

# Many ants make light work; quantifying force output of weaver ant teams

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## DECLARATION

I declare that this thesis, as a whole or in parts, has not been submitted for a higher degree to any other university or institution. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

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This thesis is formatted as a manuscript for submission to the *Journal of Experimental Biology*, with some exceptions to meet the requirements of the Macquarie University. This includes the requirement of an abstract of 200 words, 2cm margins, 1.5x line spacing, figures and tables embedded within the text.

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## Abstract

Teams benefit from increased participation to a point – where the benefit of cooperation is outweighed by the cost of coordination. In social insects, this trade-off has an opportunity to be averted, as advanced coordination emerges from self-organised, distributed mechanisms. Where observed human behaviours such as a lack of motivation and accountability in teams challenge productivity, social insect mechanisms, such as positive feedback loops, could serve to improve it. In chapter one, I discuss human, robot and social insect teams and propose collective force generation as an ideal system to observe the complexities of efficient teamwork. In chapter two, I measure forces applied by teams of weaver ants (*Oecophylla smaragdina*). During nest construction, weaver ants attach to leaf edges and self-assemble into pulling chains, folding leaves together to make nesting chambers. Here I find that weaver ants not only sustain their individual effort despite increasing team sizes, but also contribute additional force per team member, in some circumstances. Chain arrangement and body posture analysis reveal individuals within a team contribute uneven amounts of effort, potentially revealing the control mechanism generating ‘superefficient’ teamwork. Further study of social insect systems will inspire the application of control mechanisms that generate effective teamwork, for the improvement of engineered systems such as swarm robotics.

## Chapter 1: Literature Review

### *Teamwork in social insects: insights from cooperative force generation*

#### Abstract

The principles of effective teamwork are coordination and cooperation, yet the interaction between the two can often be conflicting. Counter-intuitively, in human teams doing physical work, additional team members lead to decreased output per member, due to differences in motivation and physical coordination. In social insect teams, collective behaviours give rise to innate organisation mechanisms which may overcome this phenomenon. The effect of growing team size on physical output in a social insect system is relatively unexplored. Given their impressive load carrying abilities, I put forward force generation in social insects as an ideal system to study the specifics of organisational behaviour in teams. I first outline the three potential outcomes generated by teams contingent upon individual effort. I discuss examples of force generation in social insect teams, alongside swarm robot studies to explore the potential mechanisms that govern distributed teams. I suggest the mechanisms employed by social insect teams may minimise coordination loss, and have the potential to up-regulate motivation levels. Understanding team organisation in biological complex systems will have applications in multi-agent engineered systems, such as optimisation algorithms and swarm robotics.

#### Introduction

Working in a team can provide significant benefits, allowing groups to perform tasks that are difficult or impossible for individuals to achieve alone. However, teams do not automatically benefit from increasing participation: a team's performance is strongly affected by the synchronicity of the team members' efforts. If individuals within a team do not coordinate their actions, they can hinder or cancel out the actions of others. This is commonly seen in human systems, where the scaling up of team size does not lead to predictably efficient outcomes. Within a team, various factors affect an individual's contribution, yet the combination of factors that facilitate the maximum cumulative output remain unclear (Brown and Harkins, 2020). A balance must be reached between cooperation and coordination to reach an optimal team output.

Social insect teams face this balancing act in everyday tasks, exhibiting actions underpinned by mechanisms of collective behaviour (Deneubourg and Goss, 1989). Within a collective system, every individual is unaware of the global order, acting according to simple individual-level rules

and local cues. The system performs without centralised control, each individual decision occurring in a distributed manner, minimising the potential for system failure. Despite the relatively straightforward mechanisms at play at the individual level, the collective behaviours generate resilient and organised outcomes at the level of the group (Bonabeau et al., 1997; Theraulaz and Deneubourg, 1994).

Social insects, such as ants and bees, have long been revered for their mastery of coordinated behaviours, from rational decision making to self-assembling structures (Anderson et al., 2002; Sasaki and Pratt, 2018). Honeybee (*Apis mellifera*) colonies can determine the highest-quality nest site out of multiple choices (List et al., 2008). Worker army ants (*Eciton burchelli*) arrange themselves into functional bridges to provide optimised short-cuts on foraging routes (Reid et al., 2015). A range of collective tasks, such as foraging and nest construction, involve teams of insects applying additive force on an object. These circumstances offer a quantitative insight into the effectiveness of teamwork in a decentralised system. Analysing these systems could be the key to understanding organisational behaviour in teams and how to optimise the trade-off between cooperation and coordination.

Not only is this research significant to understanding and improving human systems, but it is also highly relevant to robotics. Swarms of simple, decentralised robots working collectively by reacting to local cues are adaptive to dynamic environments and resilient to individual malfunctions (Dorigo et al., 2020; Rubenstein et al., 2014). With the potential applications in the fields of agriculture, construction, and space exploration, the actions to be employed will occur on vastly different scales (Dorigo et al., 2020). A major challenge for the future will be the design of control algorithms that are unaffected by team size. Social insects serve as inspiration for swarm robot algorithms, however, a reciprocal relationship exists, as swarm robots also serve an important role in understanding collective behaviour in natural systems. These artificial systems offer greater control in studying typically variable behaviours; therefore, this review will consider robotic research in addition to social insect research to uncover the complexities of teamwork.

Here, I propose that collective force generation in decentralised systems offers a unique quantitative insight into the specifics of cooperation on different scales. By assessing both social insect and swarm robot systems, I examine the factors that are likely to encourage optimal outputs. Firstly, to contextualise the significance of these systems, I outline relationships observed in human teams and the factors that contribute to suboptimal outputs. I then argue the social insect behaviours that generate collective force, such as foraging and nest construction, are an



ideal system to observe behavioural organisation in teams due to their resilient structural features and their self-organised behaviours. I discuss the limited literature that has explored social insects interacting with force, revealing their optimisation techniques regarding team size. Finally, I put forward weaver ants as a novel system to study team dynamics in an effort to improve the current understanding of efficient teamwork.

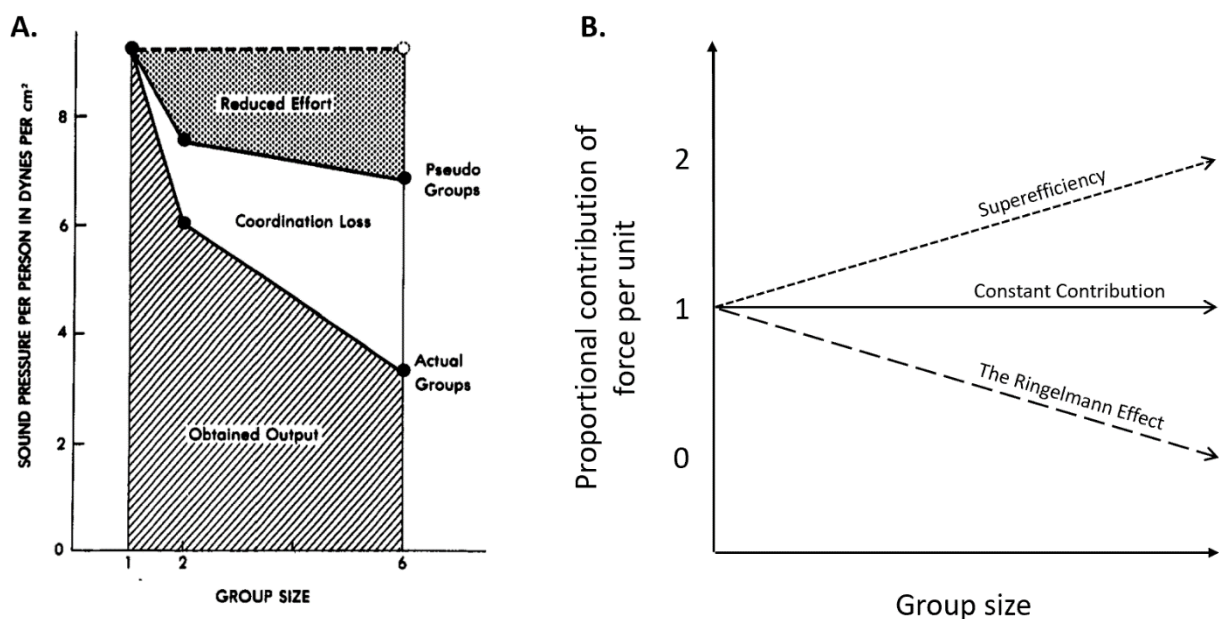
## The problem with teamwork

Teams are seen throughout nature and in the majority of human endeavours, organising individuals at an intermediate level to achieve a goal that individuals cannot complete alone (Anderson and Franks, 2003; Anderson and McMillan, 2003). According to the complexity of the task at hand, individuals work together in various arrangements. Here I define a team task to require a singular action performed by many (Anderson et al., 2001). Team output should theoretically equal the sum of each individuals' input of effort, yet, counter-intuitively, this is rarely the case. This phenomenon is a classic case study in social psychology known as the Ringelmann effect (first discovered in 1913 by Maximilien Ringelmann during a human rope pulling experiment)(Moede, 1927). When a group of human individuals were instructed to perform a combined pulling action on a common rope, the output of their efforts was predicted to be additive; four people should exert four times as much force as a single person, and eight people should exert eight times as much. Yet, in these trials' teams of eight generated less than half the force of their cumulative sum (Kravitz and Martin, 1986).

This discrepancy is attributed to two main factors. As group size increases, so does the number of 'coordination links' and the potential for system malfunction. Coordination loss features differently in each system, for example, in Ringelmann's experiments individuals would pull in slightly different directions cancelling each other's forces out. The second factor limiting team output in humans is described as 'social loafing'. Individuals are negatively affected by the presence of others due to various psychological reasons. These included feelings of a lack of responsibility and a tendency to hide in the crowd, as individual feedback is not discernible in the overall team effort (Latané et al., 1979). In some experiments, these two combined factors have been teased apart, such as in experiments involving the cumulative sound generated by groups of people clapping and cheering (Ingham et al., 1974). Individuals were found to generate more sound when they were blindfolded and falsely led to believe they had company (pseudo groups),

than when they were aware of being in an actual group. This study demonstrated that coordination loss and social loafing are both important factors leading to suboptimal team output (Fig. 1A).

Teams displaying the inverse to the Ringelmann effect will be described here as ‘superefficient teams’, where individuals contribute comparatively more effort when participating in larger groups (Fig. 1B) (Franks, 1986; Franks et al., 1999). Much like social loafing leads to the Ringelmann effect, social facilitation is a mechanism that could give rise to superefficiency. In humans, social facilitation has only been described in coaction contexts. This is where individuals perform independent tasks and the presence of others has a positive impact on the outcome (Bond and Titus, 1983). Theoretically, social facilitation should optimise a team’s output rather than maximise it – this is because if each individual was to contribute their maximum effort regardless of external factors, this would generate a ‘constant contribution’ relationship (Fig. 1B). In both constant contribution and superefficiency contexts the effect of coordination loss would have to be at a minimum. The complex social factors effecting human team outputs render the human system an ineffectual model for generating superefficiency (Karau and Wilhau, 2020). As an alternative system, I propose social insects, which are known for their altruistic (rather than selfish) behaviours (Boomsma and Franks, 2006).



**Figure 1: Individual effort with increasing cooperation within a group determines overall output.** (A) Collective sound pressure from cheering in larger teams generate a lesser outcome, more so in actual groups than pseudo groups, separating the Ringelmann effect into a result of social loafing

and coordination loss (Latané et al., 1979). (B) Three potential trends a team's output can generate; Superefficiency, where more effort per individual is contributed as team size increases; Constant Contribution, where an equal amount of effort is contributed per individual as team size increases, and; The Ringelmann Effect, where less effort per individual is contributed as team size increases.

## Social insects as a study system

Teamwork in social insects operates according to simple, local mechanisms. However, the swarm intelligence that emerges from social insect systems has inspired models that tackle problems such as transportation, communication pathways and robotic design (Bonabeau et al., 2000).

Though swarm intelligence is not exclusive to social insects, they offer a system with substantial unit numbers coupled with experimental tractability, ideal for analysis. The unique decentralised approach to a task offers solutions robust to system failure yet flexible to changing conditions (Anderson and Franks, 2003; Middleton and Latty, 2016). Through simple stimulus-response behaviour, social insects generate dynamic group-level outcomes, greater than that of the cumulative contributions from the individuals involved (Theraulaz G and Bonabeau E, 1995).

The main principle generating ordered patterns in social insect systems is self-organisation (Bonabeau et al., 1997). Random fluctuations of actions are moderated based on a feedback system, where a bifurcation point is reached subject to the parameters of the system (Garnier et al., 2007). Actions that are successful are promoted through enforcement whilst actions that are unsuccessful are either inhibited or left to subside through inactivity (Theraulaz et al., 2002). A well-known example of an applied model of swarm behaviour is the Ant Colony Optimisation algorithm (Dorigo et al., 2006). Based on ant foraging systems, the algorithm simulates how an efficient route is prioritised over time. As a worker ant forages, she lays pheromone between the nest and food source, attracting other worker ants to the trail, who then contribute their own pheromone. Over time, the pheromone trail on the shortest route is reinforced as more ants complete these trips faster. The pheromone on the longer route slowly evaporates and the traffic on the suboptimal routes subsides. The biological process has been modelled and factors such as pheromone evaporation rate were enhanced to improve the algorithms practicability. This algorithm has been applied to the classic Travelling Salesman Problem and implemented to optimise real-world transport and telecommunication networks (Bonabeau et al., 2000).

Teamwork in social insects is inherently different to teamwork in humans due to the type of control (Garnier et al., 2007). Human teams are most often under centralised control, typically

governed by a leader with global information about the environment and the teams' effort and output. Social insect colonies are under distributed control; thus every unit is unaware of the overall effort and their relative contribution to it. Rational decisions are more likely under distributed control as it avoids the possibility for information overloads (Sasaki and Pratt, 2018). Ant colonies choosing a new nest site send individual workers to evaluate a single potential nest via a threshold model and recruit based on the result (Robinson et al., 2011). Recruitment is a democratic process, with even a minority aware of superior choice, they will forego the information to create a unanimous decision on nest site (Rajendran et al., 2022). Therefore, social insect systems are inherently designed to cater for large team sizes. The amplification of random fluctuations leads to unanimous decisions and organised patterns during tasks such as foraging and nest selection. It is when these self-organised systems attempt to construct physical structures where coordination becomes a limiting factor.

Social insects extend the capabilities of a self-organised system through the additional incorporation of hardwired behavioural rules regulated by social interactions to tackle coordination challenges (Garnier et al., 2007). These inherent rules act as a baseline of behaviours which are modified on the spatiotemporal scale according to changing conditions. The complexity this can generate is best exemplified in self-assemblages (Anderson et al., 2002). These living structures are made up of individuals linked together to function at a group-level. For instance, colonies of the red fire ant *Solenopsis invicta* build rafts and towers to survive flooding events (Nave et al., 2020). The behaviours exhibited to build these structures can be achieved through four basic, qualitative rules, the expression of which is moderated by several factors. A key factor influencing expression in insect assemblages is local neighbour interaction. Likewise, in self-assembled army ant bridges, the probability of staying or leaving the structure is facilitated by the rate of traffic (Garnier et al., 2013). Despite the simple rules at play, the coordinated complexity that emerges at the group level demonstrates the potential of optimal outcomes in large teams of social insects.

Conversely, social factors may have the potential to positively effect insect effort through a mechanism such as local enhancement, otherwise known as allelomimesis (Deneubourg and Goss, 1989). If an individual perceives a neighbour performing an effectual action, they are more likely to engage in the same action. The current understanding of local enhancement involves the likelihood of performing an action (i.e., it is binary) - whether this effects the likelihood of contributing more or less effort into an action remains unclear. The experimentation on social

insects does have limitations, such as behavioural inconsistencies and uncontrollable variables, thus it is useful to have an alternative distributed system that is more amenable to control and modification. This ideal alternative is swarm robotics.

### Swarm robots as a tool for further understanding

Originally inspired by social insects, swarm robotics is an ever-growing field of research with widespread applications (Dorigo et al., 2020). A swarm robot is an autonomous robot programmed with distributed control algorithms. A single robot is useless when implemented independently, however, when deployed as a swarm they are capable of complex emergence, much the same as social insect systems (Nouyan et al., 2009). As the robots react at a local level, they are capable of adapting to novel conditions. The system is decentralised and is therefore robust to individual failure. The swarm system is capable of operating without communication, which may be essential moving forward into a highly connected world where trust between systems should not be assumed. Compared to classic centralised robots, swarm robots are more cost efficient whilst maintaining scalable, dynamic group-level results (Dorigo et al., 2020). Moreover, the 'swarm intelligence' that emerges is being used to further our understanding of biological systems.

Parameter modifications can extend robotic systems into the biologically implausible and may be able to offer further insights into the mechanisms of teamwork. Already, swarm technology has been modelled on collective biological systems with great success, employing both computer simulations and physical robots. Computer simulations are an effective way to trial behavioural algorithms without physical constraints limiting the output. However, for the swarm system to eventually be effective in a real-world scenario, testing a behaviour in real robots allows us to understand the physical challenges these robots will encounter. The Kilobot robot, inspired by bees and ants, follows three simple behaviours that allow them to self-assemble into programmed two-dimensional shapes (Rubenstein et al., 2014). Robots mimicking the collective building behaviours observed in termites have been able to build towers using bricks they can climb upon (Werfel et al., 2014). The s-bot is capable of attachment within self-assemblages to create patterns, navigate rough terrain and pull objects (Nouyan et al., 2009; Şahin et al., 2002).

Recreating these swarm systems has revealed areas that led to inefficiency within a team. In large groups often an effect of interference is seen, as more time and energy are needed to avoid collisions with neighbouring robots (Lerman and Galstyan, 2002). It has shown heterogeneity can

lead to loafing effects in load transport, as individuals must adjust to the slowest team member (Wilson et al., 2018). Differences in performance can be attributed to coordinating physical forces within a system, which in turn relies on the physical characteristics of each individual.

## Biomechanics of social insects and their assemblages

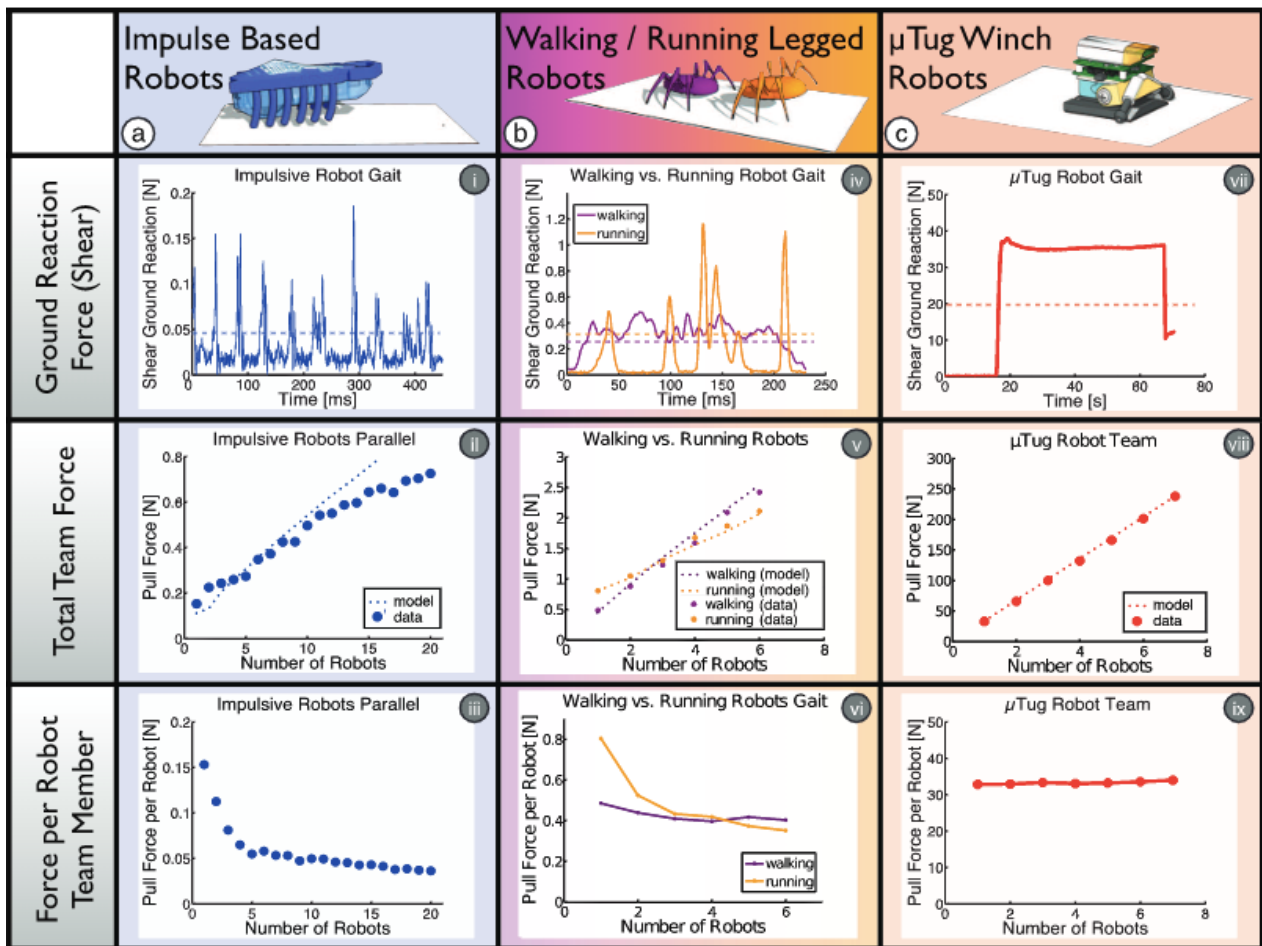
Insects offer an ideal system to study force generation as they have remarkable load carrying abilities. The applied force within any pulling system is limited to the tensile strength between the working units and the ground reaction force between the units and the contact surface (Townsend and Salisbury, 1987). In comparison to their body size, an insect's anatomy allows individuals to withstand force in great quantities.

The insect exoskeleton is made from a lightweight cuticle which offers a high level of structural strength due to the internal arrangement of chitin fibres (Gunderson and Schiavone, 1989). The exoskeleton of the ant *Formica exsectoides* can withstand a force up to 5000 times its body weight, where the critical point of failure is reached in the soft membrane of the neck joint (Nguyen et al., 2014). The ant aligns its neck axis with the load to maximise stiffness; hence, when arranged in self-assembled structures they can align these angles for maximum structural rigidity.

Load bearing is also dependent on the individuals' ability to attach to a surface. Insect tarsi (feet) generally consist of tarsal claws to grip rough surfaces and an adhesive pad (arolium) between the claws that extends when in contact with smoother surfaces (Endlein and Federle, 2008; Federle and Endlein, 2004; Federle et al., 2001). The extension of the arolium is due to the structures' inflation increased by pressure; hence, when more force is applied, the grip strengthens (Federle et al., 2001). Additionally, a behaviour likely to contribute to an insect's strength has been described as a 'freezing reflex' (Federle et al., 2000). When subjected to high disturbance such a gust of air, ants adopt a low-slung body position, maximising their attachment forces to the ground.

A system's maximum structural potential is also enhanced by the biomechanics of attachment forces. The force between an individual and the ground during movement is heavily influenced by the gait of each individual. Robot systems have been employed to compare gait dynamics in relation to force output, and more specifically how this relationship changes within teams (Christensen et al., 2016). Peak force generation is highest when exhibiting an impulsive or running gait; however, in larger teams these gaits are more difficult to coordinate, leading to a Ringelmann

effect relationship (Fig. 2a). A walking gait fares better in larger teams due to the decreased stride length and increased contact time with the ground, generating more of a constant contribution relationship (Fig. 2b). However, the most efficient gait was a winch operated robot, which exhibited a strong connection to the ground coupled with long, synchronised pulls with an even force output. Even so, without social rules to up-regulate pulling force, superefficiency will never be observed (Fig. 2c). Whilst in movement, ants employ a fast-moving tripod gait, where an individual moves three legs at a time. However, during more intensive tasks, such as cooperative transport and leaf-pulling, ants maximise their connection to the ground, moving only a single leg at a time, resembling a winch gait (pers. obs., see Fig. 4B).



**Figure 2: Study testing force generation with differing gaits.** (a) an impulse gait, (b) walking and running gaits, (c) winch gait. The first row shows the variation of force generation over time. The second row shows cumulative group force in increasing group sizes. The third row shows the relative force per robot in increasing group sizes. Note that walking and winch gaits exhibit constant contribution relationships. Data and analysis from (Christensen et al., 2016).

Within assemblages the internal attachment forces limit the systems maximum strength. Insect self-assemblages are held together via body-part connections. Within fire ant rafts, leg-to-leg connections are dominant as they can hold more than twice the load-bearing capacity of leg-to-body connections (Hu et al., 2016). The force required to separate a connected ant is around 620 dynes, which is greater than 400 times the ants' weight (Mlot et al., 2011). The superior biomechanics of insects and their assemblages allows them to safely interact with surprising amounts of force. Additionally, the collective behaviours of social insects can lead to even greater levels of stability. Next, I outline a number of examples to explore the emergent effects of biomechanics and collective behaviour have on force generation in social insect systems.

## Interactions with group size and force in insect teams

### Cooperative transport

The main example where force features as a part of the emerging display of collective behaviour is during foraging. Foraging in social insects consists of scouting trips from the nest, recruitment when a food source is located, and transportation back to the nest (McCreery and Breed, 2014). Where prey items are too large to carry as individuals, they must coordinate their efforts to work as a team - this is known as cooperative transport. Predictably, team size involved in carrying the load is driven by the weight of the prey item (Franks, 1986; McCreery et al., 2019). Superefficient ant teams have been described in cooperative transport, where groups can carry larger loads together than the sum of their individual loads, with no effect on velocity (Franks, 1986). The effectiveness of transport is entirely dependent on coordination, which is optimised by the communication of local information, such as nest location or obstacles, and the arrangement of individuals around the prey item.

The contribution of informed individuals and their ability to communicate the information to the rest of the team is essential to an efficient trip (Gelblum et al., 2015; McCreery and Breed, 2014). Information is communicated through the forces felt through the load (Feinerman et al., 2018), as ants actively align themselves according to these forces to maximise efficiency (Sudd, 1965). In an encircling arrangement (Fig. 3A), employed by *Paratrechina longicornis*, the path is optimised by the constant joining of transiently informed leaders (Feinerman et al., 2018). Typically, the ants on the leading edge pull and the ants attached to the back of the prey item lift. An informed ant will attach themselves to the front of the prey item and pull towards the nest, acquiring the leading-



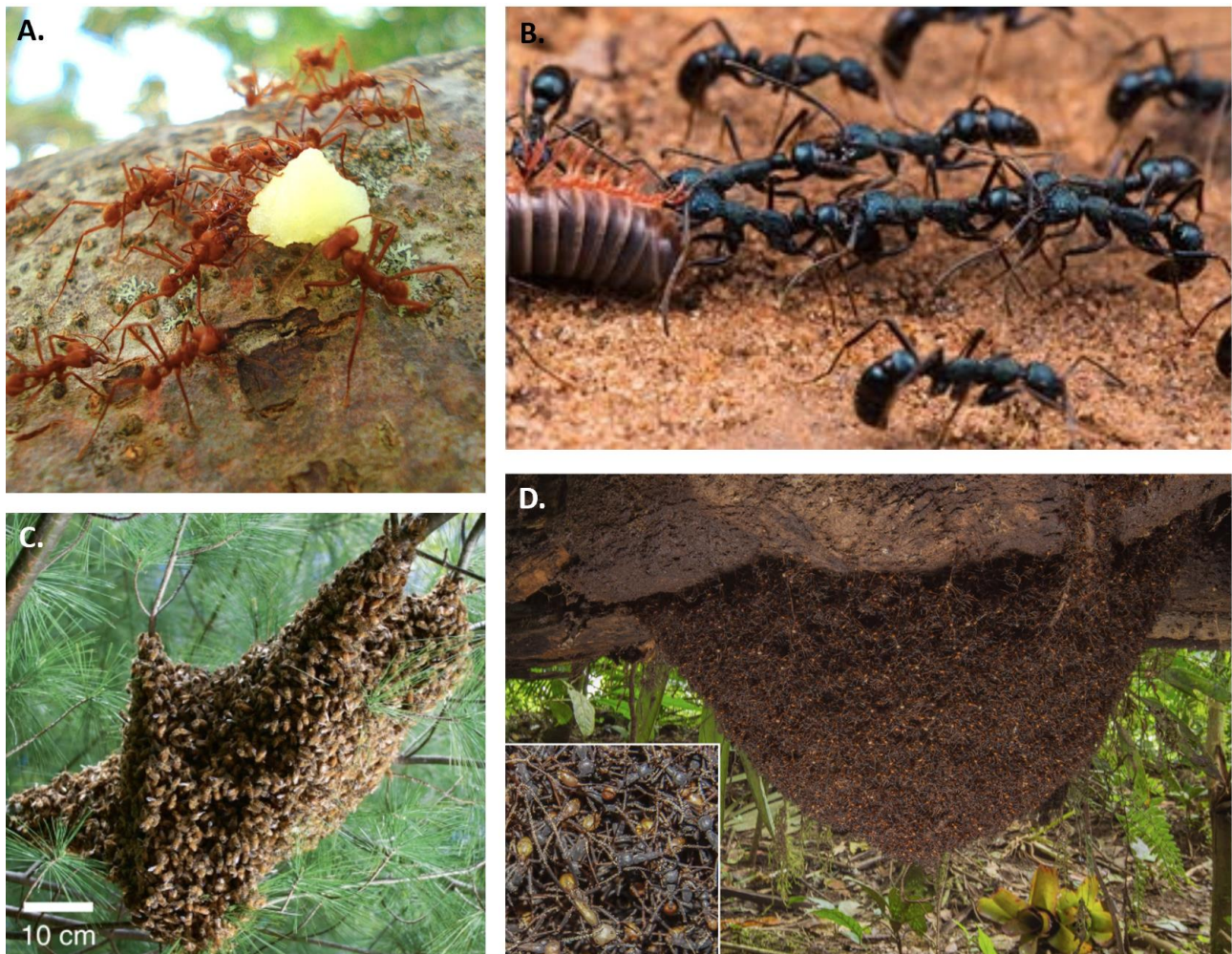
edge position. As sensory inputs are obstructed by the prey item the leading-edge ant becomes less informed over time. Subsequently, another informed ant will then attach to the item and pull in the nest's direction, gaining the leading-edge position and shifting less informed ants into lifting positions. Despite most ants being unaware of the nest location, or having differing opinions, the prey item orientation is optimised through the regular rotation of leaders. In combination with the 'transiently informed leader' control mechanism, the encircling cooperative transport is also influenced by group size. In small teams, encircling arrangements typically generate inefficient trajectories, however as team size increases an adaptive critical point is reached based on overall team size, where the group generates more ordered path trajectories, due to the weighted averaging of the internal coordination links (Feinerman et al., 2018). However, large group sizes can impact the transport speed of the load, where the speed of groups larger than five ants' plateau (Berman et al., 2011). Therefore, regulating an optimal group size involves a trade-off between speed and an ordered path trajectory.

Different species employ various arrangements where the alignment of directional forces and the heterogeneity of workers can determine the team's success (Buffin et al., 2018; Franks, 1986; Peeters and de Greef, 2015). The species categorised as 'superefficient' are swarm raiding species, *Eciton burchellii* and *Dorylus wilverthi* (Franks et al., 1999). Swarm raiders typically carry their prey forward facing, slung under the body, which eliminates rotational forces and enhances unidirectional forces. *E. burchellii* foragers join the team until the point at which optimal speed is reached, maximising efficiency (Franks, 1986). However, 88% of these teams are pairs, and efficiency is attributed to the coordination of gaits at high speeds. At the other end of the scale in terms of team size is *Leptogenys*. Individuals arrange themselves into pulling chains with up to 52 workers to drag a prey item back to the nest (Fig. 3B) (Peeters and de Greef, 2015). Whether or not this is an efficient method for prey transportation, given this high involvement, is yet to be assessed.

However, it is not always the arrangement of worker that determines foraging success. In the desert ant species *Novomessor cockerelli*, workers congregate on the leading edge of the prey item and pull backward. The larger groups tend to transport prey items slower, not due to the alignment of forces, but because the group can only travel the speed of the team's slowest member (confirmed using swarm robots) (Buffin et al., 2018; Wilson et al., 2018).

The effect of group size on a task such as foraging has been explored by employing a range of coordination algorithms in 'robot' simulations (Rosenfeld et al., 2006). The robots were

programmed to ‘forage’ by collecting as many pucks in a given time as possible, and although the transport was not collective, similar coordination issues must be overcome. All algorithms operated without communication or without prior knowledge of the terrain. The teams achieved the tasks efficiently up until a certain group size was reached. This threshold was determined by the level of interference the algorithm allowed for, thus higher coordination among units led to more effective teams. Another robotic study, that accounted for an ant’s ability to moderate collisions, still encountered a negative effect of group size due to coordination (Krieger et al., 2000). By maximising synchronicity between units, we can ensure the effective use of larger teams in artificial systems.



**Figure 3: Collective behaviours involving an interaction with force.** (A) Red ants cooperatively transporting food item with an encircling arrangement (Gabellieri et al., 2018). (B) *Leptogenys* sp. transporting a millipede back to the nest using branched pulling chains (Peeters and de Greef, 2015). (C) Honeybees (*Apis mellifera*) swarming to provide temporary shelter (Shishkov et al., 2022). (D) Army ant (*Eciton burchellii*) bivouac (Bochynek et al., 2021).

## Aggregations

Aggregations can be seen in both bees and ants to function as a temporary nest, providing security and thermoregulation. These assemblages offer an ideal system to study how the forces interacting within these living structures are actively optimised to enhance the functional capacity. In *Eciton* army ants, swarms engage in vast foraging raids, where bivouacs are assembled as often as nightly (Fig. 3D) (Schneirla et al., 1954). These assemblages, sometimes over 500,000 strong, are heterogeneous structures with dense shells and lightly packed cores (Bochynek et al., 2021). The structure optimises the distribution of weight on individuals throughout the assemblage. The individuals bear a maximum of eight times their weight at the base of the assemblage despite growing numbers of ants. Hence, despite larger load-carrying abilities the structure is organised to optimise an individual's contribution of effort.

Similarly, honeybees interlock their bodies in assemblages to form a temporary nest whilst scouts search for a permanent nest site (Fig. 3C) (Peleg et al., 2018). These structures can remain stable for multiple days as they actively adapt to environmental conditions (Peters et al., 2022). They are observed to grow in warmer temperatures, allowing air circulation through the swarm, and conversely shrink in cooler conditions. Much like army ant bivouacs, bee assemblages also share the weight distribution throughout the structure at constant scale, irrespective of swarm size (Shishkov et al., 2022). Additionally, the structure maintains this weight distribution when exposed to physical stresses. When exposed to horizontal shaking, the pendant shape flattens into a more stable state. The mechanism that allows this contraction is likely the sensing of the local change of strain forces, triggering individuals to move up the strain gradient (Peleg et al., 2018).

Another ant species known for their self-assemblages are fire ants, forming rafts and towers (Mlot et al., 2011; Phonekeo et al., 2017). When assessing tensile strength in fire ant aggregations of increasing group sizes, a general loafing trend was observed (Phonekeo et al., 2016). In this study, individual contribution is measured through tensile strength; however, this metric likely underrepresents the maximum output of a group of ants as tension centres on only a few points of contact regardless of group size. The effect was not as severe when surrounded by participating neighbours, aided by the lateral connections they provided. The raft and tower assemblages must withstand the disruptions of rising flood waters; thus, their locking mechanisms must be secure (Mlot et al., 2011). The connections are actively modulated by applying pressure through their legs and orientating themselves perpendicular to each other, reducing packing density and increasing buoyancy (Foster et al., 2014). Towers, despite working against gravity, also manage to distribute

forces evenly with a maximum tolerance of the weight of three ants (Phonekeo et al., 2017). This weight threshold also acts as a behavioural parameter regulating the growth of the tower. If an ant feels weight greater than three ants, it leaves through a tunnel at the base of the tower. This creates a continuous cycle of ants contributing to the assemblage which fine-tunes the distribution of forces through constant disassembly and regeneration. The study of self-assemblages indicates the importance of the role force plays in maintaining and optimising an assemblages' structural integrity.

### Nest Construction

Social insects are well known for their complex nest designs, some of which are constructed using the above-mentioned collective behaviours. Occasionally, in efforts to shift building materials, the insects generate force cooperatively. In honeybees (*Apis mellifera*), workers self-assemble into chains during honeycomb construction; these assemblages are known as festoons. Festoons are thought to assist construction in several ways. First, increased activity warms the wax making it malleable. Secondly, it acts as a template for new comb construction - without the presence of the hanging parallel festoons, the combs emerge unstructured. Finally, by applying rotational forces the festoons pull the structure into position (Hepburn et al., 2014). Although this pulling function has been identified, ongoing research has not quantified the torsional forces applied by teams of bees. Another understudied example of additive force during nest construction, and the main focus of this research, is the pulling chains of weaver ants (Sane et al., 2020).

### Weaver ants as a model system for teamwork and force generation

The weaver ant (*Oecophylla smaragdina*) is an arboreal species, capable of constructing highly complex self-assemblages including bridges, hanging chains, and pulling chains (Anderson et al., 2002; Crozier et al., 2010). Individual engagement in a self-assemblage is encouraged by neighbour participation through positive feedback (Lioni et al., 2001). Visual assessment is also employed to make decisions (Lioni and Deneubourg, 2004). The species' behaviour can be explained by simple decision-making and self-organisation, with direct communication not likely to contribute to the species' performance (Crozier et al., 2010; Hölldobler and Wilson, 1977).

Whilst almost all the variations of self-assemblages in weaver ants interact with force, pulling chains are the clearest example of individual force input. During nest construction, worker ants manipulate the leaf substrate by pulling the tip towards the base, or by pulling adjacent leaves



together, to form a nest chamber (Fig. 4A) (Bochynek and Robson, 2014; Hölldobler and Wilson, 1983). The amount of force required to roll or pull a leaf is more than a single ant can produce, thus, the ants attach together, via a mandible-petiole connection, into chains and pull as one (Fig. 4B). When leaves are brought into position, worker ants use semi-mature larvae as silk-producing glue-guns to weave the leaf material together (Hölldobler and Wilson, 1983). The sequence of behaviours is a complex team task requiring advanced coordination (Anderson et al., 2001).



**Figure 4: Weaver ant's during nest construction behaviours.** (A) Worker ants holding leaves together waiting for workers to weave leaf edges together with silk from larvae. (B) A pulling chain event captured during an experiment performed in chapter 2.

Also integral to the systems effectiveness is their attachment forces. Weaver ants can withstand detachment forces (measured by clinging to an accelerating centrifuge) up to 118x their own body weight (Federle et al., 2000). Compared to other insects, the weaver ant arolium features higher stability in the extended position, revealing how they are capable of remaining secure in an assemblage for long periods of time. Within a pulling chain, an ant employs a winch gate, where one leg is moved backward at a time generating intermediate pulls, maximising their ground reaction force. The detachment force at the mandible-petiole connection, is yet to be quantified. However, the connection should be more resilient than body-leg or leg-leg connections employed

in hanging chains and bridges as the downward curved mandibles lock snugly into place over the front of the leading ant's gaster.

Despite the ant's ability to assemble into chains, this is not seen during cooperative transport of prey items during foraging. Weaver ants employ an encircling arrangement to drag large prey items up tree trunks into their nests (Wojtusiak et al., 2012). Remains of lizards and small birds have been found in weaver ant nests, likely transported collectively. Remarkably, it has recently been found that regardless of load size or surface incline, cooperative transport in weaver ants features a constant prey delivery rate, a measure of speed and weight lifted per individual (Burchill et al., 2022). This suggests weaver ants are capable of a high level of physical coordination. Whether this is observed through the formation of pulling chains is yet to be seen.

With a basic understanding of the underlying behavioural mechanisms in weaver ant self-assembly, further research should analyse the productivity of teamwork from an empirical perspective. Specifically, measuring additive force per individual in pulling chains could offer an insight into the systems organisational relationship. Depending on the degree of coordination and motivation, the species could potentially exhibit a loafing, constant contribution, or facilitation relationship in increasing group sizes. However, as self-organisation is likely to optimise the structure that facilitates the maximum force output, constant contribution or superefficiency are entirely plausible.

Whether a team is capable of being superefficient depends on the level of individual effort. If an individual continuously contributes its maximum force, the upper limit to the total team effort is a constant contribution relationship. If, however, an individual contributes more effort in the local presence of others, the team's effort could generate more force when assembled into long chains than when the same size team is scattered over a wide area. This superefficiency would tend to optimise the total force needed to achieve a task. However, in some scenarios this mechanism could lead to inefficiency. When shifting a load, if the weight of the load equals the ant's maximum load carrying capacity, social facilitation would imply the ant would not contribute this effort at first and would recruit another team member to achieve the task, sequestering more workers than functionally required. There is evidence, however, that weaver ants can gauge the weight of a load. During cooperative transport, worker ants recruit additional workers to shift large loads via pheromone trails (Hölldobler, 1983). When workers were exposed to a pinned down prey item, they recruited more workers than what was needed to shift the detached object, indicating load

weight rather than load size determines task engagement. This ability, in conjunction with facilitation, could generate a superefficient team regardless of load size.

Whether or not social insects employ a social facilitation mechanism in large teams is unclear. Measuring the total and individual forces generated by behaviours such as the pulling chains in weaver ants will uncover the empirical potential of teams of social insects. By observing a superefficient team, we can resolve the interactions between these factors and recreate the relationship in robotic systems. Implementing a facilitation algorithm in swarm robots would optimise each unit's output to perform better in the presence of others, with the potential to improve the systems' overall competency.

The future could see swarms of robots assist in construction, disaster response and planetary exploration (Dorigo et al., 2020; Willmann et al., 2012). In all three of these examples, materials need to be shifted. Single robots will not be capable of shifting large loads; therefore, they will have to work together and coordinate their efforts to achieve their goal. I intend to investigate the trade-off between the addition of teammates (cooperation) and the organisation of an increasing number of physical links (coordination) in weaver ant pulling chain teams. The arrangement of individuals could offer insight into the how geometrical forces contribute to a team's success. This insight could contribute to the next generation of swarm robotic design.

## Chapter 2: Data Chapter

### Abstract

The advantage of teamwork lies in the cumulative outcome generated by the input of each team member. Yet, due to synchronisation and motivation issues, individuals can actually contribute less effort as team size grows; this is known as the Ringelmann effect. Social insects display innate patterns of organisation through simple distributed mechanisms, and therefore are optimal model systems for studying the emergence of team size effects on collective behaviour. Weaver ants (*Oecophylla smaragdina*) self-assemble into pulling chains during nest construction to fold leaves together into nesting chambers. Here, I measure the cumulative force produced by different sized teams of weaver ants to address whether a distributed system can overcome the Ringelmann effect. I find that weaver ants sustain their individual effort despite increasing team sizes. Single workers generate forces on average 80 times their body weight. This effort is not only maintained in team sizes up to 19 ants, but also increased in some circumstances. The presence of long chains has no effect in smaller teams, yet overall average chain size scales positively with individual force contribution, suggesting longer pulling chains enhance the efficiency of pulling behaviour. The body posture of ants within different sized chains suggests ants at the rear contribute comparatively more than the other ants. This study reinforces the potential of swarm-intelligence in inspiring optimisation algorithms for superefficient teams in distributed artificial systems, such as swarm robotics.

### Introduction

The advantage of employing a team to perform a physical task lies in the cumulative amount of effort from the team members. In humans, difficulties in synchronisation and motivation often serve to limit this combined effort (Ingham et al., 1974). As such, it is common to find what is known as the Ringelmann effect – where, as team size increases, individual effort decreases (Kravitz and Martin, 1986). Individuals contributing a maximum effort regardless of team size would generate a constant contribution relationship, which would give the maximum outcome for a team. Alternatively, individuals within a team could display a superefficient relationship (Franks, 1986). This is where individual effort increases with increasing team size, theoretically optimising the cumulative effort generated to reach the same goal (Bond and Titus, 1983). To achieve such optimisation, the system would need to control for the limiting factor of coordination.



In the natural world, the most impressive feats of coordination within large teams are seen in the collective actions of social insects. Advanced coordination is seen in the nest site selection and emigration behaviours of honeybees (Seeley and Buhrman, 2001), termites constructing robust, thermoregulated mounds (Korb, 2003), and army ants linking their bodies to form bridges that optimise their foraging trails along the forest floor (Reid et al., 2015). Teams of social insects tackle complex tasks in the absence of leadership by reacting to local interactions (Bonabeau et al., 1997). Sophisticated group-level outcomes emerge through the self-organising nature of the systems physical components and is promoted through simple local rules governing cooperation between neighbours (Camazine et al., 2001). Little is known about the quantitative potential a collective, distributed system has in undertaking a physical task, and how this ability scales with group size.

The weaver ant *Oecophylla smaragdina*, lives arboreally in colonies with over 500,000 workers (Hölldobler and Wilson, 1977). To provide shelter for their queen and brood they construct nests by drawing leaves together and weaving larval silk along leaf edges to enclose a nesting chamber (Crozier et al., 2010). Nests are made up of a network of chambers woven in place, built in sizes consisting of up to 300 leaves (Devarajan, 2016). To achieve the strengths needed to fold leaves of varying rigidities the workers self-assemble into living chains. Workers attach via mandible-petiole connections and pull in unison to fold a leaf onto itself, or to pull neighbouring leaves together. The weaver ant utilises an adhesive pretarsal organ known as an arolium to withstand detachment forces up to 118 times their body weight (Federle et al., 2000). However, the forces they can actively generate during an everyday task, such as nest construction, remain to be quantified.

The processes that govern social insect behaviours apply to weaver ant assemblages. The weaver ant displays dynamic, robust behaviours, capable of self-assembling pulling chains, horizontal bridges, and vertical chains (Bochynek and Robson, 2014; Hölldobler and Wilson, 1977; Lioni et al., 2001). The self-assemblages are modulated through feedback controls. In hanging vertical chains, an ant's probability of joining an assemblage depends on the existing state of neighbour engagement (Lioni and Deneubourg, 2004). Within pulling chains, positive feedback also controls the growth of chains, as individuals are more likely to join existing chains (Bochynek and Robson, 2014). Emergent effects of weaver ant mechanisms have been measured in cooperative transport. Workers surround a load and drag it back to their arboreal nests, across horizontal and vertical planes. Despite the change in forces across planes and changes in load size, the teams are able to maintain a constant rate of delivery per individual by actively up-regulating their group size

(Burchill et al., 2022). Typically, the coordination between large teams impacts group-level outcomes, leading to the Ringelmann effect. However, in growing weaver ant foraging teams, individual workers would bear lighter loads whilst travelling faster. Burchill et al. (2022) found that despite an increasing investment in the team, individual effort was still maintained for an efficient group-level outcome. During nest construction, a similar balancing act would be encountered, where the force needed to fold a leaf may require the cooperation of multiple workers. To optimise the outcome of the groups effort and be classed as a superefficient team, individuals must physically coordinate their forces and sustain or increase effort levels despite increasing team participation.

Here I experimentally address this by assessing the collective force applied by teams of weaver ants, and evaluating the factors that contribute to the overall team outcome. I built an apparatus resembling an arboreal nesting location that triggered pulling chain behaviour using an artificial leaf. I connected a load cell to the leaf tip to measure the forces applied by weaver ants of different team sizes and arrangements. Mirroring the pulling task that originally revealed the Ringelmann effect (Kravitz and Martin, 1986), I can determine whether weaver ants modulate their individual effort when in different-sized teams to avoid the loafing effect observed in humans. I aim to compare the efficiency of chains to individual ants to determine the biological advantage of forming chains. In nature, as an ant pulls on a leaf, she walks backwards until she meets resistance from the leaf, at which point she adopts a backwards extended body posture. In these experiments, all ants meet resistance as the leaf tip is tethered to the force meter via a wire, thus all postures should be extended back. Therefore, I additionally assess body posture as a metric for force contribution to uncover individual differences in contribution within the various chain arrangements. Overall, I aim to reveal whether a biological collective system can overcome loafing effects despite increasing levels of engagement and to understand the mechanisms that lead to this emergent property. This study reinforces the value in studying social insects for design inspiration in artificial distributed systems such as swarm robotics.

## Materials and methods

### Study species and experimental protocol

Experiments were conducted on six *O. smaragdina* colonies (each containing approx. 1,000-5,000 workers) collected in Townsville, Queensland in June 2022. The colonies were kept in

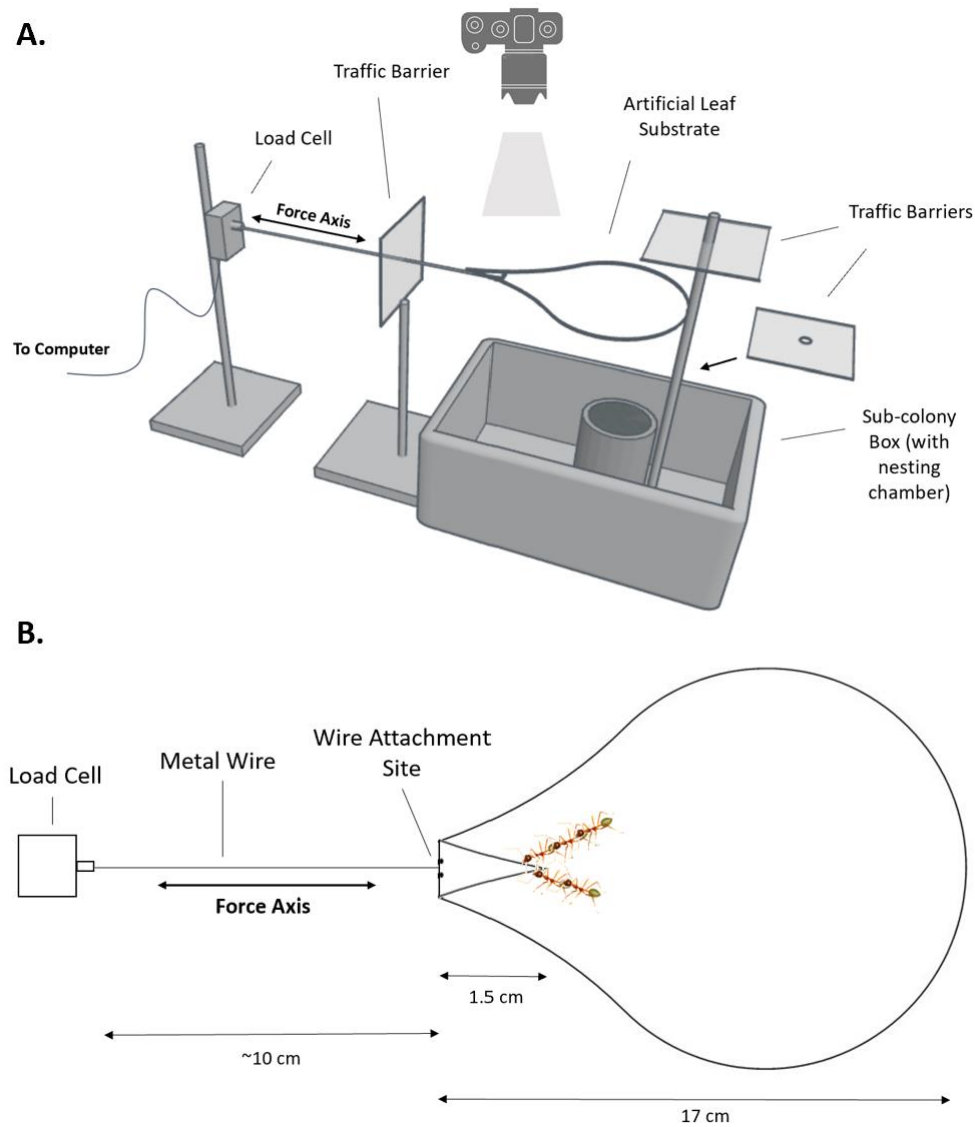
temperature-controlled rooms (28°C) and were kept in Fluon-coated containers to prevent escape. The colonies were supplied with *ad libitum* water and sugar water and fed crickets every three days. No ethics or permits were required to collect and maintain *O. smaragdina* colonies.

The experiments were filmed in indoor controlled environments. To initiate chain formation, upturned nesting chambers from whole colonies, containing several hundred to a thousand workers, were placed in a Fluon-coated plastic box. The box contained a retort stand to allow the workers access to the paper 'leaf' substrate (Fig. 1A). The teardrop shape of the leaf substrate triggered workers to self-assemble into pulling chains at the leaf tip (Bochynek and Robson, 2014). Leaf substrates were made with a Cricut™ cutting machine to ensure accurate replication.

A GSO series precision load cell with 10g capacity range (Transducer Techniques™) was used to record the real-time force in grams on a single axis (Fig. 1B), by positioning it level with the leaf tip and attaching a 15cm thread of single strand electrical wire (approx. 0.1 mm diameter). Using the manufacturer provided software (Transducer Techniques, 2022), the load cell electronically logged the pulling force output of the ant teams at 1 second intervals.

As a pulling event was initiated by the ants, the leaf tip was pulled back 3 cm, at which point the wire became taut against the wire attachment site and measurements could be taken by the load cell. A complete pulling event involved the initiation of a single worker pulling on the leaf tip, the subsequent growth and decay of chains and chain arrangements, through to when the last worker let go of the leaf tip. The rigidity of the copy paper (90 gsm) meant that several ants were required to pull in unison before the tip reached the wire attachment point and measurements could be taken. As such, I also used tissue paper substrates (17 gsm) of the same shape, so that I could record the output of a single pulling ant, and small teams.

In the higher-traffic replicates, where chains were fast-growing, a barrier was placed on the retort stand to limit the traffic accessing the leaf substrate. This slowed the growth of larger arrangements and led to a gradual decay of the chain arrangements, until all ants had detached from the leaf tip. Therefore, the timing of the traffic barrier placement was determined by the estimated growth rate of the chains. However, as each replicate featured a different sub-colony size, and therefore rate of traffic, the timing of the barrier placement was different for each trial.



**Figure 5: Experimental apparatus.** (A) Diagram of entire apparatus. (B) Diagram of dorsal view of the setup during a pulling event.

#### Data Collection

**Ant arrangements:** The videos were filmed from above, perpendicular to the leaf substrate, with a Panasonic Lumix GH-5 digital camera equipped with a Macro 30mm lens at 24 fps. The footage was synchronised with the load cell output by including the load cell software in the video field of view, and clipping the start of the video to align with the initiation of the load cell recording. In total 32 pulling events were captured, comprising 388 unique arrangements. The clips were analysed using the behavioural data-logging software BORIS (Friard and Gamba, 2016), to note the joining and leaving of ants, and at what location, i.e., attachment/detachment at the leaf tip or onto/from an existing chain. Ants that joined the arrangement for less than 5 seconds were

omitted. A unique arrangement was denoted by the joining and leaving of an ant. I then calculated total team size for each arrangement by summing the numbers of ants in all chains.

*Force calculations:* I calculated force per individual by dividing the total force by the total team size for every second. As each arrangement existed for different lengths of time, an average was calculated per unique arrangement to avoid pseudoreplication. Force measurements 10 seconds before and after the traffic barrier being attached were excluded to remove erroneous force fluctuations introduced by this procedure.

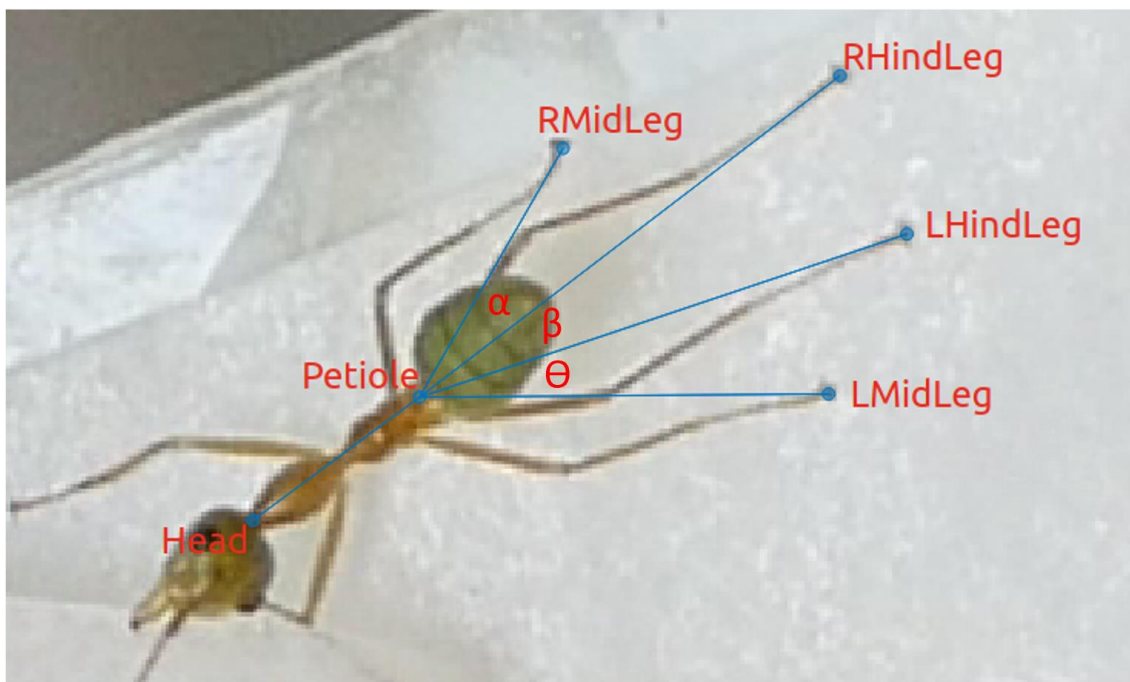
As the load cell measured force on a single axis, any major deviation in the average pulling vector could represent a loss of force measurement. To assess the extent of vector deviations in the observed chains, I measured the angle of the long axis of each chain relative to the wire using ImageJ (Schneider et al., 2012) and calculated the average pulling vector of each arrangement. The total change of average vector angle over each pulling event was calculated. I also measured the effect of pulling vector deviation on my load cell setup (Fig. S1). In three replicates, there was an average negative force output from single-ant arrangements, which was attributed to disturbances from unusual traffic on the leaf tip and wire. Force fluctuations due to traffic were observed when the force meter was unloaded, thus the three instances of negative outputs likely occurred when the pulling force applied by the individual ant was close to zero. However, as the traffic effected these single ant arrangements, this cannot be confirmed, thus I omitted these arrangements from the data ( $n = 3/388$  arrangements, 0.008% of the data).

*Growth/decay phases:* Time (in seconds) was considered a predictor variable and the force relationship for growth and decay of each pulling event were compared. The growth and decay phases were defined by the point of maximum force in each pulling event, with the time before the maximum force denoted as growth, and the time after as decay. As each pulling event had a different duration, the proportion of time before and after this point was calculated and compared using a linear mixed model.

*Worker size:* The body size of 20 workers from each colony ( $n = 120$ ) was measured to assess the effect on force output. Workers unengaged in the pulling behaviour were randomly selected and labelled from the video frames by an individual blinded to the replicate condition. ImageJ was used to calibrate images using a 1 cm scale bar attached to the leaf substrate, and then to measure the thorax length of the workers in mm (Fig. S2). Force difference among colonies was compared to average worker size and worker size was concluded to have a minimal effect (Fig. S3).

Regardless, worker size was also compared against average chain size, to ensure there were no confounding effects on my main findings (Fig. S4). 20 workers from four colonies ( $n = 80$ ) were then weighed to the nearest 0.001 g to determine the force generated in relation to mean body weight.

*Body Positioning:* The posture of pulling ants was assessed to explore the variation in force outputs. Body and leg positions were measured for individual pulling ants, as well as ants within two- and three-ant chains. For the individual pulling ants, 20 frames were extracted across all replicates for each of 7 force values in increments of 0.1g between 0.1 and 0.7g, where a single ant was known to be pulling. The same was done for two-ant and three-ant chains. Where possible an even number of random frames were taken from unique arrangements to avoid pseudoreplication. ImageJ was used to measure the body posture. The extension of the four back legs was calculated by measuring the distance from the petiole to the tarsi and dividing these lengths by the thorax length to account for any differences in worker size. Additionally, I assessed the spread of the legs of each worker by averaging the between the two hind legs ( $\beta$ ), between the right hind leg and the right mid leg ( $\alpha$ ), and between the left hind leg and left mid leg ( $\theta$ ) (Fig. 6).



**Figure 6: Measurements taken to indicate posture;** the length of the thorax, the length of the four back legs, the three angles between the legs.

To assess posture within a chain, random frames of unique arrangements of one-, two- and three-ant chains were extracted. Frames were taken from when the chain of interest existed in isolation, however as there were only three instances of three-ant chains in isolation, I used alternative instances where a coexisting single chain was not in close proximity to the three-ant chain. Under these constraints, I obtained 28 one-ant chain frames from 14 unique instances, 32 two-ant chain frames from 8 unique instances, and 21 three-ant chain frames from 7 unique instances. ImageJ was used to record the same measurements as above for each ant. Within two- and three-ant chains, the average leg extension and average leg angle was compared between the first ant (attached to leaf tip) and second ant (attached to first ant), and so on.

### Statistical Analysis

All statistical tests were performed in R version 4.2.1 (R Core Team, 2021) using the *tidyverse* package. All linear models were assessed using the *lme4* package version 1.1-29 (Bates et al., 2015). Model diagnostics were performed using the simulations-based approach in the *DHARMa* package version 0.4.6, testing the fitted models' dispersion and outliers. To control for differences between colonies (worker size) and experimental set-ups I included both colony and replicate nested random effects.

In assessing effects of team size and average chain size on individual force contribution, all linear mixed effect models used a square root transformation on the response variable to meet the residual normality assumption. The first model tested whether the force per individual was influenced by the total number of ants participating in chains, the phase of the system (growth or decay), or the interaction between these factors. A second model tested whether force per individual was influenced by the total number of ants participating in chains. A third model assessed whether the force per individual was influenced by the average chain size. Lastly, a fourth assessed whether the average chain size, the total number of ants participating in chains, or the interaction among these variables influenced the force per individual.

I used a further linear mixed effect model to assess the posture measurements as predictor variables with the response variable of force output, for individual pulling ants. To determine the best posture predictors, I calculated and compared corrected Akaike information criterion (AICc) values for simple linear models with a single posture predictor. For the leg extension measure I compared the average leg extension between all four back legs to the average leg extension between the two hind legs. For the leg angle measure I compared the average angle between all

four back legs  $((\alpha + \beta + \Theta)/3)$  to the angle between the hind leg ( $\beta$ ). The best predictors were the average leg extension between all four back legs and the angle between the two hind legs ( $\beta$ ). The residuals from the individual linear models featured irregular distributions, which were made regular by combining them into one model and including an interaction term.

ANOVAs were carried out to assess the force differences between different chain arrangements and differences between an ants' posture in different chain positions. Post-hoc tests were undertaken to determine the significance of specific comparisons. If the overall ANOVA was significant then the assumptions were checked with the plot function.

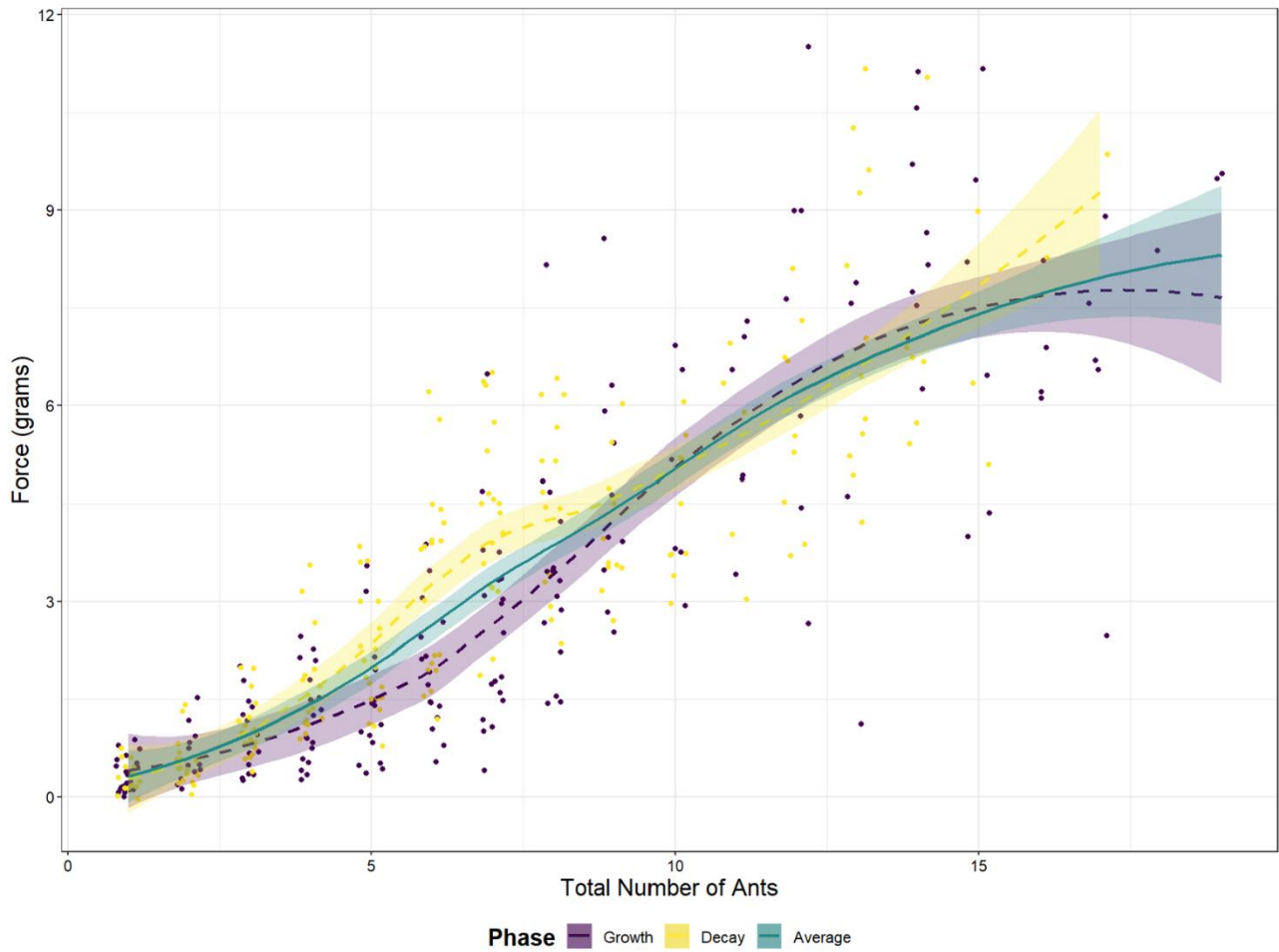
## Results

### Effects of Team Size on Individual Force Output

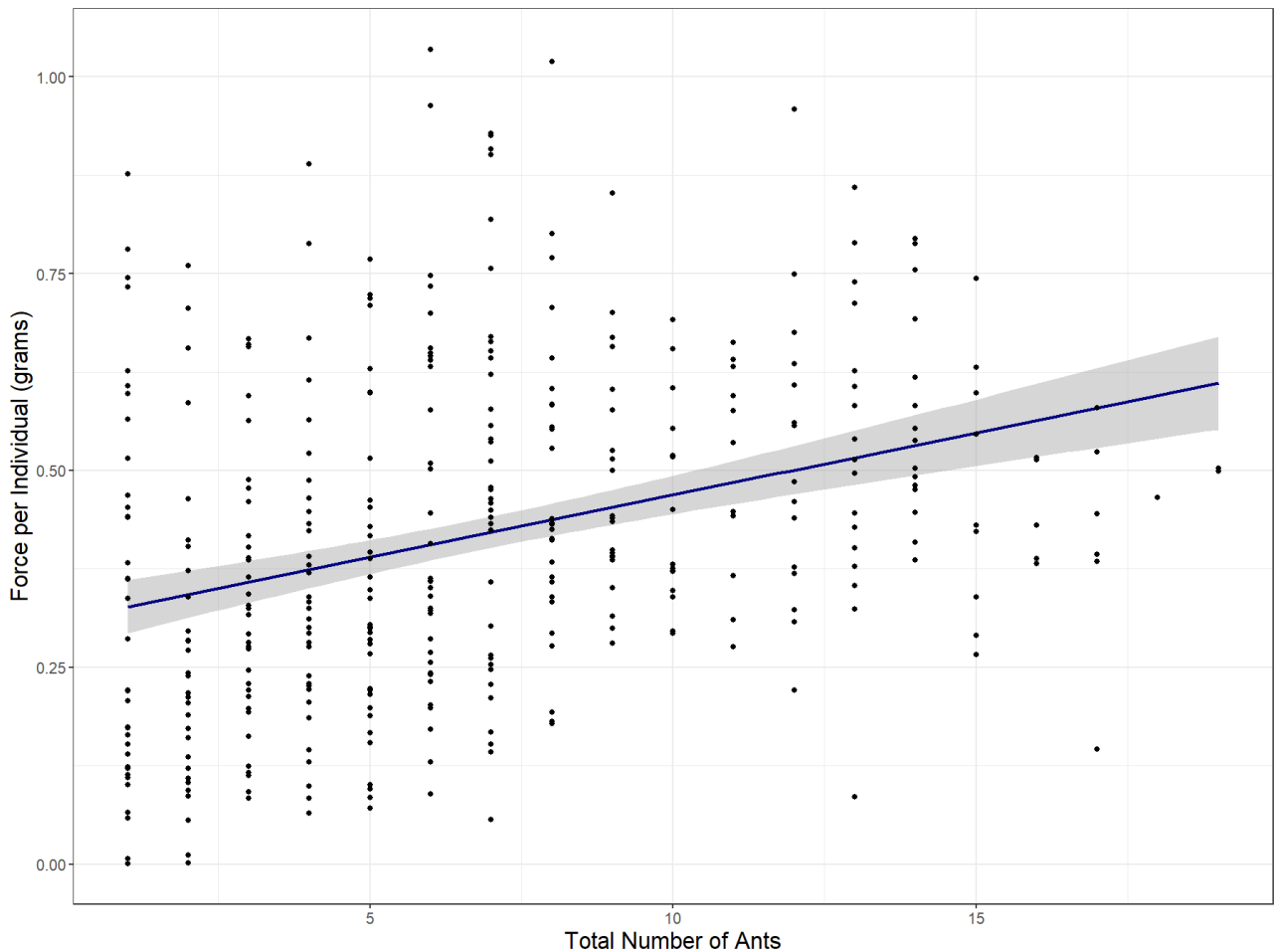
I measured the cumulative force generated by teams of ants ranging from 1 to 19 ants. As additional ants attached and detached to the arrangement the force increased and decreased steadily, rather than in a step-like pattern (Fig. S5). Regardless of team size, workers contributed  $0.406 \pm 0.0109$  (mean  $\pm$  s.e.m) grams of force, with a maximum of 1.03 grams of force. Using the average of my colonies' weight measurements ( $0.00504 \pm 0.000162$  grams) I deduce weaver ants are capable of actively generating 80 times their own body weight on average, and a maximum of 208 times their body weight while pulling.

In some replicates, the growth and decay phases featured a difference in overall force between the same sized teams. However, over all replicates this difference between these two phases averaged out. The growth and decay relationships are graphed using a local area regression in Figure 7. Phase had no interaction effect on the overall force output ( $p = 0.530$ ); therefore, I combined the two phases into one dataset for further analyses (Fig. 8). I found a significant effect of team size on individual contribution ( $p < 2e-16$ ). In other words, as an individual joins the arrangement, slightly more force per individual is contributed (slope = 0.0202).





**Figure 7: Total force output for different sized teams, during the growth and decay phases of pulling events.** Solid circles represent the average force for each unique arrangement. The curves are local area regressions for the growth phase (purple), decay phase (yellow) and average of both phases (blue). Shaded areas represent the 95% confidence interval.

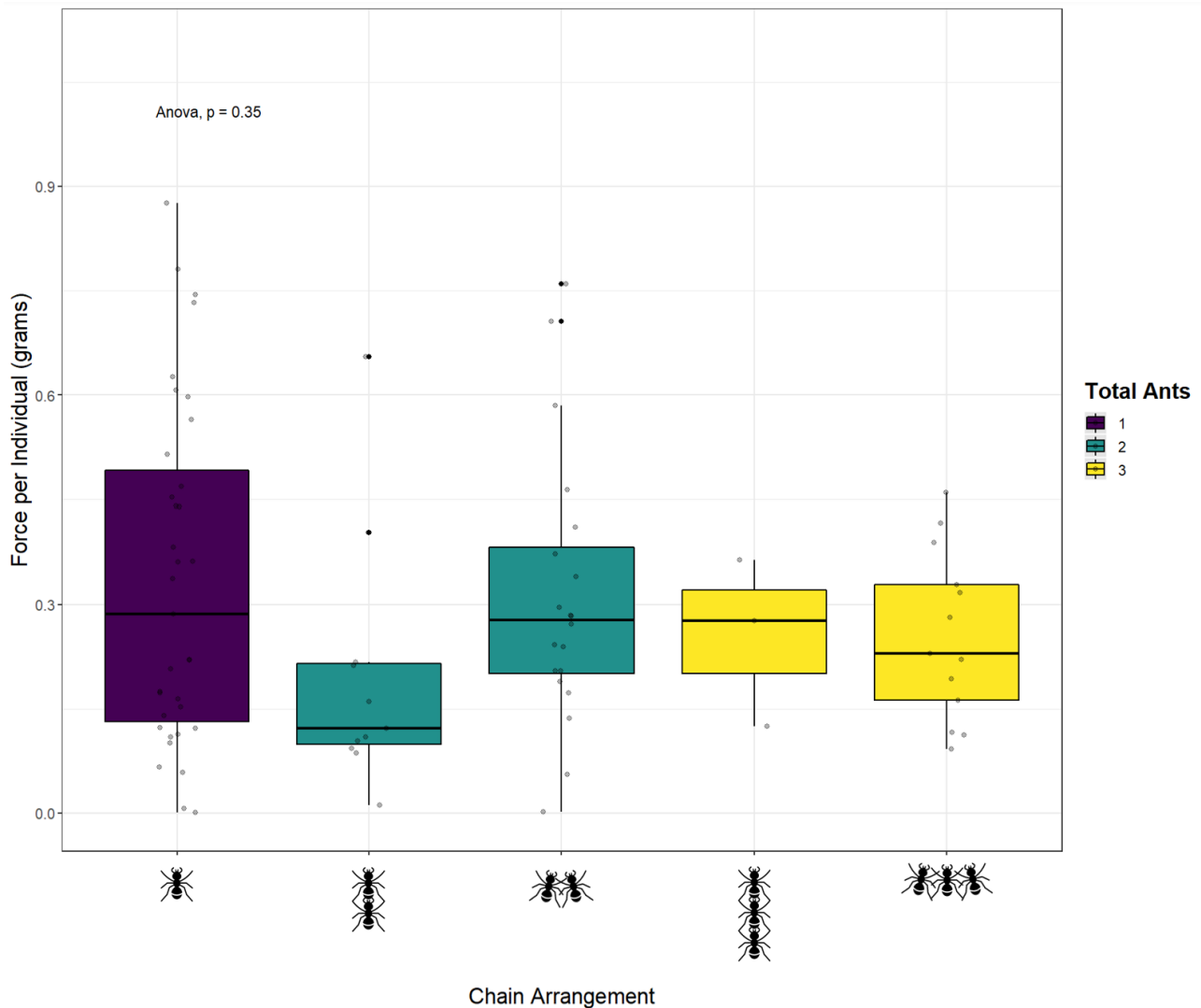


**Figure 8: Linear relationship between the force per individual and the total number of ants.** Solid circles represent the average force per individual for each unique arrangement. Shaded area is the 95% confidence interval.

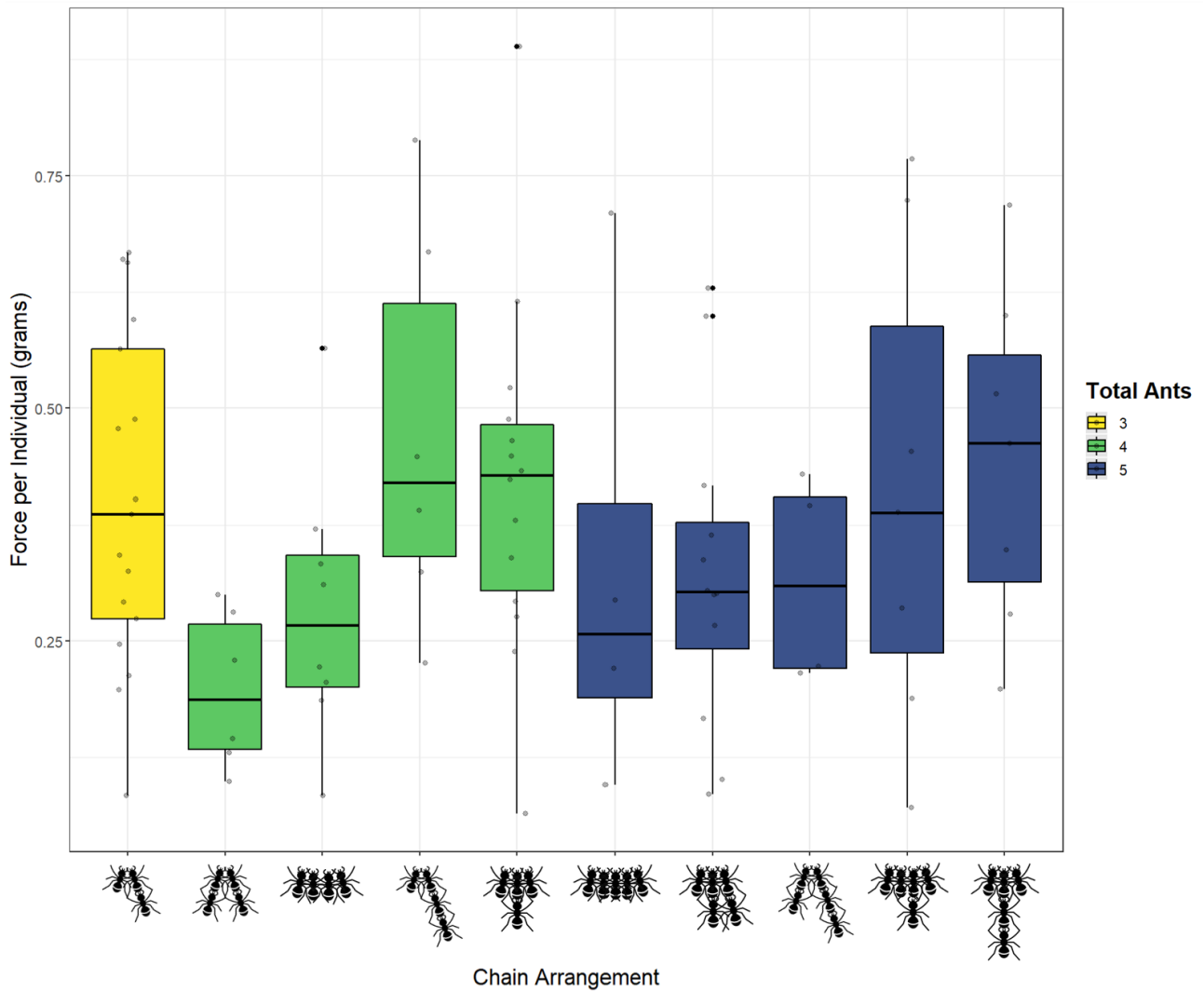
#### Differences in Chain Arrangements

Within my replicates, chain size varied between 1 and 5 ants with an average of 1.71 ants. To assess the effect of individual effort within a chain, I can compare the force output of different arrangements with the same total ants (Figs 9, 10). The cleanest comparison is that between a single multi-ant chain and its corresponding arrangement of the same number of individuals pulling separately (Fig. 9). I found no significant differences between these arrangements in team sizes up to three ants, i.e., there is no clear trend between ants within a chain and the same number of ants pulling separately, as ants in a chain exert slightly less force in two ant teams and slightly more force in three ant teams. It should be noted the three-ant chain only arose on three different circumstances; thus, more data would need to be collected to confirm these results. In arrangements larger than 3 ant teams the chain arrangements become more varied and the sample size for each unique arrangement becomes smaller, therefore statistical comparison is not

performed (Fig. 10). However, it can be observed teams consisting of many individual pulling ants tend to contribute less than teams with the longer chain arrangements.

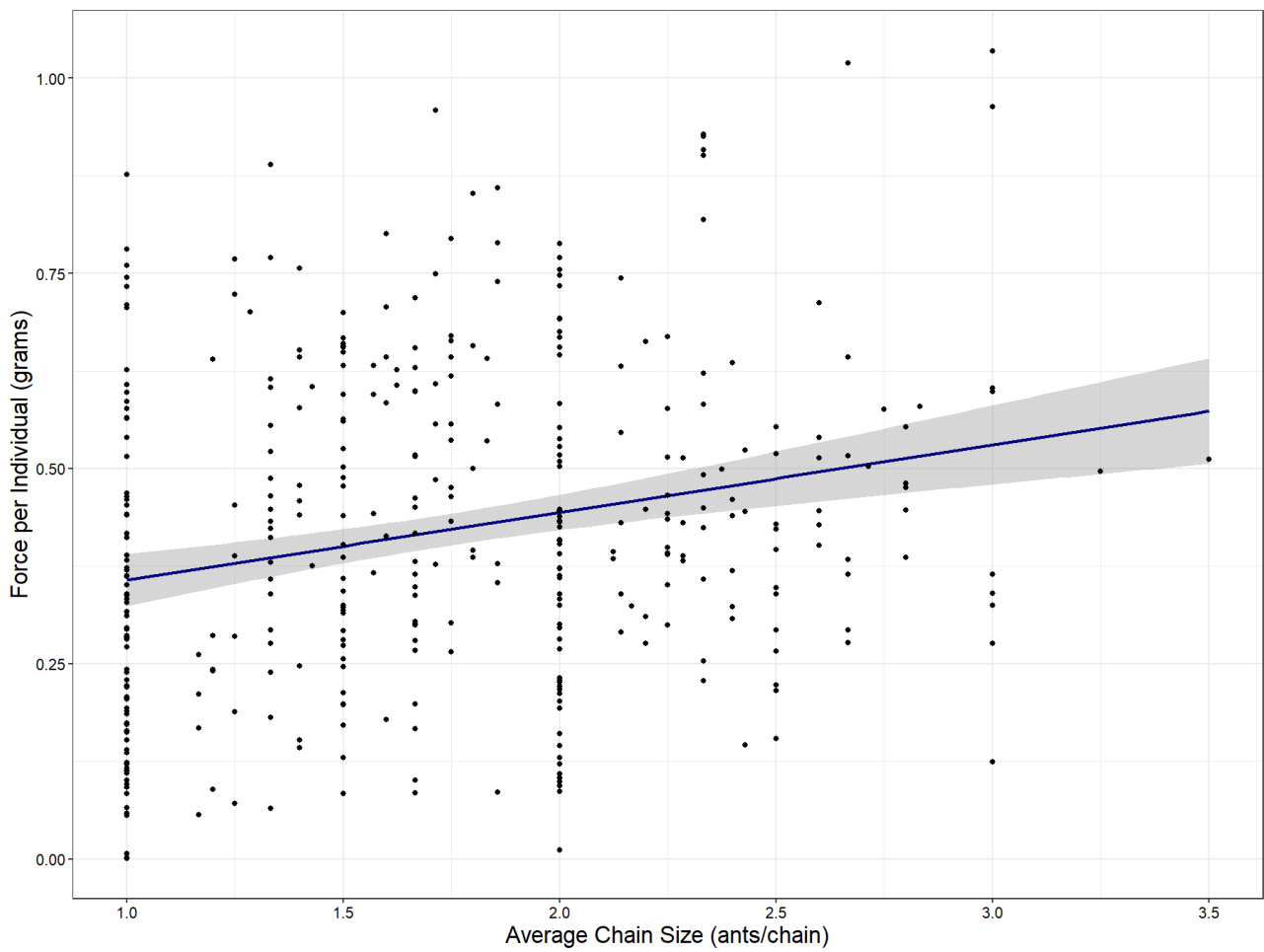


**Figure 9: Force per individual in arrangements of up to three ants.** Shaded circles represent average force per individual for each unique arrangement. The box plots show the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the filled circles are outliers.



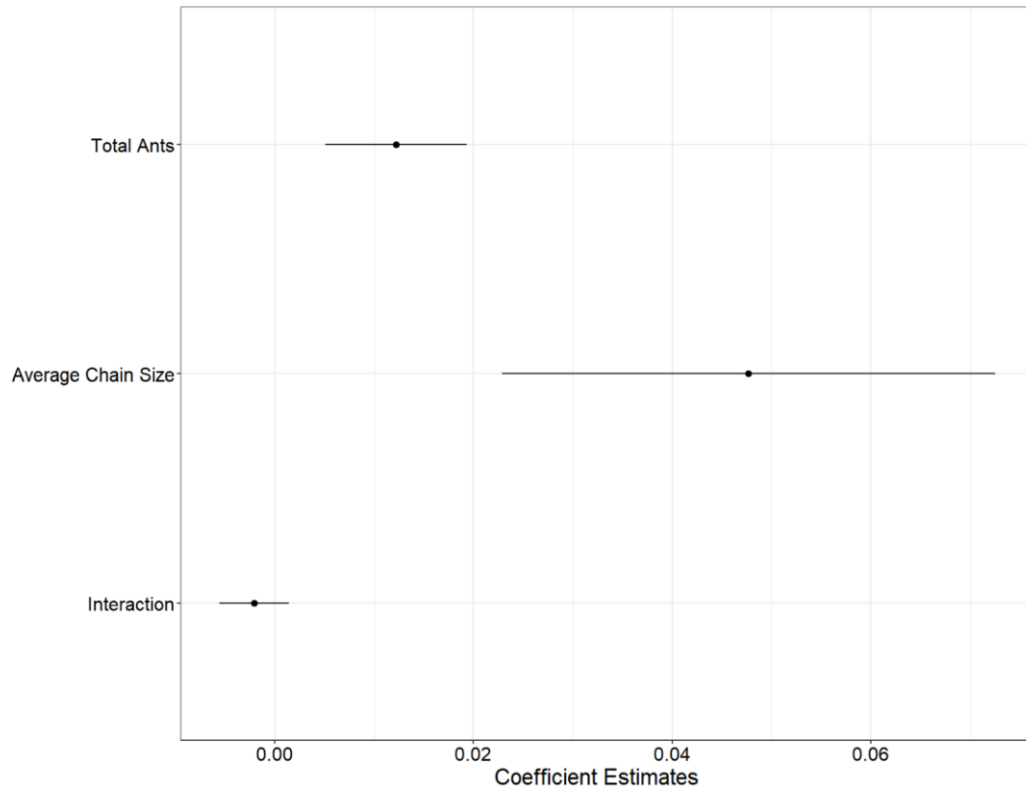
**Figure 10: Force per individual in arrangements of three to five ants.** Shaded circles represent average force per individual for each unique arrangement. The box plots show the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the filled circles are outliers.

To understand whether chain size effects individual force contribution I look at the average chain size for each unique arrangement. While the range of pulling vectors increases with the addition of more chains, I can dismiss an effect of force loss through changes in the average pulling vector throughout these larger replicates as the maximum vector difference does not enter the range of significant force loss in the load cell setup (Fig. S1). Ants contribute more force as average chain size increases (Fig. 11) ( $p = 1.05\text{e-}12$ ). I found no significant interaction between average chain size and total number of ants. ( $p = 0.228$ ). However, average chain size serves as a better predictor of force per individual than the total number of ants (Fig. 12A). The model shows a normal distribution of variance across replicates and colony (Fig. 12B).

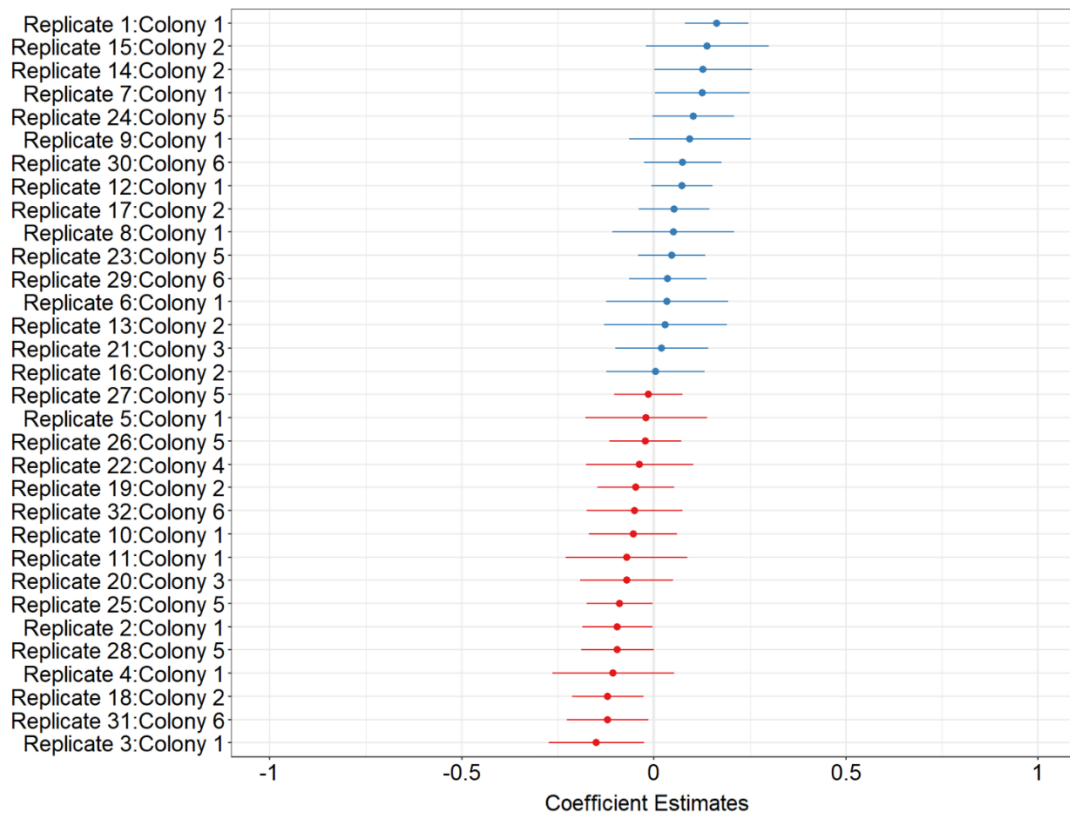


**Figure 11: Linear relationship between the force per individual and the average chain size.** Solid circles represent the average force per individual for the average chain size of each unique arrangement. Shaded area is the 95% confidence interval.

A.



B.

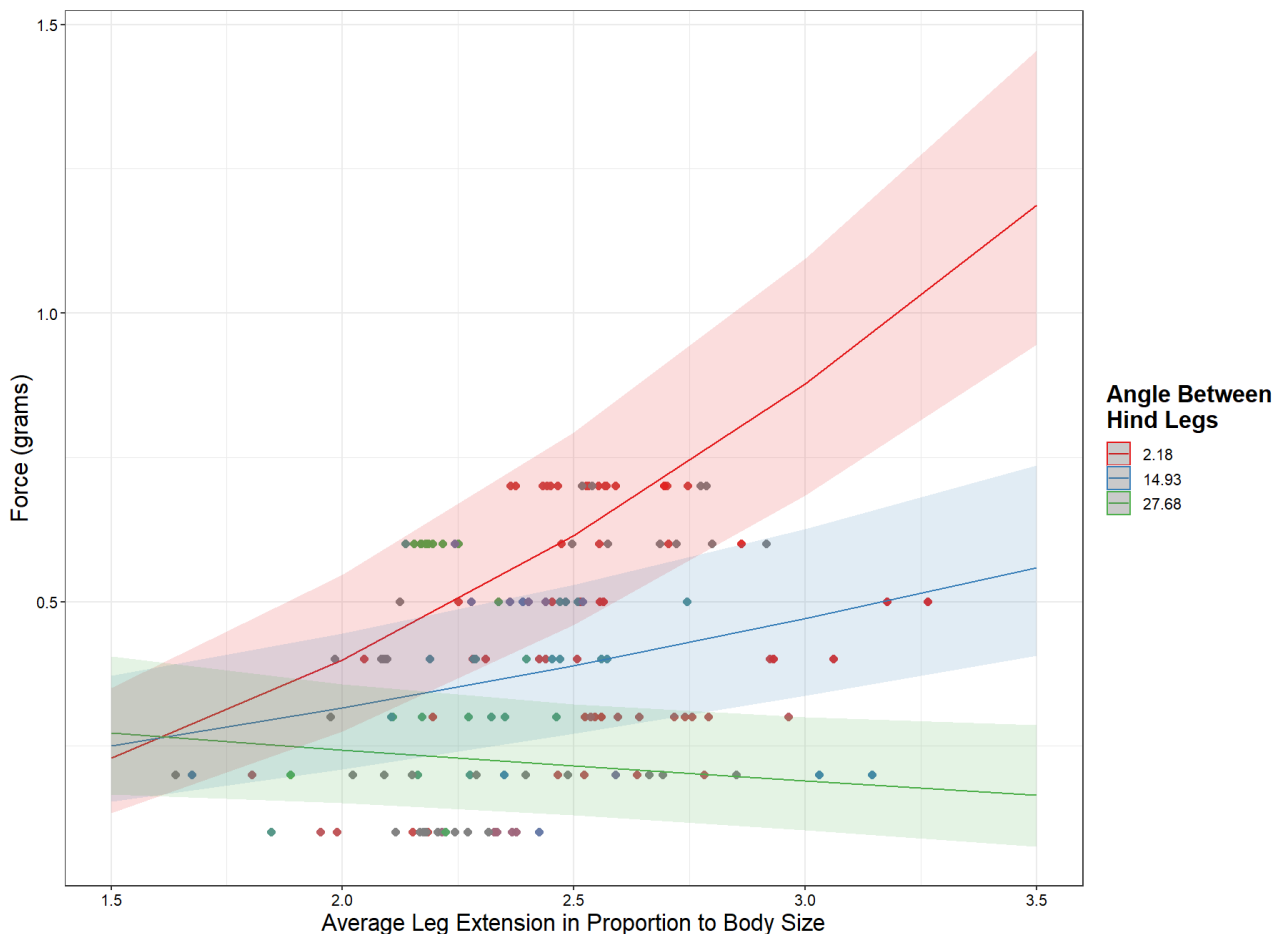


**Figure 12: Standardised relative effects of predictors on the force per individual.** (A) the relative strengths of fixed effects; the total number of ants, the average chain size and their interaction. (B) The relative strengths of random effects; replicate ID nested with colony ID.

## Ant Posture Analysis

I found that the posture of individual ants pulling in isolation correlates with that ants force contribution. The extension of all four back legs and the single angle between the two hind legs are the best predictors for force output ( $\Delta\text{AICc}_{\text{extension}} = 23.58$ ,  $\Delta\text{AICc}_{\text{angle}} = 54.45$ ). The more extended the four back legs are, the larger the force ( $p < 2 \times 10^{-16}$ ). The smaller the average angle is, i.e., the closer the hind legs are to each other, the larger the force ( $p = 0.00032$ ). The extension of the legs is a better predictor of force than the angle ( $\Delta\text{AICc} = 44.70$ ).

Additionally, there is a significant interaction between leg extension and leg angle ( $p = 4.77 \times 10^{-9}$ ). Figure 13 shows prediction curves for leg extension at different sized angles. At identical leg extension, ants with larger angles between their hind legs generate less force. In other words, leg extension must be directed backwards to generate larger forces.



**Figure 13: Interaction between the angle between the hind legs and average back leg extension on the force output of a single ant.** Postures with small angles (red curve) and a large extension are more conducive to higher force outputs than postures with large angles (green curve) and large extensions. Filled circles represent the exact force output at the time where the posture measures were taken. Solid lines are the predicted effects of the interaction between the

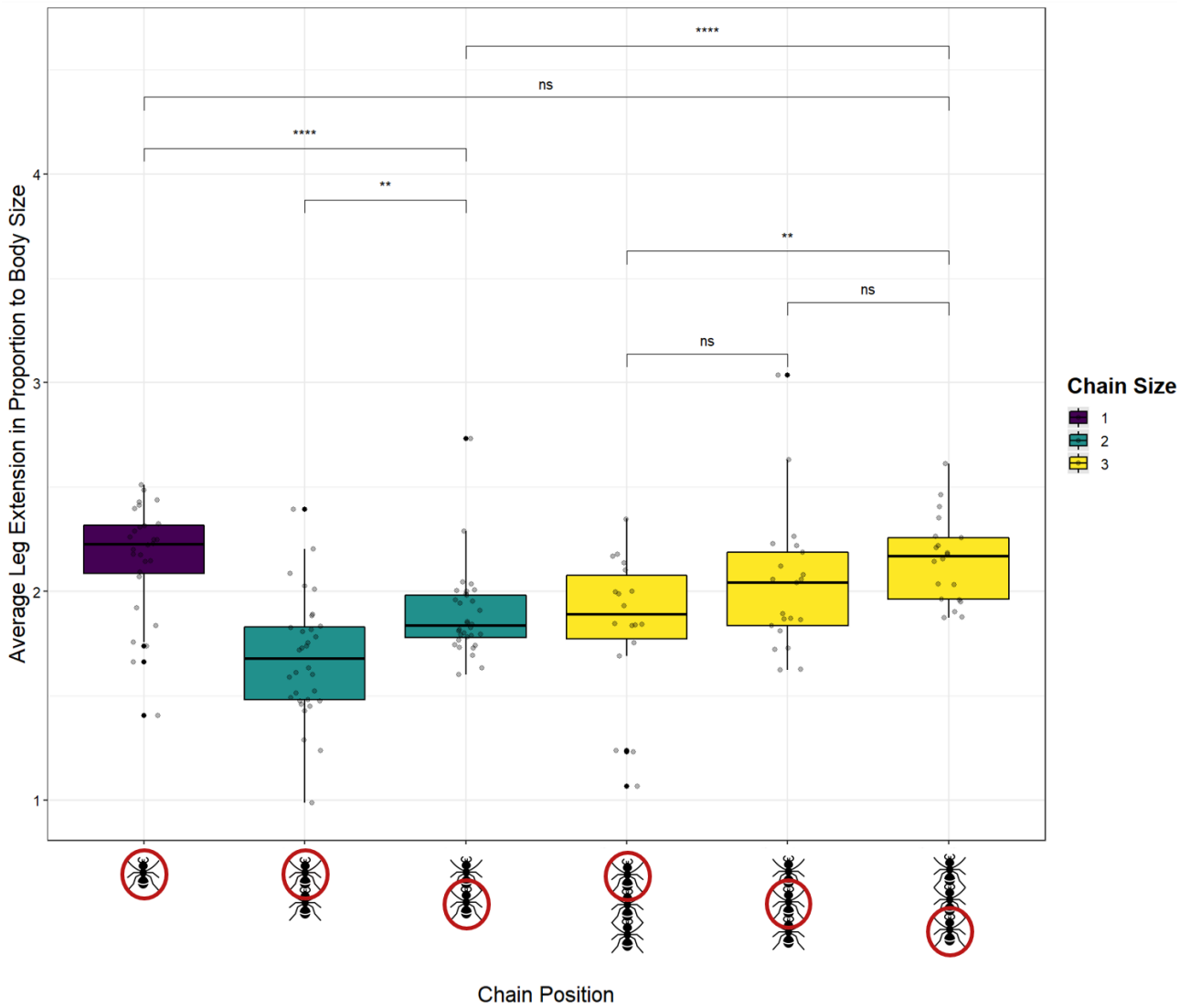
extension of the legs and the angle between the legs. Shaded regions represent the 95% confidence interval.

Additionally, I found that the posture of an ant is influenced by its position within a chain. Comparing the leg extension and leg angles of ants in the different positions found in one-, two- and three- ant chains, overall, I found significant differences ( $\text{ANOVA}_{\text{extension}}: p = 9.53 \times 10^{-12}$ ;  $\text{ANOVA}_{\text{angle}}: p = 3.01 \times 10^{-8}$ ). Comparisons of interest were between ants occupying different positions within a chain, and between the rear-most ant of different chain sizes (Figs 14, 15). A post-hoc analysis was performed on the remaining pairs (Tables S1, S2).

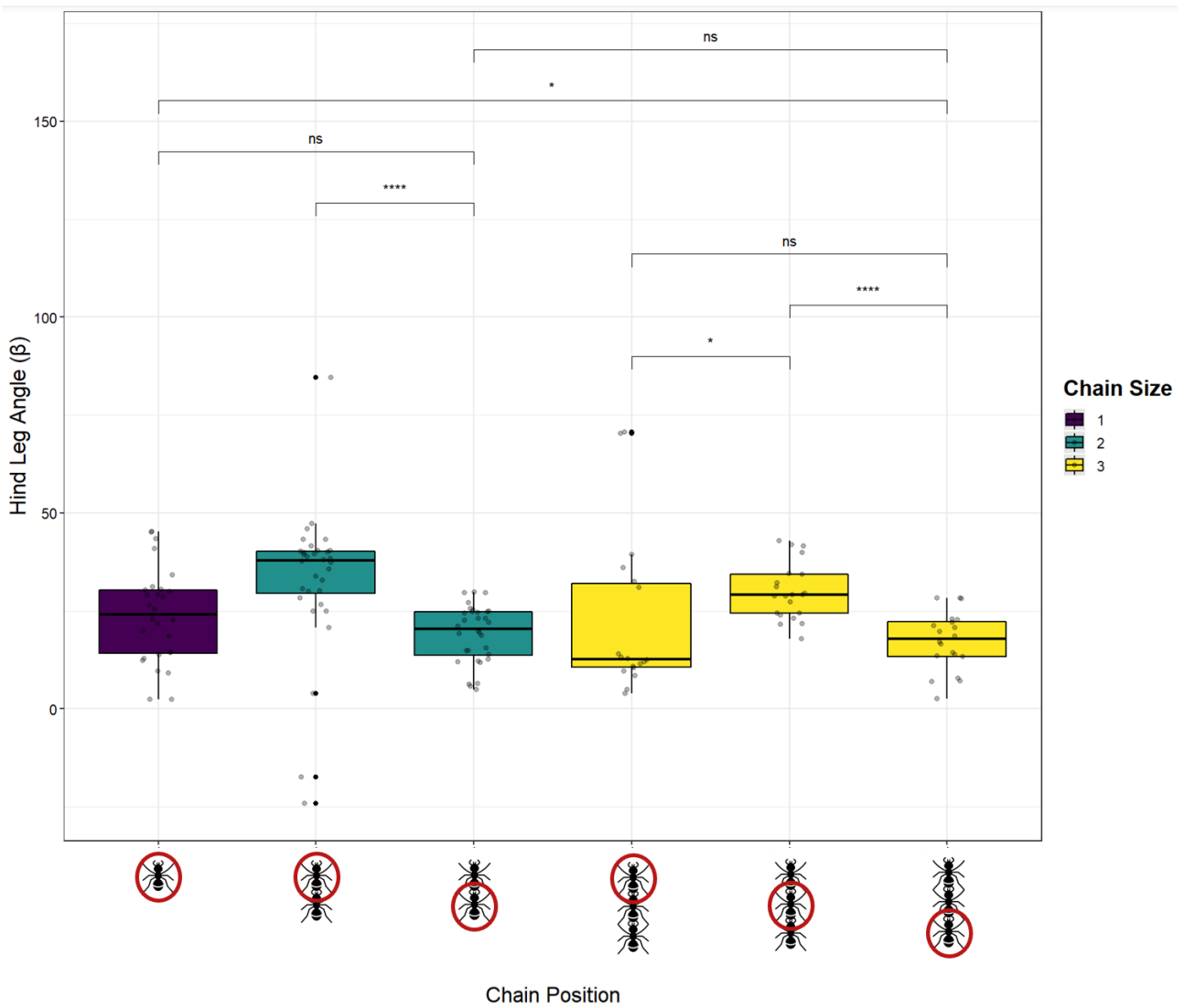
Within two-ant chains, the extension of the four back legs significantly differs depending on an ant's position, with ants in the rear of the chain having greater leg extension (Fig. 14). Three-ant chains featured a similar trend, with the ant in the last position having significantly more stretch than the ant in the front position. The leg extension of the middle ant did not differ significantly from that at the front or rear of the chain. In comparing the leg extension of the ants at the rear positions within different chain sizes, I found that ants pulling individually and ants in the rear of a three-ant chain are significantly more stretched out than the rear ant in two-ant chains, but there was no significant difference between individuals and the rearmost ant in three-ant chains.

The hind leg angle within two-ant chains significantly differs depending on an ant's position, with the ants at the rear of the chain having a smaller angle (Fig. 15). However, the angles within a three-ant chain did not follow a trend, where the ants in the front and rear position both have significantly smaller angles than the ant in the middle position. In comparing the leg angle of ants at the rear positions within different chain sizes, I found the hind leg angle in the rear ant of the three-ant chain was significantly smaller than ants' pulling individually, however there was no significant difference between these ants and the rear ant of the two-ant chain.





**Figure 14: Comparison of average back leg extension in different positions in one-, two-, and three- ant chains.** Longer leg extension is conducive to a higher individual force generation. Shaded circles represent the average leg extension from each frame captured. The box plots show the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the filled circles are outliers.



**Figure 15: Comparison of angle between hind legs in different positions in one-, two-, and three-ant chains.** Smaller angle is conducive to a higher individual force generation. Shaded circles represent the angle between the hind legs from each frame captured. The box plots show the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the filled circles are outliers.

## Discussion

This study finds teams of weaver ants can generate substantial amounts of force, and through emergent coordination, can overcome the Ringelmann effect. As team size increased individuals contributed slightly more effort, classing them as a superefficient team. The difference in force generated in the growth and decay phases of the chain arrangements was negligible, dismissing an overall effect of a stabilising hysteresis on the system (McCreery et al., 2022). Moreover, I found the average chain size of each arrangement to be the best predictor for the increase in individual contribution, such that the presence of larger chains facilitates more force from the overall team.

This suggests that the presence of chains plays a significant role in enhancing the efficiency of the behaviour.

The body posture analysis revealed that there may be unequal force contribution within a team depending on the positioning within different sized chains. I found ants that had both a longer extension of the four rear legs and a smaller angle between the hind legs (i.e., were more stretched out along the longitudinal axis) contributed the greatest amount of force. I found that ants pulling individually, and the ants in the rear of a chain were most likely to adopt this posture. Thus, efficiency through chain formation is likely due to the rear ants in larger chains contributing more effort.

It cannot be conclusively determined the mechanisms that lead to this discrepancy of individual force contribution. However, I can speculate about potential contributing factors based on this study's experimental results and comparable social insect studies. I put forward social facilitation as an overarching mechanism that could describe motivational differences within teams. Through simple stimulus-response behaviour, individuals could actively up-regulate their force contribution in the presence of more teammates, and/or longer chains.

A social facilitation effect could theoretically arise through positive feedback, with the input into the feedback loop being the size of their team and the response being to contribute more effort. However, individual ants are unaware of global order and therefore their exact team size - they only respond to their immediate surrounds. These local cues are perceived by three main sensory modalities in ants; visually observing neighbours engaging in a behaviour (Lioni et al., 2001), chemically sensing concentrations of pheromones (Crozier et al., 2010; Deneubourg and Goss, 1989), or mechanically sensing the forces of pulling/being pulled within an assemblage (Feinerman et al., 2018; Sudd, 1965). Tactile cues may allow ants to perceive their immediate neighbours within a chain, and to modulate their individual effort accordingly. Ants may thus vary their contribution to the team depending on their position in the chain, as suggested by my posture analysis. Visual assessment of the team size prior to joining may also feature as an input affecting individual contribution. A similar mechanism has been observed in the ant *Myrmecocystus mimicus* during combat between colonies, where the ants compare the numbers of the opposing attack force by 'head counting' (Lumsden and Hölldobler, 1983). A visual approximation of team size could account for the comparative increase in individual effort in larger teams as seen in this study's results.

While this form of physical cooperation is rare in the natural world, the closest analogue is cooperative transport of a prey item (Feinerman et al., 2018), as both behaviours share the same basic task of shifting a load as a team. In most studies of cooperative transport, force measurements are typically estimated by the weight of the load and transport speed, indicating the vector sum of the collective effort. Superefficient teams were first described in the swarm-raiding army ant *Eciton burchelli*, where large foraging parties expand over forest floors, retrieving a range of different sized prey items (Franks, 1986; Franks et al., 1999). Larger loads are carried cooperatively, slung under the body of two or more workers. Superefficiency was measured as a ratio of load weight to worker weight, and was mainly attributed to the transportation method eliminating rotational forces and synchrony of worker gaits.

Pulling chains, however, must align rotational force vectors to pull in a unanimous direction. Similarly, in encircling cooperative transport arrangements, a conflict in the rotational forces on the load can result in a deadlock (Gelblum et al., 2015). In these cases, ants likely use the forces felt through the load to align their inputs (Feinerman et al., 2018; Sudd, 1965). Newly attached ants have more updated information on the nest location and contribute comparatively more effort than the others to influence the load (Gelblum et al., 2015), thereby optimising the alignment of forces towards the nest. This control mechanism may align with my findings, as newly attached ants in pulling chain arrangements are typically those at the rear of a chain, contributing larger forces.

If such a control mechanism regulated this system, there would be a difference in individual effort over the period of their engagement, starting larger and slowly declining. For instance, ants may actively downregulate their effort due to fatigue or a loss of motivation. Such a mechanism would act as a negative control for social facilitation, as when the joining of individuals is low and task success (leaf tip movement) is low, individuals contribute gradually less force, until the point they choose to leave. While I did not specifically test this, in this case I would expect to see a difference in overall force between the growth and decay phases, as the decay phase is more likely to contain a higher proportion of ants which have been pulling for longer, and vice versa. I did not observe such a result. Further evidence of an individual's contribution over time in the growth and decay phases of chain formation is needed to address this hypothesis, and specifically address the possibility and influence of fatigue.

Changes to the behaviour of only the last individual in a chain are unlikely to be the sole contributing factor to the superefficiency observed, as if this was the case, average chain length

would have a negligible effect on individual force contribution. There are, however, physical constraints such as crowding that can restrict the effort of individuals in smaller chains. Ants attached closer to the leaf tip are more crowded and have less space to extend their legs due to the presence of ants beside them or ants attached to them. Additionally, in large team sizes, single ants were observed attaching to the leaf tip on top of other chains, unable to connect all their legs to the ground, and thus likely contributing less force. However, this behaviour is not futile as they offer a connection point for a growing chain. Similarly, in larger chains it was observed that the ant attached to the tip was occasionally lifted from the ground by the force behind her, again likely contributing little to the overall effort (though perhaps serving as ‘ropes’ to connect the elevated leaf tip to the ground). Ants at the rear of a chain however, especially when chains are long, are further away from the tapered leaf tip and have more space to extend their legs further from their body and more in line with their body axis. Therefore, the superefficiency of chains, despite the potential for loafing by front-positioned ants, is further evidence for the higher contribution of the rearmost ants in the chain, as suggested by my posture analysis. Further posture analysis of larger arrangements, comparing posture in ants close to the tip and ants further from it could test this theory. An automated positioning software, such as DeepLabCut™ may assist in this assessment.

Ants have a famously high power-to-weight ratio (Nguyen et al., 2014). Various methods have been employed to determine this metric, which typically involve measuring a maximum detachment force. The standard method places an ant on a centrifuge and the rotational speed is slowly increased until the ant detaches (Federle et al., 2004). Using this technique, the average weaver ant can withstand 118.4 times their body weight of force before detachment (Federle et al., 2000). At a maximum, ~13mN was recorded which is around 200 times their average body weight. In this study, I found a smaller average force, at only 80 times their body weight and a similar maximum force, at 200 times their body weight. However, the forces applied in this study are inherently different to detachment forces – I specifically measure the amount of active force an ant chooses to employ when pulling. To the best of my knowledge, I have recorded the highest power-to-weight ratio of any ant recorded under the conditions of active, voluntary force. The fact that within pulling chains ants generally pull at less than their maximum capability is further evidence for their ability to regulate force output at both the individual and collective level.

## Future research

The potential for these findings to inspire swarm robotic designs has been explored in Chapter 1, however, as mentioned, swarm robotics will also be crucial in future research in distributed team outcomes. Though in this study I have estimated individual force contribution through body posture, an accurate measurement of individual effort in a team may be possible through the use of swarm robots. Each robot's contribution can be modified and monitored, allowing the input of a behavioural mechanism such as social facilitation to evaluate the emergent quantitative force relationship. In theory, the application of superefficient robot swarms would minimise the energy needed to complete a task. For example, during disaster response a team of robots may be deployed to shift a large load. The effort contributed by individual robots to shift the load would be minimised until a larger team, with combined power sufficient to shift the load, is recruited, at which point maximum effort would be employed. However, as there are multiple metrics contributing the efficiency of the overall system, including the number of robots sequestered and time taken to complete the task, a balance must be reached to optimise the overall outcome.

Our experiments show that weaver ants actively contribute their maximum effort given the right conditions; large teams featuring long chains with aligned force vectors. Further behavioural research could test the stated hypotheses to uncover the potential control mechanisms. This could be achieved by further analysis into this behaviour to measure factors such as the joining and leaving probabilities of individual ants in addition with their interaction rates, to assess their effect on individual participation, persistence, and effort contribution. Whilst in nature the main challenge would be the continuous, unanimous movement of the leaf tip, my experimental setup allowed individuals to orient themselves once when they attach to the tip and then maintain that posture. Therefore, the effect from competing vectors between chains is likely small, minimising competition and potentially facilitating the superefficiency seen. Comparing this study's outcomes to the outcomes of an untethered system (i.e., a freely moving leaf-tip), would provide an interesting comparison to assess the effect that task success (perceived as tip movement) has on the overall feedback loop, by comparing the same metrics this study employed.

## References

- Anderson, C. and Franks, N. R.** (2003). Teamwork in Animals, Robots, and Humans. *Adv. Study Behav.* **33**, 1–48.
- Anderson, C. and McMillan, E.** (2003). Of Ants and Men: Self-Organized Teams in Human and Insect Organizations. *Emergence* **5**, 29–41.
- Anderson, C., Franks, N. R. and McShea, D. W.** (2001). The complexity and hierarchical structure of tasks in insect societies. *Anim. Behav.* **62**, 643–651.
- Anderson, C., Theraulaz, G. and Deneubourg, J.-L.** (2002). Self-assemblages in insect societies. *Insectes Soc.* **49**, 99–110.
- Bates, D., Mächler, M., Bolker, B. M. and Walker, S. C.** (2015). Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **67**, 1–48.
- Berman, S., Lindsey, Q., Sakar, M. S., Kumar, V. and Pratt, S. C.** (2011). Experimental study and modeling of group retrieval in ants as an approach to collective transport in swarm robotic systems. *Proc. IEEE* **99**, 1470–1481.
- Bochynek, T. and Robson, S. K. A.** (2014). Physical and Biological Determinants of Collective Behavioural Dynamics in Complex Systems: Pulling Chain Formation in the Nest-Weaving Ant *Oecophylla smaragdina*. *PLoS One* **9**, 1–7.
- Bochynek, T., Schiffers, F., Aichert, A., Cossairt, O., Garnier, S. and Rubenstein, M.** (2021). Anatomy of a superorganism -- structure and growth dynamics of army ant bivouacs. *ArXiv*.
- Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S. and Camazine, S.** (1997). Self-organization in social insects. *Trends Ecol. Evol.* **12**, 188–193.
- Bonabeau, E., Dorigo, M. and Theraulaz, G.** (2000). Inspiration for optimization from social insect behaviour. *Nature* **406**, 39–42.
- Bond, C. F. and Titus, L. J.** (1983). Social facilitation: A meta-analysis of 241 studies. *Psychol. Bull.* **94**, 265–292.
- Boomsma, J. J. and Franks, N. R.** (2006). Social insects: from selfish genes to self organisation and beyond. *Trends Ecol. Evol.* **21**, 303–308.
- Brown, A. J. and Harkins, S. G.** (2020). Chapter 9 - Social Facilitation and Social Loafing: Opposite Sides of the Same Coin. In *Individual Motivation within Groups* (ed. Karau, S. J.), pp. 297–330. Academic Press.
- Buffin, A., Sasaki, T. and Pratt, S. C.** (2018). Scaling of speed with group size in cooperative transport by the ant *Novomessor cockerelli*. *PLoS One* **13**, 1–14.
- Burchill, A. T., Pavlic, T. P., Pratt, S. C. and Reid, C. R.** (2022). Weaver ants regulate the rate of prey delivery during collective vertical transport. *bioRxiv*.
- Camazine, S., Deneubourgh, J.-L., Franks, N. R., Sneyd, J., Theraulaz, G. and Bonabeau, E.** (2001). *Self-Organization in Biological Systems*.

- Christensen, D. L., Suresh, S. A., Hahm, K. and Cutkosky, M. R.** (2016). Let's All Pull Together: Principles for Sharing Large Loads in Microrobot Teams. *IEEE Robot. Autom. Lett.* **1**, 1089–1096.
- Crozier, R. H., Newey, P. S., Schlüns, E. A., Robson, S. K. and Biol Ellen Schlüns, D. A.** (2010). A masterpiece of evolution-Oecophylla weaver ants (Hymenoptera: Formicidae). *Myrmecol. News* **13**, 57–71.
- Deneubourg, J. L. and Goss, S.** (1989). Collective patterns and decision-making. *Ethol. Ecol. Evol.* **1**, 295–311.
- Devarajan, K.** (2016). The Antsy Social Network: Determinants of Nest Structure and Arrangement in Asian Weaver Ants. *PLoS One* **11**, e0156681.
- Dorigo, M., Birattari, M. and Stutzle, T.** (2006). Ant colony optimization. *IEEE Comput. Intell. Mag.* **1**, 28–39.
- Dorigo, M., Theraulaz, G. and Trianni, V.** (2020). Reflections on the future of swarm robotics. *Sci. Robot.* **5**, 1–3.
- Endlein, T. and Federle, W.** (2008). Walking on smooth or rough ground: passive control of pretarsal attachment in ants. *J. Comp. Physiol.* **194**, 49–60.
- Federle, W. and Endlein, T.** (2004). Locomotion and adhesion: dynamic control of adhesive surface contact in ants. *Arthropod Struct. Dev.* **33**, 67–75.
- Federle, W., Rohrseitz, K. and Hölldobler, B.** (2000). Attachment forces of ants measured with a centrifuge: better 'wax-runners' have a poorer attachment to a smooth surface. *J. Exp. Biol.* **203**, 505–512.
- Federle, W., Brainerd, E. L., McMahon, T. A. and Hölldobler, B.** (2001). Biomechanics of the movable pretarsal adhesive organ in ants and bees. *Proc. Natl. Acad. Sci. U.S.A.* **98**, 6215–6220.
- Federle, W., Baumgartner, W. and Hölldobler, B.** (2004). Biomechanics of ant adhesive pads: frictional forces are rate- and temperature-dependent. *J. Exp. Biol.* **206**, 67–74.
- Feinerman, O., Pinkoviezky, I., Gelblum, A., Fonio, E. and Gov, N. S.** (2018). The physics of cooperative transport in groups of ants. *Nat. Phys.* **14**, 683–693.
- Foster, P. C., Mlot, N. J., Lin, A. and Hu, D. L.** (2014). Fire ants actively control spacing and orientation within self-assemblages. *J. Exp. Biol.* **217**, 2089–2100.
- Franks, N. R.** (1986). Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli*, Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **18**, 425–429.
- Franks, N. R., Sendova-Franks, A. B., Simmons, J. and Mogie, M.** (1999). Convergent evolution, superefficient teams and tempo in Old and New World army ants. *Proc. R. Soc. B: Biol. Sci.* **266**, 1697–1701.
- Friard, O. and Gamba, M.** (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* **7**, 1325–1330.



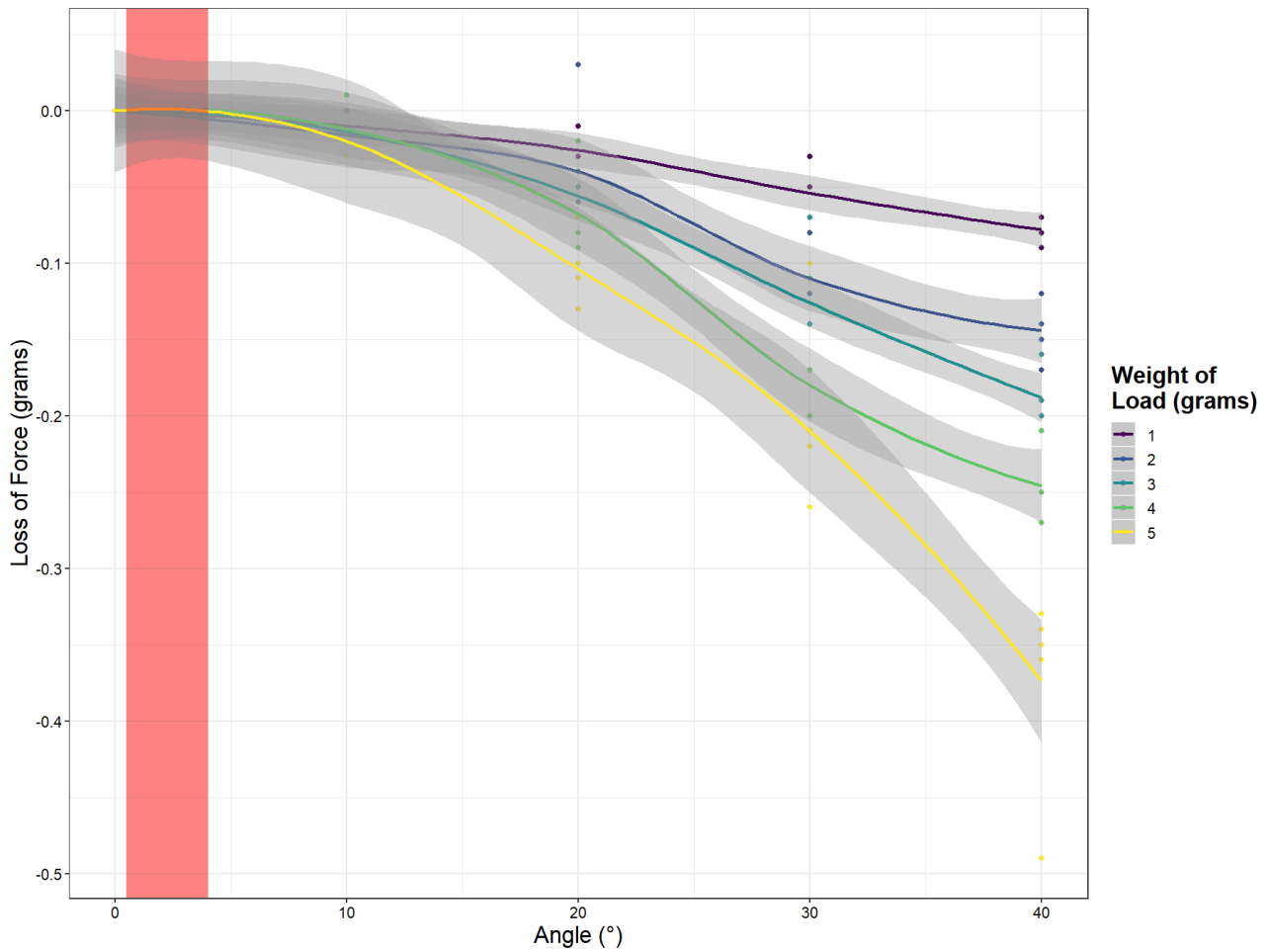
- Gabellieri, C., Tognon, M., Pallottino, L. and Franchi, A.** (2018). A study on force-based collaboration in flying swarms. In *Swarm Intelligence*, pp. 3–15. Springer Verlag.
- Garnier, S., Gautrais, J. and Theraulaz, G.** (2007). The biological principles of swarm intelligence. *Swarm Intell.* **1**, 3–31.
- Garnier, S., Murphy, T., Lutz, M., Hurme, E., Leblanc, S. and Couzin, I. D.** (2013). Stability and Responsiveness in a Self-Organized Living Architecture. *PLoS Comput. Biol.* **9**, 1–10.
- Gelblum, A., Pinkoviezky, I., Fonio, E., Ghosh, A., Gov, N. and Feinerman, O.** (2015). Ant groups optimally amplify the effect of transiently informed individuals. *Nat. Commun.* **6**, 1–9.
- Gunderson, S. and Schiavone, R.** (1989). The insect exoskeleton: A natural structural composite. *JOM* **41**, 60–63.
- Hepburn, H. R., Pirk, C. W. W. and Duangphakdee, O.** (2014). *Honeybee Nests Composition, Structure, Function*. Springer Science & Business Media.
- Hölldobler, B.** (1983). Territorial Behavior in the Green Tree Ant (*Oecophylla smaragdina*). *Biotropica* **15**, 241.
- Hölldobler, B. K. and Wilson, E. O.** (1977). Weaver Ants. *Sci. Am.* **237**, 146–155.
- Hölldobler, B. and Wilson, E. O.** (1983). The Evolution of Communal Nest-Weaving in Ants: Steps that may have led to a complicated form of cooperation in weaver ants can be inferred from less advanced behavior in other species. *Am. Sci.* **71**, 490–499.
- Hu, D. L., Phonekeo, S., Altshuler, E. and Brochard-Wyart, F.** (2016). Entangled active matter: From cells to ants. *Eur. Phys. J. Spec. Top.* **225**, 629–649.
- Ingham, A. G., Levinger, G., Graves, J. and Peckham, V.** (1974). The Ringelmann effect: Studies of group size and group performance. *J. Exp. Soc. Psychol.* **10**, 371–384.
- Karau, S. J. and Wilhau, A. J.** (2020). Social Loafing and Motivation Gains in Groups: An Integrative Review. In *Individual Motivation within Groups: Social Loafing and Motivation Gains in Work, Academic, and Sports Teams*, pp. 3–51. Academic Press.
- Korb, J.** (2003). Thermoregulation and ventilation of termite mounds. *Sci. Nat.* **90**, 212–219.
- Kravitz, D. and Martin, B.** (1986). Ringelmann Rediscovered: The Original Article. *J. Pers. Soc. Psychol.* **50**, 936–941.
- Krieger, M. J. B., Billeter, J. B. and Keller, L.** (2000). Ant-like task allocation and recruitment in cooperative robots. *Nature* **406**, 992–995.
- Latané, B., Williams, K. and Harkins, S.** (1979). Many hands make light the work: The causes and consequences of social loafing. *J. Pers. Soc. Psychol.* **37**, 822–832.
- Lerman, K. and Galstyan, A.** (2002). Mathematical Model of Foraging in a Group of Robots: Effect of Interference. *Auton. Robots* **13**, 127–141.
- Lioni, A. and Deneubourg, J.-L.** (2004). Collective decision through self-assembling. *Sci. Nat.* **91**, 237–241.

- Lioni, A., Sauwens, C., Theraulaz, G. and Deneubourg, J.-L.** (2001). Chain Formation in *Oecophylla longinoda*. *J. Insect Behav.* **14**, 679–696.
- List, C., Elsholtz, C. and Seeley, T. D.** (2008). Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms. *Proc. Royal Soc. B* **364**, 755–762.
- Lumsden, C. J. and Hölldobler, B.** (1983). Ritualized combat and intercolony communication in ants. *J. Theor. Biol.* **100**, 81–98.
- McCreery, H. F. and Breed, M. D.** (2014). Cooperative transport in ants: A review of proximate mechanisms. *Insectes Soc.* **61**, 99–110.
- McCreery, H. F., Bilek, J., Nagpal, R. and Breed, M. D.** (2019). Effects of load mass and size on cooperative transport in ants over multiple transport challenges. *J. Exp. Biol.* **222**, 1–10.
- McCreery, H. F., Gemayel, G., Pais, A. I., Garnier, S. and Nagpal, R.** (2022). Hysteresis stabilizes dynamic control of self-assembled army ant constructions. *Nat. Commun.* **13**, 1–13.
- Middleton, E. J. T. and Latty, T.** (2016). Resilience in social insect infrastructure systems. *J. R. Soc. Interface* **13**, 1–13.
- Mlot, N. J., Tovey, C. A. and Hu, D. L.** (2011). Fire ants self-assemble into waterproof rafts to survive floods. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 7669–7673.
- Moede, W.** (1927). Die Richtlinien der Leistungs-psychologie. *Ind. Psychotech.* **4**, 193–209.
- Nave, G. K. Jr., Mitchell, N. T., Chan Dick, J. A., Schuessler, T., Lagarrigue, J. A. and Peleg, O.** (2020). Attraction, Dynamics, and Phase Transitions in Fire Ant Tower-Building. *Front. Robot. AI* **7**, 25.
- Nguyen, V., Lilly, B. and Castro, C.** (2014). The exoskeletal structure and tensile loading behavior of an ant neck joint. *J. Biomech.* **47**, 497–504.
- Nouyan, S., Groß, R., Bonani, M., Mondada, F. and Dorigo, M.** (2009). Teamwork in self-organized robot colonies. *IEEE Trans. Evol. Comput.* **13**, 695–711.
- Peeters, C. and de Greef, S.** (2015). Predation on large millipedes and self-assembling chains in *Leptogenys* ants from Cambodia. *Insectes Soc.* **62**, 471–477.
- Peleg, O., Peters, J. M., Salcedo, M. K. and Mahadevan, L.** (2018). Collective mechanical adaptation of honeybee swarms. *Nat. Phys.* **14**, 1193–1198.
- Peters, J. M., Peleg, O. and Mahadevan, L.** (2022). Thermoregulatory morphodynamics of honeybee swarm clusters. *J. Exp. Biol.* **225**, 1–9.
- Phonekeo, S., Dave, T., Kern, M., V. Franklin, S. and L. Hu, D.** (2016). Ant aggregations self-heal to compensate for the Ringelmann effect. *Soft Matter* **12**, 4214–4220.
- Phonekeo, S., Mlot, N., Monaenkova, D., Hu, D. L. and Tovey, C.** (2017). Fire ants perpetually rebuild sinking towers. *R. Soc. Open Sci.* **4**, 1–14.
- R Core Team** (2021). R: A Language and Environment for Statistical Computing.

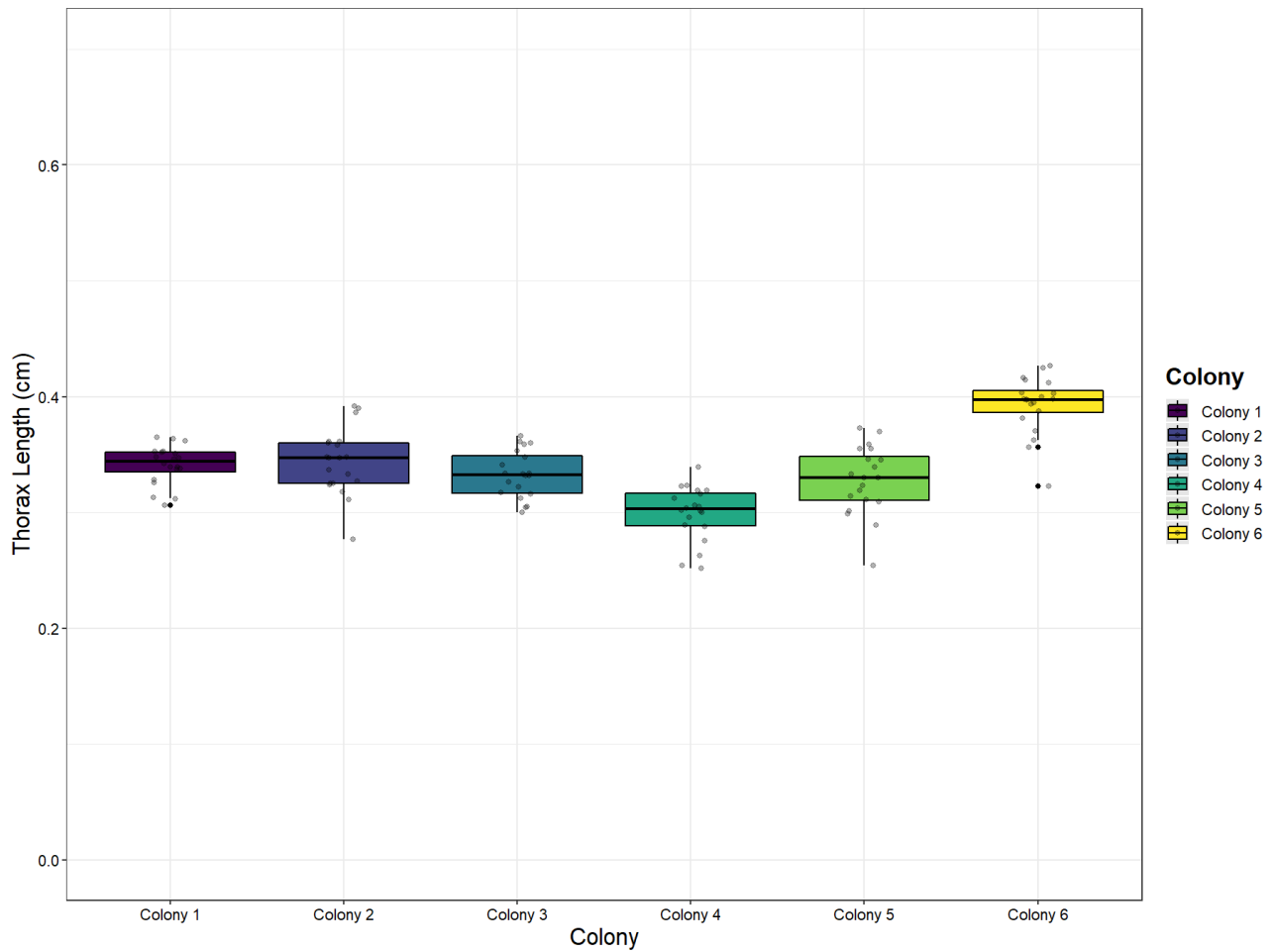
- Rajendran, H., Haluts, A., Gov, N. S. and Feinerman, O.** (2022). Ants resort to majority concession to reach democratic consensus in the presence of a persistent minority. *Curr. Biol.* **32**, 645–653.
- Reid, C. R., Lutz, M. J., Powell, S., Kao, A. B., Couzin, I. D. and Garnier, S.** (2015). Army ants dynamically adjust living bridges in response to a cost-benefit trade-off. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 15113–15118.
- Robinson, E. J. H., Franks, N. R., Ellis, S., Okuda, S. and Marshall, J. A. R.** (2011). A Simple Threshold Rule Is Sufficient to Explain Sophisticated Collective Decision-Making. *PLoS One* **6**, 1–11.
- Rosenfeld, A., Kaminka, G. A. and Kraus, S.** (2006). A study of scalability properties in robotic teams. In *Coordination of Large-Scale Multiagent Systems*, pp. 27–51. Springer US.
- Rubenstein, M., Cornejo, A. and Nagpal, R.** (2014). Programmable self-assembly in a thousand-robot swarm. *Science (1979)* **345**, 795–799.
- Şahin, E., Labella, T. H., Trianni, V., Deneubourg, J. L., Rasse, P., Floreano, D., Gambardella, L., Mondada, F., Nolfi, S. and Dorigo, M.** (2002). Swarm-bot: Pattern formation in a swarm of self-assembling mobile robots. *IEEE Trans. Syst. Man Cybern.* **4**, 145–150.
- Sane, S. P., Ramaswamy, S. S. and Raja, S. V.** (2020). Insect architecture: structural diversity and behavioral principles. *Curr. Opin. Insect. Sci.* **42**, 39–46.
- Sasaki, T. and Pratt, S. C.** (2018). The Psychology of Superorganisms: Collective Decision Making by Insect Societies. *Annu. Rev. Entomol.* **63**, 259–275.
- Schneider, C. A., Rasband, W. S. and Eliceiri, K. W.** (2012). NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671–675.
- Schneirla, T. C., Brown, R. Z. and Brown, F. C.** (1954). The Bivouac or Temporary Nest as an Adaptive Factor in Certain Terrestrial Species of Army Ants. *Ecol. Monogr.* **24**, 269–296.
- Seeley, T. D. and Buhrman, S. C.** (2001). Nest-site selection in honey bees: how well do swarms implement the “best-of-N” decision rule? *Behav. Ecol. Sociobiol.* **49**, 416–427.
- Shishkov, O., Chen, C., Madonna, C. A., Jayaram, K. and Peleg, O.** (2022). Strength-mass scaling law governs mass distribution inside honey bee swarms. *Sci. Rep.* **12**, 1–10.
- Sudd, J. H.** (1965). The Transport of Prey by Ants. *Behaviour* **25**, 234–271.
- Theraulaz, G. and Deneubourg, J.-L.** (1994). Swarm Intelligence in Social Insects and the Emergence of Cultural Swarm Patterns. In *The Ethological Roots of Culture*, pp. 107–123. Springer Netherlands.
- Theraulaz, G., Bonabeau, E., Nicolis, S. C., Solé, R. v., Fourcassié, V., Blanco, S., Fournier, R., Joly, J.-L., Fernández, P., Grimal, A., et al.** (2002). Spatial patterns in ant colonies. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 9645–9649.
- Theraulaz G and Bonabeau E** (1995). Modelling the Collective Building of Complex Architectures in Social Insects with Lattice Swarms. *J. Theor. Biol.* **177**, 381–400.

- Townsend, W. T. and Salisbury, J. K.** (1987). The effect of coulomb friction and stiction on force control. In *IEEE International Conference on Robotics and Automation*, pp. 883–889. IEEE.
- Transducer Techniques** (2022). DPM-3 Data Logging Software.
- Werfel, J., Petersen, K. and Nagpal, R.** (2014). Designing collective behavior in a termite-inspired robot construction team. *Science (1979)* **343**, 754–758.
- Willmann, J., Augugliaro, F., Cadalbert, T., D’Andrea, R., Gramazio, F. and Kohler, M.** (2012). Aerial Robotic Construction towards a New Field of Architectural Research. *Int. J. Archit. Comput.* **10**, 439–460.
- Wilson, S., Buffin, A., Pratt, S. C. and Berman, S.** (2018). Multi-robot replication of ant collective towing behaviours. *R. Soc. Open Sci.* **5**, 1–13.
- Wojtusiak, J., Godzińska, E. J. and Dejean, A.** (2012). Capture and retrieval of very large prey by workers of the African weaver ant, *Oecophylla longinoda* (Latreille 1802). *Trop. Zool.* **8**, 309–318.

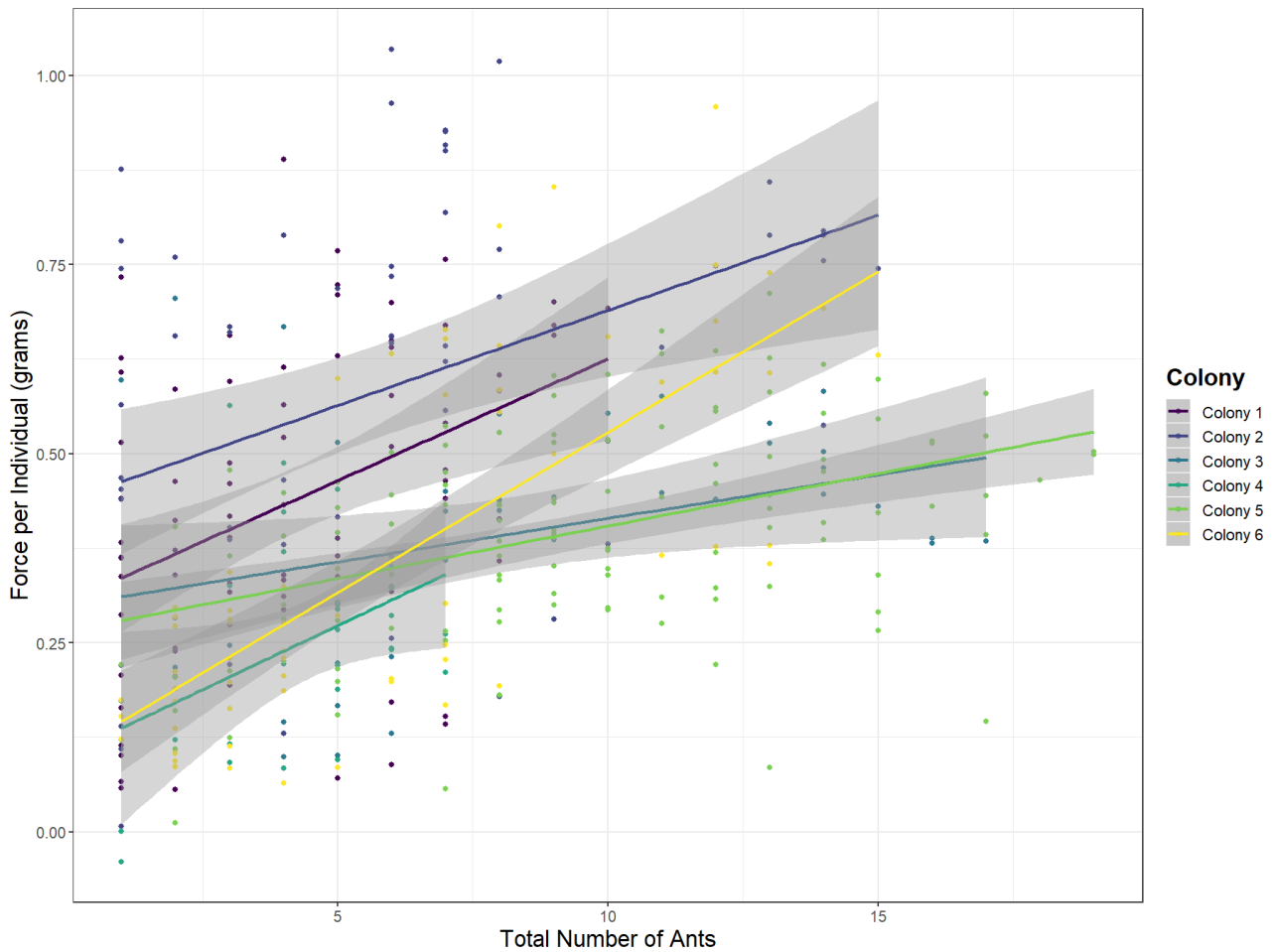
## Supplementary Materials



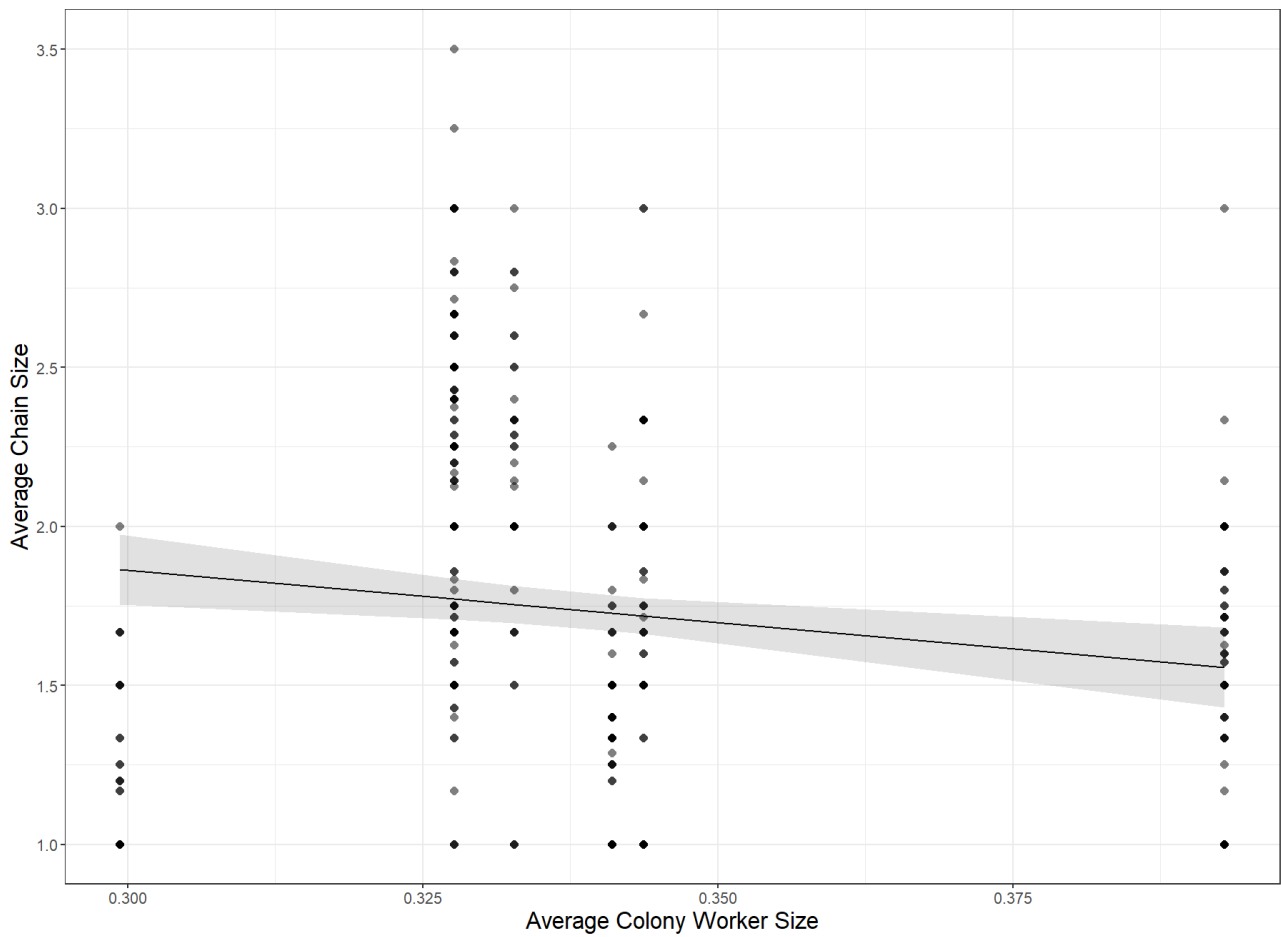
**Figure S16: Representation of force loss due to pulling vector change with different loads.** Data was measured by attaching known loads to load cell and measuring the force loss at different angles (n= three measurements per angle and load). The red shaded area represents the range of vector angles observed in the pulling chain dataset. Hence, I am confident that loss of force detection due to chain vector did not occur in this dataset. Solid lines are a local area regression, and the grey shaded area is the 95% confidence interval.



**Figure S17: The thorax length in different colonies.** Shaded circles represent the thorax length of a single ant. The box plots show the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the filled circles are outliers.

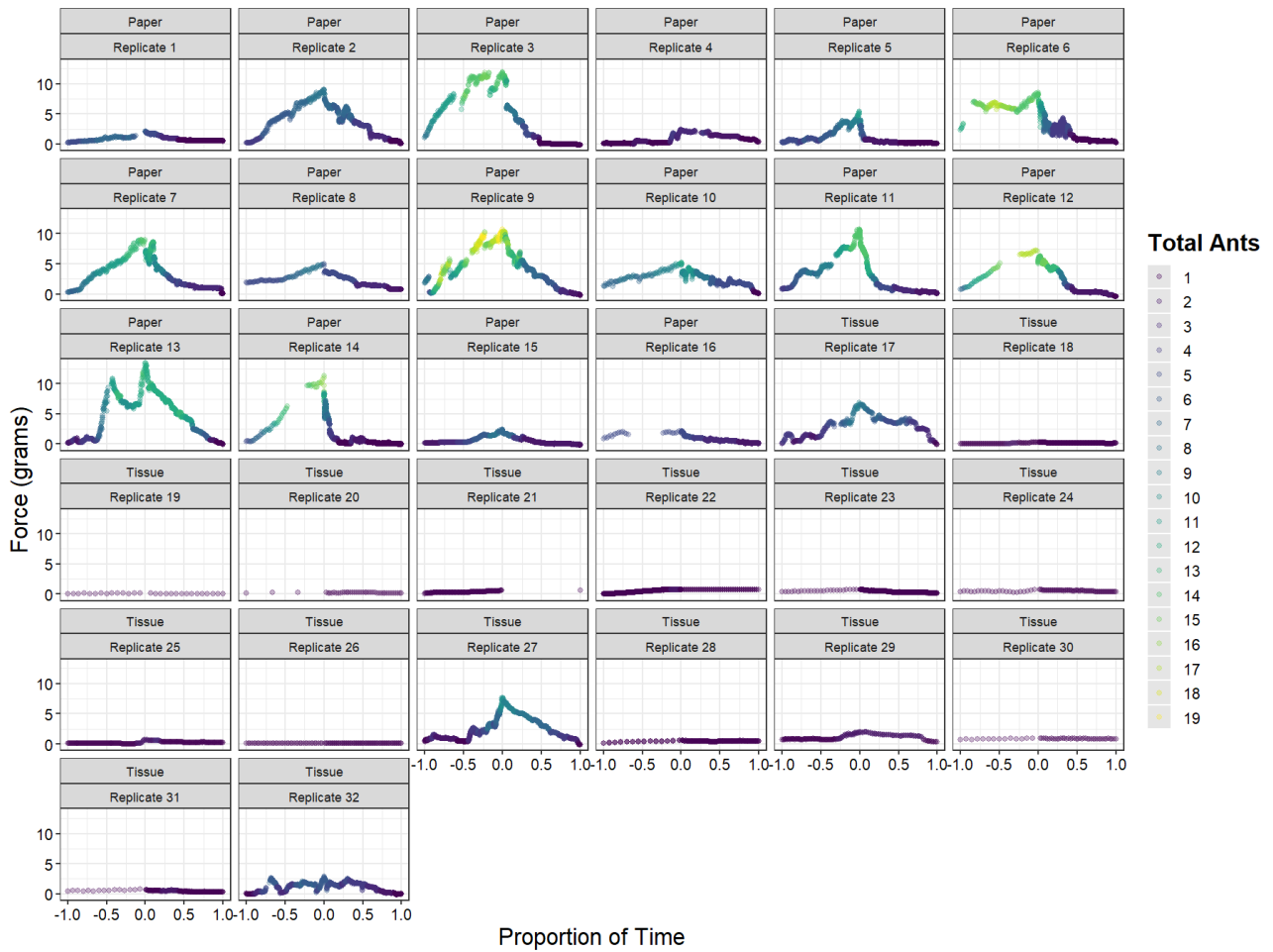


**Figure S18: The force relationship in different colonies.** The colonies with the smallest (Colony 4) and largest (Colony 6) mean worker size overlap almost completely and have a nearly identical trajectory, indicating that worker size was not an important factor in this dataset. Solid circles represent the average force per individual for each unique arrangement. Shaded area is the 95% confidence interval.
















**Figure S19: The spread of chain size data among colonies.** The relationship is significantly negative ( $p = 0.00383$ ), therefore not confounding the positive relationship average chain size has with force per individual. Solid circles are the average chain size for each unique arrangement. Shaded area is the 95% confidence interval.





**Figure S20: Growth and Decay of chain arrangements in all 32 replicates.** Data points represent the force recorded every second shown on a proportional time scale, where zero represents the point of maximum force. Gaps in data were omitted due to disturbances by traffic barrier placement.

**Table S1: Tukey post-hoc results from the differences between the rear leg extension in different chain positions**

Chain position comparison	Estimate	Lower CI	Upper CI	Adjusted p-value
 vs 	-0.11	-0.20	-0.03	<b>0.00</b>
 vs 	-0.00	-0.09	0.08	1.00
 vs 	-0.04	-0.13	0.04	0.67
 vs 	-0.18	-0.25	-0.10	<b>0.00</b>
 vs 	-0.09	-0.17	-0.02	<b>0.01</b>
 vs 	0.11	0.02	0.21	<b>0.01</b>
 vs 	0.07	-0.02	0.16	0.24
 vs 	0.06	-0.03	0.15	0.33
 vs 	-0.02	-0.11	0.06	0.98
 vs 	0.04	-0.05	0.13	0.75
 vs 	0.17	0.09	0.26	<b>0.00</b>
 vs 	0.09	0.01	0.18	<b>0.02</b>
 vs 	0.13	0.05	0.21	<b>0.00</b>
 vs 	0.05	-0.03	0.13	0.48
 vs 	0.08	0.01	0.15	<b>0.02</b>

**Table S1: Tukey post-hoc results from the differences between the hind leg angle in different chain positions.**

Chain position comparison	Estimate	Lower CI	Upper CI	Adjusted p-value
 vs 	-0.33	-1.37	0.71	0.94
 vs 	-0.65	-1.65	0.36	0.43
 vs 	0.74	-0.25	1.73	0.26
 vs 	1.26	0.36	2.16	<b>0.00</b>
 vs 	-0.42	-1.31	0.47	0.75
 vs 	-0.32	-1.43	0.80	0.96
 vs 	1.07	-0.03	2.18	0.06
 vs 	-1.59	-2.62	-0.57	<b>0.00</b>
 vs 	0.09	-0.93	1.10	1.00
 vs 	-1.39	-2.46	-0.32	<b>0.00</b>
 vs 	-1.91	-2.90	-0.92	<b>0.00</b>
 vs 	-0.23	-1.21	0.75	0.98
 vs 	-0.52	-1.50	0.46	0.64
 vs 	1.16	0.20	2.13	<b>0.01</b>
 vs 	-1.68	-2.55	-0.81	<b>0.00</b>