Nipponaphis monzeni*) heal breaches in gall walls through localized soldier mobilization and eruption (KUTSUKAKE & al. 2019). New insights on collective walling behaviors therefore have the potential to inform an array of strategies for conflict resolution among insect societies.

Ephemeral walling behavior in army ants may also illuminate similar processes at drastically different levels of biological organization. How cells interact with one another during the formation of cysts, how platelets adaptively form scabs and how they dismantle, or how cell membranes composed of phospholipid bilayers emerge from molecules with simple rules of interactions are all processes that share a decentralized establishment of barriers between what is "outside" and what is "within". However, these processes are also difficult to observe. Being able to follow individual-level investment in such transient structures can lead to models for understanding naturally evolved strategies for re-allocating a limited resource from a primary task (walking) to a secondary task (posturing) that improves the efficiency of the first (REID & al. 2015). Furthermore, directly studying the interaction between an abstract border and the ants that implement it provides unique opportunities to test and refine supposedly general models of top-down causation that are normally restricted to biochemical application (AULETTA & al. 2008). For example, emergent walling structures in army ants are higher-order structures that help to better understand the fine-grained behaviors of individual posturing ants just as three-dimensional folds of an RNA molecule add causal efficiency by reducing the degrees of freedom of the biopolymer subunits. Whether and how hypotheses generated by easily observable social-scale phenomena can inform new ways of thinking about these processes remains an exciting avenue for future investigation.

Acknowledgments

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