REVIEW ARTICLE

Aggressive behavior across ant lineages: importance, quantification, and associations with trait evolution

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Abstract

Aggressive behavior, or lack thereof, is vital to the success of a social insect colony. A diversity of aggressive behaviors are exhibited in varying degrees by workers across ant species. To better understand this suite of behaviors, we review the extensive literature around ant aggression in order to assess the importance of aggression to the success of ant lineages, the ways in which aggression has been quantified in the literature, and potential correlations between aggression and other key functional traits. Our new contributions to this body of literature include an interaction framework for contextualizing the variation of behaviors, a new suggested scale for quantifying aggressive behaviors, and finally an investigation into traits that are correlated with aggression across ant lineages. Based on our phylogenetic comparative analyses, we find a negative correlation between eye length and aggression and that body size, worker polymorphism, and potentially participation in mutualisms with plants and other insects are evolutionarily linked to an increase in aggressive behavior.

Keywords Social insects · Formicidae · Aggression · Fighting · Defense

Introduction

A social insect colony consists of a reproductive queen and non-reproductive workers, which can vary from a few to millions of individuals (Burchill and Moreau 2016; Hölldobler and Wilson 1990). Due to the structure of social insect colonies, with reproductive success being tied to the ability to gain and defend resources against enemies and competitors, aggressive behaviors are vital to the success of the colony (Abbot 2022). Because it is essential for survival, expression or lack of aggressive behavior is also linked to the reproductive success of an organism and is therefore an important factor in the evolution of species (Modlmeier and Foitzik 2011). We define aggressive behavior as a behavior exhibited by at least one individual that threatens or harms another for the purpose of defense, obtaining prey, and/or competitive/reproductive advantage. This definition comes from several working definitions throughout the literature

(Carroll and Janzen 1973; Alekseyenko et al. 2013; Manfredini et al. 2018). In ants specifically, behaviors that are categorized as aggressive within many contexts are, in no particular order: mandibular flaring, gaster flexion, stinging, use of chemical defense, pulling/grabbing, lunging/charging, and biting (See Fig. 1).

Despite the fact that aggressive behaviors are oftentimes needed to defend a social insect colony, there remains a striking amount of variation not only across large taxonomic groups but also among species and even colonies (Abbot 2022; Oster and Wilson 1978). Across social insects, there have been recorded variations in aggressive defense strategies. In many termite species, a distinct soldier caste, characterized by specialized mandibles and glands, is primarily responsible for aggressive defense against predation (Stuart 1969; Traniello 1981; Thorne 1982; Miura and Maekawa 2020). Within Hymenopterans, aggression varies among groups and species. Solitary cicada-killer wasps (*Sphecius speciosus*) will aggressively defend their nest (Pfennig and Reeve 1989). Some solitary bees exhibit both intra- and interspecific aggression (Batra 1978). In subsocial bees, actively reproductive females are more aggressive than pre- and post-reproductive females (Rehan and Richards 2013). For eusocial hymenopterans, defensive aggression is most often directed toward individuals that are not members of

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Fig. 1 Illustrations of ants exhibiting distinct aggressive behaviors: (1) gaster flexing and lunging (2) gaster flexion with mandible gaping (3) biting, stinging, and pulling/grabbing

Oecophylla
Mandible gaping
Gaster flexing

Myrmecia
Gaster flexing
Lunging

Pogonomyrmex
Biting
Stinging
Pulling
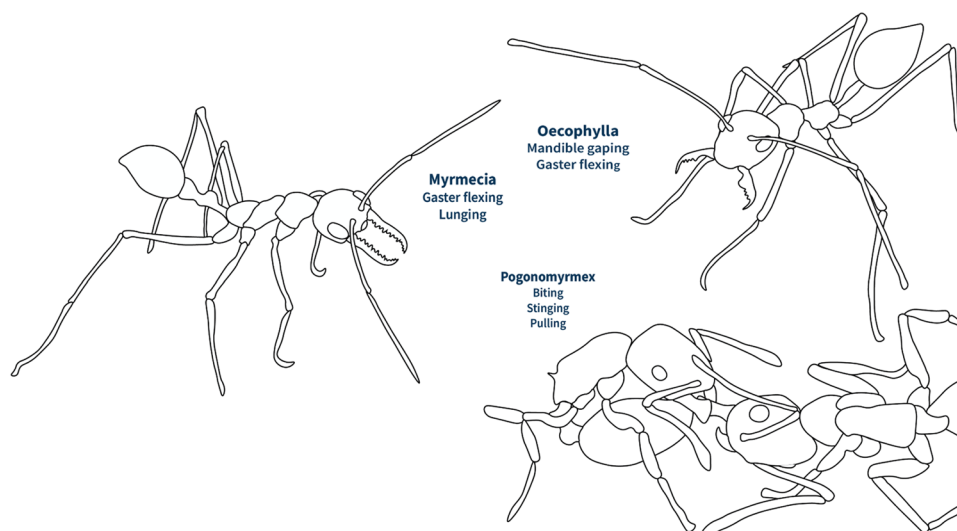
the colony, although there are cases where it is instrumental within the colony (Manfredini et al. 2018). Paper wasps use cues to assess if an individual is a rival to reduce aggressive competition and even use aggression to determine social rank (Tibbetts and Lindsay 2008; Thompson et al. 2014). Eusocial honey bees will use aggression to defend their nest when disturbed with varying levels of intensity (Alaux et al. 2009). Aggressive nest defense is present across all social Hymenopterans, but within ants (Formicidae), an entirely eusocial family, there is still striking variation in aggressive interactions across the family.

Aggressive collective defense and warfare is instrumental to the survival of ant lineages as it is both known from extant and extinct lineages (Barden and Grimaldi 2016). Although aggressive behavior can be successful in defining territories, safeguarding resources, and protecting against enemies, it is also energetically costly and risky (Stuble et al. 2017; Arnott and Elwood 2008; Vieira and Peixoto 2013; Grether et al. 2017; Carroll and Janzen 1973; Lach et al. 2010). Carroll and Janzen (1973) defined aggression in ants as a tradeoff between (1) the risk of losing workers and energy and (2) the gain of new resources. Therefore, when and where aggressive behaviors are exhibited is indicative of various life history traits of the colony (Carroll and Janzen 1973).

Aggression can be directed toward intra- and interspecific interactions. In this review, we will examine both. Here, we focus on aggression displayed by workers, however, there is extensive literature on queen aggression (Rissing and Pollock 1987; Medeiros et al. 1992; Bourke et al. 1994). Less is known about male aggression, but it has been explored in *Cardiocondyla* (Kinomura and Yamauchi 1987; Yamauchi 2005; Heinze et al. 2005).

In this review, we aim to provide a framework for contextualizing the variation in aggressive behaviors and responses focusing on the worker caste across ant lineages, suggest a new scale for quantifying aggressive behavioral responses, and finally test for correlation between aggression and various other traits across ant lineages while controlling for phylogeny.

Part I: Framework for contextualizing behavioral variation

Under what conditions aggressive behavior is exhibited across ant lineages varies tremendously. Here, we propose a framework for understanding the levels at which variation can be introduced in an encounter. In order for a behavior to be initiated, there must be something to react to. In the study of behavior, this is called a stimulus. Once a stimulus is presented to an organism, then it must be perceived. When something is perceived, then the organism must evaluate the risk or reward of engaging in a potential interaction with the stimulus. Finally, the organism acts according to the previous step. At each of these steps, there is potential for variation to be introduced. This entire pathway is outlined in Fig. 2.

Stimuli

A stimulus is something that is presented to an organism that may cause a behavioral response. There are various stimuli that ants must react to within their environment to be successful. Stimuli could be prey, predators, competitors, mutualists, a neutral organism, or environmental.

Perception

How different ant lineages perceive threats is heavily dependent on their investment in different sensory structures. Some ants may have high visual investment and acuity,
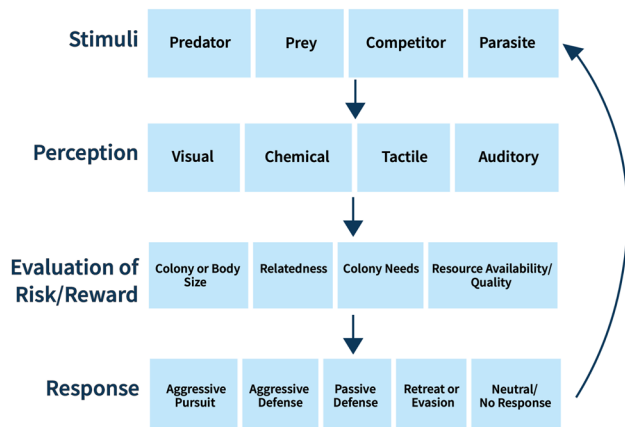
Fig. 2 Framework for understanding ant behavioral interactions

whereas some worker ants are completely blind. Ants often use chemical communication in the form of pheromones. For example, some ants have alarm pheromones whereas others use other ways to communicate to the colony that a threat is present. It has also been shown that ants also use tactile and auditory cues, although these are not as heavily used. Nevertheless, at this level of our framework, we still observe a high amount of variation as to how the ants are sensing the stimulus.

Evaluation of risk and reward

Aggression can be energetically costly (Huber and Kravitz 2010). Game theory states that in resource-centered conflicts, the reward of an interaction has to outweigh the potential costs (Smith 1974; Smith 1982). Having the ability to evaluate the threat and alter a behavior accordingly can be vital to the success of an ant colony. Some colonies may be able to take greater risks than others; for example, Batchelor and Briffa (2011) in their study of red wood ant (*Formica rufa*) aggression discuss the fact that colonies have a resource holding potential (RHP) (Batchelor and Briffa 2011). RHP indicates the fighting ability of a colony or individual based on experience, resource value, and motivational state (Batchelor and Briffa 2011). RHP can indicate which colonies are more likely to enter a fight based on the ability of the colony. Furthermore, due to the cost of aggression, colonies that are in better condition (larger size, high energetic levels, weaponry, experience, etc.) should be able to afford to engage in more aggressive interactions (Arnott and Elwood 2008; Vieira and Peixoto 2013; Grether et al. 2017). A social insect colony has numerous potential resources for predators and parasites and, therefore, they must be able to defend themselves. When attacked, colonies have the option to defend their colony or retreat, by moving deeper into their nest or to another location, in order to survive

the interaction (Haight 2006; Edmunds 1974; Judd 1998; London and Jeanne 2003). There are many factors that may affect which of these actions a colony may take, such as ability to recruit fighters, to relocate quickly, or to retreat into the nest to avoid the enemy. For some colonies, one or more of these options may not be viable. Some species also exhibit "ritualized" contests where colonies can show strength and size. These displays are often used to avoid costly aggressive interactions or fights. Examples of this behavior can be found in *Tetramorium immigrans*, *Myrmecosystus mimicus*, and *Iridomyrmex purpureus* (Ettershank and Ettershank 1982; Lumsden and Hölldobler 1983; van Wilgenburg et al. 2005; Hoover et al. 2016; Sano et al. 2018).

Response

The ultimate response of the individual or colony can vary and is highly dependent on the previous steps of our framework. An aggressive pursuit may result when a predator encounters a prey organism. Aggressive defense is when a colony or individual uses aggressive behaviors in order to defend a nest or territory. Passive defense is when the nest is defended without the use of aggressive behaviors, such as a *Cephalotes* or *Colobopsis* majors blocking a nest entrance with its phragmotic head. A retreat or evasion of threat may happen when an individual or colony can effectively avoid an altercation altogether, with perhaps the aid of a hidden nest entrance or quickly running away from a threat.

Some species go beyond the defense of their own nest and maintain an area around the nest to which they defend. Ants establish these territories by means of aggression, signaling, and avoidance (Adams 2016; Hölldobler 1979). Aggression in this context refers to massive fights that occur at boundaries to create partitioned space. The intensity of these fights can vary, ranging from massive battles to the death to slight tussles that only result in a few casualties (Adams 2016; Ettershank and Ettershank 1982; van Wilgenburg et al. 2006; Rockwood 1973; Brown 1959; Thomas et al. 2007; Plowes et al. 2014). This variation is a result of a number of factors. Mabelis (1978) describes the seasonality of territorial wars among *Formica polyctena* colonies and how it is driven by food availability. These battles occur when other protein sources are scarce and the casualties from the battle are consumed by the enemy colony (Mabelis 1978). When other food sources become more bountiful, the colonies are far less aggressive toward each other (Mabelis 1978). Therefore, territoriality stems from both nest defense and resource acquisition (Mabelis 1978). Furthermore, some arboreal tropical species, like *Oecophylla longinoda*, *O. smaragdina*, *Azteca trigona*, and *Dinomyrmex gigas*, have guards that constantly patrol the edges of their colonies' territory in a threatening state (Hölldobler 1979; Adams 1990; Adams 1994; Pfeiffer and Linsenmair 2001).

There are two major hypotheses that contextualize intra-specific aggressive responses for social taxa: the Nasty Neighbor and the Dear Enemy hypotheses. It is thought that the Nasty Neighbor Effect may be more prevalent in social insects than the Dear Enemy Effect, but there remains variation in results from many studies (Sanada-Morimura et al. 2003). The Nasty Neighbor hypothesis states that a species will show more aggression toward colonies that they are always in contact with and less aggressive to stranger colonies (Fisher 1954). This hypothesis is supported by studies in *Pristomyrmex pungens, Pogonomyrmex barbatus,* and *Oecophylla smaragdina* (Gordon 1989; Newey et al. 2010). Conversely, the Dear Enemy Hypothesis posits that less aggression would be shown to neighbor colonies than to stranger colonies (Temeles 1994). Lower aggression toward familiar neighbors is seen in *Acromyrmex lobicornis, Acromyrmex octospinosus, Leptothorax nylanderi, Pheidole tucsonica* and *Pheidole gilvescens* (Jutsum et al. 1979; Heinze et al. 1996; Langen et al. 2000; Dimarco et al. 2010).

Species that are behaviorally dominant, using chemical defense or caste-specific defensive roles, affect the access of resources for other species that are less dominant and/or aggressive (Stuble et al. 2017). Ants must be competitive for resources in order to sustain their social lifestyles. Studies of interspecific dominance rely on context, meaning their dominance score is dependent on what other species are present (Warren et al. 2020; Andersen and Patel 1994; Gibb and Hochuli 2003; Gibb and Hochuli 2004). When resources are in short supply, competition becomes stronger, and animals seeking these limited resources often harm one another in the process (Lang and Benbow 2013). Furthermore, some ants have certain defensive traits, such as a sting, while others do not. Therefore, a stinging response to a threat is not possible in every ant lineage. There is also a tradeoff among defensive traits across ant lineages (Blanchard and Moreau 2017).

Part II: Quantification of aggressive behaviors

There are a plethora of studies from numerous research groups that attempt to translate aggressive behavior into a numerical value for scientific purposes. Here, we address the advantages and shortcomings of using various techniques to quantify ant aggression.

Identifying aggression

In order to quantify a suite of behaviors, you must first identify them. The behaviors that are commonly recognized as aggressive within ants are biting, mandibular opening, gaster flexing, increased antennation (sometimes), lunging/charging, grabbing/pulling, and/or stinging or using chemical defense (Lach et al. 2010; Newey

et al. 2010; Holway et al. 1998; Suarez et al. 1999; Giraud et al. 2002; Roulston et al. 2003; Bengston and Dornhaus 2014; Guerrieri et al. 2009). Some of these behaviors are overtly aggressive, like biting or stinging/using chemical defenses. On the other hand, some of the other behaviors must be examined within the context of the behavior, such as increased antennation or mandibular opening. If we stick to the definition of aggression that was presented in the introduction, we should not categorize all of these behaviors as aggressive. In most studies, more than one of these behaviors is used to identify aggression within individuals. In some cases, only one behavior is examined.

Previous scales

Most studies that quantify aggression follow a scale from not aggressive to fighting until injury or death. See Online Resource 3 for all studies included. The scales vary but many follow the general outline established by Holway et al. (1998), Suarez et al. (1999), Giraud et al. (2002), Tsutsui et al. (2003), and Roulston et al. (2003). In these scales, the lowest number on the scale (a score of 0 or 1) indicates no aggressive interaction and the highest (a score of 4 or 5) indicates prolonged aggression or fighting. These scales label behaviors such as biting, lunging, use of sting/chemical defense as aggressive and behaviors such as avoidance and ignoring as not aggressive. Bengston and Dornhaus (2014) proposed a different type of scale which has negative values for behavior that is not aggressive, 0 representing neutral behavior, and positive numbers indicating aggressive interactions (Bengston and Dornhaus 2014). Furthermore, several studies have used a similar scale and have also taken into account the duration of aggressive behaviors and the total interaction time, creating an aggression index (Newey et al. 2010; Guerrieri et al. 2009). This can be very informative as intuitively there would be a lot of variability among colonies, species, or even heavily dependent on context like the state of the colony and the degree of the threat being presented to a colony. The scale approach to quantifying aggressive behaviors has both strengths and weaknesses. Firstly, the scale is a very versatile tool. It can be used across many different ant groups and contexts with little to no alterations. It can be simplified or made more complex by incorporating the frequency of behaviors, duration of behaviors, and number of individuals interacting by utilizing relatively simple equations. Conversely, the scale approach is dependent on ordinating behaviors. Another weakness is that a scale requires that a research group apply a number to a behavior or set of behaviors. This suggests that a transition from a behavior scored as a 1 to 2 is equated to the transition from 2 to 3. This fails to account for any nuances that may occur between integers or stages.

New aggression scale

We recognize the shortcomings of using scales to quantify aggressive behaviors, but also acknowledge that they are currently the best tool we have that could allow for comparative studies across ant lineages. Here, we suggest a new scale that can be applied to all clades of ants and therefore could allow for large-scale comparisons in the future (Table 1). This scale is based on scales from (Suarez et al. 1999) and (Bengston and Dornhaus 2014). Avoidance and escape are counted as a negative value as they are behaviors that are distinctly not aggressive and are actually removing the individual from the interaction altogether. Antennation and olfactory inspection are counted as zero as they are sensory behaviors and thus are neutral, this behavior would occur in the presence of a "friend" or "enemy". Numbers 1–4 of the scale are typical behaviors exhibited by ants when engaging in aggressive interactions. The behaviors are always exhibited in the order they are shown in the scale in all 106 studies examined for this review (see Online Resource 3). The novelty of the proposed scale is that it is general and can be applied to all groups of ants. Therefore, the scale can be useful for comparative analyses in the future. Furthermore, reporting the exact behaviors exhibited in behavioral studies within supplemental materials will continue to make aggression studies more repeatable.

Part III: Traits correlated with aggression

For the purpose of this review, species were determined aggressive or not by reviewing the literature. For each species included, we located published behavioral tests, behavioral observations, natural history notes, nestmate recognition studies, or dominance tests that indicated whether or not the species tends to be aggressive or evasive and timid toward non-nestmates (other ants, other invertebrates, or vertebrates). Naturally, the behavioral data can be variable and only species that had clear indications that they are aggressive or evasive and timid were included. For full references of behavioral data, see Online Resource 1.

**Table 1** Scale for quantifying ant aggression

Aggression scale	
− 1	Avoidance or escape
0	Antennation; olfactory inspection
1	Mandible gaping and/or gaster flexing; threat posture
2	Lunging or pursuit or chasing
3	Biting and/or pulling
4	Use of chemical defense or sting

Based on levels of variation in on our framework of aggressive behavior (Fig. 2), we included the following traits and discussed how they may impact how aggressively a colony may respond to a threat: worker polymorphism, body size, eye length, polygyny, presence of sting, presence of chemical defense, predatory diet, mandible length, scape length, latitudinal range and participation of mutualisms. Then, we use phylogenetic comparative methods to evaluate the correlation between these traits and aggression within our data set while controlling for phylogeny. Detailed methods and results can be found in Online Resource 4. In short, we used the phylogeny of Nelsen et al. (2018) and scored 171 species as aggressive or non-aggressive from the evaluation of over 200 published works (Fig. 3; Online Resource 1 and 4). We used both Pagel's Model of Correlated Evolution for binary traits as well as the Threshold Model, which can be used for binary and continuous traits, to investigate potential correlations (Pagel 1994; Felsenstein 2012; Revell 2014).

We found that worker polymorphism is correlated with aggressive behavior ($p = 0.009$; Online Resource 2). Within eusocial colonies, some individuals serve in caste-specific active defense roles and are present in *Camponotus*, *Pheidole*, and *Atta*, among other genera (Detrain and Pasteels 1992; Salzemann and Jaffe 1991; Wilson and Hölldobler 1985). Defense or fighting is normally only conducted by a small percentage of the colony. In species with larger workers or majors, they are overrepresented at the site of conflict (Adams 1994; Pfeiffer and Linsenmair 2001; Hölldobler 1981; Hölldobler 1983). This is due to the fact that majors and larger workers are often more aggressive, more efficient fighters, less likely to withdraw from a fight, and more likely to win a fight (Batchelor and Briffa 2011; Nowbahari et al. 1999; Tanner 2008; Fluker and Beardsley 1970; Kamhi 2015; Larsen et al. 2014). Therefore, the presence of a major or soldier caste may be correlated with aggressive nest defense. Furthermore, it must be noted that the major worker's role in a colony is not solely defensive, so, therefore, these results do not indicate that major is always the most aggressive caste in a colony, but rather there is a correlation between a species having majors and being noted as aggressive within the literature.

We also find that body size is correlated with aggression ($r = 0.338$; Online Resource 2). To our knowledge, the relationship between body size and aggression has only been explored in one ant species *Cataglyphis niger* (Nowbahari et al. 1999). In non-social invertebrates, body size is directly related to individual aggression, therefore, a similar trend could be occurring in social insects but at the colony level instead (Huber and Kravitz 2010). The size of an individual or their opponent is also important in head to head agonistic interactions. For example, within *Cataglyphis niger*, individuals that are larger are more likely to engage in fighting than

Fig. 3 Phylogeny of the ants included in our analysis. Phylogeny from Nelsen et al. (2018). Again for these analyses 171 species were coded for being aggressive or non-aggressive from a survey of the published literature. Results presented are a summary of 1000 stochastic character maps of aggression across ant lineages. Blue indicates the apparent absence of aggression, while red displays that aggressive behavior has been seen within the species
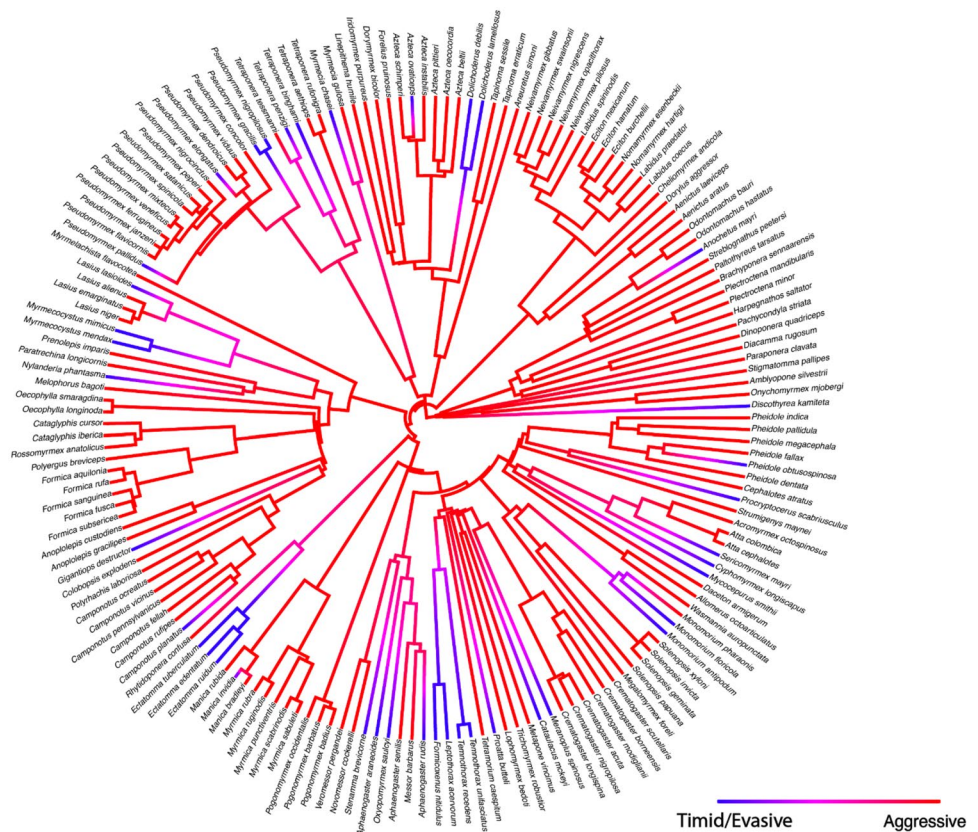
those that are smaller (Nowbahari et al. 1999). However, the size of an ant could be extremely important to its physical capabilities and ability to avoid conflict. The relationship between body size and behavior has been well studied for many types of organisms and behaviors (Dial et al. 2008). With such a large range in body sizes across ants, this presents a unique opportunity to explore how this variation could be interacting with behavioral outputs.

We find that there is a negative correlation between eye length and aggression ($r = -0.4035$; Online Resource 2). In ants, morphological traits strongly associated with sensory capabilities such as eye length and scape length have been shown to be correlated with environmental pressures (Weiser and Kaspari 2006; Gibb et al. 2015; Gibb and Parr 2013; Guilherme et al. 2019; Jelley and Barden 2021; Sosiak and Barden 2021). We find that ants with relatively smaller eyes are correlated with aggression. One group that may be driving this correlation could be the army ants which are all recognizably aggressive toward non-nestmates while having extremely reduced or absent eyes in the worker caste (Kronauer 2020).

We found that there was no correlation between aggression and polygyny ($p = 0.715$), presence of sting ($p = 0.814$), presence of chemical defense ($p = 0.360$), and predatory diet ($p = 0.143$), mandible length ($r = 0.321$), scape length ($r = 0.418$), and latitudinal range ($r = 0.052$) with the

included taxa, and marginal correlation between mutualisms and aggression ($p = 0.078$) (Online Resource 2). It has been proposed that polygyny could increase aggression toward a broader range of species, due to the fact that when a colony has multiple queens or is polydomous, the colony gives up discriminatory power and must maintain a higher level of aggression to all organisms it encounters (Hölldobler and Wilson 1990). However, we find no correlation which may suggest that no matter dispersed a colony is, recognizing non-nestmates may be important for all ant species. The possession of a sting or chemical defense at first is thought to be a hallmark of ant aggressive defense, however, sting or chemical defense has been lost multiple times across ant lineages (Kugler 1979). This may be due to the fact that use of a functional sting negatively correlates with a suite of other defensive traits including spines, large eye size, and large colony size (Blanchard and Moreau 2017). Although having a sting is very important for individual level defense, there may be other traits that might be more useful in terms of defending at the colony level. The presence of a sting may also be more important for defense against vertebrates or for subduing prey, than for fighting other ant colonies (Kugler 1979; Robinson et al. 2023). Predatory ants may be observed being aggressive more than other ants, due to their need to exhibit aggressive behaviors to obtain prey. Army ants are a notorious group of aggressive ants and are

highly predatory (Kronauer 2020). Mandible length can be indicative of biting ability, with biting being a key behavior exhibited during aggression (Püffel et al. 2021). On the other hand, specialized mandibles in ants also tend to be longer and may indicate prey type rather than fighting capabilities. There are several groups of organisms that symbiotically interact with ants due to their ability to defend resources and/or deterrence of herbivores. These interactions have resulted in tightly fit mutualisms between ants and other organisms. The two major and well-studied types of mutualisms with ants are those that they form with plants and with sap sucking insects (Banks 1962; Way 1963; Shingleton et al. 2005). The ant-acacia mutualism is the most well-known of the ant-plant mutualisms, with several studies conducted in Central and South America focusing on *Pseudomyrmex* species and their varying degrees of aggressiveness (Janzen 1966; Janzen 1967; Janzen 1975; Beattie 1985; Ward 1991; Davidson and McKey 1993; Ward and Downie 2005; Rubin and Moreau 2016).

There are several traits that could not be tested in a phylogenetic context due to insufficient data that we believe could be related to variation in aggressive behavior in ants. These include colony size, diet, foraging, resource availability, environmental factors, and colony parasitism. Colony size is often associated with elevated levels of aggression, as larger colonies normally have a greater workforce that allows individuals to specialize in defense, there are a greater number of disposable individuals, or increases chances of winning an aggressive contest (Batchelor and Briffa 2011; Amador-Vargas et al. 2015; Porter and Jorgensen 1981). Carbohydrates are the main fuel of ant worker behaviors, including those mediating aggressiveness (Grover et al. 2007; Barbieri et al. 2013; Rudolph and Palmer 2013; McGlynn and Parra 2016; Wittman et al. 2018). Therefore, access to certain food resources may affect energetic ability for certain behaviors. Foraging and aggression may be linked neurologically (Howe et al. 2016). Foraging style may impact the likelihood of engaging in aggressive interactions, and some foraging styles rely heavily on the foragers ability to defend food sources when discovered (Cerdá et al. 2013; Vepsäläinen 1982; Morrison 1996; Cerdá et al. 1997). Aggressive defensive behavior also reflects environmental factors such as climate, resource distribution, risk of infection, or desiccation risk (Gordon 2019; Segev et al. 2017). In *Temnothorax rugatulus,* there are latitudinal differences in risk taking and spatial distribution of nests (Bengston and Dornhaus 2014). Animals are more aggressive when resources, like nests, are defensible (Sundström et al. 2004). There are some nest structures or locations that may be more defensible than others. Arboreal territories may be easier to defend than other types of nests (Adams 2016; Jackson 1984; Blüthgen et al. 2004). On the other hand, if an ant colony is well hidden or the nest is structurally sound, the colony may be able to retreat into the nest to easily avoid predators and the use of aggressive behaviors is not necessary (Haight 2006). There may also be an increase of aggression in colonies that have a higher instance of dulotic or kidnapper ant species that target them (Jongepier and Foitzik 2016). Frequent exposure to enemies in a laboratory setting can make *Pristomyrmex pungens* and *Oecophylla smaragdina* colonies more aggressive (Ruiz-Guajardo et al. 2017; Blüthgen et al. 2004).

Concluding remarks

Highly contextualized and variable aggressive behavior across ant lineages is undoubtedly important to the success of the group. Our framework provides context for the introduction of variation at each level of an aggressive interaction that is applicable to all ants. Using a scale that is created to fit all ant taxa will allow for more large-scale studies of the variation of aggressive behavior in ants. Also using a scale that incorporates non-aggressive and aggressive behaviors can provide nuance to quantifying aggressive interactions in many contexts. Finally, we show that worker polymorphism, body size, and relative eye length is correlated with aggression across ant lineages. There is also marginal support for mandible length, worker polymorphism, and having mutualist partners for being linked to aggression in ants. This shows potential for further investigation of the correlations between behavioral and functional traits, perhaps more centered on key radiations of ants.

Ants occupy almost all terrestrial ecosystems across the globe. In these environments, ants are interacting with other organisms in a multitude of impactful ways (predation, competition, prey, modifying the environment, engaging in mutualisms, etc.). Furthermore, behavior is dynamic and variable. Understanding the nuances of ant aggressive behavior can help parse apart how ants have risen to become so dominant and integral in biological communities across the globe. Future research that focuses on behavioral differences within key clades of ants while also accounting for phylogenetic relationships, morphological attributes, and ecological interactions is a logical next step for working to combine the fields of ant behavior, systematics, and ecology. Furthermore, future work could also focus on comparative queen and male aggression. Not only is this impactful for the myrmecological research community, but also for social insect researchers and beyond.

Declarations

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