DYNAMICS OF SELF-ASSEMBLED STRUCTURES IN *ECITON* ARMY ANTS

MATTHEW JAMES LUTZ

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Adviser: Iain D. Couzin

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Abstract

Army ants of the genus *Eciton* are among the most well-studied of the social insects. Their sophisticated social organization, nomadic lifestyle, and role as top predators in tropical ecosystems have interested researchers for decades, revealing much about their biology, behavior and ecological significance. This work has had significant impact across disciplines, generating fundamental insights for the study of self-organization and providing inspiration for emerging fields like collective robotics. However, an important aspect of army ant behavior has been relatively understudied: the structures that *Eciton* ants build out of their own bodies. Understanding the mechanisms by which these structures form, their dynamic properties and their adaptive function at the colony level is the focus of this dissertation.

In the chapters that follow, I present the results of a series of field experiments conducted in Panama over the last few years, along with a set of models aimed at elucidating the mechanisms underlying the formation of self-assembled structures. I show that self-assemblages are a fundamental aspect of the behavior of the two most conspicuous and well-studied species of army ant, *Eciton burchellii* and *Eciton hamatum*, and provide significant adaptive benefits at the colony level. The deployment of self-assemblages by these two species is a key innovation that has contributed to their dominant ecological position as top predators in the tropical forests of the New World. While other social insects form self-assemblages for specific tasks and under certain conditions, no other animals rely so heavily on this unique behavior as a fundamental aspect of their ecology.
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Introduction

Evolution and behavior of army ants

The term “army ants” is a functional definition for a group of species that share a suite of behavioral and morphological traits known as the *army ant adaptive syndrome* (Gotwald 1995), adaptations that have enabled these ants to become dominant predators throughout the tropics (Rettenmeyer 1963; Schneirla 1971; Wilson 1971; Kaspari & O’Donnell 2003). These interrelated traits include obligate collective predation, nomadism, and highly specialized queens that are permanently wingless (Kronauer 2009). Colonies are large, and reproduce by fission (Rettenmeyer et al. 2010). Maintaining a large colony size on a primarily carnivorous diet appears to require the adoption of a nomadic lifestyle, an observation initially made by Wheeler (1928). The interdependence of these attributes has been commented on repeatedly (Schneirla 1954; Wilson 1958), culminating in the currently accepted set of traits that define the syndrome, and thus the group (Brady 2003; Kronauer 2009). While some combination of these traits occur in a number of ant species, until recently the “true army ants” were generally agreed to consist of three subfamilies: Aenictinae, Ecitoninae, and Dorylinae (Wilson 1964). However, these have all recently been subsumed under the single subfamily Dorylinae, along with three other groups formerly considered part of the dorylomorph clade (Brady et al. 2014).

Within the revised Dorylinae subfamily, the army ants are now generally agreed to consist of 5 genera in the New World (*Cheliomyrmex, Labidus, Eciton, Neivamyrmex,* and *Nomamyrmex*), comprising 147 species, and 3 genera in the Old World (*Aenictus, Aenictogiton,* and *)
and *Dorylus*), comprising 184 species (Brady & Ward 2005; Brady et al. 2014). The evolutionary history of this group has been the subject of much debate, primarily over the origin of the army ant syndrome, and a longstanding theory held that this combination of traits had arisen independently in the New World and the Old World, with similarities due to convergent evolution (Gotwald 1979). However, recent phylogenetic analyses generally support the monophyly of all the army ants listed above (Brady 2003; Moreau et al. 2006). Complicating the picture, the origin of this monophyletic army ant group was most recently estimated at approximately 79 mya (Brady et al. 2014), which implicitly challenges a previous hypothesis that the New World and Old World army ants diverged from a common ancestor after the breakup of Gondwana (approximately 100 mya). This inconsistency has not yet been addressed, and further phylogenetic work will likely continue to clarify the early history and development of the army ant syndrome.

**Group predation**

While most ant species deploy solitary scouts to search the environment independently, recruiting nestmates upon the discovery of a food source, army ants always forage as a group, cooperating to flush out, capture and overwhelm prey. This adaptation has enabled the exploitation of prey types not accessible to individual foragers, specifically large arthropods and the brood from colonies of other social insects (Wilson 1958). The most extreme examples of this collective predatory behavior take the form of swarm raids, characteristic of certain species of *Eciton* and *Labidus* in the New World and *Dorylus* in the Old World. These can stretch for up to 200 m and take in tens of thousands of arthropod prey items per day (Franks et al. 1999). Although not typical for most army ants, swarm raids have been the subject of numerous
dramatic descriptions and anecdotes, including common tales of army ants entering buildings and clearing out resident arthropods (Gotwald 1995). Swarm raids, in their size and impact, represent the most visible manifestation of the army ant syndrome, demonstrating the evolutionary success of this suite of adaptations in ways that are easily perceived from a human perspective. However, the vast majority of army ant species are far less conspicuous, raiding in columns beneath the leaf litter or underground, and preying specifically on other ant colonies (Kaspari & O’Donnell 2003).

**Nomadism**

Army ant colonies do not inhabit and construct a permanent nest in one location as is typical for many ant species, but periodically migrate *en masse* to a new site. It is thought that this nomadic lifestyle evolved to avoid depleting the prey in a given area (Wheeler 1910; Schneirla 1957), a coadaptation that accompanied the development of group predation (Wilson 1958; Wilson 1971). The frequency of colony movements, as well as the typology of nest construction, varies widely among species. Most New World army ants change location on a regular basis during the nomadic phase (described below), constructing a temporary nest, or *bivouac*, out of their own bodies that is dismantled and rebuilt with each emigration (Schneirla et al. 1954). This is true both for above-ground dwelling ants like some *Eciton* species, and underground species like most of the genus *Neivamyrmex* (constituting the majority of Neotropical army ant species). In contrast, many Old World army ants excavate longer lasting nests in the ground (Berghoff et al. 2002) and may occupy a site for months before moving (Schöning et al. 2005). While relatively little is known about the nesting or emigration behavior of many Old World hypogaeic (underground-dwelling) ants compared to the more easily
observed surface-dwelling species, it appears that these ants have a less dramatic impact on prey communities (Berghoff et al. 2003). This may explain why these primarily underground-dwelling species tend to remain at one nest site for longer periods, lending support to the prevailing theory that prey depletion is key to the development and frequency of nomadism.

Reproduction

The queens of army ant colonies are permanently wingless, which means they do not undertake mating flights, as in most other ants. Rather, the queen remains in her natal colony and mates with winged males that have dispersed from other colonies (Franks 1980; Kronauer 2009), and colonies reproduce by fission, dividing into two roughly equal parts (Schneirla 1971). The mating system is polyandrous, and in species where mating has been observed the queen typically mates with 10-20 males, resulting in mixed parentage (Kronauer et al. 2007a). Queens are specially adapted to produce large numbers of eggs with a gaster (abdomen) capable of greatly expanding during egg production, a condition known as dichthadiigyny. In the extreme case of the surface-dwelling *Dorylus* species of Africa, commonly referred to as driver ants, a queen may lay up to 250 million eggs in her lifetime, enabling massive colonies containing millions of individuals (Kronauer & Boomsma 2007).

Living above and below ground

Despite the fact that they constitute the vast majority of army ant species, underground-dwelling (hypogaeic) army ants have been the subject of far less scientific study than the conspicuous and well-known surface dwelling (epigaeic) species (Berghoff et al. 2002). The ecological importance of lesser studied and primarily hypogaeic species is clear, and may rival or
even exceed that of the well-known above ground species. For instance, Neotropical lowland forests can support guilds of as many as 20 different species of army ants, most of these hypogaeic (O’Donnell et al. 2005). The raids of all these species combined have significant impacts on prey communities that may be comparable to those of the more conspicuous epigaeic species (Kaspari & O’Donnell 2003). However, this bias is so prevalent in the literature that frequently the term “army ant” is used as shorthand to refer simply to one of the two common Eciton species, Eciton burchelli or Eciton hamatum. The epigaeic Old World army ants of the genus Dorylus are often referred to by their common name as driver ants, and have also been well described and studied (Gotwald 1995). Of course, much of the work that has been done on the more accessible surface-dwelling species has revealed important insights that apply to all army ants. While this dissertation follows a similar path in its focus on the charismatic Eciton species, it is important to recognize the position of these ants within the larger group, in order to understand the evolutionary pressures and ecological forces that shape the particular traits of interest here. The genus Eciton diverged only 17.8 mya, from a lineage that had been primarily underground for 60 million years before that (Bulova et al. 2016; Brady et al. 2014). Further studies focusing on hypogaeic species will be critical both to clarify the evolutionary history of this unique group, and to better understand the adaptations made in response to surface living.

**Study species: Eciton burchelli and Eciton hamatum**

The chapters that follow will focus on two species of Neotropical army ant, Eciton burchelli and Eciton hamatum. These ants are conspicuous and abundant, and widely distributed throughout the tropics of Central and South America. They forage above ground, during the day, and live in large colonies of 100,000-500,000 individuals for *E. hamatum* and up to 700,000
individuals for *E. burchellii* (Rettenmeyer 1963; Schneirla 1971; Powell & Franks 2007). All of these factors have made the two species particularly well-studied due to their relative accessibility. They are keystone predators in the leaf litter of the tropical forests they inhabit (Boswell et al. 1998; O’Donnell et al. 2007), and play an important ecological role in structuring the communities on which they prey (Franks & Bossert 1983; Otis et al. 1986; Kaspari et al. 2011).

The epigaeic (above-ground) lifestyle of *E. burchellii* and *E. hamatum* has contributed to their relative success as predators by enabling these ants to exploit new niches, while also introducing a host of new selection pressures. Both species are extremely sensitive to high temperatures, which constrains their foraging effectiveness by confining their raids strictly to forested areas, one obvious cost of living above ground (Meisel 2006). Another significant cost of an epigaeic lifestyle is increased predation pressure, a factor that may have driven the adoption of strictly nocturnal emigrations, since the colony is at greatest risk when transporting the queen during these movements. The ability to detect light and dark is a crucial adaptation required to make such behavioral adjustments to surface living, and in fact *Eciton* ants re-developed the toolkit for sight in response to life on the surface, after diverging from the rest of the mostly sightless Dorylinae an estimated 17.8 mya. The *Eciton* visual system is capable of detecting changes in light levels, with a significantly larger optic lobe relative to brain size compared to other army ants (Bulova et al. 2016). In addition to development of the visual system, the increased environmental and sensory complexity of living above ground has also selected for increased brain size. *Eciton* workers have significantly larger brains relative to their body size than other army ants (Bulova et al. 2016). It is possible that this increase in brain size has enabled many of the complex behavioral adaptations that are described here.
The most significant pressure introduced by living entirely above ground is the pressure of time. Temporal constraints affect almost every facet of the life of these two Eciton species, and these have shaped many aspects of their behavior and morphology (Franks et al. 1999). As a consequence of their nightly emigration schedule, both E. burchellii and E. hamatum raid exclusively during daylight hours (Schneirla 1971). This requires the self-organized coordinated activity of up to 200,000 workers, over an area that can stretch as far as 200 meters from the bivouac, tasked with locating, killing and efficiently transporting enough prey (up to 30,000 items) to feed the colony and its developing larvae. The need to accomplish all this within a strict time window (12 hours or less) has resulted in a unique set of morphological and behavioral adaptations, some of which will be the focus of this dissertation.

The bivouac

For both E. burchellii and E. hamatum, the focal point of colony activity is the bivouac, or temporary nest. This structure is formed from the interconnected bodies of the ants themselves, hanging in chains that eventually connect into curtains and ultimately into a continuous structure with defined internal spaces (Rettenmeyer 1963; Schneirla 1971). Bivouacs are typically constructed in semi-sheltered locations, commonly hanging from the underside of a log or between the buttress roots of a tree, and may also be built in elevated locations hanging from the branches of trees (Schneirla et al. 1954). When spanning directly from a sheltered surface to the ground, the usual form is cylindrical, but this shape is frequently adapted to the surrounding geometry and bivouacs may take the form of a continuous curtain when spanning between roots, a sack-like structure when hanging from a tree branch, or a variety of intermediate forms (Schneirla 1971). The bivouac serves as a shelter and an incubator for the
brood of the colony, and provides active thermoregulation (Schneirla et al. 1954; Jackson 1957). In colonies of *E. burchellii* studied in Panama, temperatures within the bivouac were consistently maintained around 28.5°C, varying by only 2°C, while external temperatures varied as much as 7°C (Franks 1989). Temperature regulation is also a factor in the selection of bivouac sites, with *E. burchellii* bivouacs located in sheltered or subterranean sites more frequently in areas of higher elevation with more climatic variation (Soare et al. 2010).

**Activity Phases**

The periodic emigrations of both *E. burchellii* and *E. hamatum* take place according to a temporal cycle with two phases, the *nomadic* and the *statary* phase (Rettenmeyer 1963; Schneirla 1971). These phases are related to the condition of the brood, which develops in distinct but overlapping cohorts (Franks 1980; Kronauer 2009). Nightly emigrations, in which the entire colony moves to a new site up to 100 m away, dismantling and rebuilding the bivouac, occur during the nomadic phase. For *E. burchellii*, this phase lasts approximately 14 days, during which the brood consists of larvae that have voracious appetites and must be fed, imposing a significant nutritional demand on the colony (Franks 1980; Franks & Fletcher 1983; Kronauer et al. 2007b; Wilson et al. 2011). In the statary phase, typically lasting around 20 days, emigrations cease and the colony remains in one location, with the bivouac usually built in a sheltered site. The queen lays a new batch of eggs that hatch toward the end of this phase, estimated at around 80,000 for *E. hamatum* and 200,000 for *E. burchellii* (Schneirla 1971), and the previous larvae enclose into cocoons. With both cohorts of brood in a quiescent state as eggs and pupae respectively, adult workers have to feed only themselves, and thus foraging activity is greatly reduced, with smaller raids that occur less frequently, on average 13 out of the 20 days (Franks
At the end of the statary phase, a new group of callow workers ecloses from these cocoons, an event that excites the workers into activity and triggers the first emigration, initiating the switch back to the nomadic phase (Schneirla 1957).

This stereotyped activity cycle is costly, in that it places severe time constraints on raiding activities during the long nomadic phase, when emigrations need to begin at dusk each day, forcing *Eciton* ants to raid (and emigrate) at an extremely high pace. Although it does impose significant costs, the rigid behavioral pattern is an adaptive response to certain prey dynamics (Franks 1980; Britton et al. 1996). Both *Eciton burchellii* and *Eciton hamatum* primarily prey on other social insect colonies. Social insects constitute over half the diet of *E. burchellii*, while *E. hamatum* specializes exclusively on this prey type (Powell 2011). After a raid, these social insect prey colonies are slow to recover, and thus *Eciton* colonies need to frequently move to new areas while avoiding returning to previous sites too quickly (Franks 1982; Franks et al. 1999). During the nomadic phase in both species, the overall direction of each day’s raid is oriented to avoid areas covered on previous days. This strategy allows for continual access to new prey patches (Franks & Fletcher 1983), and has been shown to outcompete less costly “hypothetical ancestral” strategies with shorter nomadic phases and emigration lengths under conditions where prey are slow to recover (Britton et al. 1996).

**Foraging behavior and patterns**

*Eciton burchellii* are generalist predators, feeding on a variety of arthropod prey in addition to ants, while *Eciton hamatum*, like most army ants, specialize on raiding other ant colonies (Schneirla 1971; Gotwald 1995). This difference in prey specialization results in different patterns of foraging behavior between the two (Deneubourg et al. 1989; Franks et al. 1999).
E. burchellii conduct dramatic swarm raids containing up to 200,000 individuals, in which a swath of ants on average 8 meters wide (Franks 1980; Kaspari et al. 2011) surges across the forest floor in search of prey, moving at around 15 meters per hour (Willis & Oniki 1978). As animals are flushed from the leaf litter, ants swarm around captured prey, attacking and overwhelming even relatively large arthropods. Colonies of E. burchellii cannot grow if they sustain losses of even 1% or 2% per day, so a massive number of ants is required at the front of the swarm in order to overcome prey and minimize losses (Bourke & Franks 1995).

Prey items that are too unwieldy to be carried are dismantled into smaller pieces for transport. The mandibles of E. burchellii cannot cut through the cuticle of prey items, making the size of pieces difficult to control (Rettenmeyer 1963; Powell & Franks 2005). Large or awkward items that cannot be further broken down are typically transported by teams of workers. These teams are superefficient, in that they can transport an item as a group that, if fragmented, they would be unable to carry individually in pieces (Franks et al. 1999). Although raids occur predominantly along the ground, columns of raiding ants often ascend the trunks of trees as well to capture prey up to 20 meters above ground (Rettenmeyer 1963; Franks 1980). Ants laden with prey return from the front of the swarm along a network of trails coalescing into a principal trail connected to the bivouac, covering an average distance of 105 m (Franks & Fletcher 2003). This principal trail maintains a consistent flow of bidirectional traffic, with ants delivering prey to the bivouac and outbound ants returning to forage at the front of the swarm, fluctuating from 3 to 12 ants in width (Powell & Franks 2007).

In contrast, Eciton hamatum conducts so-called “column raids” typical of most other army ants, a function of their specializing on other ants as prey, although they occasionally raid colonies of social wasps as well (Rettenmeyer 1963). In either case, they take almost exclusively
brood from the colonies they raid (Powell & Franks 2006). The narrow exploratory front of this raiding system is typically less than 1 m wide, and prey delivery is more sporadic than the nearly continuous flow of prey generated by swarm raiding (Rettenmeyer et al. 1983; Powell & Franks 2006). However, the raids of E. hamatum always consist of multiple independent trails that branch out in different directions for up to 300 m from the bivouac (Schneirla 1933; Rettenmeyer 1963; Bartholomew et al. 1988), ultimately providing for sustained prey intake even if individual raids are temporarily unsuccessful due to the patchy distribution of prey (Powell 2011). Although the impressive swarm raids of E. burchellii have long been perceived to have a greater impact on prey populations (Schneirla 1971), the amount of prey collected by E. hamatum colonies on average (38.2 g / day) has been shown to be comparable to that of E. burchellii (42 g / day), suggesting that swarm raiding and column raiding are strategies that achieve relatively similar success from different prey types (Powell 2011).

In both species, the foraging raid begins shortly after dawn, and progresses with peaks and lulls of activity throughout the day, with a well-established trail network usually formed by the middle of the day. By dusk, the colony begins the process of moving to a new bivouac site, even as foragers are still returning with prey (Schneirla 1933). Both E. burchellii and E. hamatum possess eyes with just a single facet, and cannot form images although they can detect changes in light (Rettenmeyer 1963; Bulova et al. 2016). Communication between individuals and sensing of the environment, other than detection of light levels, occurs through olfaction via the antennae and through touch. When foraging, Eciton ants utilize a process known as mass recruitment to alert other ants to a newly discovered food source, through a combination of chemical and tactile signaling. This recruitment mechanism has been estimated as the most effective and rapid of all ant species (Chadab & Rettenmeyer 1975).
Eciton ants deposit chemical pheromones in the environment during all stages of the foraging process. While exploring, finding prey, and returning to the bivouac, individuals periodically drag their gaster along the substrate, depositing chemical trails that consist of hindgut material (Blum & Portocarrero 1964). These trails are persistent, and it has been suggested that they may be detected and followed up to weeks after being deposited (Schneirla 1971). Upon encountering a potential source of prey, an individual ant returns to the nearest raid column while depositing pheromone, then runs in either direction and contacts other workers with her antennae. This process is repeated multiple times, and initiates a cascade as a number of ants who are recruited to the prey source perform the same activity, attracting even more workers. In this manner 100 workers or more can be diverted from the main trail to a new prey source within one minute (Chadab & Rettenmeyer 1975). In addition, E. burchellii workers may also use alarm pheromone, which is produced from a gland in the head, as a means to recruit help while subduing large prey items, since deliberately laying a recruitment trail is not feasible without losing the prey. This is supported by the fact that alarm pheromone provokes a strong response from non-major workers in E. burchellii, while in E. hamatum it serves to attract primarily major workers, who only participate in defense and not in prey capture (Lalor & Hughes 2011).

Castes and division of labor

A morphologically diverse workforce, with individuals of different sizes or shapes performing specialized roles, is thought to evolve such that certain morphologies match specific tasks, an arrangement that would benefit the colony as a whole by increasing organizational efficiency (Oster & Wilson 1978; Bourke & Franks 1995). Such a division of labor among
morphologically distinct castes, known as physical polyethism, occurs in around 20% of ants (Sendova-Franks & Franks 1999), most often in species with highly developed social organization. Both Eciton burchellii and Eciton hamatum are highly polymorphic (Topoff 1971), and 4 worker castes have been described: majors, submajors, medium workers and minors (Franks 1985), ranging in size from 4 to 14 mm (Rettenmeyer 1963). However, only the majors and submajors are morphologically distinct from the rest of workers. The major workers of both species are immediately recognizable, with large heads (over 2.5 mm) that are lighter in color than the rest of the body, and unique sickle-shaped mandibles (Feener et al. 1988). These are often referred to as “soldiers,” reflecting their specialized role in colony defense. Among non-major workers, size distributions are continuous, but morphology changes significantly in a narrow region, defining the submajor caste in both species (Powell & Franks 2006).

Although they account for only around 3% of workers, submajors play an important role for both E. burchellii and E. hamatum as prey transport specialists, making up 26% of all porters of prey (Franks et al. 1999). In both species, prey items are held in the mandibles and carried beneath the body (Bartholomew et al. 1988; Powell & Franks 2005), a strategy that allows for rapid transport, as demanded by the time-constrained Eciton lifestyle. Most other ants carry heavy loads in front of or above their bodies, which is more efficient but reduces speed (Traniello 1989). The faster below-body transport method of Eciton limits prey size to the space under the legs, resulting in a strong relationship between ant size (specifically leg length and head size) and the size of prey carried (Franks et al. 1999). Although generally faster, below-body transport constrains loading efficiency and causes friction with the substrate, as larger loads must be partially dragged (Powell & Franks 2005). This is especially true for E. burchellii, given the often awkward geometry and large size of the dismantled pieces of non-ant prey they
transport. Correspondingly, the submajor caste in *E. burchellii* is especially exaggerated, suggesting that the difficulty of transporting non-ant prey (resulting from the invasion of a new niche) drove the evolution of these transport specialists. This is supported by the fact that strong selection for transport efficiency is to be expected in *E. burchellii*, since less efficient transport can significantly affect overall prey delivery, and thus colony fitness (Powell & Franks 2006). These exaggerated submajors have longer legs relative to body size (Topoff 1971), which increases loading space allowing for the transport of larger prey, and larger heads and mandibles that enable the stronger grip needed to hold large prey firmly against the forces of friction from dragging (Powell & Franks 2005).

While not as exaggerated in morphology, *E. hamatum* submajors are also prey transport specialists, an adaptation that increases transport efficiency when carrying larger ant prey. Thus there is a positive relationship between prey variety and worker diversity, and other *Eciton* species that prey on monomorphic ants (and thus carry only uniformly sized prey) do not have a submajor caste at all (Powell & Franks 2006). Primarily in *E. burchellii*, again due to the size and awkward geometry of non-ant prey items, teams led by submajors also specialize in transporting prey. Below-body transport appears to facilitate the formation of teams, since two or more ants can easily line up one behind another to carry a linear prey item (Franks et al. 1999). Prey retrieval groups demonstrate a consistent division of labor, with different task requirements in different spatial positions. In teams, the largest ant is almost always the front runner, and teams consisting of large and small ants are able to bring the velocity of large prey items up to the standard speed of the foraging column (Franks et al. 2001). A more informal kind of team organization occurs at the front of the swarm, where a clear division of labor is exhibited as prey
are captured and subdued primarily by groups of mid-sized workers, after which submajors arrive to assist with retrieval and transport (Powell & Franks 2006).

The high degree of polymorphism found in *E. burchelli* and *E. hamatum*, and extreme specializations like the development of an exaggerated submajor caste, may be facilitated by the army ant mating system, through genetic variation for caste determination and polyandry (Jaffé et al. 2007). Queens mate with 10-20 males, resulting in a number of different worker patrilines (subgroups of full sibs) within each brood (Kronauer 2009), and ultimately greater diversity within the colony as different brood cohorts develop into workers and intermix. Genetic effects contribute to caste determination in *E. burchelli*, as different patrilines may be biased towards producing different ratios of worker morphologies (Jaffé et al. 2007). Variation in body size is apparent in the larvae (Schneirla 1971), suggesting that the mechanisms by which genetic effects translate into different size phenotypes may involve influencing the interactions between workers and developing larvae, affecting the rate of development and thus body size (Hughes et al. 2003; Jaffé et al. 2007).

Polyandry is presumed to be an integral part of the army ant syndrome, occurring in many army ant species that do not exhibit polymorphism (Kronauer et al. 2007a). This implies that the colony-level genetic diversity that results from polyandry is not necessarily associated with high levels of worker diversity. However, worker polymorphism and intercolonial genetic diversity are positively correlated across ant taxa (Fjerdingstad & Crozier 2006). It is likely that high levels of genetic diversity do indeed facilitate the development of both large colony sizes and highly polymorphic worker castes (Hughes & Boomsma 2007), but these traits will only emerge in response to appropriate selection pressures, such as those described here for *Eciton*. If polyandry is in fact common to all army ants, this group should offer a useful framework for
comparisons among species regarding the evolution of worker diversity under different constraints.

**Impact on prey communities**

While the impact of nearly all army ant species on their prey communities is considerable, the conspicuous swarm raids of *E. burchellii* have long been thought to have a particularly strong effect on the leaf litter arthropod community (Schneirla 1971). However, the precise extent of this impact is not yet well understood. It has been suggested that regular raids by *E. burchellii* sustain diversity in the leaf litter community by creating patches at different stages of succession (Franks & Bossert 1983; Britton et al. 1996). Prey densities of non-social insects in a raided area have been said to return to normal levels after 10 days, while social insect prey may take up to 200 days to recover (Franks & Bossert 1983). However, both the prey capture efficiency and overall impact of *E. burchellii* raids have been challenged.

One observational study estimated that 80% of arthropods at the front of the swarm escaped predation by ants, although some of these may have ultimately been captured by ant-following birds (Otis 1986). More quantitatively, recent experiments found no consistent significant effect of *E. burchellii* raids on invertebrate density or biomass, with the smaller swarm-raiding species *Labidus praedator* having a more detrimental effect on prey populations in areas that were subject to a raid (Kaspari et al. 2011). This disparity is thought to result from the fact that *E. burchellii* are somewhat limited in their prey capture abilities by their large size, with long legs that confine them to moving across the top of the leaf litter, where they miss smaller prey items that can escape through small gaps in the litter (Kaspari et al. 2011). An attempt to quantify the impact of an entire army ant guild in the Neotropics, which may consist
of up to 20 species in one area, estimated a frequency of 1.22 raids / m^2 per day (Kaspari & O’Donnell 2003), much higher than the estimated frequency of *E. burchellii* raids alone, with a 50% chance of any point in the forest being raided once every 240 days (Franks & Bossert 1983).

A better understanding of the ecological effects of *Eciton* raids is emerging, along with those of other army ant species. While the daily prey intake of *E. hamatum*, estimated at 38.2 g or 120 g/km^2, is less than many mammalian top-predators in the Neotropics, the ecological significance of this predation may be greater than just the raw biomass consumed since the prey consists of other ant species, each of which in itself may play an ecologically important role (Powell 2011). Similarly, *E. burchellii* often preys on large ant species, the periodic removal of which may release resources for other less dominant species (Kaspari & O’Donnell 2003). However, rather than indiscriminately harvesting whatever crosses their path, as has been perceived (Franks & Fletcher 1983), *E. burchellii* specializes on high biomass patches. When encountering poor patches, they leave larger fractions of prey behind, depleting proportionally more in rich patches, explaining why overall they may have a less severe impact on prey in a given area than previously thought (Kaspari et al. 2011). The tendency of the swarm raid to press on, rather than spending time searching through low quality patches, is likely driven by high colony-level energy demands and the general need to maintain a high tempo (Franks et al. 1999).

**Ant birds and myrmecophiles**

In addition to their impact on prey communities, *Eciton burchellii* are ecologically important for their interactions with a vast number of other animal species. A total of 557 species have been recorded associating with *E. burchellii* colonies, and around 300 of these species
depend on the ants for their existence (at least in part), constituting the largest animal association centered on one species (Rettenmeyer et al. 2010). This list includes birds, beetles, mites, butterflies, flies, wasps, springtails, bristletails and millipedes, some of which are parasitic, some commensal (Rettenmeyer et al. 2010). Tachinid and stylopod flies parasitize arthropods fleeing the swarm, further extending the devastation of the raid.

In addition, around 50 species of birds regularly follow E. burchellii swarms, feeding on escaping arthropods as they flee the ants (Willis & Oniki 1978), although a total of over 200 bird species have been at least observed foraging at swarm raids (Rettenmeyer et al. 2010). In total, there are 29 species of obligate ant-following birds, and a swarm may be accompanied by as many as 50 individuals from 20 different species at once, although most of these will be opportunistic followers (Willis & Oniki 1978). Obligate ant followers need to monitor an average of 3 colonies to ensure an active swarm (Touchton & Smith 2011) These birds maintain a dominance hierarchy, with dominant species like the ocellated antbird feeding at the richest sites at the front of the swarm and defending these areas (Touchton & Wikelski 2015). The presence of ant-following birds is another cost attributable to above-ground foraging, and especially to the conspicuous swarm raids of E. burchellii, as these birds reduce the ants’ foraging efficiency, taking prey that would otherwise be captured (Wrege et al. 2005).

**Traffic organization and self-assemblages**

The organization of traffic is a fundamental challenge for many ant species, especially those with large colony sizes, where the effective coordination of massive numbers of foragers is essential for colony-level success. The analogous importance of traffic organization – vehicular, pedestrian and informational – for the functioning of human societies is clear (Couzin & Franks...
2003, Dussutour et al. 2004; Fourcassié et al. 2010), and strategies for the distributed control of human traffic systems inspired by ant behavior are increasingly common (e.g. Hoar et al. 2002; Narzt et al. 2010). Foraging traffic in ant colonies is bi-directional, and different species utilize a range of strategies to accommodate this and minimize disruptions (John et al. 2004; Burd 2006). The black garden ant *Lasius niger* avoids delays in foraging by regulating density when crossing a narrow surface to minimize encounter rates, with individuals forming alternating clusters of outgoing and incoming ants (Dussutour et al 2005). These ants also regulate crowding on their trails by depositing less pheromone under crowded conditions, which they assess at an individual level by monitoring the number of contacts they experience (Czaczkes et al. 2013). Likewise, under crowded conditions an increasing number of head-on collisions and pushing between ants can also lead to the partial rerouting of traffic over an alternate route, resulting in optimal foraging behavior (Dussutour et al. 2004).

Traffic is even more complex for species that live in large colonies and transport external loads like army ants and leaf cutting ants. Most of these species forage in one place for extended periods, and construct trunk trails, smooth surfaces which they maintain clear of debris to facilitate the flow of foraging traffic (Burd et al. 2002; Dussutour et al. 2007), the costs of which are generally small compared to their long-term benefits (Howard 2001). Since the construction of trunk trails is a common adaptation to accommodate traffic that has arisen independently in unrelated taxa (Powell & Franks 2007), it might also be expected that individual behavioral strategies would evolve to maximize the flow of traffic on trails, due to the inherently cooperative nature of ant foraging and selection at the level of the colony. However, this is not generally the case (Burd et al. 2002). Leaf cutting ants of the species *Atta cephalotes* do not appear to adjust their behavior to accommodate bi-directional flow, resulting in frequent head-on
encounters that slow traffic, although it has been proposed that these interactions may promote information exchange (Burd & Aranwela 2003). In contrast to human traffic, where individuals modify their behavior to avoid collisions, traffic in *Atta* generally behaves more like a fluid, and despite frequent collisions, rates of flow are highest when traffic is bidirectional (Burd et al. 2002). However, when spatially constrained on a narrow trail, *Atta* ants do follow priority rules, with outbound ants stopping and giving way to laden ants returning to the nest. As in *L. niger*, this leads to the formation of alternating groups of outbound and inbound ants (Dussutour et al. 2009). In addition, foraging efficiency is higher under crowded conditions, suggesting that trails may be maintained at an optimal width that does not result in maximizing overall speed (Dussutour et al. 2007). Through these mechanisms, maximum flow and high efficiency are achieved at high densities by modulating velocity, as foragers are constrained to run below their maximum speed (Burd et al. 2002; Powell & Franks 2007). Since these ants forage on long-lasting resources and are active both night and day, adaptations that would maximize foraging speed have not been selected for.

*Time-constrained foraging in Eciton*

In contrast, *Eciton* ants are likely to be under strong selection pressure for adaptations that promote the efficient transport of prey, reductions in which can lead to significant decreases in overall prey delivery (Powell & Franks 2007). In particular, during the time-constrained foraging of the nomadic phase, reductions in prey intake can have severe impacts on colony fitness. This is due not to the energetic demands of the workers themselves, but rather to the necessity of feeding the ravenous larvae, whose nutritional demands dominate the colony during this time (Kronauer et al. 2007b; Willson et al. 2011). The larvae, spread widely throughout the
bivouac so as to contact as many workers as possible, actively provoke workers to forage with tactile signals consisting of sharp writhing movements that elicit an excitatory response when they strike workers (Vowles 1955; Schneirla 1971). The high level of urgency within the bivouac during the nomadic phase indicates the importance of effective foraging during this time for colony survival. Critically, the ultimate size of a new worker cohort is limited by daily prey intake, and any reduction in prey delivery will thus have a strong effect on colony growth (Powell & Franks 2006). Colonies that grow faster may be able to reproduce by fission faster, which typically occurs within 3 years for successful colonies (Bourke & Franks 1995), while colonies that do not maintain positive growth rates run the risk of dying out.

As a consequence of these pressures, traffic on Eciton trails is among the most highly organized of all ant species, and a number of adaptations enable Eciton to maintain some of the highest running speeds among ants (Hurlbert et al. 2008). In E. hamatum this can vary from 5 cm/s to 13 cm/s, with a consistent positive relationship between worker size and running speed, since workers with longer legs and larger bodies can run faster (Powell & Franks 2007; Hurlbert et al. 2008). This variation in running speeds may contribute to the consistent oscillations that emerge in Eciton traffic flow, resulting from physical interactions and analogous to the dynamics of vehicular traffic (Garnier 2013). However, unlike most ant species, average running speed is not drastically affected by transport due to the below-body carrying method, and Eciton hamatum sustain average speeds of around 8cm/s for ants both with and without prey (Bartholomew et al. 1988; Powell & Franks 2005). Due to their frequent emigrations and patchily distributed prey, they cannot rely on the construction of trunk trails to facilitate the flow of foraging traffic, necessitating other behavioral adaptations to maximize traffic flow and speed.
These adaptations include the spontaneous formation of lanes and the modification of the environment with self-assemblages.

**Lane formation**

Unlike the species described above, both *E. burchellii* and *E. hamatum* actively avoid collisions, and the traffic along their trails generally maintains a segregation of lanes between outgoing and incoming ants. The formation of lanes reduces the number of collisions and resulting decelerations between ants, increasing the overall speed and flux of traffic (Couzin & Franks 2003; Burd 2006). In *E. burchellii*, this can take the form of a distinct three-lane spatial structure along the primary trail, with ants returning to the bivouac occupying a center lane while outgoing ants form two lanes on either side. The lane structure emerges from a self-organizing process, as returning ants have a lower turning rate during avoidance maneuvers than outbound ants (Couzin & Franks 2003). Since ants within the raid have a sense of direction, it is likely that this asymmetry in turning behavior has been selected for, although the reduced agility of prey-laden ants may also contribute to the resulting pattern. The three-lane structure is thought to be more stable than a two-lane system due to differences in pheromone deposition between outbound and inbound ants (Couzin & Franks 2003).

**Self-assemblages and self-organization**

In addition to the self-organized formation of lanes, *Eciton burchellii* and *Eciton hamatum* facilitate the flow of foraging traffic by deploying self-assembled structures to modify the environment. The rarity of these structures in the raids of other *Eciton* species suggests they are an adaptive response to the time-constrained lifestyle of these ants (Powell & Franks 2007).
By modifying the environment to increase the flow of traffic in various ways, these temporary structures provide benefits similar to those of the longer-lasting trunk trails constructed by other species, and may have evolved as an alternate strategy as part of their nomadic lifestyle (Powell & Franks 2007). The bivouac is the most complex of all the self-assembled structures created by these ants, serving the most important role for the colony (Schneirla 1954), and the processes underlying its formation and maintenance are still not entirely understood. However, it will remain a subject for future work. Here, I focus in particular on the self-assembled structures created by *E. burchelli* and *E. hamatum* that are deployed in the course of their foraging activities as a means of managing the flow of traffic. These structures are highly responsive, and integral to the foraging success of these species, as will be shown.

Generally, self-assembly is understood to refer to systems in which only the constituents of the final structure take part, as opposed to template-directed assembly, in which spatial information is imposed externally (Miller 1976; Sendova-Franks & Franks 1999). Since self-assembled structures emerge from locally-mediated interactions between individual units, the concept of self-assembly is related to self-organization (Camazine et al. 2001), and the majority of self-assembling processes are also self-organizing (Sendova-Franks & Franks 1999). To differentiate between these two terms, self-assembly has been described more specifically as a process in which a well-defined structure results from a specific number of components, and is determined by their geometry and strength of interactions (Gerhart & Kirschner 1997; Sendova-Franks & Franks 1999). While most examples of self-assembly in biology occur at the molecular or cellular level (Miller 1976), the term has also been used to describe the phenomenon known as *social resilience* in certain ant colonies, whereby workers re-establish their positions and roles after a disturbance, reorganizing themselves back into a functional colony (Sendova-Franks &
Franks 1999). Here, I will use it more specifically to refer to the assembly of physically coherent functional structures by social insects.

Self-assemblages in insect societies have been described as “intermediate-level parts,” functional units that are adaptive at the colony level, yet consist of multiple individuals. Crucially, the functionality of these units only emerges at an intermediate level, and is not present within the individuals themselves (Anderson et al. 2002). As an analogy, these may be viewed as the tissues and organs of a complex insect society, and it has been argued that such units represent an overlooked level of organization within insect societies (Anderson et al. 2001). Specifically, insect self-assemblages are defined as structures formed when multiple individuals grip onto one another (Lioni 2001). Around 18 different types of these structures have been identified in insect societies among ants, bees and wasps, with varying degrees of organization and functionality (Anderson et al. 2002). Generally, their formation is associated with large colony size and high levels of social organization. They are formed and maintained by self-organizing processes, and often an individual’s probability to join a structure depends on locally-sensed properties (Lioni & Deneubourg 2004).

**Self-assemblages in Eciton**

While many of the self-assemblages formed by other social insects occur only under certain conditions, for *Eciton burchellii* and *Eciton hamatum* the formation of these structures is a regular and fundamental aspect of their behavior. In addition to the bivouac, as previously discussed, self-assemblages are used primarily as a way to modify the environment to facilitate the flow of traffic. The simplest of these structures are “plugs,” consisting of single or multiple ants filling small holes in the leaf litter with their bodies, that are present on almost every meter
of principal trail (Powell & Franks 2007). Both *E. burchellii* and *E. hamatum* workers show a strong preference for smooth surfaces, and their foraging trails often take advantage of elements in the environment that allow for long, uninterrupted runs over fallen trees and logs, lianas, rocks, and even smaller sticks. However, the primary terrain with which they interact consists of the heterogeneous surfaces that make up the leaf litter. Over terrain with high rugosity (surface roughness), the mean speed of workers is negatively impacted, especially when carrying prey. Generally, *Eciton* workers achieve high mean velocities by maintaining a consistent positive relationship between body size and running size (Powell & Franks 2005), however this breaks down when they encounter rough terrain. Over surfaces with high rugosity, all prey-laden ants are forced to run at the same speed as the smallest ants (Powell & Franks 2007). Plugs are formed by generalist workers (non-majors or submajors) as a way to smooth the terrain in order to counteract this. Workers size-match their bodies to appropriately sized holes, creating smoother surfaces that allow prey-laden foragers to attain maximum speed, contributing to an overall increase in the mean speed of traffic, and thus the rate of prey intake for the colony (Powell & Franks 2007).

Bridges are the other most common type of self-assemblage formed by *E. hamatum* and *E. burchellii*. In contrast to many dramatic early descriptions (e.g. Wheeler 1921), these bridges are typically not massive structures used to cross over bodies of water or obstacles (although these may occur under rare circumstances), but rather modest structures that are distributed frequently throughout the foraging trail system. They are typically concentrated in the highest numbers close to the bivouac along the primary trail, where traffic is greatest (pers. observation). This is due mainly to the fact that bridges are highly responsive to traffic. In a previous study, we found that the time spent by an ant as part of a bridge increases as a function of traffic flow.
(Garnier et al. 2013). In experiments where bridges were removed, they re-formed quickly in the same location, but consisted of fewer ants, suggesting some redundancy in the initial process of formation (Garnier et al. 2013). We found that bridges were robust to moderate perturbations and typical oscillations in traffic, but highly responsive to large disruptions. When traffic was stopped on a trail, bridges were consistently dismantled within a few minutes. This response results from local sensing, as individual ants detect the flow of traffic over a bridge, presumably by assessing the rate of contacts (Garnier et al. 2013). The probability of an ant to join or leave a bridge in response to this sensory input is an exponential function of traffic flow, ensuring that bridges rapidly form in response to high traffic and are less likely to form under low traffic conditions (when the cost of locking up workers in a bridge may not be warranted). Further, time spent in a bridge is positively influenced by the number of surrounding ants, resulting in stable structures even if bridges reduce in size in response to lower traffic (Garnier et al. 2013).

Through these self-organizing mechanisms, bridges form and dismantle as needed in response to the highly variable traffic conditions of *Eciton* raids. Like plugs, bridges enable these ants to maintain high rates of traffic over unpredictable terrain, estimated to average 144 ants/min (+/- 15 SE) for *E. burchellii* and 86.4 ants/min (+/- 7.4 SE) for *E. hamatum* (Lalor & Hughes 2011), resulting in a net gain in prey intake for the colony (Powell & Franks 2007).

**Description of chapters**

This dissertation represents a comprehensive study of the self-assembled structures created by *Eciton* army ants as integral components of their foraging network. I show that these structures dynamically respond to local conditions of foraging traffic, adapting their geometry to improve the flow of traffic in various ways, and ultimately serving to increase the prey intake.
rate of the colony. In the first chapter, I demonstrate that the bridges formed by *Eciton hamatum* are used to create shortcuts by moving the foraging trail to a more efficient path over time. Bridges move to a point that represents a cost-benefit tradeoff for the colony, where the cost of locking up workers in a bridge begins to outweigh the benefit of the shortened path. In the second chapter, I describe a type of structure called *scaffolding*, created by *Eciton* ants traversing vertical surfaces. I show that these structures emerge in response to disruptions in the flow of traffic caused by the difficulty of prey-laden ants in navigating vertical surfaces. Through a process of negative feedback, the formation of these structures serves to re-organize the flow of traffic, with the emergent benefit of catching ants and prey items from falling.

The third chapter examines another category of structures, *flanges*, formed when foraging traffic moves along a narrow substrate. Ants cling to either side of the substrate to effectively widen the path of travel. I show that these structures form in response to different factors than either bridges or scaffolding, resulting from a context-dependent individual level response. Finally, I present a spatially explicit, agent-based model that is capable of reproducing the formation of different kinds of structures in response to environmental geometry and traffic conditions. I use the model to test hypotheses about the individual-level rules that generate the various structures described in previous chapters depending on context.
Army ants dynamically adjust living bridges in response to a cost-benefit tradeoff

Abstract

The ability of individual animals to create functional structures by joining together is rare and confined to the social insects. Army ants of the genus *Eciton* form collective assemblages out of their own bodies to perform a variety of functions that benefit the entire colony. Here we examine ‘bridges’ of linked individuals that are constructed to span gaps in the foraging trail. These living bridges are uniquely complex in both their dynamic properties and the number of animals involved, and so are of considerable interest for understanding emergent structures in complex systems. How these structures adjust themselves to varied and changing conditions remains poorly understood. Our field experiments showed that ants continuously modified their bridges, such that these structures would lengthen, widen and change position in response to traffic levels and environmental geometry. Ants initiated bridges where their path deviated from the direction of incoming traffic and moved the bridges over time to create shortcuts over large gaps. The final position of the structure depended on the intensity of the traffic and the extent of path deviation, and was influenced by a cost-benefit trade-off at the colony level, where the

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1 Adapted from Reid CR*, Lutz MJ*, Powell S, Kao AB, Couzin ID, Garnier S. (2015) Army ants dynamically adjust living bridges in response to a cost-benefit trade-off. *Proceedings of the National Academy of Sciences*. 112 (49) 15113-15118 *co-first authors*
benefit of increased foraging trail efficiency was balanced by the cost of removing workers from the foraging pool to form the structure. To examine this trade-off, we quantified the geometric relationship between costs and benefits revealed by our experiments. We then constructed a model to determine the bridge location that maximized foraging rate, which qualitatively matched the observed movement of bridges. Our results highlight how animal self-assemblages can be dynamically modified in response to a group-level cost-benefit trade-off, without any individual unit having information on global benefits or costs.

Introduction

Scenarios requiring the coordination of many individual units to accomplish higher-level tasks are common to systems at many scales in biology (Camazine et al. 2001). Yet we have little understanding of how environmental forces and evolutionary constraints shape the interactions between individuals that give rise to complex organization at the group level. This remains a fundamental problem for our understanding of systems as diverse as developmental processes, the interactions of neurons in the brain, collective navigation in animal groups and vehicular traffic (Berdahl et al. 2013; Helbing 2001; Couzin 2009).

The physical joining of discrete units to create composite functional structures at the group level is a subset of these problems that has previously been studied in microscopic systems such as the multicellular ‘slug’ of the cellular slime mold Dictyostelium discoideum (Savill & Hogeweg 1997). Larger, more complex self-assemblages of multi-cellular individuals appear to be confined to the social insects (Anderson et al. 2002), where well-known examples include the floating rafts created by the fire ant Solenopsis invicta (Mlot et al. 2011) and the living chains formed by weaver ants of the genus Oecophylla (Lioni et al. 2001). For surface-dwelling army
ant species of the new world genus *Eciton*, the regular formation of self-assembled structures is fundamental to colony survival, as they are used for both shelter (the bivouac, or temporary nest), and as a means to organize and expedite traffic along the foraging trail.

*Eciton* army ants are nomadic social predators that hunt primarily other ants and some arthropods throughout Central and South America (Powell & Franks 2006; Rettenmeyer et al. 1983; Powell 2011). Raids occur mainly in the leaf-litter, where the ants use strength in numbers to overwhelm their prey, and a colony typically harvests around 40 grams dry weight of prey per day from an area a few hundred meters across (Powell 2011). Unsurprisingly, this level of localized raid intensity can have a significant impact on prey populations (Powell 2011; Franks 1982; Franks & Bossert 1983; Kaspari et al. 2011), but the army ants avoid local prey depletion by conducting regular colony emigrations to new, potentially prey-rich patches of the forest (Powell 2011; Franks 1982). These ants therefore live an exceptionally time-constrained lifestyle (Powell & Franks 2005), where maximizing prey intake during the day’s raid must be followed by high-speed and efficient colony relocation. For both foraging and emigration, high levels of traffic are critical for maximizing overall transport efficiency (Couzin & Franks 2003). This high traffic flow is achieved in part by exceptionally fast running speeds of up to 14cm/s for both prey-burdened and unburdened ants (Powell & Franks 2005), and sustained average speeds of around 8cm/s (Hurlbert et al. 2008) along foraging trials that typically range between 100 and 200m in length (Powell 2011). However, the leaf litter that blankets the forest floor contains many holes, uneven surfaces, and diversions that can slow traffic (Powell & Franks 2005, Powell & Franks 2007). *Eciton* workers deal with these obstacles by filling holes and spanning gaps with their bodies, providing a living roadway for their nestmates to run over.
Previous work has shown that individual workers plug small potholes with their bodies, smoothing and widening paths to allow for an increased rate of traffic flow and prey delivery rates. These benefits are likely to more than offset the cost of dedicating a significant proportion of foragers to pothole plugging (Powell & Franks 2007). *Eciton* army ants also build complex ‘bridges’ of multiple linked individuals that span larger gaps (Garnier et al. 2013). The ants use these bridges as the leaf litter terrain demands, such that long stretches of tens of meters over relatively smooth terrain (e.g. large logs and fallen branches) may contain no bridges, whereas areas of particularly rough and broken terrain may contain multiple bridges per meter of trail. The composition of each bridge also varies from just a few individuals spanning a small hole, to many hundreds fully suspended across gaps tens of times larger than an individual ant. This variation in the deployment and composition of army ant bridges further highlights the uniquely dynamic and complex nature of these self-assembled animal structures, but we know very little about them. Previous studies examined the responsiveness of these bridges to traffic flow, demonstrating that they are robust to small perturbations in traffic, yet highly responsive to large interruptions, breaking apart within a few seconds when traffic was stopped (Garnier et al. 2013). What remains unknown is how the presence, shape, and position of bridges are established, and how these may benefit the collective actions of the colony.

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

**Materials and Methods**

The focal species was *Eciton hamatum* (Fabricius), and all data were collected from Barro Colorado Island (BCI), Panama. All experiments were conducted during daylight hours between February and August 2014. *E. hamatum* workers spend the day foraging, establishing a primary trail and several secondary trails by late morning, with bidirectional traffic connecting the bivouac to the raid site. We conducted our experiments along the primary raiding trail, finding a suitable location to set up our apparatus and filming equipment before inserting our experimental apparatus into the existing trail. To accomplish this, we located sticks and small branches along the trail on which ants had been running, which were thus coated in trail pheromone. Removing these, we inserted our apparatus into the interrupted trail, using the pheromone-coated sticks to construct makeshift ramps on either side of our apparatus, which was mounted on tripods approximately 40 cm above the forest floor. To encourage the re-routing of traffic, we placed additional leaves from the trail, along with ants, onto the side platforms. After a period of 10-30 minutes, the trail had fully re-established over our apparatus.
Figure 1 | a) Experimental apparatus from above. θ indicates the angle of separation between the platforms, in this case set to 20°. Over 30 minutes, the bridge has moved the distance $d$ from its initiation point at the intersection of the platforms to its current location. See Materials and Methods for explanations of the empirical measurements $d$, $w$, $b$ and $D_{\text{max}}$, and the cost-benefit model for descriptions of $L_A$, $L_T$, $L_1$, $L_0$ and $L_E$. The position of $L_T$ corresponds to the position of the main trail axis, as described in the text. The width ($w_A$) and length of each movable platform section was 3.3 cm and 24 cm, respectively. b) apparatus with $\theta$ set to 12°. Hinges are shown as circles. c) apparatus with $\theta$ set to 60°. The surface area of a bridge, used to estimate costs, is shown in blue, while the reduction in travel distance is shown with red dashed arrows, for the same distance ($d$).

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

**Data Collection and Analysis**

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

We measured how the collective action of the ants modified various bridge properties over time, performing our analyses for each minute of the experiments by selecting the final frame from each minute of the video data. Fig. 1a shows graphically the properties of the bridge we measured. Using the ImageJ software (v1.46r, http://imagej.nih.gov/ij/), we measured where the inner and outer edges of the bridge intersected a line drawn through the center of the space between the hinged platforms \((D_{\text{max}} \text{ in Fig. 1a})\). We measured the absolute distance that the inner edge of the bridge moved from the junction of the two platforms \((d)\). Bridge width \((w)\) was determined by calculating the distance between the inner and outer edges of the bridge. Knowing the angle \(\theta\), and the length of \(d\), we used basic trigonometry to determine the length of the inner edge of the bridge \((b \text{ in Fig. 1a})\), and the trapezoidal surface area of the bridge for each minute of the experiments.
In addition to changes over time, we were interested in how the ants modified the structure of their bridges under different traffic conditions. We measured traffic along the trail by counting how many ants passed a point one quarter of the way along one of the platforms of the apparatus, in both directions, over each minute of the experiments.

The change in position of the bridge over time was analyzed using a generalized linear model (GLM) with 3 main effects: time, angle $\theta$, and traffic intensity as measured above. The time variable was transformed using a hyperbolic function to account for the slowing down of the bridge movements with time. The parameters of the hyperbolic function (i.e. the growth speed and the asymptote) were estimated by fitting a hyperbolic curve to the data of each experiment separately and taking the median value for each parameter. Within-group correlation was modeled as an autoregressive process of order 1. Using the Akaike Information Criterion (AIC), a comparison of the different combinations of the 3 main effects and their interactions showed that the best model included time, angle $\theta$ and traffic intensity, and the interactions between time and angle $\theta$, and between time and traffic intensity. Model diagnostics were performed using graphical procedures (Q-Q plot and standardized residuals vs fitted values).

**Model parameter estimates**

The center of each hinge point is 0.98 cm from the end of each platform. The length of the apparatus arm between the two hinges is thus $L_0 = 24 - 2 \times 0.98 \, cm = 22.04 \, cm$, and the width of the apparatus arm is $w_A = 3.3 \, cm$. Therefore, $L_A = 13.95, 25.36, 35.01,$ and $35.36 \, cm$, for apparatus angles $\theta = 12^\circ, 20^\circ, 40^\circ,$ or $60^\circ$, respectively, and $D_{\text{max}} = 6.93, 12.49, 16.45,$ and $16.61 \, cm$. From video observations, we estimate the dimensions of an ant to be $l_n = 0.691 \, cm$ and $w_n = 0.107 \, cm$ and the density of ants moving across the apparatus to average 0.42 ants/cm,
which is compatible with the literature (Bartholomew et al. 1988). We estimate the ratio between bridge width and length to be \( \omega = 4.7990^{0.5014} \). We set \( L_T \), the length of the foraging trail not part of the experimental apparatus, to 100 cm (see bridge spacing estimates in SI), with the total number of ants \( N \) determined by \( (L_T + L_A) \) and the overall density of ants.

**Results**

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

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

**Figure 2** | Bridge movement as a function of a) experimental time, b) angle \( \theta \), and c) traffic intensity. Each dot represents the position of a single bridge for each minute of each experiment. These values are partial residuals computed from a Generalized Linear Model (GLM) as described in the text: they represent the relationship between a given independent variable and the bridge position, given that the other two independent variables are also in the model. The solid line and its semi-transparent envelope represent the best fit of the GLM for each independent variable and its 95% confidence interval.

**Geometric model of the cost-benefit relationship**

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

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

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

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

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

where \( w_\theta \) is the ratio between the width and the length of a bridge, as a function of the angle \( \theta \). The value of \( w_\theta \) corresponds to the slope of the linear regression in Fig. S1.

The theoretical costs (in geometric terms) increase non-linearly (as \( d^2 \)) with bridge movement (Fig. S2a), increasing much more rapidly for higher angles \( \theta \). The theoretical benefits, in terms of travel distance saved by installing a bridge as a shortcut, increase linearly (as \( d \)) for all angles as bridges move further toward the main trail axis (Fig. S2b). The benefits increase at a faster rate for smaller angles because the longer bridges required at larger angles offset some of the benefits in total path length reduction. To verify our theoretical cost-benefit relationship, we compared the theoretical curves to the cost-benefit relationship of actual bridges (Fig. 3).

Our geometric quantification of the cost-benefit relationship in army ant bridges shows that the cost of sequestering workers increases faster than the benefit gained from reducing travel distance. In order to demonstrate that this cost-benefit relationship is responsible for bridge movement ceasing before travel distance along the trail is minimized, we extended the geometric
model to the following cost-benefit optimization model of bridge construction. This model assumes that the colony tends to maximize traffic density on their trails as a means to improve traffic output (e.g. increased prey retrieval, shorter migration time). This is compatible with previous studies showing that several army ant behaviors are directly involved in improving traffic conditions on the trails (Couzin & Franks 2003; Powell & Franks 2007).

![Figure 3](image)

**Figure 3** | The relationship between costs and benefits for bridges at 4 different angles $\theta$. Dashed lines are theoretical cost-benefit relationships as computed from our model (and depicted in Fig. S3). Each dot shows the distance saved and surface area of an individual bridge at any point in time. Solid lines are LOESS curves built from the experimental data for each angle $\theta$ that help visualize the general trends in the data.

**Cost-benefit optimization model of bridge dynamics**

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

If a bridge is built across the apparatus at some distance \( d \) from the junction, then the length of the bridge will be \( b = 2dtan(\theta/2) \) (Fig. 1). Consequently, this will decrease the total foraging trail length to \( f = L_T + b + (1 - d/D_{\text{max}})L_A \), where \( D_{\text{max}} \) is the maximum distance that the bridge can travel given the constraints of the apparatus and is given by \( D_{\text{max}} = L_A\cos(\theta/2)/2 \). The bridge incurs a cost to the colony by decreasing the number of available foraging ants by an amount \( n_b = w_0b^2(1 - w_0\tan(\theta/2))/(l_nw_n) \), where \( w_0 \) is the ratio between the width and the length of the bridge, and \( l_n \) and \( w_n \) are the length and width, respectively, of an average ant when occupying a position within the bridge structure. The density of ants on the foraging trail in the presence of a bridge becomes:

\[
\rho = \frac{N - n_b}{f}. \tag{3}
\]

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

\[
\begin{align*}
\[4\] & \quad d^* = \frac{\cos(\theta/2)}{2(1 - \sin(\theta/2))} \left[ (L_T + L_A) - \sqrt{(L_T + L_A)^2 - \frac{N l_n w_n \{1 - \sin(\theta/2)\}^2}{w_0 [1 - w_0 \tan(\theta/2)] \sin(\theta/2)^2}} \right]
\end{align*}
\]

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

\[
\begin{align*}
\[5\] & \quad d^* = \frac{\cos(\theta/2)}{2(1 - \sin(\theta/2))} \left[ (L_T + L_A) - \sqrt{(L_T + L_A)^2 - \frac{AN l_n w_n \{1 - \sin(\theta/2)\}^2}{w_0 [1 - w_0 \tan(\theta/2)] \sin(\theta/2)^2}} \right]
\end{align*}
\]

By fitting the resulting equation [5] to the data, we find a very good fit to the data for \(A = 17.02\) (95% confidence interval [15.22, 18.82]) (Figure 4b). The optimal bridge migration distance decreases as the apparatus angle increases, and increases as the overall density of ants on the foraging trail increases (Fig 4a), which agrees with the behavior of the ants in our experiment (Fig. 2b, c).
Figure 4 | (a) The optimal bridge position $d$ as a function of apparatus angle $\theta$ for different ant densities. Other model parameters are as described in Materials and Methods section. (b) Comparison between the predicted final position of the bridge (solid line) and the experimental observations (dots) as a function of the angle $\theta$. The value of parameter $A$ (the only free parameter of the model) was chosen to best fit the experimental observations. Note that changing its value would only affect the numerical outcome of the model, not the general shape of the relationship. The experimental observations reported in this figure are partial residuals computed from a Generalized Linear Model (GLM) as described in the text.

Discussion

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

Our density-based model of bridge dynamics demonstrates that such a trade-off is likely to result from attempts to maximize the foraging rate. The model shows that, given the properties of the traffic along the trail, there exists a bridge position where the cost of sequestering workers in the bridge structure outweighs the benefit gained from reduced travel distance. Our data do not allow us to claim that the positions at which bridges stopped in our experiments are indeed the optimal positions predicted by this idealized model. This is because our model assumes that ants attempt to maximize traffic density. In reality, traffic theory indicates that they should increase traffic only up to a critical density that maximizes traffic flow, and beyond which interactions between individuals would cause slowdowns. Measuring this critical density would be very difficult in field conditions, where it is nearly impossible to control – and in particular to increase – the traffic flow. It is likely that the ants have a number of regulatory mechanisms that naturally keep traffic below the critical density (Couzin & Franks 2003; Dussutour et al. 2004; John et al. 2009; Hönicke et al. 2015). Nevertheless, assuming that ant traffic never exceeds this critical density, our model makes two clear predictions: the distance moved by the bridge should
decrease with the increasing angle of the apparatus, and for all angles, bridges should move further as traffic increases. Our experimental results match these two predictions very well, supporting the hypothesis that the position and size of army ant bridges result from a cost-benefit trade-off.

There may be several factors contributing to the value of the free parameter $A$ in our cost-benefit model. While the model treated each individual equally (by simply counting the number of ants on the trail and the number of ants in the bridge), there are substantial differences between bridge-building ants and non-bridge-building ants. The submajor caste of *E. hamatum* rarely participates in bridge-building but contributes highly disproportionally to foraging, in terms of the likelihood of carrying a prey item, the size of the prey item carried, and running speed (Powell & Franks 2006; Powell & Franks 2005). Furthermore, our preliminary observations suggest the ants contributing to bridge-building tend to be younger individuals that are visibly more timid in the raid traffic and lack foraging experience. Together, these factors reduce the cost of ants joining the bridge and account for at least some of the value of the free parameter $A$.

The most likely mechanism by which army ant bridges adjust to their environment is through individuals modifying their likelihood to join or leave a structure based on interaction rates. Ants in the structure are responsive to changes in traffic, increasing their likelihood to leave when traffic levels drop below a critical threshold (Garnier et al. 2013). When a bridge forms at an angle between two surfaces, as in our experimental apparatus, traffic conditions vary along the bridge’s cross-section. Ants seeking the shortest path tend to create a higher traffic flow along the inner side of the bridge (closer to the main trail axis), and lower traffic flows along the outer side, where the path is longer. Passing workers thus experience higher interaction
rates on the inner side and are more likely to attach to the structure here (Garnier et al. 2013). Conversely, ants on the outer edge are contacted less, and are more likely to leave the structure. These localized processes of construction and deconstruction in response to a cross-sectional traffic gradient are likely to result in a dynamic structure that steadily moves toward the main trail axis, shortening the overall path of travel.

Our study was necessarily focused on the local dynamics of single bridges occurring on sections of the greater foraging network. To understand the overall colony-level costs and benefits, it would be necessary to quantify both the number of ants per bridge and the number of bridges in an entire foraging network. Powell and Franks (2007), using the closely related E. burchellii, calculated that the cost-benefit trade-off of building plugs versus contributing to prey retrieval should yield a net gain for the colony under a range of realistic scenarios (pothole plugs can be thought of as ant bridges with one to a few individuals). Nevertheless, under their worst case estimate, with the loss of one prey item for every plug-ant and a total of 20% of total foragers dedicated to plugs, daily intake of prey could drop by as much as 79%. Hence, accurate measures of the proportion of available foragers locked up in bridge structures will be critical for a global, colony-level representation of the cost of bridges to foraging colonies. Similarly, it is clear that the presence of bridges should yield energetic gains at the colony level from increased prey delivery rates, both through minimizing the path length from raid site to bivouac and from the cumulative increase in speed gained by smoothing rough sections of terrain. However, for global, colony-level calculations of the cost-benefit trade-offs of bridge building, it would be necessary to accurately measure the path length of the trail established by the ants, the number and size of bridges along the trail, and the total path shortening that the bridges provide. This is beyond the scope of the present study (though see Supporting Information for an estimate of
colony-wide bridge investment), but will be critical for extending our results here on the localized net gain of bridges to the collective benefit at the whole-colony level.

Future work should also examine how *E. burchellii* responds to the cost-benefit trade-off induced by bridge-building. The foraging behavior of *E. burchellii* differs from that of *E. hamatum* in that the former species most often utilizes a single branching trail that is focused in one direction only, and connected to the bivouac by a common, ‘trunk’ trail (Schneirla 1971). Colony size is also typically much larger in *E. burchellii* than *E. hamatum*, further contributing to higher traffic flow and prey delivery rates in *E. burchellii* at the level of individual trails (Powell 2011; Franks 1982; Garnier et al. 2013; Franks 1985), but not necessarily greater colony-level biomass intake when *E. hamatum*’s multiple trail foraging system is considered (Powell 2011). If all workers are utilizing the same trunk trail (as opposed to the 2-3 separate radiating trails of *E. hamatum* (Powell 2011), then colony-level bridging costs may be lower as less terrain may need to be bridged, and benefits may be higher because the entire prey-laden workforce will benefit from all bridges on the common trail. However, *E. burchellii* bridges may also need to be wider given the higher average traffic flow, and more obstacles may need to be bridged to accommodate the generally wider trail. If *E. burchellii* has also evolved to make a cost-benefit trade-off in bridge-building, we might therefore expect informative differences between species in the distance and rate of bridge migration, further improving our understanding of the cost-benefit trade-offs inherent to collectively solve these problems.

Another important area for future work is the role of structural forces in regulating the growth, movement and stability of bridges. Our experiments demonstrate that a consistent length/width ratio is maintained as bridges increase in size, which suggests that the probability to join or leave a bridge may be influenced by structural forces as well as traffic dynamics. For ants already in a
bridge, the decision to remain or leave may be influenced by increasing or decreasing tension forces on the legs, while for ants crossing a bridge, the decision to join may be influenced by the relative stability of the structure.

In a previous study, the bridge structure was shown to emerge in a decentralized manner, from simple interactions influenced by local information on the traffic intensity and the presence of gaps along the trail (Garnier et al. 2013). The present study provides quantitative insights into the functional importance of the self-assembly process for the foraging efficiency of the colony. We show that self-assembling bridges can adjust to features of the landscape that are unpredictable from the organism’s perspective, and appear to balance construction costs with foraging benefits. As such, these structures demonstrate the adaptive value of biological self-assembly even in complex, multi-cellular organisms (Anderson et al. 2002; Kushner 1969; Whitesides & Grzybowski 2002), and may inform the design of artificial self-assemblages, at the interface of materials science, robotics and architecture (Soleymani et al. 2014; Werfel et al. 2007; Stewart 2006; Napp & Nagpal 2014; Yoshida et al. 1998; Hosokawa et al. 1998; Gro et al. 2006; Trianni et al. 2006).

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invaluable support. Thanks to Devanand Saraswati for key assistance with experiments, and two anonymous reviewers for comments on the manuscript.
Growth of self-assembled structures in *Eciton burchellii* is driven by a negative feedback control response

**Abstract**

The coordination and control of traffic is fundamental to the functioning of complex transport networks, both in biological systems and in human society. For social insects with large colonies, efficient coordination of foraging traffic is essential. *Eciton* army ants have evolved a number of strategies to maximize the prey intake rate of the colony, including the building of structures to facilitate the flow of traffic along foraging trails. Worker ants use their own bodies to build temporary structures that respond to the flow of traffic and alter the environmental geometry over which traffic is moving. Here we investigate ‘scaffolding’ structures that are formed when the foraging trail crosses an inclined surface. These structures form as the result of a self-organizing process, as ants respond to local information about the geometry of the environment and the properties of traffic. We conducted field experiments on *E. burchellii* trails to examine scaffolding formation and size under a variety of traffic and geometric conditions. Our results show that scaffolding structures formed more quickly and consisted of more ants at steeper angles, and were unlikely to form at all when the surface angle was close to horizontal. The dynamics of the formation of these structures varied in response to particular traffic conditions. In addition to surface angle, the amount of prey being transported along the trail had
a significant influence on the formation and size of structures, suggesting that scaffold-forming behavior may have evolved as a means of minimizing the loss of prey items in particular. To further investigate this, and to test a possible individual-level rule underlying the formation of these structures, we devised a simple model based on negative feedback control that qualitatively reproduces the dynamics of scaffold formation. These results show how a simple individual-level response to environmental and traffic factors can lead to a robust control strategy at the group level.

**Introduction**

The efficient transport of individuals, materials and information is critical for the functioning of many systems in biology and human society. This is especially true for social insects, where the survival of the colony depends on the coordination of foraging traffic for the collection and transport of resources through the environment (Couzin & Franks 2003; Dussutour et al. 2004; Burd 2006), just as human cities rely on the organized transport of goods and information to function effectively (Kerner 1998; Chowdhury et al. 2000; Louf & Barthelemy 2014). In engineered systems, both the complexity and scale of traffic problems are continually increasing, driven by rapid advances in technology and the interconnectedness of global networks (Hoar et al. 2002; Kennedy et al. 2015). Emerging technological developments involving complex networks like Smart Cities, the Internet of Things, and the coordination of autonomous vehicles will likely rely on methods of distributed, rather than hierarchical control (Karnouskos & de Holanda 2009; Batty et al. 2012). Distributed control systems rely on local sensing and communication, and are more robust under dynamic conditions than systems using top-down control (Sinopoli et al. 2003; Ogren et al. 2004).
**Negative feedback, robustness and proportional control**

Robustness, or the ability of a system to maintain functionality against external and internal perturbations, is ubiquitous in biology and a fundamental feature of complex evolvable systems (Kitano 2004). Understanding how this property is achieved in biological systems at multiple scales is a challenge with broad implications (Janssen et al. 2007). At the cellular level, robustness often results from a combination of positive and negative feedback, with negative feedback playing a stabilizing role (Stelling et al. 2004). While methods of distributed control inspired by social insect colonies generally focus on the power of positive feedback mechanisms to find optimal solutions (Bonabeau et al. 2000; Reid et al. 2011), negative feedback can play an important role in avoiding potential suboptimal solutions that can result from positive feedback alone (Beckers & Deneubourg 1990; Sumpter & Beekman 2003). For example, *Lasius niger* ants respond to crowding on the trail by reducing their deposition of pheromone, downregulating the positive feedback recruitment signal on that section of trail (Czackzkes et al. 2013).

Proportional control is a negative feedback-based mechanism for regulating some variable of a system’s behavior around a set point by means of a control loop. The difference between the current value of the variable and its set point is continuously measured, and a correction is applied based on the magnitude of this error (Pachter et al. 1996). In biological systems, proportional control mechanisms have been demonstrated in animals for the regulation of temperature (Hammel et al. 1963) and energy usage (Hainsworth et al. 1981). In mechanical systems, one or two additional terms are usually added to the correction $P$ to provide for additional stability, the integral term $I$ which accounts for the error over time, and the derivative $D$ which adjusts for the current rate of change of the error, resulting in a PID or proportional-integral-derivative controller (Venkatashankar & Chidambaram 1994; Ang et al. 2005). Here we
describe a distributed version of a proportional controller in a biological system. *Eciton burchellii* army ants respond to a disturbance in the flow of traffic based on local sensing of the rate of contacts between individuals, triggering a negative feedback loop by which the system regulates itself through proportional control at the group level.

*Self-assemblages in E. burchellii*

*Eciton burchellii* ants are forced to operate at a fast pace during their daily foraging raids in order to maintain the high rates of prey delivery necessary to support the developing brood of their massive colonies (Rettenmeyer 1963, Schneirla 1971). This strict time constraint has led to a number of unique adaptations. *E. burchellii* are able to maintain some of the highest running speeds among all ants (Powell & Franks 2005), and are known to spontaneously form lanes to increase the efficiency of traffic along their foraging trails (Couzin and Franks 2003). They also form self-assemblages, structures created when individual ants join their bodies together. These structures have been observed in a number of insect species with complex social organization, and are considered as intermediate-level parts of insect societies, functional adaptive units that exist at a level between the individual and the entire colony (Anderson & McShea 2001). For *Eciton* army ants, these structures serve two primary purposes: as shelter, in the case of the bivouac or temporary nest structure (Schneirla 1971), and as a means of improving the flow of traffic during raids and emigrations (Garnier et al. 2013, Powell & Franks 2007). Previous work on the bridges formed by *Eciton hamatum* showed that these structures are not static, but respond to traffic and environmental geometry to create shortcuts that benefit the colony (Chapter 1). The probability of an individual ant within a structure to leave or remain in a structure is a function of
the rate of contacts experienced (Garnier et al. 2013), but the mechanism underlying the decision to join a structure remains unexplained.

Here we examine a previously unstudied type of self-assembled structure in *Eciton burchellii*. We call these structures scaffolding because of their resemblance to the temporary support structures built around human construction projects. They form where a section of *E. burchellii* trail crosses a vertical or nearly-vertical surface like the face of a rock, a large buttress root, or the wall of a building. However, these structures do not form in every such instance, as trails often traverse steeply inclined surfaces without any scaffolding (personal observation). To form a scaffold, individual ants remove themselves from the flow of traffic and grip the inclined surface with their tarsi, remaining motionless to create a living platform with their bodies. These structures can be sparse, with only a few widely dispersed ants stopped along a surface, or extremely dense, with hundreds of ants attached both to the substrate and to one another, creating a deep structure that projects out into space.

To understand the role of these structures and the dynamics of their formation, we asked the following questions: 1. When and how do scaffolding structures form, and what are the key factors that drive their initiation and ultimate size? 2. At an individual level, what cues trigger an ant to stop and join a scaffolding structure? 3. Do these structures have adaptive benefits at the colony level, and if so, what are the benefits? To address these questions, we conducted field experiments that allowed us to manipulate the angle of a surface traversed by an established *E. burchellii* raiding trail and measure the spontaneous formation of scaffolding structures. We show that these structures predictably and repeatedly form as the result of interactions between environmental geometry and traffic dynamics, and identify the variables important to their formation and growth. To explain how the growth dynamics of scaffolding structures result from
local interaction rules, we developed a model of structure growth by negative feedback based on a proportional control mechanism. We assessed the fit of the model by comparing predicted growth curves with the experimental data.

**Materials and Methods**

*Experimental setup and protocol*

Field experiments were conducted in the seasonal tropical forest of Barro Colorado Island, Panama, in daylight hours during the dry season in January and February 2015. Three different colonies of *Eciton burchellii foreli* (Mayr), all in the nomadic phase, were located and used in experiments for 2 or 3 days each. Experiments were performed along the primary raiding trail, where traffic is most consistent throughout the day, within 50m of the bivouac. Each morning a suitable location along this trail was found, with enough space to set up the experimental apparatus and recording equipment. A break was created in the existing trail by removing sticks and leaves from the substrate, and the apparatus inserted into the resulting gap. Disrupted forager traffic was redirected up onto both ends of the apparatus by using the displaced sticks and leaves as makeshift ramps, covered in pheromone from the existing traffic. Experiments began once a continuous traffic flow had re-established over the apparatus.
Figure 1 | Diagram of experimental apparatus showing width of the adjustable central panel covered with sandpaper (a) and the removable spacer, shown in red in (b), used to adjust the angle of the surface.

The experimental apparatus consisted of two platforms that were 3D-printed from PLA filament (a non-toxic, corn-derived resin), each mounted on a flexible tripod approximately 10-15 cm above the ground, linked together by a removable hinged panel (Fig 1). The slope of this center panel could be set from nearly horizontal (20 degrees) to fully vertical (90 degrees) in 10-degree increments with an interlocking system of 3D-printed spacers. The center panel was covered with 220-grit sandpaper to provide an ecologically realistic surface that ants were capable of gripping, as tested in pilot experiments (Fig. 2b). To ensure the relative accuracy of
the angles, a field compass with spirit level was used to adjust the side platforms to be level and in plane with one another when setting up the apparatus each day.

To begin each experiment, traffic was interrupted temporarily as the adjustable surface was cleared of all ants and re-set to one of the 8 treatment angles. Once the surface was fixed back in place, ants began a tentative process of exploration. In order to account for the temporal variability of this phase, an experiment was considered to start only when the first ant had completely crossed the surface, re-establishing the trail and the flow of traffic. Each experiment was recorded for 10 minutes from this starting point. A total of 89 experiments were conducted, with 10, 11 or 12 trials completed for each of the 8 angle treatments from 20-90 degrees.

Data Collection

Videos were filmed with a high definition camcorder (Panasonic HDC-300) at 30 fps. The camera was mounted on a tripod and positioned at an angle approximately perpendicular to the surface being filmed, at a distance of approximately 60 cm. After initial processing of the video footage, 2 experiments were discarded due to poor lighting conditions, leaving a total of 87 experimental videos for analysis. The slope of the hinged surface was the only factor directly manipulated in the experiment. However, there are many potentially important variables that may be associated with the formation of scaffolding structures. The other factors we measured fluctuate throughout the course of a raid. This variation allowed us to observe the system under different combinations of factors to determine which conditions had an influence on the ultimate size of the scaffolding structures formed.
Figure 2 | (a) Diagram of the image subtraction process used to measure the area of the scaffolding structure. Each box shows the result of the algorithm at a different point in time for an example video, from early in an experiment (L) to the end of the experiment (R). Grey areas indicate moving ants, which are not counted in the area calculation. Black areas indicate ants that have stopped along the surface. The final area of the structure at the end of the experimental time is shown in red. (b) Example frame from a video of one of the experiments.

Traffic flux and directionality: Traffic flow was measured for each experiment by visual analysis of the videos (see Fig. 2b for an example). The number of ants crossing the edge of the sandpaper surface in each direction was counted. 5 counts were taken over 30-second increments.
evenly spaced over the course of each experiment to account for fluctuations in traffic, and averaged to give an estimate of mean total flux in ants/second. The proportion of bidirectional traffic was calculated by dividing the mean flux in the non-dominant direction by the total traffic.

*Prey-laden ants:* The number of prey-laden ants were counted visually, by identifying and tallying the number of ants carrying prey items for the duration of each experiment. The total number of ants carrying prey for each experiment was divided by 600 seconds to give a value in ants carrying prey / second.

*Scaffolding area measurement:* The change in size of scaffolding structures over time was measured using a custom image subtraction algorithm in Matlab. Adjacent frames of the video were compared to detect and record whenever an ant remained stationary (joined a structure) rather than moving with the flow of traffic (Fig. 2a). Output from the software was given in pixel area, which was then rescaled by comparison with manual counts to give a biologically relevant value, the number of ants making up the structure. Scaling values were calculated using the following regression equation ($R^2 = 0.96$), where $N_S$ is equal to the number of ants in a structure and $A$ is equal to the area of the structure in pixels:

$$[1] \quad N_S = 4.31 + 407.65(A)$$

*Falls from platform:* To give a rough estimate of how often ants fell off the structure at each angle in the absence of scaffolding structures, the number of falls were counted for the first 5 minutes of each video, before structures were fully formed.
Data Analysis

Size analysis of scaffolding structures and falling rate

Experimental data were analyzed with the statistical package R, version 3.2.5 (R Development Core Team 2009). For the full data set, generalized additive models were fitted using the gam() function from the mgcv package (Wood 2006; Wood 2011) to examine the effects of surface angle and the observed traffic variables on the ultimate size of scaffolding structures formed. GAMs with negative binomial distributions were used due to nonlinearities in the observed traffic data (apparent only over the entire data set) and overdispersion. Further analyses were conducted on a subset of the experiments with $\theta \geq 50$ to examine the effects of the traffic variables under conditions when structures were likely to form. These data were analyzed with generalized linear models using the glm.nb() function of the MASS package (Venables & Ripley 2002) and the glm() function (quasipoisson) from the stats package. In both cases, model selection was performed by starting with a saturated model including all of the potential variables of influence and their interactions, to a limit of three-way interactions. Non-significant interactions and effects were removed iteratively, until all terms remaining had an effect with $p < .05$. A similar process was used to examine the effect of surface angle and traffic variables on the likelihood of ants to fall from the surface, using generalized linear models with gamma distribution.

Growth analysis of scaffolding structures

For analysis of the growth dynamics of scaffolding structures over time, a negative exponential growth model was derived to test the hypothesis of negative feedback control by the process described below. Model fitting was performed with the nls() function of the stats
package to determine weighted nonlinear least-squares estimates of the parameters for growth curves from individual experiments. The default Gauss-Newton algorithm was used, which attempts to minimize the sum of squares of the error between the data and predicted values from the model, starting from initial parameter estimates and revising these over a number of iterations.

**Proportional control model**

When ants formed a scaffolding structure, the structures grew over the course of each experiment, typically reaching a stable size within the experimental time frame of 10 minutes. (See growth curves for each angle treatment in Figure 5 below). To characterize the rate at which structures grew, and to examine a possible mechanism underlying their formation, a simple model of proportional control was developed. The hypothesis underlying the model, based on the results presented below and on observations, is that prey-carrying ants drive the formation of scaffolding structures. A narrative description of the model is as follows:

- At higher angles, ants carrying prey have a more difficult time keeping their footing than non-laden ants, forcing them to slow down more.
- This creates a disruption in the flow of traffic, detected by individual ants as an increase in some cue (we will later suggest that this cue may be related to the rate of contacts between individuals, but the model is agnostic to its particular nature).
- As structures grow, prey-laden ants increasingly rely on the structure to proceed, segregating traffic and increasing the overall flow, eventually reducing the disruption cue to a baseline level.
The model is based on a proportional controller, a simplified version of a proportional-integral-derivative (PID) controller, a feedback loop-based control mechanism commonly found in industrial systems. For simplicity, this version consists only of the proportional term, which typically contributes the majority of the controller response (Riviera et al. 1986). The controller output \( u \) at time \( t \) is equivalent to:

\[
[2] \quad u(t) = K_p \, e(t)
\]

where \( K_p \) is a scaling factor (set equal to 1 here), and \( e \) is an error value defined as the difference between a desired set point \( SP \) and the current measured value of the process variable \( PV \):

\[
[3] \quad e = |SP - PV|
\]

Since \( K_p \) is set to 1, \( e = u \) in the current model. The error in the system is defined in terms of a cue \( C \), the rate of change of which is detectable by an individual ant \( i \). Ants have some memory capacity and can detect changes in the rate of a stimulus like contact rate, for example (Gordon 1999). The baseline rate of the cue \( C_{\text{typ}} \) is a function of the traffic variables density \( D \), prey \( P \) and proportion of bidirectionality:

\[
[4] \quad C_{\text{typ}} = f(D, P, B)
\]
The initial elevated rate of the cue $C_E$ experienced on an inclined surface is also a function of these three variables, with the addition of a variable $\theta$ denoting the angle of surface inclination, since surfaces at higher angles are increasingly difficult to traverse for prey-laden ants.

$$[5] \quad C_E = f(C_{typ}, \theta)$$

$C_E$ is then the initial value of $C$ at $t = 0$ for a particular set of angle and traffic conditions, and the difference between these two terms constitutes the detected error in the system, and thus the controller response:

$$[6] \quad u(t) = \Delta C(t) = |C_{typ} - C(t)|$$

Since the elevated level of the cue $C$ is reduced by the formation of scaffolding structures as prey-laden ants are diverted from the main flow of traffic, we can define $C(t)$ as a function of the size of the structure at time $t$. Since most of the scaffolding structures observed grew to a stable size over the course of each 10-minute experiment, we assume that $\Delta C$ is reduced in proportion to the size of the structure at $t$. We define the ultimate size of a structure as $\alpha$, which also varies as a function of the traffic properties, especially the amount of prey and the angle of the surface $\theta$, as described above.

$$[7] \quad \alpha = f(D,P,B,\theta)$$
Therefore, $C$ is reduced at a rate specific to the traffic conditions and angle of the surface in proportion to $\alpha$ such that:

\[
[8] \quad C(t) = C_E (\alpha - A(t)) = u(t)
\]

where $A(t)$ is the number of ants in a structure at time $t$. Since the set point $SP$ of the system is equal to 0 (where $C = C_{bp}$, the baseline level of the cue, indicating no traffic disruption), $C(t)$ is equivalent to $u(t)$, the controller response. As the overall size of the structure $A$ is the control variable of the system, we can write a differential equation describing the growth of a structure:

\[
[9] \quad \frac{dA}{dt} = C_E (\alpha - A_t)
\]

Solving for Eq. 9 results in:

\[
[10] \quad A_t = \alpha \left( 1 - e^{-C_E t} \right),
\]

a negative-exponential growth curve with a form equivalent to some simple models of plant growth (Jones et al. 1986; Fekedulegn et al. 1999). The parameter $C_E$ thus represents the growth rate of the structures when they are small, with $\alpha$ giving the asymptote of the growth curve as the growth rate goes to zero.
Results

Determinants of scaffolding structure size

Scaffolding structures formed more frequently and reached larger stable sizes at higher surface angles $\theta$ (Figure 3). Below 40° ($N = 20$), only one significant structure formed (defined as a stable structure consisting of 10 or more ants). At 40° and above ($N = 67$), the angle of the surface $\theta$ had a significant effect on the size of structures formed, which increased with higher angles $\theta$ ($\theta = 40^\circ$: $p = .009, z = 2.61$; $\theta = 50^\circ$: $p = .0024, z = 3.04$; $\theta = 60^\circ$: $p < .001, z = 4.56$; $\theta = 70^\circ$: $p < .001, z = 4.67$; $\theta = 80^\circ$: $p < .001, z = 5.01$; $\theta = 90^\circ$: $p < .001, z = 5.37$).

Figure 3 | Size of structures at the end of each experiment, measured as the number of ants in a structure divided by the length of the central panel (10 cm), for each of the 8 different angle treatments.
The amount of prey being transported (measured as number of prey-laden ants per second) also had a significant positive effect on structure size (smooth term, GAM: $X^2 = 38.47, p < .001$)(Figure 4). Overall, the best fitting model (GAM, negative binomial) including $\theta$ as a factor variable and the amount of prey as a continuous variable explained 85.2% of the deviance in the size of structures. Traffic density and the proportion of bidirectional traffic were not found to have significant effects on scaffolding size, and there were no significant interactions between any of the effects when including the entire data set. Predicted values from the overall model are shown in Figure 4, along with the data for individual experiments.

**Figure 4** | Curves are predicted values from a generalized additive model including surface angle $\theta$ (treated as a factor), and the amount of prey-laden ants as predictor variables, as described in the text. Shaded areas are 95% prediction intervals. Points are
values from the data, with each point representing one experiment. Colors for all indicate
the treatment angle $\theta$.

Few structures formed at low angles, making it difficult to assess the influence of variables other
than the surface angle when structures did form (Figure 5). To examine more closely the effects
of traffic variables on the formation of structures, we confined additional analysis to the subset of
experiments with $\theta \geq 50$. With this reduced data set a GLM was fitted, with the surface angle $\theta$
again showing the strongest significant effect ($t = 9.07, p < .001$). Additionally, in this model the
proportion of bidirectional traffic had a significant negative effect on structure size ($t = -2.86, p =
.006$), and the model revealed a more complex set of interactions between the other traffic
variables. A significant negative effect on structure size was found from a three-way interaction
between bidirectionality, prey rate and traffic rate ($t = -2.30, p = .0089$), while significant
positive effects were found from two-way interactions between prey rate and traffic rate ($t =
4.63, p < .001$), bidirectionality and prey rate ($t = 3.34, p = .0017$), and bidirectionality and traffic
rate ($t = 3.02, p = .00318$).
Figure 5 | Results from all experiments, grouped by angle treatment. At low angles (from 20-40 degrees), structures rarely formed and were sparse when they did. At higher angles structure size and growth rate varied as a function of traffic conditions.

Determinants of falling rate

Ants were more likely to fall from the surface at higher angles \( \theta \) (Figure 6). A GLM with gamma distribution \((F = 38.36 \text{ on } 9 \text{ and } 77 \text{ DF, Adjusted } R^2 = .80, p < .001)\) was fitted to examine the effect of angle and traffic variables on the number of ants falling over the first half of each experiment, before scaffolding structures were fully in place. Both the amount of prey \((t = 5.66, p < .001)\) and traffic rate \((t = 4.46, p < .001)\) had a significant effect on the number of falls. In addition, the surface angle \( \theta \) had a significant effect in proportion to the slope of \( \theta \) (\( \theta = 30^\circ: p = .032, t = 2.179; \theta = 40^\circ: p < .001, t = 3.78; \theta = 50^\circ: p = .0024, t = 3.04; \theta = 60^\circ: p < .001, t = 4.56; \theta = 70^\circ: p < .001, t = 4.67; \theta = 80^\circ: p < .001, t = 5.01; \theta = 90^\circ: p < .001, t = 5.37\)).
Figure 6 | Rate of falls (in fallen ants / minute), for experiments at each of the different angle treatments. Falls were counted over the first 5 minutes of each trial, before structures were fully complete.

Negative feedback proportional control model

The negative exponential equation derived from the proportional control model was fit to the growth curves from the data to estimate the parameters $C_1$ and $\alpha$ for each experiment.

Examples of the fitted curves and estimated coefficients for experiments with $\theta = 90^\circ$ are shown in Figure 7.
Figure 7  |  Curves from the exponential growth model fit to data from individual experiments with $\theta = 90^\circ$, labeled with parameter estimates for $\alpha$ and $C_i$. 95% prediction intervals are shown in grey.

Although goodness-of-fit can be difficult to assess for nonlinear models, a pseudo-$R^2$ measure was calculated for each curve to provide some indication of fit. Curves, estimated coefficients and estimated errors for all experiments where the model was fitted can be found in Appendix B. Since structures rarely formed below $\theta = 50^\circ$, we confined attempts to fit the model to experiments with $\theta \geq 50^\circ$. Of these experiments ($N = 56$), substantial structures formed in 48 cases (defined as structures consisting of 10 or more ants). The model was successfully fit to 45 of these growth curves, with a “good fit” (defined as a value of pseudo-$R^2 > .75$) achieved for 30 of these.
Table 2 | Summary of negative exponential model fits

<table>
<thead>
<tr>
<th>Experimental angle $\theta$</th>
<th>50</th>
<th>60</th>
<th>70</th>
<th>80</th>
<th>90</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N$ experiments</td>
<td>11</td>
<td>12</td>
<td>11</td>
<td>12</td>
<td>10</td>
<td>56</td>
</tr>
<tr>
<td>Structures formed</td>
<td>6</td>
<td>11</td>
<td>9</td>
<td>12</td>
<td>10</td>
<td>48</td>
</tr>
<tr>
<td>Negative exponential growth model fit to data</td>
<td>6</td>
<td>9</td>
<td>8</td>
<td>12</td>
<td>10</td>
<td>45</td>
</tr>
<tr>
<td><em>Model fit with pseudo-$R^2 &gt; .75$</em></td>
<td>3</td>
<td>4</td>
<td>7</td>
<td>9</td>
<td>7</td>
<td>30</td>
</tr>
</tbody>
</table>

The parameters $C_i$ and $\alpha$ were extracted from each fitted curve, and fell within the range of values shown in Figure 8, which gives a sense of the curves described by the relationship between the terms. Estimates for each combination of $C_i$ and $\alpha$ are shown in Figure 9.

![Figure 8](image_url) Growth curves output from a simple simulation model of Eq. 9 with $\Delta t = 1 \text{ s}$. The model was run for a range of parameter values representative of the data, showing the relationship between $C_i$ and $\alpha$ within the experimental time frame.
The relationship of the estimates for parameter $\alpha$ to potential explanatory variables were modeled with a negative binomial GLM, showing a significant effect of surface angle $\theta (z = 7.60, p < .001)$ and a significant interaction effect between prey rate and traffic rate ($z = 3.79, p < .001$). No consistent relationship could be determined between the estimated values of the growth rate $C_i$ and potential explanatory variables, perhaps due to the relatively small sample size of the curves fit.

![Figure 9](image_url)

**Figure 9** | Parameter estimates from the negative exponential model for experiments with $\theta = 50^\circ - 90^\circ$. Error bars are the 95% confidence interval for estimated values. Convex hulls shaded by color for each angle treatment.

**Discussion**

The results described here show that the self-assembled scaffolding structures constructed by *Eciton burchellii* ants across inclined surfaces function as a self-organized, distributed system.
of traffic control. Scaffolding structures are responsive to the dynamic conditions of foraging traffic and environmental geometry, and are adjusted through a process of negative feedback analogous to a proportional controller. The growth rate and size of structures are emergent properties that arise as the result of local sensing and decision making. In particular, ants respond to a cue related to traffic disruption to initiate or join a structure. This cue is driven primarily by the amount of prey being transported at any given time, as prey-laden ants are forced to reduce their speed more than non-laden ants when traversing an inclined surface, causing a disruption in traffic. As structures are formed, prey-laden ants are diverted out of the main flow of traffic onto the scaffolding structure to regain their footing. Thus, a negative feedback process emerges whereby larger structures remove more prey-laden ants from the primary flow, reducing the traffic disruption and the level of cue that leads to the formation of structures. By this process, structures are stabilized at a rate and size that is a function of a particular set of traffic variables. However, this function is a complex set of interacting variables, and there are regions of parameter space that are more or less favorable for the formation of structures.

Highly bidirectional traffic flow affects the growth of structures in unpredictable ways. We attribute this to the increased disruption of traffic that accompanies higher levels of bidirectional flow. In terms of the proportional control model described here, this results in a higher baseline value of the individual-level cue indicating traffic disruption, essentially diluting the signal and making it more difficult for ants to detect a change in the cue due to the inclined surface. This would help to explain the negative relationship between bidirectionality and structure size, as well as the complex effect on structure size of the interactions between bidirectionality, traffic and prey. While the model proposed here makes no assumptions about the individual-level cue by which ants detect a disruption in traffic, it is likely related to the rate
of contacts between individuals. Contact rate is a cheap and robust cue that requires little processing, since it does not require counting of individuals (Gordon & Mehdiabadi 1999). Other ant species use contact rate as a cue to inform decisions (Green and Gordon 2007) and to estimate the density of colony-mates (Gordon et al. 1993; Czaczkes et al. 2013). In *E. burchellii*, previous work has demonstrated the importance of contact rate for the stability of self-assembled structures (Garnier et al. 2013; Powell & Franks 2007). In Chapter 4, I will test the hypothesis that contact rate serves as a cue to indicate traffic disruption leading to the formation of scaffolding structures.

The rate of prey delivery had the strongest positive effect on structure size of the three traffic variables measured. Previous work on the bridges formed by *E. burchellii* had shown that traffic rate had a significant influence on the growth and dynamics of structures, with an ant’s probability to join a structure an increasing nonlinear function of the traffic rate (Garnier et al. 2003; Chapter 1). This simple rule and its inverse (describing an ant’s probability to remain in a structure after joining) explained the stability and responsiveness of bridge structures. However, our analysis revealed that traffic rate only had an effect on structure size in combination with other traffic variables. Like bridges, scaffolding structures facilitate the flow of traffic and ultimately increase the rate of prey delivery. However, they emerge through a different process and serve a different function. Bridges and plugs are relatively common along the raiding trail, and provide small modifications to the environment that result in a significant increase in prey delivery for the colony (Powell & Franks 2007). Scaffolding structures are rare, and emerge in response to a disruption in traffic. They serve the dual function of preventing ants and prey items from falling while also improving traffic flow.
The fact that we were able to achieve a good fit between the negative exponential model and the growth curves for only 30 out of 56 potential experiments can be attributed to a few factors. First, goodness-of-fit can be difficult to assess with nonlinear models, and our cutoff value for the pseudo-$R^2$ measure was arbitrary. Other growth models like the Michaelis-Menten model of enzyme kinetics (Michaelis & Menten 1913) or the related Monod equation for bacterial growth (Monod 1949) can be fit to the data as well, but offer no biological justification. By deriving the negative exponential solution from a hypothetical mechanism of negative feedback control, we proposed a biologically relevant model to explain both the growth dynamics and function of scaffolding structures. However, the model describes the growth of structures under ideal conditions, without accounting for any variation in traffic conditions. As discussed in the description of the proportional control model, the parameters $C_i$ and $\alpha$ are a function of the particular conditions of traffic and environmental geometry (surface angle) for each experiment. This assumes that the parameters would be fixed in response to the values of the traffic variables at the beginning of the experiment, without changing over time.

A visual examination of the curves for each experiment with 95% prediction intervals (Appendix B) reveals that nearly every instance where the prediction interval is wide corresponds to an experiment where the rate of growth of the structure changed at one or more points during the experiment. Since structure size within a given angle treatment is a complex function of traffic rate, the rate of prey delivery and the proportion of bidirectionality, any variation in the growth rate of structures can be due to changes in one or more of these traffic patterns during the course of the experiment. Traffic on *E. burchelli* trails is highly variable, showing periodic oscillations resulting from speed differences and contacts between individuals with a median period of around 3.4 seconds. However, it has been shown that bridges are stable
to these regular variations in flow (Garnier et al. 2013). We would expect that scaffolding structures respond similarly to these oscillations, suggesting that variations in the growth rate of scaffolding structures result from changes in either the rate of prey delivery or bidirectional traffic. While the proportion of bidirectional traffic does vary widely over the course of a raid as the ratio of incoming to outgoing ants shifts (Rettenmeyer 1963; Schneirla 1971), these shifts typically occur over longer timescales than the 10 minutes of each experiment.

These variations are therefore most likely due to changes in the amount of prey-laden ants. The rate of prey delivery can vary widely and unpredictably for both *E. burchellii* (Franks 1982) and *E. hamatum* (Powell 2011). This is due primarily to the patchy nature of prey distribution, and to the existence of “booty caches” along the trail where prey items are dropped temporarily during the raid (Franks 1985; Schneirla 1971). These caches are periodically cleared, resulting in a large influx of prey items. Given our findings and the model presented here, we expect scaffolding structures to be highly sensitive to such fluctuations in prey delivery. However, further analysis is needed to tune the model to the effect of within-experiment variation in prey delivery rate.

The results presented here provide new insight into a behavioral adaptation in an important social insect predator that is driven by unique ecological constraints. We have added to an increasing base of knowledge regarding the mechanisms underlying the formation of complex self-assembled structures (Powell & Franks 2007; Garnier et al. 2013), a topic with considerable implications for the emerging field of swarm robotics (Kube & Bonabeau 2000; Werfel et al. 2014). Our findings support other recent work demonstrating the importance of negative feedback for regulation in social insect colonies (Grueter et al. 2012; Czaczkes et al. 2014). The model of proportional control in social insects we have described achieves stability through
negative feedback driven by local sensing, a potential improvement over previous biologically inspired systems of distributed control (Di Caro & Dorigo 1998; Passino 2001). More broadly, our study provides a clear example of how robustness can be maintained in biological systems through a self-organized negative feedback process.

Acknowledgments

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Infrastructure on demand: *Eciton burchellii* army ants self-assemble to widen paths in response to traffic bottlenecks

**Abstract**

We examined a context-dependent subtype of the broader class of self-assembled structures formed by the army ant *Eciton burchellii* to facilitate the flow of foraging traffic. Flange structures are formed when traffic is constricted along a narrow path like a stick or vine. Under such conditions, individual ants will stop along the edge of the surface, using their bodies to effectively widen the path for other crossing workers. We describe the results of field experiments demonstrating that flange structures consistently and repeatedly form under these conditions. We show that the growth of flanges is significantly influenced by the dynamics of traffic flow over time, as has been shown previously for the bridge structures formed by *E. burchellii*. However, we demonstrate that flange structures are responsive to a different set of traffic variables than bridges, and that the dynamics of flanges differ from those of bridges in fundamental ways. The formation of flange structures is strongly influenced by the proportion of bidirectional traffic on the trail, and these structures form more rapidly than bridges under a wider range of conditions. We discuss why the rapid deployment of flanges is important for *E. burchellii*, and how the same individual-level mechanism can create structures with different response dynamics under different conditions of environmental geometry. We use results from
an individual-based simulation model to inform a new hypothesis about the growth dynamics unique to flanges, reflecting the particular role of these structures.

Introduction

While many organisms are capable of modifying their environment adaptively, the structures built by social insects like some species of termites and ants are unrivaled in their complexity. Typically, social insects modify their environment using stigmergy, where individuals deposit information in the environment that serves as a cue to others (Grassé 1960). By such a process, intricate structures are built without requiring any direct communication between individuals or overall plan (Theraulaz & Bonabeau 1995). This highly successful adaptation has arisen in many social insect species (Wilson 1971), and the concept has been influential for a wide variety of fields outside of biology (e.g. Parunak 1997; Dorigo et al. 2000; Valckenaers et al. 2004). However, stigmergy is useful primarily for social insects that remain in one place for long periods of time. In the Neotropical army ants Eciton burchellii and Eciton hamatum, an entirely different strategy of environmental modification has been selected for.

These ants maintain a nomadic lifestyle without a permanent nest, instead building a temporary nest structure out of their own bodies that is frequently dismantled and moved to a new location (Schneirla 1954). In addition, they form smaller structures out of their own bodies that function as environmental modifications that facilitate the flow of traffic on their raiding trails, anastomosing transport networks that can extend for hundreds of meters. These self-assemblages are fundamental to the efficient operation and fitness of Eciton colonies (Powell & Franks 2007), and perform as a distributed system of environmentally-responsive infrastructure that is unique among social insects. Unlike processes of environmental modification that rely on
stigmergy alone, the self-assemblages built by Eciton ants adapt over time to dynamic conditions in the environment and respond to changes in foraging traffic by adjusting their geometry (Chapter 1). Self-assemblages have been described metaphorically as akin to the tissues and organs of complex insect societies (Anderson et al. 2002), and while other social insects form similar structures under certain conditions, in no other species are self-assemblages such a fundamentally integrated aspect of ecology and behavior. This makes Eciton ants an ideal system for examining the processes by which individual behavioral traits are selected for their capacity to facilitate a rapid and coordinated response at the level of the colony. The results presented here complement recent work revealing how individual-level rules may be tuned in E. burchellii and E. hamatum to achieve distributed control through environmental modification (Couzin & Franks 2003; Powell & Franks 2007; Garnier et al. 2013).

We examined a previously unstudied type of structure formed by Eciton burchellii ants when foraging traffic is constrained along a narrow surface. These constrictions create bottlenecks in the flow of traffic, congested zones with complex dynamics that exist in nearly all traffic systems under certain conditions. Bottlenecks and spontaneous jamming have been well studied in vehicular and pedestrian traffic (Arnott 1993; Kerner 1998; Moussaid et al. 2012) and also in ants (John et al. 2004; Dussutour et al. 2005; Fourcassié et al. 2010). Based on previous observations, we hypothesized that any bottlenecks formed would be alleviated by a number of ants widening the path of travel by forming “flanges” out of their own bodies, consisting of one or more rows of ants attached along the side of the thin pathway. We conducted a series of field experiments in which we were able to trigger and observe the formation of flange structures under realistic traffic conditions. We hypothesized that flange structures would grow in a predictable pattern in response to certain traffic conditions, and that ants would adjust the size of
structures over time to accommodate changes in traffic. Our observations led to another hypothesis about the individual rules that ants use to decide whether to initiate or join a structure, which we support with results from an individual-based model. Our results show how a simple set of individual-level behavioral rules can lead to the emergence of context-specific structure types without involving complex sensing or decision-making processes.

**Materials and Methods**

*Experimental setup*

Experiments were carried out on Barro Colorado Island (BCI), Panama in February, 2003 with three different colonies of the study species, *Eciton burchellii foreli*. Each experiment was performed along the principal raiding trail, where a break in traffic was created and the experimental apparatus inserted. Traffic was redirected over the apparatus, constructed from wood and consisting of two ramps connected by a bridge with a removable middle section, the experimental surface (Fig. 1). The experimental surface was 14 cm long, with a 10cm by 0.3cm restricted section to simulate the geometry of a narrow stick or vine that the ants often traverse, a condition under which flanges had been observed. It was hypothesized that this narrow constriction would induce the formation of flanges, and it did in every trial. Traffic was first re-established over a simple wide bridge between the two ramps, after which experiments began according to the following procedure.
Figure 1 | Apparatus design, showing the full ramp structure (a) and the removable wide central surface (b), indicating location of the replaceable experimental surface (c). Adapted from (Powell and Franks 2007).

**Experimental protocol**

Once the normal rate of traffic was re-established over the simple wide bridge, this surface was replaced with the flange bridge, but with a wide section of bridge in the middle section, and traffic was again allowed to re-establish over the new surface. At this point, traffic was paused and the wide middle section was replaced with a restricted middle section (the experimental surface). Traffic on the trail was then allowed to flow, and the experiment commenced. Starting at this point, each trial was filmed from above for 5 minutes. At the end of
5 minutes, traffic was again paused. Ants crossing the apparatus at this point were allowed to finish, until the experimental surface was free of crossing ants. The experimental surface was then removed, with the remaining flange ants still attached, and placed into a Ziploc bag that was immediately sealed and put on ice. Those ants remaining as part of a flange at the end of each trial were then counted and measured back in the lab. 10 replicates were performed with each of the three colonies, for a total of 30 trials. Each within-colony replicate used a new one of 10 experimental surfaces, which were all washed with mild detergent and water and wiped down with alcohol before use with a new colony.

Figure 2 | Example of a flange structure. A frame captured from a video of one of the experiments after 3 minutes of experimental time. The lower wood surface is the base of the ramp structure shown in Fig. 1a.
**Data Collection**

Videos were filmed with a high definition camcorder mounted on a tripod above the apparatus at 30 fps. The video footage was cropped to 5 minutes from the beginning of each experiment for consistent analysis.

*Traffic flux, prey rate and directionality:* Traffic flow was measured for each experiment by visual analysis of the videos. The number of ants crossing the apparatus in each direction was counted. Counts were taken for each 15-second increment over the course of the experiment to measure fluctuations in traffic, and these were averaged to give an estimate of mean total flux in ants/second for each experiment. Ants carrying prey were identified and counted for each 15-second increment as well. The proportion of bidirectional traffic was calculated by dividing the mean flux in the non-dominant direction by the total traffic.

*Flange area measurement:* For one set of experiments (with the colony E03_11), the size of flange structures over time was measured using a custom image subtraction algorithm in Matlab. Adjacent frames of the video were compared to detect and record whenever an ant remained stationary (joined a structure) rather than moving with the flow of traffic. Output from the software was given in pixel area, which was then scaled in relation to the counts of flange ants removed at the end of each experiment. For the entire data set, a value for the area of the structure (rather than a discrete count of ants) was estimated for analyses requiring area calculations according to the scaling equation

\[ N_{ants} \cdot 0.0833 = Area \ (cm^2) \]
**Flange ant counts and morphological measurements:** The ants remaining in each structure at the end of a trial were counted and measured in the lab. The right back leg length of each ant was measured to the nearest 0.15 mm, using a dissecting microscope fitted with an ocular micrometer. The back leg length has a tight scaling relationship with overall size as measured by dry weight (Powell & Franks 2005), allowing for conversion between the two measures.

**Agent-based model of self-assemblage formation:** To test a hypothesis about the individual-level rules by which ants join flange structures and to help explain their growth dynamics, a spatially explicit agent-based simulation model was used. For a complete description of the model, see Chapter 4. The model was used qualitatively to test predictions and generate new hypotheses. Values for all other parameters were held constant while the proportion of bidirectional traffic was set at two levels, 0.0 and 0.5. The growth of flange structures was monitored over time by counting the number of ants in a structure. Additionally, the number of ants attempting to join a structure at any given time step was counted. The model was run for 7200 time steps, equivalent to 144 seconds of experimental time, to examine the initial growth phase of structures.

**Data Analysis**

Data were analyzed with the statistical package R, version 3.2.5 (R Development Core Team 2009). With a data set comprising the mean values for the three traffic variables over each experiment and the final structure size at the end of each experiment, the effects of potentially
influential traffic variables on the ultimate size of flange structures were examined by fitting generalized linear models with the quasipoisson method of the glm() function of the stats package. Mixed effects models were initially explored, but the influence of colony as a random effect was not significant. Model selection was performed to find the simplest explanatory model, starting with a saturated model that included all potentially influential terms and their interactions. Non-significant terms and interactions were removed until only variables with significant effects remained. Further analyses were performed on the time series data from experiments with one colony (E03_11), for which growth data of flange structures over time was extracted. These included the calculation of Pearson product-moment coefficients to assess correlations between variables, and the fitting of Loess curves and linear models to examine trends in the data.

Results

Determinants of flange size

The final size of flange structures (measured as the number of ants in a structure at the end of each experiment) was significantly influenced by the mean proportion of bidirectional traffic during the course of the experiment ($p = .0027, t = 3.300$) and the mean rate of prey delivery ($p = .0144, t = 2.616$) (GLM, quasipoisson). The influence of colony was not significant, either as a random or fixed effect, and no significant effect was found from the rate of traffic flow. No significant interactions were found between the traffic variables. The average area of flange structures at the end of an experiment was 4.748 cm$^2$ ($SD = 2.325$). Summed with the initial area of the narrow path (since flanges extended this on either side), the average usable road area at the end of an experiment was 9.748 cm$^2$, an increase in area of 94.96%.
Figure 3 | Curve representing predicted values from the GLM of the ultimate size of flange structures (total number of ants in the structure at the end of each experiment) at different levels of bidirectional traffic. Shaded area shows the 95% prediction interval of the model. Points are results from individual experiments, colored according to colony.

Dynamics of flange growth

A Pearson product-moment coefficient was calculated to examine whether the growth rate of structures was significantly correlated with time. As shown in Figure 4, the growth rate of structures was highest at the beginning of experiments, and showed a significant negative correlation with time ($r(187) = -0.338$, $p < 0.001$).
Figure 4 | Growth rate of flange structures as a function of time for colony E03_11. Loess curve fit to the data for all experiments to visualize the general relationship, with 95% confidence interval shown in grey.

A Pearson product-moment coefficient was also calculated to examine the relationship between the growth of structures and bidirectional traffic. A significant correlation was found ($r(187) = 0.447$, $p < 0.001$), and Loess curves were fit to the data to further assess the relationship between the growth of structures and bidirectional traffic (Fig. 5).
Figure 5 | Loess curves fit to the data for 9 individual experiments with colony E03_11 showing (a) the growth dynamics of structures over time and (b) the dynamics of bidirectional traffic over time.

The proportion of bidirectional traffic varied less within each experiment than either prey rate or traffic rate for the experiments that were analyzed in-depth over time (Fig. 6).
The agent-based model qualitatively captured the rapid growth dynamics of flange structures (Figure 7a). Additionally, the number of ants checking whether to join a structure (a procedure that is induced by an ant’s proximity to an edge), was observed to be consistently correlated with the transition in the slope of the growth curve of scaffolding structures (example curves in Figure 7b). We present this as a qualitative result although analyses have not been
performed to assess significance because the general relationship is consistent and repeatable in the simulation model under different combinations of parameters.

Figure 7 | (a) Two example growth curves output from the simulation model after 7200 time steps, equivalent to 144 seconds of experimental time. Red points and smooth curve are the result of a simulation run with the value for bidirectional traffic set to 0.0. Blue points and curve are output from the model run with the maximum value of 50% bidirectional traffic. For both, traffic rate = 8.0 ants / sec. and prey proportion (as a percentage of total
traffic) = 10%. (b) shows results from the same simulation run, counting the number of ants that have attempted to join a structure present in the simulation at any given timestep. Ants arrive and leave the model continuously from either side (see Chapter 4), with around 140 ants in the simulation at any time at the level of traffic shown here.

Discussion

Our results show that flange structures form rapidly and consistently as a response to bottlenecks created when traffic flow is constricted along a narrow surface. Structures formed in every experiment that we conducted, and on average their formation nearly doubled the effective road width, increasing the capacity of the trail and eliminating any initial bottleneck. The formation and growth of flanges was significantly influenced by the proportion of bidirectional traffic flow and the rate of prey delivery over the course of each experiment. The rate of flange growth was highest at the beginning of each experiment, and declined over time.

We have demonstrated that flanges are fundamentally different than the bridges also formed by Eciton burchellii in their structure, function and growth dynamics. Our analysis of these structures has revealed another level in the kit of adaptive responses available to Eciton army ants by means of temporary modification of the environment through the formation of self-assemblages. From what we have shown, it appears that flanges are deployed as a rapid, self-organizing response to disturbance. They typically form downstream from a bottleneck in traffic, when the flow of traffic rushes forward along a narrow path. The apparent responsiveness of flange structures to disruptions in traffic flow suggests that they provide another form of negative feedback control similar to the scaffolding structures described in Chapter 3. However, further analyses of the experimental data over time are necessary to examine the particular correlations between flange structure and traffic dynamics in order to make any assertions about causality.
Given their constrained geometry and the correspondingly straightforward process by which they form, flanges should provide a useful model for asking fundamental questions about the individual rules that give rise to self-assemblages. The simulation model we introduced briefly implements a simple rule for the formation of structures that proves to be quite robust, and offers a potential mechanism to explain the emergence of flange structures. An encounter with an edge in the environment can trigger the response by which an ant attempts to join a structure. If there are no other ants already part of a structure in the immediate area, the ant will likely turn away from the edge. The initiation of a structure from scratch tends to occur rarely, because ants can only initiate structures where two surfaces meet at an angle. However, once a structure is initiated, ants encountering an edge are more likely to join if another ant is already present. This triggers a positive feedback loop as more ants continue to join.

The situation induced by the flange apparatus (or any narrow surface where flanges typically form) allows this positive feedback cascade to progress rapidly. As a worker ant traverses the narrow surface, she is constantly in contact with an edge, and thus maintains a consistently high probability to join a structure. If there are already ants in the structure, she will continue forward (with a high probability of joining) until finding an available space. Since ants in a flange structure cling to the side of the surface, space is essentially limited (although large structures can form under the right traffic conditions). Once all the easily accessible spaces are occupied, the cascade should subside (as shown in Fig. 7b). Further damping the response, as the flange structure effectively widens the path of travel, new ants crossing the surface are less likely to encounter an edge and trigger the joining mechanism.

Another, perhaps complementary, explanation for the rapid emergence of flange structures is the self-organized formation of lanes that occurs on Eciton burchellii trails. Lane
formation also emerges from a simple individual rule, as ants returning to the bivouac tend to turn at a lower rate than outbound ants. Inbound ants thus end up occupying one central traffic lane, while outbound ants have a tendency to use one of two outer lanes (Couzin and Franks 2003). Given this behavior, the significant influence of bidirectional traffic on the formation of flanges is not surprising. Returning ants should be expected to maintain their position in the center of the narrow path, while outgoing ants should dodge to the edge of the surface to avoid collisions. Further analyses of traffic data from the experiments described here should provide additional insights and offer a means of testing these hypotheses.

We have demonstrated another adaptive function of self-assembled structures in *Eciton* army ants, one that is highly context-dependent and seems to be particularly effective, although more thorough quantitative analysis is required before we can assess the particular adaptive value of this response. The rapid formation of flange structures demonstrates how simple and general individual rules that lead to the emergence of complex behaviors at the group level can be highly tuned to perform a particular function under certain conditions.

**Acknowledgments**

I gratefully acknowledge the work of Scott Powell, who designed and conducted the experiments described here and whose expertise has been invaluable in the course of analyzing the data and writing the manuscript. Some of the video analysis was carried out by a team of undergraduate students at the University of Konstanz under the supervision of Alexander Bruttel, to whom I am indebted for coordinating a difficult operation. Finally, I thank Iain Couzin for supporting this research and enabling my work both in the US and Germany.
An agent-based model to simulate the formation and dynamics of self-assembled structures in *Eciton* army ants

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**Abstract**

The self-assembled structures formed by *Eciton* army ants are a unique example of how natural selection can select for behaviors in social insects that have no apparent utility at an individual level, but provide an adaptive benefit at the level of the colony. These structures can function as shortcuts or to smooth the terrain over which foraging traffic moves, increasing the rate of prey delivery by either decreasing distance traveled or increasing the speed of prey-laden foragers. However, little is known about the individual rules that produce this complex group-level behavior. To examine what individual sensory inputs and behavioral outputs might combine to produce this behavior, I developed a spatially-explicit agent-based model. I evaluated the results of the model against experimental data from two sets of experiments with two different species of ants, *Eciton burchellii* and *Eciton hamatum*. The model reproduces two different kinds of structures formed, under different conditions of environmental geometry, and reproduces the movement dynamics of army ant bridges, under traffic conditions matching the experimental data. I use the model to test hypotheses generated by previous experimental work about the individual-level behaviors underlying the formation of structures.
Introduction

Understanding how higher-level order emerges as a result of local interactions among individuals of limited cognitive capacity and sensing ability is a fundamental problem in biology, with broad implications across disciplines (Levin 1992; Couzin 2009). Within the general domain of these systems, described as self-organizing (Camazine et al. 2003), the term “swarm intelligence” describes the capacity of systems consisting of simple agents to perform complex tasks beyond the capabilities of a single individual (Garnier et al. 2007). Examining the behavior of systems that exhibit properties of swarm intelligence has generated valuable insights in many fields, including for the design of multi-agent systems in an engineering context (Leonard 2014). A key challenge for understanding (and potentially controlling) the emergent behavior of such systems is ascertaining the individual-level rules that lead to complex group-level behaviors (Berdahl et al. 2013). Given the difficulty of extracting such rules directly from experimental data, agent-based simulations can provide a powerful tool to complement experimental approaches in testing hypotheses about individual behaviors (Couzin et al. 2002; Couzin et al. 2005; Torney et al. 2010).

In particular, agent-based models have proven useful for the study of social insect behavior. For species like Eciton burchellii and Eciton hamatum, which can be extremely difficult to keep in a lab setting, simulation models have been critical for both generating and testing hypotheses about foraging behavior (Deneubourg et al 1989; Sole et al. 2000) and traffic organization (Couzin & Franks 2003). I have taken a similar approach to investigating the individual-level rules that lead to the formation of self-assembled structures. The experiments described in the previous chapters led to a number of hypotheses about individual behavior, which I test here.
**Hypothesis 1:** The first hypothesis is that the same individual-level rule (or set of rules) should be capable of generating the variety of structures that *Eciton* army ants build, depending on the environmental and behavioral context. This hypothesis underlies the basic structure of the model, and should be supported to some degree if the model can reproduce the range of desired behaviors with simple individual rules.

**Hypothesis 2:** The second hypothesis involves the particular environmental cue by which an ant is induced to initiate or join a structure. Informed by field observations and experiments, I hypothesize that whenever structures span across empty space (as in a bridge), they must be initiated at an angle between two edges, by which an initiating ant can grip onto some surface with the tarsal claws of both front and back legs. This rule has been demonstrated in pothole plugging behavior (Powell & Franks 2007), and was observed repeatedly in the experiments from Chapters 1 and 3. Once the initial ant is in place as a “cornerstone”, more ants can join around the same location. Ants stopped as part of a structure then provide a cue for others to join through a positive feedback process.

**Hypothesis 3:** The third hypothesis relates to a potential cue derived from interactions between individuals. Ants may have a variable probability to initiate or join structures that is a function of the number of contacts (or collisions) they detect while moving in the flow of traffic.

The chapters presented here, along with previous work on self-assemblages in *Eciton burchellii* (Powell & Franks 2007; Garnier et al. 2013), have revealed a number of variables that influence the formation of structures. However, these are primarily macroscopic properties relating to the dynamics of foraging traffic and environmental geometry. Discerning individual rules from these properties is difficult due to the number of variables involved. For instance, in the experiments and model of Chapter 1, we showed that the distance moved by bridges
represents a cost-benefit tradeoff at the colony level, but the individual rules that have been selected for to enable this remarkable collective behavior are unclear. The model presented here replicates the formation process of both bridges and flanges, and captures the movement dynamics of bridges under different angle treatments and traffic conditions. I use experimental data from previous chapters to identify the individual-level parameter ranges that produce bridges and flanges with the appropriate size, growth and dynamics corresponding to particular traffic properties. The emergence of context-specific structure types is achieved through a simple set of individual rules, supporting Hypothesis 1 above.

The robust performance of the model demonstrates the importance of initiating structures at an angle or intersection between surfaces, supporting Hypothesis 2 as well. The third hypothesis, about the role of contact rate as a cue for the formation of structures, is supported in some contexts but not in others. I show that contact rate may play an important role in the formation of scaffolding structures as a means of detecting traffic disruption (as hypothesized in Chapter 2), but that this cue is not required for the formation of realistic bridges and flanges.

**Methods: Model Description**

I developed a spatially-explicit agent-based model to simulate the process of self-assemblage formation in *Eciton* army ants as a result of local interactions. The goal of the simulation was to determine a simple and robust set of individual rules capable of generating different kinds of structures depending on environmental context. The model was tested in three different spatial scenarios replicating the three different experiments described in the previous chapters. The bridge apparatus from Chapter 1 across the same four angle treatments, the inclined angle surface from Chapter 2, and the constrained geometry of the flange apparatus
from Chapter 3. However, the scaffolding environment of the model was used only to simulate the difficulty of traversing the surface to examine traffic dynamics to test the hypothesis from Chapter 2. In the other two cases, the model was able to reproduce the temporal dynamics of the structures formed under a wide range of parameters. The model is implemented in the agent-based modeling environment NetLogo (5.3.1; Wilenski 1999). Many of the parameter values, as well as significant components of the movement procedures and interaction rules, are adapted from the model of self-organized lane formation in *E. burchellii* by Couzin and Franks (2003). I have tried to maintain the same notation wherever possible to permit comparison between the models. The pheromone detection procedure is a simplified version of the orientation model of Calenbuhr and Deneubourg (1992). Some elements of the NetLogo implementation, such as the pheromone deposition and diffusion procedures, are inspired by the ant foraging model of Czaczkes (2014), and the avoidance procedure is adopted from the flocking model of Wilenski (1998). The model description that follows is organized according to the ODD (Overview, Design concepts, Details) framework (Grimm et al. 2006).

**Overview**

**Purpose**

The purpose of the model is to understand how complex self-assembled structures are formed and adjusted by *Eciton* army ants as a result of simple individual rules, in response to dynamic local conditions.
Figure 1 | A snapshot of the model visualization, with the background image set to the bridge apparatus with an angle of 40°. Outbound ants are represented as blue, returning ants red. Bridge ants are shown as grey or orange, with orange ants indicating the initiation points of structures.

Entities, state variables and scales

The model is spatially explicit, with ants represented as a number of agents $N$. These agents interact with one another, and with a two-dimensional environment consisting of a 400 x 300 grid of patches. Each patch is a square of 2 x 2 pixels in the model space, corresponding to a real-world size of 1 mm$^2$. Time progresses in discrete steps $t$, with the difference between each time step $\Delta t = 0.02$ s of real-world time. The number of agents in the simulation at any time $t$ is a function of the traffic rate $F$, which is an input to the model. Agents arrive in the world by a pseudo-random process influenced by $F$. At each time step, the heading of each agent and the position of most agents are updated in parallel, as described below. Also at each time step, every patch in the environment that ants have interacted with is updated according to the amount of pheromone that has been deposited or that has diffused. Ants only move on patches colored...
white (representing the apparatus surface), unless a self-assembled structure has been built over the black patches (representing empty space). The apparatus geometry is loaded in as a .png image file at the beginning of each run. An example of the model visualization is shown in Fig 1.

Ants are modeled to scale with the environment, with a realistic distribution of sizes approximating the size ranges and proportions of different worker castes. The model can also be run with uniform-sized workers to test the effect of size variation on the formation of structures. Caste proportions are approximated from (Franks 1985), with major workers excluded due to their relative scarcity among raiding ants, and the fact that they do not participate in the building of structures. The proportions of other castes, as well as their size distributions, are as follows:

<table>
<thead>
<tr>
<th>Worker caste</th>
<th>proportion of ants in model</th>
<th>size range of β in model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minim</td>
<td>22 %</td>
<td>0.4 cm – 0.65 cm</td>
</tr>
<tr>
<td>Medium</td>
<td>74.55 %</td>
<td>0.7 cm – 1.0 cm</td>
</tr>
<tr>
<td>Submajor</td>
<td>3.15 %</td>
<td>1.0 cm – 1.2 cm</td>
</tr>
</tbody>
</table>

Table 1 | Worker caste proportions and size ranges

Each ant i occupies space at a position vector \(c_i\) and maintains a heading with a direction vector \(v_i\). The body length of an ant \(\beta_i\) is set as each ant arrives in the model, and is assigned in a range in proportion to each caste. Overall, body sizes \(\beta_i\) in the model range from 0.4 – 1.2 cm (with the major caste excluded). The head of an ant \(i\) at time \(t\) is thus at a point \(c_i(t) + \frac{1}{2} \beta_i v_i(t)\). The antennae extend 45° ahead to either side, at a distance \(\phi_i\) defined as \(\frac{1}{2} \beta_i\). For simplicity, however, the antenna zone is defined in the model as a sector subtending 90°, centered at \(c_i\) and extending in front of an ant to a distance \(r_p\). This defines the first of two sensory zones. The
second zone is defined by an area closer to the body, as a circle centered at \( c_i \) with radius \( r_d \). A summary of the model parameters is given below.

<table>
<thead>
<tr>
<th>Values</th>
<th>Description</th>
</tr>
</thead>
</table>
| \( \beta_i \) | body length of ant \( i \) | **Morphological parameters**
| 0.4 cm to 1.2 cm | This range represents a realistic distribution of sizes across 3 of the 4 worker castes. Major workers are excluded from the model, since they only constitute 0.3% of workers within a raid and do not participate in forming structures. Proportions of each caste and size estimates approximated from back leg length measurements in (Franks 1985) as in Table 1. |
| \( \alpha \) | 90° | angle of sector with center \( c \) defining antenna sensory zone |
| \( r_d \) | 0.5 \( \times \) \( \beta \) | radius of circle with center \( c \) defining body sensory zone |
| \( r_p \) | 1.5 \( \times \) \( \beta \) | length of sector with center \( c \) defining antenna sensory zone |
| \( \theta_A \) | 1000° s\(^{-1}\) | turning rate avoidance |
| \( \theta_P \) | 500° s\(^{-1}\) | turning rate pheromone |
| \( \theta_E \) | 1000° s\(^{-1}\) | turning rate away from edge |
| \( \theta_O \) | 1000° s\(^{-1}\) | turning rate to orientation preference |
| \( \epsilon \) | 15° | turning error is a random variate drawn from a Gaussian distribution with mean of 0 and standard deviation = \( \epsilon \) |
| \( u_{\text{min}} \) | 2 cm s\(^{-1}\) | minimum speed |
| \( u_{\text{des}} \) | 4.7 cm s\(^{-1}\) to 7.6 cm s\(^{-1}\) | desired speed |
| \( \mu \) | 50 cm s\(^{-2}\) | acceleration rate |

**Movement variables (updated each \( \Delta t \))**

<table>
<thead>
<tr>
<th>Values</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( c_i )</td>
<td>( x, y )</td>
</tr>
</tbody>
</table>
\( v_i \quad x, y \) heading vector of ant \( i \)

\( d_i \quad x, y \) desired heading vector of ant \( i \)

\( g_i \quad x, y \) internal orientation vector of ant \( i \)

\( u_i \quad u_{\text{min}} \text{ to } u_{\text{des}} \) current speed of ant \( i \)

---

**Behavioral parameters**

\( \rho \quad 0.01 \text{ to } 1 \) contact memory decay rate

\( \rho_b \quad 0.01 \text{ to } 1 \) contact memory decay rate for ants in structure

\( p \quad 0.01 \text{ to } 0.25 \) scaling factor from \( k \) to \( P_j \)

\( k_{\text{max}} \quad 50 \) maximum contacts \( k \) in memory

\( m_{\text{max}} \quad 50 \) maximum contacts \( m \) in memory

\( h \quad 1 \text{ to } 10 \) parameter adjusting the weight given to head-on collisions

\( Q \quad .001 \) amount of pheromone deposited (unitless)

---

**Behavioral variables (updated each \( \Delta t \))**

\( P_j \quad 0 \text{ to } 1 \) probability to join structure (can also be fixed)

\( P_{L} \quad 0 \text{ to } 1 \) probability to leave structure (can also be fixed)

\( k_i \quad 0 \text{ to } k_{\text{max}} \) running count of contacts experienced by an ant \( i \)

\( m_s \quad 0 \text{ to } m_{\text{max}} \) running count of contacts experienced by an ant \( s \) while part of a structure

---

**Environmental and general parameters**

\( L_q \quad x, y \) location of patch \( q \)

\( d \quad .001 \) proportion of pheromone diffused:

a proportion \( d \) of the pheromone value of each cell is subtracted from patch \( q \) and distributed to the 8 neighboring cells at each \( \Delta t \)

\( \Delta t \quad .02 \text{ s} \) length of model time step
Environmental variables (updated each $\Delta t$)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_q$</td>
<td>0.0001 to 1</td>
<td>pheromone concentration at patch $q$</td>
</tr>
<tr>
<td>$w_q$</td>
<td>TRUE / FALSE</td>
<td>walkability of patch $q$</td>
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</tbody>
</table>

Traffic parameters

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T$</td>
<td>0 to 10.0</td>
<td>traffic rate (flux) in ants/s</td>
</tr>
<tr>
<td>$T_B$</td>
<td>0 to 0.5</td>
<td>proportion of bidirectional traffic</td>
</tr>
<tr>
<td>$T_P$</td>
<td>0 to 0.5</td>
<td>proportion of ants carrying prey</td>
</tr>
</tbody>
</table>

Table 2 | Model variables and parameters

Process overview and scheduling

What follows is a general description of the model processes, with a detailed description of each procedure found below under *Submodels*. The main behavioral procedure consists of two steps, where each ant $i$ first updates its heading, and then attempts to move in this direction. If movement is not possible during the second step, the ant either attempts to join a structure or further adjusts its heading. The separation of these two steps is fundamental to the behavior of the model, and is based on observations of army ant building behavior. Structures are initiated when an ant cannot move into the space immediately before it, but experiences pressure from the traffic of ants behind. Ants only initiate a structure when there is a surface to grasp both ahead and behind. Structures grow when other ants join, but these ants must also experience some empty space in order to trigger the behavior (i.e. on the sides of a bridge).

At each time step $\Delta t$, an individual ant $i$ first checks the surface ahead at the tip of each antenna to see if it can proceed in the current direction. If it detects empty space, it turns towards a walkable surface. If it detects a walkable surface at both antenna tips, it then checks its
interaction zones for neighbors. If other ants are detected within either the antenna zone \( r_p \) or the body zone \( r_A \), it adjusts its heading away from these neighbors to avoid collisions. If these ants are ahead, it slows down, otherwise it accelerates. If no other ants are within the interaction zones, it attempts to detect the pheromone concentration at the end of each antenna. When pheromone is detected, it turns in the direction of the highest concentration. In summary, the steps by which an ant updates its direction vector \( \mathbf{v}_i \) are:

**Edge detection >>**

If empty space detected: *Turn towards walkable surface.*

If walkable surface ahead:

**Collision avoidance >>**

If ants to avoid: *Turn away from neighboring ants.*

If no ants to avoid:

**Pheromone detection >>**

If pheromone detected: *Turn towards highest concentration.*

If no pheromone detected: *Maintain current heading*

Once the direction vector \( \mathbf{v}_i \) has been updated, an ant checks to see if it can proceed forward at its current speed. If there is a surface ahead, the location vector \( \mathbf{c}_i \) is updated by moving along the direction vector \( \mathbf{v}_i \) at the current speed \( u_i \). If there is no walkable surface ahead, depending on its probability to join \( P_J \), the ant checks the local area to see if it should join a structure. If it finds a suitable location, it joins or initiates a structure at this point. \( P_J \) is a function of the number of collisions an ant experiences. The rules for where to join a structure are described further below. After joining a structure, an ant remains immobilized with a probability to leave \( P_L \), a function of the number of contacts experienced while part of the structure, and leaves when \( P_L \) reaches 0.
Movement check >>

If walkable surface detected: *Move forward at current speed.*

If empty space ahead:

**Self-assemblage check >>**

If \( P_j \) is low: *Return to edge detection, update v, again.*

If \( P_j \) is high:

**Find location to join >>**

If no ants: *Must find a corner location.*

If ants already in structure: *Find a location with enough space to fit.*

**Design concepts**

*Emergence:* The model simulates the emergence of self-assembled structures from a set of simple individual behaviors, in that there is no explicit rule dictating when or how structures should form. The rate of contacts between individuals increases the probability of individuals to join or remain in a structure. Along with the spatial conditions required for an ant to join or initiate a structure, this is sufficient to generate different types of structures (bridges or flanges) in response to the geometry of the environment.

*Sensing and Interaction:* When moving, individuals interact with and respond to other ants within their sensory zones. Ants within a structure sense contacts from other ants passing over the structure. Individuals interact with their environment by detecting the type of surface ahead (either the apparatus surface or an ant structure) to avoid falling into empty space, and by detecting the concentration of pheromone deposited by other ants.

*Stochasticity:* Sensory error and environmental noise are simulated by adjusting the desired direction vector \( d_i \). At each time step, this vector is rotated by a turning error \( \varepsilon \), a random
variate drawn from a Gaussian distribution. In a time step \( (t) \) when an individual \( i \) is not able to move forward along its updated direction vector \( \mathbf{v}_i \), initiation of the decision process for joining a structure is triggered by drawing a random number from 0 to 1 and comparing this to the probability to join \( P_J \) of ant \( i \). If \( P_J = 1 \), an ant will always attempt to join.

Observation: Many of the model parameters, including the maximum turning rates and rate of acceleration are drawn from observations of \textit{E. burchellii} trail running as described by Couzin and Franks (2003). The overall concept of the model, in particular the decision point to join a structure and the decision rules, are drawn from my observations of structures during the course of field experiments.

**Details**

**Initialization**

The environment is initialized as a grid of 400 x 300 patches consisting of 2 x 2 pixels, each of which are colored black or white based on an imported .png image representing the geometry of the apparatus for each experiment. There are no ants and no pheromone in the environment at the beginning of each run. As the model runs, ants arrive from both sides of the world at a rate determined by the traffic rate \( T \) and proportion of bidirectional traffic \( T_B \). The proportion of prey-laden ants is set by the parameter \( T_P \). The \( y \)-coordinate of newly arriving ants is a Gaussian-distributed random variate centered on the hypothetical trail center (which varies for each background type) with standard deviation of 1 cm. This generates an arriving trail of ants with a width in the range of typical observed trail widths. Initial values for the contact rate \( k \), and thus the probability to join a structure \( P_J \), of each ant \( i \) are set to 0. Newly arriving workers
are sized according to the predetermined distribution of worker castes and size ranges described above.

**Figure 2** | Snapshot of the model running with background environment set to the “flange” apparatus. Blue = outgoing ants; Red = incoming ants; Green = prey-laden incoming ants.

**Input**

Inputs to the model include the traffic rate and the proportion of bidirectional traffic, which are set before each run to evaluate the model performance against the experimental data for the same values. The background geometry is also an input, and can be selected from one of the 4 different angles or the flange apparatus.

**Submodels: Movement rules**

**Edge detection:** A moving ant \( i \) detects the surface type at the ends of the left and right antenna, respectively. If a walkable surface (either platform or bridge) is detected at both locations, the ant proceeds to the interaction behaviors (described below). If a walkable surface is
detected at only one location, left or right, the ant turns in that direction by $\theta_E$, updating its direction vector:

$$\mathbf{v}_i(t + \Delta t) = \mathbf{v}_i(t) \cos \theta_E + \mathbf{v}_i(t) \sin \theta_E + \mathbf{v}_i(t)(1 - \cos \theta_E).$$

If no walkable surface is detected, the ant moves backwards at its current speed and turns to one side or the other with a probability of 0.5.

**Separation:** If a walkable surface is detected ahead, an ant $i$ checks within its sensory zone for potential collisions with neighbors. This zone consists of a sector extending in front of the ant a distance $r_p$ from the ant’s center with an internal angle $\alpha$, representing the sensing zone of the antennae, and a circle with radius $r_d$ from the ant’s center representing a zone encompassing the body and closest leg segments. If any other ants $j$ are detected in this zone, the ant attempts to avoid collisions by turning towards a desired vector $\mathbf{d}_i$:

$$\mathbf{d}_i(t + \Delta t) = \sum_{j \neq i} \frac{\mathbf{c}_i(t) - \mathbf{c}_j(t)}{|\mathbf{c}_i(t) - \mathbf{c}_j(t)|}$$

If the difference between its present heading and the desired vector $\mathbf{d}_i$ is less than the maximum turning rate $\theta_A$, it will set its heading $\mathbf{v}_i(t + \Delta t)$ to match $\mathbf{d}_i$, otherwise it will turn $\theta_A$ degrees towards it. If any ants $j$ are detected within the antenna zone specifically, the ant reduces its speed $u_i$ at the rate of acceleration $\mu$, resulting in:
\[ u_i(t + \Delta t) = u_i(t) - \mu \Delta t \]

If any ants \( j \) are detected within a smaller zone \( r_c \) defined as the collision zone, the ant is determined to have made a collision. This causes an ant \( i \) to increase its count of contacts \( h \) by the number of ants \( j_c \) detected. If any ants \( j_c \) in the collision zone are detected moving in the opposite direction of ant \( i \), the ant is determined to have made a head-on collision with ants \( j_h \). This causes an ant \( i \) to reduce its speed by double the rate of acceleration \( \mu \), and to increase its count of contacts \( k_i \) by the parameter \( h \), a factor representing the relative importance given to head-on collisions. If \( h = 1 \), these are treated the same as regular collisions. Thus the updated count of contacts after each step is:

\[ k_i(t + \Delta t) = k_i(t) + j_c(t) + hj_h(t) \]

Since ants do not have an infinite memory, we assume some constant decay rate for the contact count \( k \), represented by the parameter \( \rho \). When no contacts are experienced, \( k_i \) is updated as:

\[ k_i(t + \Delta t) = k_i(t) - \rho \Delta t \]

If ants \( j \) are detected within the body zone \( r_d \) only, the ant increases its speed by the rate of acceleration \( \mu \). If no ants are detected in either zone, the ant attempts to detect pheromone in its local environment.
**Pheromone detection:** If an ant \( i \) has detected a walkable surface, and found no other ants to avoid within its sensory zone, it assesses the surface at the ends of its left and right antenna for the presence of pheromone. The amount of detectable pheromone is limited by the pheromone detection threshold \( C_{\text{min}} \). If a concentration exceeding this threshold is detected, a comparison is made between the concentration at the left antenna \( C_L \) and the concentration at the right antenna \( C_R \), with \( \Delta C = C_L - C_R \). The detectable level of difference between the two concentrations can be tuned with the parameter \( C_{\text{dif}} \). If the concentration of pheromone on one side or the other is higher, the ant attempts to turn towards the direction of the higher concentration at a rate \( \theta_D \) corresponding to the proportional difference:

\[
\theta_D = \frac{\Delta C}{\max\{C_L, C_R\}} \cdot 22.5^\circ
\]

If \( \theta_D > \theta_P \) (the maximum pheromone turning rate), the ant turns in this direction by \( \theta_P \). If no pheromone is detected, or if no difference is detected between the two concentrations, an ant does not adjust its heading in response to pheromone. The heading \( \mathbf{v}_i(t + \Delta t) \) is updated by \( \theta_D \) or \( \theta_P \) as in [1]. Whether an ant detects pheromone or not, it accelerates by \( \mu \) since there are no surrounding ants to avoid, up to a maximum speed \( u_{\text{max}} \).

**Directional preference:** Whenever an ant \( i \) detects a walkable surface and either avoids neighbors or detects pheromone, it also orients towards a preferred direction (depending whether it is moving left or right) with an internal orientation vector \( \mathbf{g}_i \), limited by the maximum orientation turning rate \( \theta_O \). This simulates the ability of ants to orient towards a preferred direction on the trail, whether going out to forage or returning to the bivouac. The vector \( \mathbf{g}_i \) is
added to either the desired avoidance or pheromone vector \( \mathbf{d}_i \) at each time step a surface is detected.

**Turning error:** To simulate error and sensory noise, the final updated direction vector \( \mathbf{v}_i \) is rotated by an additional angle \( \varepsilon \), a random variate drawn from a Gaussian distribution with mean of 0 and standard deviation of 10 (this is an adjustable parameter).

**Movement:** Once the direction vector \( \mathbf{v}_i \) has been updated, an ant \( i \) performs a check to see if it can move from its new orientation by examining the surface directly in front of it. If the result of this check is negative, it assesses whether or not to build a bridge at the location (described below). If the result is positive, it updates its location vector by moving forward at its updated speed \( u_i \) along its new direction vector:

\[
\mathbf{c}_i(t + \Delta t) = \mathbf{c}_i(t) + \mathbf{v}_i(t + \Delta t) \Delta t \quad u_i
\]

**Submodels: Self-assemblage rules**

**Probability to join structure:** If, after updating its directional vector \( \mathbf{v}_i \), an ant \( i \) is unable to move forward, it decides whether to initiate or join a structure in the current location. This process is triggered with probability \( P_J \), a function of the number of contacts an ant has experienced recently, \( k_i \), scaled by a factor \( p \) to within a range of 0 to 1. The results of this scaling are capped at 1, placing an upper bound on the number of contacts that can influence an individual’s probability to join a structure. At each time step a random floating point number from 0 to 1 is drawn and compared with the \( P_J \) of ant \( i \) to determine whether or not it should try
to join a structure. If $P_J$ is greater than the random draw, it will attempt to join. Thus if $P_J = 0$ it
will never attempt to join, if $P_J = 0.5$ it will attempt to join on roughly 50% of the time steps it
runs the procedure, and if $P_J = 1$ it will always attempt to join.

**Joining behavior of initial ant:** If the $P_J$ of an ant $i$ dictates that it should attempt to join
a structure, it assesses the local environment for a suitable location. First, it checks if there are
already any ants in its sensory zone that are part of a structure. If there are no ants in a structure,
it attempts to locate a corner on which to attach. This behavior is based on observations of ant
structures in the field, which are almost always initiated at a corner between two surfaces, since
the initial ant must have something to grasp in order to form a structure. This rule is critical for
the realistic emergence of structures in the model, and is implemented by assessing the color of
the environmental patches within the sensory zone. Black patches represent empty space, while
white patches represent the apparatus surface. In order to initiate a structure, an ant $i$ must detect
a black patch that is surrounded by at least 5 neighboring white patches, indicating an
intersection with another surface rather than a straight edge. If this condition is true, the ant will
stop in its current position and change its status from a mobile ant to a structure ant, enabling
future ants to use its body as a walking surface. If this condition is not true, indicating that the
ant is standing along a straight edge, it will run the edge detection procedure described above in
order to turn away.

**Joining behavior of additional ants:**

If other ants are already in a structure, an ant $i$ will join in its current location unless there
are more than 2 ants already occupying the space. This approximates the amount of overlap
between ants in structures from observations. If there are too many ants already in the current position, an ant \( i \) will move itself to another suitable location within its sensory zone and attempt to join there. If no other suitable locations can be found, the ant will turn away from the edge and continue moving.

**Behavior when in structure:**

At every time step, each ant \( s \) that is part of a structure keeps count of the number of contacts from crossing ants in a variable \( m \). This count is limited to \( m_{\text{max}} \). As with the contact count \( k \) for moving ants, this is reduced whenever an ant in a structure does not experience a contact by a rate \( \rho_a \):

\[
[6] \quad m_s(t + \Delta t) = m_s(t) - \rho_a \Delta t
\]

with an ant \( s \) leaving a structure when \( m = 0 \). Upon leaving, an ant finds a suitable place to begin moving again by following the edge detection procedure.

**Submodels: Pheromone dynamics**

The model implements a simplified version of pheromone deposition and diffusion. Since the pheromone detection rule is simply a comparison between two concentrations, realistic values for \( Q \), the amount of pheromone placed with each deposit, and \( d \), the diffusion constant, are not necessary to generate realistic trail following behavior. An ant \( i \) deposits an amount of pheromone \( Q \) at every time step it detects a walkable surface ahead by adding \( Q \) pheromone to
the patch \( q \) it occupies at time \( t \). Every patch \( q \) diffuses a proportion \( d \) of its current concentration \( C_q(t) \) to its 8 neighboring patches at each time step.

**Methods: Simulation runs**

*Contact rate in scaffolding formation*

In Chapter 2 a growth model was described for scaffolding structures with a negative feedback mechanism. The model proposed that individual ants are sensitive to some cue by which they detect disruptions in traffic due to the differential slowing of prey-laden ants. It was hypothesized that this cue was related to the rate of contacts experienced by an individual ant. It was not possible to visually assess the contact rate and detect changes in this variable from the video footage, since ants move at an extremely high rate and make frequent contact with other individuals (especially when traffic density is high). Visual scoring of the videos also would have necessitated a qualitative determination as to what constituted a contact. For these reasons, the current agent-based simulation model was used to test the hypothesis about contact rate and scaffolding structures. The model was run for 10 repetitions of each of the following combinations, for a total of 4320 runs:

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Traffic flux (ants/s)</td>
<td>1, 2, 3, 4, 5, 6, 7, 8</td>
</tr>
<tr>
<td>Prey proportion (% traffic)</td>
<td>0% 2.5% 5% 7.5% 10% 12.5% 15% 17.5% 20%</td>
</tr>
<tr>
<td>Proportion bidirectional (% traffic)</td>
<td>0, 10, 25</td>
</tr>
<tr>
<td>Prey-laden ants slowed further?</td>
<td>TRUE, FALSE</td>
</tr>
</tbody>
</table>

*Table 1 | Parameters of agent-based model used to estimate contact rate*
These parameters were chosen to match the range of variables measured in the experiments from Chapter 2. The model was run for 1500 time steps, equivalent to 30 seconds of experimental time. The hypothesis (that contacts are increased when prey-laden ants slow down more than non-laden ants traversing an inclined surface) was tested by varying the last parameter listed above. Half of the simulations were control runs, in which prey-laden ants always traveled at a baseline speed equal to 80% of their usual speed when not carrying prey. In the other half of the runs, the treatment variable was adjusted, forcing laden ants to slow by an additional 50% when crossing a simulated inclined surface.

Contact rate in bridge and flange formation

To test the hypothesis that the rate of contacts between individuals acts as a cue to join a bridge or flange structure, I ran a series of simulations where the probability to join was instead a fixed value. I tested a range of values for $P_J$, which determined the proportion of time steps during which an individual would attempt to join a structure (if also encountering an edge). Each simulation was run for 3000 time steps (equivalent to 1 minute of experimental time) for 10 runs at each of the following combinations of traffic parameters, split between the flange apparatus and the 20° angle apparatus.

<table>
<thead>
<tr>
<th>Parameters for simulation sets A1 and B1</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T$</td>
</tr>
<tr>
<td>$T_B$</td>
</tr>
<tr>
<td>$T_P$</td>
</tr>
<tr>
<td>$p$</td>
</tr>
</tbody>
</table>
Results

Contact rate as a cue to join scaffolding structures

An independent-samples t-test was conducted to compare the aggregated mean contacts between the treatment condition (increased slowing of prey-laden ants on an incline) to the control condition (where all ants were slowed by the inclined surface in proportion to their baseline speed). The aggregated mean number of contacts was significantly higher in the simulation runs with the “increased slowing behavior” activated ($M = 11.86, SD = 7.19$) than the control condition ($M = 8.62, SD = 5.46$) when comparing across all simulation runs; $t(1162100) = 290.8, p < .001$. Due to the extremely large sample size, Cohen’s $d$ statistic was calculated to estimate the effect size, with ($d = 0.51$), suggesting a moderate level of practical significance.

To further investigate the possible role of increased contacts as a cue to traffic disruption, the effect of increased slowing by prey-laden ants on contact rate was examined under different traffic conditions. Data from the simulation runs was subset according to the proportion of bidirectional traffic at three levels, representing the general range of values in the data, from zero bidirectional traffic to a moderately high level of 25%. While significant at all three levels, the strength of the effect differed depending on the proportion of bidirectional traffic (Table 3).
<table>
<thead>
<tr>
<th>Proportion of bidirectional traffic</th>
<th>0</th>
<th>10%</th>
<th>25%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Contacts (prey ants additional slowing)</td>
<td>$M = 11.15$</td>
<td>$M = 11.55$</td>
<td>$M = 12.69$</td>
</tr>
<tr>
<td></td>
<td>$SD = 6.24$</td>
<td>$SD = 6.80$</td>
<td>$SD = 8.10$</td>
</tr>
<tr>
<td>Contacts (uniform slowing)</td>
<td>$M = 7.09$</td>
<td>$M = 7.88$</td>
<td>$M = 10.81$</td>
</tr>
<tr>
<td></td>
<td>$SD = 3.76$</td>
<td>$SD = 4.67$</td>
<td>$SD = 6.24$</td>
</tr>
<tr>
<td>$DF$</td>
<td>388344</td>
<td>356600</td>
<td>451060</td>
</tr>
<tr>
<td>$t$</td>
<td>248.84</td>
<td>212.37</td>
<td>86.25</td>
</tr>
<tr>
<td>$p$-value</td>
<td>$&lt; 2.2e^{-16}$</td>
<td>$&lt; 2.2e^{-16}$</td>
<td>$&lt; 2.2e^{-16}$</td>
</tr>
<tr>
<td>Cohen’s $d$</td>
<td>.800 (med-high)</td>
<td>.643 (medium)</td>
<td>.253 (small)</td>
</tr>
</tbody>
</table>

**Table 3** | Summary of mean contacts comparison from simulation model

**Figure 3** | Regression lines fit to the data from Chapter 2 showing the generally negative relationship between the proportion of bidirectional traffic and structure size.

The negative effect of bidirectional traffic on the size of structures demonstrated in Chapter 2 can be seen in Figure 3. To investigate this relationship and the complex interactions involving prey rate, traffic rate and bidirectional traffic found in the GLM described in Chapter 2, the
parameter space of the simulation model output was examined in depth. Treating prey proportion (the proportion of ants carrying prey), traffic rate (in ants/s) and the proportion of bidirectional traffic as factors with discrete levels, the difference in mean contact rate between the two treatments described above for each unique combination of factor levels was analyzed. The primary variable of interest was the proportion of bidirectional traffic. The differences in mean contacts across all three levels of bidirectional traffic were visualized to try to understand the complex interactions between variables (Figure 4).
Figure 4 | The parameter space of the simulation model at different levels of the variables Traffic rate and Proportion of prey-laden ants at three different levels of Bidirectional traffic:
(a) Proportion of bidirectional traffic = 25%; (b) Proportion of bidirectional traffic = 10%; and (c) Proportion of bidirectional traffic = 0%. On the left, cells are colored based on the difference in mean contacts as a function of the manipulated variable (prey-laden ants moving more slowly on the inclined surface). On the right, cells are shaded based on the significance level of the difference (t-tests were conducted for each combination of factors with the manipulated variable set to TRUE or FALSE). Significance criteria was defined as $p < .00001$.

Comparing the difference in mean contacts at each combination level of factors in the presence or absence of the test variable (whether prey-laden ants moved more slowly) showed that when the proportion of bidirectional traffic was high (Fig. 4a), additional slowing had less of an impact on the mean contact rate. The strongest effects of the additional slowing of prey-laden ants on the rate of contacts were seen with no bidirectional traffic (Fig. 4c), when both traffic rate and the proportion of prey laden ants was high.

*Contact rate not a necessary cue for bridge and flange formation*

The use of a fixed value for probability-to-join did not have a significant overall effect on the ability of bridges and flange structures to form, although at lower fixed values of $P_J$, structures formed less frequently and were smaller (Figure 5). This analysis also revealed the formation of flange structures to be more robust than bridges to reduced values of $P_J$, with flanges forming more consistently and reaching larger than bridges under the same traffic conditions and joining probabilities (Figures 5, 6).
Figure 5 | Comparison between the mean sizes of bridges (light grey) and flanges (dark grey) formed at 4 different levels of $P_{\alpha}$, for two different traffic regimes. (a) shows results with traffic flow rate = 8 ants / sec. (b) shows results with traffic flow rate = 2 ants / sec.
Figure 6 | Comparison of total counts of structure sizes formed over all simulation runs, for the same conditions as Figure 5. Bridges at 20 degrees shown in red, Flanges shown in blue.
Discussion

The model presented here demonstrates that a simple individual-level rule can produce a range of different self-assembled structures in *Eciton* army ants. These different structure types emerge due to context-dependent interactions between traffic variables and environmental geometry, and do not require complex decision making or sensing abilities. I have shown that the use of contact rate as a cue to join structures is not required for the formation of bridges or flanges. In the model described here, these structures emerge just as readily and exhibit realistic dynamics of growth and movement when individuals have a constant probability to join. The particular value of this parameter does have a large influence on the formation of structures, but the alternative approach is equally sensitive. The rate of contacts must be scaled to a probability according to some function that is just as arbitrary as setting a constant value and tuning this parameter. However, the results I presented here testing the hypothesis from Chapter 2 suggested that contact rate could play an important role for the formation of scaffolding structures.

One possible explanation for this relates to the very different function of scaffolding structures (which form rarely and in response to a disruption) and bridges (which are relatively common along the trail and provide incremental improvements in the flow of traffic). It is possible that such a cue is context-dependent. However, the question needs to be addressed empirically. With the model described here, I have demonstrated that contact rate is not essential for the formation of structures, but can make no further predictions. To properly address the question of contact rate and how it affects the formation of self-assembled structures, a computational method should be developed to analyze the video data from our experiments.
I have presented an individual-based model that is able to qualitatively reproduce the formation and dynamics of self-assemblages under realistic traffic and environmental conditions. The model relies on a few simple rules – crucially, that free-spanning structures can only be initiated at a juncture between two edges. In the model I developed, without this rule structures begin emerging from the edge of the surface at random locations, and begin to grow due to positive feedback. Even if a gravity-type rule is implemented that prevents structures from moving out into space, it is difficult for structures to achieve stability. This juncture rule is based on numerous observations, but it would be good to test empirically as well. In addition, the edge-detection algorithm should be checked and improved by video analysis of ants interacting with the edges of structures. Finally, sensitivity analysis needs to be performed on the model. There are many parameters in the current iteration, some of which have been added to test particular questions and some of which were based on earlier hypotheses. The relative importance of parameters should be estimated so that the overall parameter space of the model can be greatly reduced.
Appendix A

Supplementary information for Chapter 1

Estimate of colony-wide bridge investment

To project how the results of our experiment might scale up and to infer the broader effects that bridges have at the colony level, we can make some estimates by combining our field observations with those in the literature. A typical E. hamatum trail network can extend 200 meters from the bivouac (Schneirla 1971). Along these trails, bridges are patchily distributed, clustering in areas of particularly rough terrain (Schneirla 1971; Powell & Franks 2007). Based on our observations, we estimate that naturally occurring bridges contain on average 10 individuals. The distribution of bridges along a trail can vary widely, depending on terrain and traffic levels. On the low end, we estimate 1 bridge per meter of trail. However, it is not uncommon to see lengths of trail with upwards of 10 bridges per meter. Given these figures, as a cursory approximation, we can thus estimate a range for the total number of ants sequestered in bridges at somewhere between 2,000 and 20,000 ants. For a typical colony of 100,000 ants (Schneirla 1971), bridges then occupy somewhere between 2-20% of the total population. If we further consider that a large proportion of the colony (perhaps up to half) remain at the bivouac throughout the day and take no part in foraging, these structures certainly segregate a substantial portion of the available foragers.
**Video of bridge movement**

Movie S1  |  Time lapse showing the position of a bridge over time, with the apparatus set to an angle $\theta$ of 20°. Each frame advances 5 minutes into the experiment. Available online at:  
www.pnas.org/content/112/49/15113.abstract?tab=ds

**Bridge length vs. bridge width**

![Figure A1](image)

**Figure A1**  |  Bridge width as a function of bridge length for each angle $\theta$. Each circle shows the width and length of a single bridge at any point in time. Solid lines are linear regressions for each angle $\theta$. Shaded areas are the 95% confidence region.
Geometric costs and benefits

Figure A2 | Theoretical costs (a) and benefits (b) as a function of distance moved by the bridge toward the main trail axis for different θ angles. In (a), the cost function takes into account the widening of bridges observed as they move towards the main trail (Fig. S1).
Appendix B

Supplementary information for Chapter 2

Negative exponential growth model fits by experiment

The following are summary data from the process of fitting the negative exponential growth model. Fits to the model were attempted for experiments with $\theta > 50^\circ$, since structures did not consistently form below this threshold. Traffic data for each experiment is given for clarity, although these data were not used in the model fitting process. $C$ and $\alpha$ are the parameters estimated from the model, and these are given along with their 95% confidence intervals. A pseudo-$R^2$ measure was calculated to assess the goodness-of-fit as described in the text. Fits with pseudo-$R^2 > 75\%$ are shaded in grey. Relative standard error measures are given for both $C$ and $\alpha$. NA indicates experiments where no fit to the model was achieved.
\[ \theta = 90^\circ \]

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</tr>
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**Table B1** | Experimental data, parameters fit from model and goodness-of-fit measures for experiments at \( \theta = 90^\circ \). Shaded areas indicate curves fit to data with pseudo-\( R^2 > 75\% \). NA indicates experiments where no model fit was achieved.
Figure B1 | Curves from negative exponential growth model fit to data for experiments with \( \theta = 90^\circ \). Shaded areas indicate 95% prediction intervals. Experiments where no fit was achieved are excluded.
\[ \theta = 80^\circ \]

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<td>54</td>
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<td>0.41</td>
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<td>71%</td>
<td>85%</td>
<td>90%</td>
<td>71%</td>
<td>85%</td>
<td>73%</td>
<td>76%</td>
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<td>97%</td>
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<td>4.18%</td>
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<td>4.61%</td>
<td>0.76%</td>
<td>7.35%</td>
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<td>96%</td>
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**Table B2** | Experimental data, parameters fit from model and goodness-of-fit measures for experiments at \( \theta = 80^\circ \). Shaded areas indicate curves fit to data with pseudo-\( R^2 > 75\% \). NA indicates experiments where no model fit was achieved.
\[ \theta = 80^\circ \]

**Figure B2** | Curves from negative exponential growth model fit to data for experiments with \( \theta = 80^\circ \). Shaded areas indicate 95% prediction intervals. Experiments where no fit was achieved are excluded.
### $\theta = 70^\circ$

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**Table B3** | Experimental data, parameters fit from model and goodness-of-fit measures for experiments at $\theta = 70^\circ$. Shaded areas indicate curves fit to data with pseudo-$R^2 > 75\%$. NA indicates experiments where no model fit was achieved.
Figure B3 | Curves from negative exponential growth model fit to data for experiments with $\theta = 80^\circ$. Shaded areas indicate 95% prediction intervals. Experiments where no fit was achieved are excluded.
\( \theta = 60^\circ \)

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Table B4 | Experimental data, parameters fit from model and goodness-of-fit measures for experiments at \( \theta = 60^\circ \). Shaded areas indicate curves fit to data with pseudo-\( R^2 > 75\% \). NA indicates experiments where no model fit was achieved.
Figure B4  |  Curves from negative exponential growth model fit to data for experiments with $\theta = 60^\circ$. Shaded areas indicate 95% prediction intervals. Experiments where no fit was achieved are excluded.
\[ \theta = 50^\circ \]

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Table B4: Experimental data, parameters fit from model and goodness-of-fit measures for experiments at \( \psi = 50^\circ \). Shaded areas indicate curves fit to data with pseudo-\( R^2 > 75\% \). NA indicates experiments where no model fit was achieved.
\[ \theta = 50^\circ \]

**Figure B4**  | Curves from negative exponential growth model fit to data for experiments with \( \theta = 50^\circ \). Shaded areas indicate 95\% prediction intervals. Experiments where no fit was achieved are excluded.
References


http://ccl.northwestern.edu/netlogo/models/Flocking. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.


