

**EVOLUTIONARY AND ECOLOGICAL PRESSURES SHAPING SOCIAL WASPS
COLLECTIVE DEFENSES**

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ABSTRACT

Social insects are well-known for their aggressive (stinging) responses to a nest disturbance. Still, colonies are attacked due to the high-protein brood cached in their nests. Social wasps have evolved a variety of defense mechanisms to exclude predators, including nest construction and coordinated stinging response. Which predatory pressures have shaped the defensive strategies displayed by social wasps to protect their colonies? We reviewed the literature and explored social media to compare direct and indirect (claims and inferences) evidence of predators attacking individuals and colonies of wasps. Individual foraging wasps are predominantly preyed upon by birds and other arthropods, whereas predators on wasp brood vary across subfamilies of Vespidae. Polistinae wasps are predominantly preyed upon by ants and Passeriformes birds, whereas Vespinae are predominantly preyed upon by badgers, bears, and hawks. Ants and hornets are the primary predators of Stenogastrinae colonies. The probability of predation by these five main orders of predators varies across continents. However, biogeographical variation in prey-predator trends was best predicted by climate (temperate vs. tropical). In social wasps' evolutionary history, when colonies were small, predation pressure likely came from small mammals, lizards, or birds. As colonies evolved larger size and larger rewards for predators, the increased predation pressure likely selected for more effective defensive responses. Today, primary predators of large wasp colonies seem to be highly adapted to resist or avoid aggressive nest defense, such as large birds and mammals (which were not yet present when eusociality evolved in wasps), and ants.

KEYWORDS: Aggression behaviour; Nest defense; Individual and colony predation; Raid; Polistinae; Stenogastrinae; Vespinae

INTRODUCTION

Social insects are perhaps best known for the fierce collective defense of their nests and the ability to deliver painful stings (e.g., *Pseudomyrmex* species in ant acacias; Schmidt, 2016; Sumner, Law and Cini, 2018). Wasps in particular have a special reputation for stinging; indeed, for millennia, human cultures throughout the world have taught their children to recognize the local wasp phenotype (for example, the aposematic yellow and black stripes of Vespinae in temperate regions) and to fear and avoid social wasps (Sumner et al., 2018; Lester, 2018; Jones, 2019). Despite widespread public recognition of the defensive talents of social wasps, we know remarkably little about the ecological and evolutionary forces driving the evolution of their defensive behaviors. The defensive behaviors of any organism evolve in response to selective pressures exerted by their predators; yet, little is known about the predators of social wasps (Fig. 1a). Although anecdotal reports are present in the literature, direct evidence of wasp predation is surprisingly scarce. To understand the (co)evolution of defensive behaviors in social wasps we require a holistic understanding of who these predators are and to what extent these predator-prey relationships can be explained by ecological and/or evolutionary traits.

The defense apparatus of social wasps

The sting apparatus of the Aculeata (ants, bees, and wasps) is an anatomical and physiological derivative of the ovipositor in female Hymenoptera, able to penetrate the skin of vertebrate predators and inject pain-inducing venom (Shing and Erickson, 1982). In the Hymenoptera, the apparatus is theorized to have initially evolved in solitary wasps in the role of paralyzing prey, a behavior observable in extant solitary wasps (Schmidt, 2004). However, in addition to using the sting apparatus during foraging, non-social hunting wasps (e.g., Pompilidae and Mutilidae) may sting vertebrate predators in self-defense, injecting highly painful venomous cocktails (Schmidt, 2016). This defense mechanism helps to explain why non-social wasps seems to have very few natural predators (Schmidt and Blum, 1977; Schmidt, 2004).

In social Hymenoptera, stinging and biting are often used to deter potential enemies. When a colony perceives a threat, non-reproductive adult females engage and sting and/or bite potential predators, often cooperatively (Starr, 1985; Nouvian et al., 2016). The venom injected via stinging often can translate into intense pain. Vertebrate predators associating social insect individuals or colonies with negative experiences may learn to avoid them (Schmidt, 2016). This associative learning can be further reinforced by the aposematic coloration of many social bees and wasps (Vidal-Cordero et al., 2012).

Several lines of evidence support the effectiveness of the stinging response as an anti-predator strategy. In fact, the defensive stinging behavior is widespread amongst Hymenoptera families (e.g. Formicidae, Kugler, 1979; Apidae, Nouvian et al., 2016; and Vespidae, Starr, 1985). Also male hymenopterans (lacking the sting apparatus) may mimic the stinging abdomen movements of females

when caught by a predator (Schmidt, 2016; Giannotti, 2004). Similar behavior is displayed by many non-stinging insects that are Batesian mimics of the aposematic coloration of bees and wasps (e.g. arctiid moths, Simmons and Weller, 2002; hoverflies, Rashed and Sherrat, 2007; Penney et al., 2014; robber flies, Brower et al., 1960).

Social wasps as prey

Eusocial wasp (referred to from here on simply as “social wasp”) colonies are by definition characterized by overlapping generations, a reproductive division of labor, and cooperative brood care (Wilson, 1971). At the peak of its cycle, a typical social wasp colony includes a nest (the architecture of which varies across taxa), one or a few reproductives (“queens”), non-reproductive workers, and developing brood (Spradbery, 1973). The brood is defenseless, and immature wasps are essentially parcels of lipid and protein, a bounty for a skulking predator (Spradbery, 1973; Ying et al., 2010). Non-reproductive workers protect the brood through primary or secondary colony defenses. Primary defenses, usually related to the choice of nesting site or nest architecture, operate before a predator initiates any prey-catching behavior (Edmunds, 1974), and decrease the chance that an encounter will take place between the colony and a potential predator. Secondary defenses, such as active behavioral responses, come into play after the potential predator has encountered a nest (see below).

Generally, predators that attack social wasp nests fall into two major groups: arthropods and vertebrates. Due to their size differences and different means of finding and attacking wasps, the two pose different kinds of threats. Because social wasps have evolved virtually non-overlapping means of defense against these predator categories, we will often distinguish arthropod versus vertebrate predation when discussing social wasp defense strategies below.

Primary defense: before predators arrive

Nesting out of reach. Ants are cursorial hunters that reach their prey on foot. There is probably no natural substrate, especially in the tropics, that is entirely free of scouting-and-recruiting ants, but some sites experience lower levels of predation pressure than others. Wasps that form relatively small colonies and build small nests – many *Polistes*, *Mischocyttarus*, *Leipomeles*, and others – on the undersides of leaf blades likely experience lower exposure to patrolling ants than do those that nest on trunks and branches (Jeanne, 1979). The mass-foraging army ants (*Eciton* spp.) are extreme examples of ant predation in the tropics, as they cover the ground and climb vegetation in a moving mass, plundering whatever cannot escape (Chadab, 1979a). However, because *Eciton* raid from the ground-up, it is possible that wasps that nest high enough in the canopy enjoy the benefit of a dilution effect. Additionally, trees and shrubs growing in water are likely completely immune from attack. The small trees, shrubs, and dead snags standing in a meter or more of water along the shores of Gatun Lake in Panama are favored nesting sites of *Polistes canadensis* (Rau, 1933). Similarly, seasonally flooded habitats in the Amazon basin are probably largely *Eciton*-free (RLJ and SO, pers.

obs.). *Dolichovespula maculata* and *Polistes* spp. nests are particularly common in tree branches overhanging rivers in the southeastern United States (KJL, pers obs). Such sites could plausibly shield nests from mammalian predators as well, and though this has not been demonstrated, these hypotheses are eminently testable in environments where social wasp colonies face well-known predation pressures, as we later discuss.

Some paper wasp species frequently nest in dense vegetation and on plants sporting spines or thorns, which can be inaccessible to birds and mammals (Richards, 1978). Nesting on vertical and/or relatively flat surfaces, such as tree trunks, walls and eaves of buildings, is typical for some Neotropical Epiponini genera (*Metapolybia*, *Synoeca*, *Clypearia*, and *Nectarinella*) and sometimes observed in other genera (some species of *Polybia*, *Chartergellus*, and *Parachartergus*, as well as many independent founding Polistini; Jeanne, 1975; Richards, 1978; Edwards, 1980). These sites likely reduce access to nests by climbing and flying vertebrate predators.

Among the vespine wasps there are aerial and cavity/ground-nesting species. Some species of *Vespa* and *Vespula* use abandoned rodent holes or cavities in man-made structures or trees to initiate their nests in early spring (Matsuura and Yamane, 1990; Akre et al., 1980; Edwards, 1980). As the nests grow, workers gradually expand the cavities by excavating the surrounding dirt, insulation, or decayed wood (Fig 1b). The only visual evidence of these nests is the traffic of foragers entering and exiting the nest, providing some camouflage against enemies, such as humans, that rely heavily on visual cues. Other vespine species build aerial nests. These can be as high as 40 meters from the ground and thus inaccessible to most non-flying predators (Feás and Charles 2019).

Nesting in association with other species. *Dolichoderus* and *Azteca* ants, especially *Az. chartifex* and allies, form huge colonies that can densely occupy entire trees and defend them and their surroundings against other ants, including *Eciton* (Delabie, 1990; Somavilla et al., 2013). Some Neotropical paper wasps build nests regularly, and in some cases obligately, in close association with these ants. The most intimate associations involve some Epiponini wasps. Some species of *Agelaia* build their nests in cavities inside the large, arboreal carton nest of *Az. chartifex* (Richards, 1978). A somewhat less intimate but more common co-nester is *Polybia rejecta*, which constructs its nest within a few centimeters of the ants' nest, or even in contact with it (Servigne et al., 2020). Wasps respond behaviorally to ant foragers near their nests. A combination of physical ejection of ant workers, wing-buzzing behavior, and the elimination of their scent trails (see secondary defenses, below) maintains an ant-free zone around the wasps' nest entrance (Servigne et al., 2020) and helps to offset opportunistic attacks by associated ant colonies. In drier habitats, where *Az. chartifex* is absent but *Eciton* occurs, wasps may nest in association with other ants. For example, in Quintana Roo, Mexico, and Guanacaste, Costa Rica, Epiponini wasps nest in myrmecophytic acacias occupied by *Pseudomyrmex* spp. (Joyce, 1993; Dejean et al., 1998; Espelie and Hermann, 1988). Numerous species of myrmecophyte have evolved intimate relationships with other species of ants, many of

which can keep *Eciton* from their host plant. Several species of wasps in the genera *Angiopolybia*, *Pseudopolybia*, and *Mischocyttarus* nest on these plants, thereby gaining protection from army-ant predation (Herre et al., 1986).

Nesting in trees defended by *Azteca* ants, described above, may afford social wasps some protection against vertebrates as well as army ants. Some species of host ants sting vertebrates that contact their host trees (e.g., *Pseudomyrmex* species in ant acacias; Young, et al., 1990). The relationship is mutualistic: in a study in French Guiana, none of 42 *Az. chartifex* nests with one or more *Polybia rejecta* colonies in close association were attacked by birds, whereas nine of the 88 wasp-free nests of the ant were attacked by woodcreepers (Dendrocolaptinae) and by a woodpecker (*Celeus flavus*; Le Guen et al., 2015). *Polybia rejecta* is especially aggressive and at least partially effective at defending against these and other vertebrate predators. By building its nest as close to the *Azteca* nest, and often in contact with it, the wasps provide protection for the ants against these birds and possibly anteaters. Several species of independent-founding polistines also nest not just on trees with *Azteca* nests, but on myrmecophyte plants (those in close association with ant colonies) such as *Cordia* spp., *Tococa* spp., and others. These are probably commensal relationships, with the wasps gaining protection from *Eciton*, but contributing nothing to benefit the host ants (Jeanne, In press). Although nesting with ants is much rarer in Africa and Asia than in the Neotropics, the wasp *Polybioides tabidus* has been reported to nest with the aggressively stinging ant *Tetramorium aculeatum* in Cameroon (Dejean and Fotso, 1995).

Some arboreal wasp nests are joined by passerine birds that nest nearby; birds use existing wasp nests as cues for nest-site selection and will build near artificial *Polybia rejecta* nests (Joyce, 1993). Avian nesting partners could offer protection to the wasps if the birds mob approaching vertebrate predators such as raptors and monkeys (Sandoval and Wilson, 2012).

Tolerance to human presence in some species of social wasp may play a role on determining which predators target their colonies. For instance, some species of Polistini and Mischocyttarini wasps are synanthropic in the Neotropics, often nesting on man-made structures; on the other hand, most Epiponini wasps tend to rely more on natural structures such as vegetation, and their diversity tends to be relatively reduced in highly urbanized areas (Detoni et al., 2018). Thus, it is possible that the predators of synanthropic social wasps are somewhat limited to other animals that also tolerate human presence. On the other hand, nesting on buildings may result in nests that are more conspicuous to predators (e.g., young *Dolichovespula* colonies are much easier for humans to notice on buildings than in trees; KJL, pers obs). If this increases detection and later predation by predators such as birds, then the use of buildings as a nest site could be seen as an ecological trap.

Crypsis. Adaptive nest crypsis is a response to selective pressure imposed by visually hunting predators, almost always vertebrates. Paper wasp nests exhibit several putative adaptations that likely decrease their visual detection by predators by decreasing contrast from, or increasing their

resemblance to, the background. In some cases, wasps may nest on substrates where their nests visually match the background. This effect can be enhanced by mosses and liverworts growing on the nest paper (Barbosa et al., 2016; Milani et al., 2020). Nest envelopes of the epiponine wasp *Leipomeles dorsata* constructed beneath leaf blades can closely resemble the leaf substrate, even mimicking the venation of the leaf (Richards, 1978). Overall shapes of nests can evolve to lessen recognition by vertebrates, such as the stick-like nests of some Mischocyttarini and Polistini species (Starr and Hook, 2006; Silveira et al., 2015; Vesey-Fitzgerald, 1950; Richards, 1978).

Nest crypsis may also be a strategy adopted by Vespinae. *Vespula* spp. may benefit from constructing their nests underground, but *Dolichovespula* produce large, aerial nests that often hang from trees (Akre et al., 1980). However, the nests can still be difficult to locate. The paper envelope can blend in with both the bark/stems of the tree it is built inside and may also be able to provide camouflage amidst vegetation or other background if hanging from trees (Feás and Charles, 2019; KJL pers. obs.).

Aposematism. An alternative strategy for both nests and groups of adult wasps is to be visually conspicuous. Well-defended nests are often placed relatively high in tree canopies, often along forest or river edges. Pale nest paper contrasts with surrounding vegetation. *Polybia striata*, *P. scutellaris*, *Chartergus* spp., and *Epipona niger* exemplify this pattern (Richards, 1978; Jeanne, 1975). For groups of individuals, the sunflower-like radial array of pale-colored adults of *Apoica pallens* resting on the underside of their open nest elicits a startle response, at least in humans, when first spotted from below (RJL pers. obs.).

Chemical repellents. Independent-founding Polistinae (Polistini, Mischocyttarini, and Ropalidiini) and foundress queens of young colonies of Vespinae apply an ant-repelling glandular product to the nest petiole. The ant-repellent secretions are produced by specialized exocrine glands on the terminal sternite of the gaster (van der Vecht's gland; Jeanne, 1970a; Keeping, 1990; Kojima, 1992; Post and Jeanne, 1981; Martin, 2017). This gland is often secondarily lost during the evolution of the Epiponini lineages that employ non-repellent means of ant defense (see secondary defenses, below; Smith, O'Donnell and Jeanne, 2001; London and Jeanne, 2000). Similarly to the independent-founding Polistini, in the Vespini, at least one species (*Vespa velutina*) has been shown to utilize ant repellents on its nest during the foundation stage of the colony cycle (Martin, 2017).

Sticky traps. Members of the genera *Nectarinella* and *Leipomeles* (Epiponini) erect sticky-tipped stalks around the access to their nests (Mateus and Noll, 1997; Schremmer, 1977; Jeanne, 1975). This appears to be an effective defense against scouting-and-recruiting ants for wasp species with small colonies and with body sizes in the range of these predators, for whom active defense is less reliable.

Hardened nests. The exceptionally tough carton envelope of some arboreal-nesting swarm-founding species may be impenetrable to arthropod raiders, including chewing ants. In some species (e.g., *Chartergus artifex*) the inter-comb passageways within the nest are narrowed to the size of a brood cell (RLJ, pers. obs.), possibly an adaptation allowing a single wasp to effectively block access to brood-laden combs by ants that have entered the lower chambers.

The nature of the nest material can also have important effects on the capacity of the nest itself to withstand mechanical attacks by vertebrate enemies. The extremely dense and tough carton of *C. artifex*, for example, may be able to resist attacks by monkeys and birds (RLJ, pers. obs.). The transition from wood pulp (paper) to mud as a nesting material has occurred twice in the genus *Polybia*; in both mud-nesting lineages, nests are highly robust to mechanical damage, and may at least narrow the range of species that can penetrate them. *P. emaciata* workers often retreat into the nest upon mechanical disturbance, apparently relying on the nest as a fortress-like defense (O'Donnell and Jeanne, 2002). Similarly, the hard mud nests of some Stenogastrines (e.g. *Liostenogaster flavolineata*) may afford them greater survival than the paper nests of their close relatives (e.g. *Parischnogaster* spp; SS pers. obs).

Secondary defenses: behavioral responses to predator arrival

Physical predator removal: Due to the relevance of ants as threats to Neotropical colonies, wasps have developed anti-predator behaviors dedicated specifically to repel ant invaders from their nests. If a foraging ant makes its way onto a nest, a defending wasp may dart at it, grab it in the mandibles, and toss it from the nest or fly off with it and drop it (Chadab, 1979b). If ant foraging persists, swarm-founding wasps (Epiponini) recruit nestmates to encircle the access point and repel the intruders with semi-synchronous bursts of wing-buzzing. The mini-blasts of air are often effective in causing the ants to turn around and exit the nest (Chadab, 1979b; Jeanne, 1991). Following an ant invasion to their nest, wasps extensively mandibulate or lick the traversed surface, apparently expunging the ants' trail pheromone or scent (West-Eberhard, 1989). Whether the behavior removes the chemical or covers it up, possibly with the labial gland secretion used in nest construction, has not been determined. Although less well documented than the tropical examples, ground-nesting *Vespula* wasps defend their colonies from Argentine ants (*Linepithema humile*) and Red Imported Fire Ants (*Solenopsis invicta*) by darting at and biting ant foragers exploring the nest entrance (KJL, pers. obs.). How wasps repel the abundant subterranean foragers of these species, particularly early in colony development, is unknown.

Vibro-acoustic warnings: When facing bigger predators, namely vertebrates, adult epiponine wasps in at least three genera (*Synoeca*, *Chartergus*, *Polybia rejecta*, *P. sericea*) respond to vibrations of the nest or its substrate by rhythmically and synchronously striking or drumming against the nest

carton, thereby generating characteristic sounds that are audible to humans over distances of five meters or more (Evans and West-Eberhard, 1970; Taylor and Jandt, 2020; SO, pers. obs.). Grazing livestock seem to learn to avoid patches of grass and bushes around *P. sericea* colonies, possibly by associating their alarm sound to eventual stinging (F. Prezoto, pers. comm.). *Protonectarina sylveirae* makes a characteristic high-pitched sound when attacking (Richards, 1978). When their nest is disturbed, *Vespa mandarinia* workers closely approach the intruder in flight while loudly snapping their mandibles (Schmidt, 2016; RLJ, pers. obs.).

Visual displays: Several species of Polistinae in the genera *Agelaia*, *Apoica*, *Brachygastra*, *Epipona*, *Polistes*, *Polybia*, *Synoeca*, and as well as *Ropalidia revolutionalis* (Hook and Evans, 1982), engage in visual warning displays, such as gaster-flagging, when the nest is disturbed (O'Donnell et al., 1997; Figure 1c). In response to a disturbance, workers on the nest (or on the vertebrate intruder that caused the disturbance) raise and wave the gaster, extrude the sting, and fan the wings. In some species, the gaster is conspicuously colored, suggesting its use as a visual signal, either as a threat to predators or to communicate with nestmates. In disturbed *Polistes* spp. nests (in Malaysia), both workers and males display raised forelegs, providing a visual signal to the potential predator (Turillazzi, 2003).

Chemical responses: The existence of alarm pheromones has been demonstrated in many large-colony species across different subfamilies (Maschwitz, 1964; Veith et al., 1984; Kojima, 1994; Sledge et al., 1999; Jeanne, 1981; Cheng et al., 2017), as well as some small-colony species (Post et al., 1984; Bruschini et al., 2006). These compounds are released either at the nest or when workers sting their aggressor, and serve to recruit in-nest workers to engage in defensive behavior, as well as to attract defending workers to a specific target. Notably, experiments have failed to demonstrate venom-associated alarm pheromones in some small-colony wasps (London and Jeanne, 1996; Keeping, 1995), further suggesting that the selective pressures behind colony defense have been varied, and have produced a number of different strategies.

In what may be a specialized defense against small vertebrate predators, *Parachartergus colobopterus* and *P. fraternus* use chemicals in defense of the nest by spraying its venom in a fine mist that travels several centimeters (Jeanne and Keeping, 1995; Mateus, 2011). The nests are built on tree trunks and are visually cryptic, which may narrow the range of potential predators to small gleaning birds, for which an eyeful of the sticky venom may be a more effective deterrent than stinging (Jeanne and Keeping, 1995).

Hiding. Contrary to popular perception of wasps being aggressive every time they are disturbed (Sumner et al., 2018), some species exhibit remarkable timidity, either fleeing or hiding in response to disturbance, despite possessing a functional stinging apparatus (Hermann and Chao, 1984;

O'Donnell and Jeanne, 2002; Strassmann et al., 1990). Some species of *Mischocyttarus*, for example, and will often hide behind their nests or, if sufficiently disturbed, fly away – avoiding a direct confrontation of any kind (Hermann and Chao, 1984; RLJ and MD, pers. obs.). Even more drastic is the response of some Stenogastrinae wasps, which may simply “drop” from the nest when threatened (SS, pers. obs.). While this may confuse a potential predator, or redirect their attention away from the nest, it also leaves the brood completely undefended.

Absconding. When all defensive tactics fail to repel a predator, it can be in the colony's best interest for the adults to abandon the nest and their brood, thus saving themselves for the opportunity to re-nest elsewhere. In an intriguing overlap with responses to vertebrate attacks, Neotropical swarm-founder adults readily abandon their nests when threatened by army ants (mostly *Eciton* that raid above ground; in some cases, rapid absconding can be triggered by encounters with just a few *Eciton* workers, or by their odor alone; Chadab, 1979b). Observations suggest that rapid absconding may be coordinated via the wasps' alarm pheromone (Chadab, 1979b).

Repeated strikes on nests by avian predators such as Red-throated Caracaras (Class: Aves, Family: Falconidae) initially induce coordinated stinging attacks, but eventually the defenders shift to rapid departure of all adults (McCann et al., 2013). Following absconding events, surviving adults in swarm-founder colonies first cluster, then move to re-nest in a new location by following a pheromone trail (Sonnentag and Jeanne, 2009).

In contrast to most polistine wasps, temperate zone *Vespula* and *Dolichovespula* colonies almost never abscond in the face of persistent or catastrophic predator attacks. This is presumably because the short seasonality of their colonies limits them from obtaining fitness gains by rebuilding a new nest following the loss of the original. Similarly, in Neotropical genera such as *Agelaia*, the scarcity and quality nesting sites may select against absconding. While adults may leave the nest during ant raids, they return after the predators are gone, and try to rebuild the colony in the same site (O'Donnell and Jeanne, 1990). Exceptionally, *Vespa velutina* adults may abandon underground nests and brood when under attack by ant predators and try to re-establish their colonies elsewhere (XF, pers. obs.).

Stinging: The most notorious response to disturbance in a social wasp colony's arsenal is the painful and dangerous sting of large-bodied species such as *Vespa* and *Synoeca* (Xuan et al., 2010; de Castro e Silva et al., 2016), and the vigorous stinging attacks by tens to hundreds of workers in large-colony species like *Vespula* and *Agelaia*, in which potential predators can receive hundreds of stings (Vetter et al., 1999). Workers are initially alarmed by movement, vibration of the nest, or by volatiles in mammalian breath (Jandt et al., 2020; Landolt et al., 1998).

Despite being the most well acknowledged active collective response to disturbance in wasps, the sting is the weapon of last resort against vertebrates. Aggressiveness in response to threats varies

widely among species. The effectiveness of the sting as a defense against vertebrates is partly a function of the size of the colony and the size of the wasp. The sting of many wasp species is ineffective against a wide variety of vertebrate predators. Large numbers of epiponine colonies are taken with apparent impunity by monkeys and birds, and vespine nests are commonly attacked by large mammals and birds (see Results). Yet if the defenders are aggressive enough and numerous enough, they can be effective. A study in French Guiana found that nests of *Polybia rejecta*, remarkable for its aggressiveness when defending its nests, suffered no vertebrate attacks, whereas other less aggressive epiponines did (Le Guen et al., 2015).

If a nest is sufficiently provoked, collective or group stinging defense is coordinated, often by alarm pheromones comprised of volatiles released with venom. Similar to alarm pheromones, vibratory signals may be used to recruit wasps inside the nest to the outside in preparation for further action (Strassmann et al., 1990; Jeanne and Keeping, 1995; Taylor and Jandt, 2020). The intensity and duration of collective defense by some species suggests a strong selection pressure exerted by nest predators, though we have yet to understand the links between predation frequency and type and the interspecific variation in defensive behaviors exhibited by social wasps. Colonies within a species can also vary greatly in the magnitude of the collective defensive response, which can be, but is not always, associated with colony size and developmental stage (Brito et al., 2018; Jandt et al., 2020; London and Jeanne, 2003).

Who are the primary predators of social wasps?

Today, a complete spectrum of solitary to eusocial species is represented within the monophyletic lineage of Vespidae (Jandt and Toth, 2015; Figure 2), wherein eusociality evolved independently at least twice (Huang et al., 2019; Hines et al., 2007), making it one of the best systems for studying the co-evolution of predator-prey relationships and of coordinated colony defense. To understand why social wasps have evolved these primary and secondary methods of collective defense, we first need to ask: Who are the predators of social wasps? Various predators have been sparsely identified in the literature, including other social wasps (Jeanne and Hunt, 1992; Turillazzi, 1984; Gadagkar, 1991), ants (Jeanne, 1972; Bruch, 1923; Tindo et al., 2002), birds (Birkhead, 1974; McCann et al., 2010; van Bergen, 2019; Huang et al., 2004) and mammals (Ying et al., 2010; Bigelow, 1922; Perry and Manson, 2008). Do social wasps that use different primary and secondary defensive strategies receive the same predation pressure from each of these taxonomic groups; and/or is that predation pressure consistent across different regions where these wasps are biogeographically located? Moreover, by including novel data sources in our search, such as social media (Nyffeler and Vetter, 2018) we may find evidence of predator-prey relationships overlooked in the literature. Here, we review the published literature and compile records from social media on the predation on vespid wasp individuals and colonies to (1) identify the predators of social wasps; (2) explain any consistent patterns of variation in who the predators are with regards to biogeography, evolutionary and

ecological traits; and (3) relate the findings above to the evolutionary history of social wasps and their predators.

METHODS

Literature search

We searched ISI Web of Science, Scopus, Google Books, and Google Scholar databases for publications on the predation of specific wasp taxa by systematically combining the taxonomic group (e.g. “Wasp”, “Vespidae”, or “Polistinae”) with the terms “predator of”, “predation on” and “attack on” (e.g. [“Vespula”] AND [“predator of” OR “predation on” OR “attack on”]). The terms “predator” and “predation” alone were avoided due to social wasps being predators themselves, with most of the search results turning up literature focused on their ecological role as predators. Books, chapters, and reviews on social wasp biology were scanned for additional references of predation of social wasps. For each reference (from literature to other media searched), we noted: (i) the predator taxa, (ii) wasp prey, (iii) whether the predation event targeted an adult wasp or the colony, (iv) the geographic location of the observation, (v) the medium in which the reference was found, and (vi) which type of evidence did the reference constitute (defined in “Data analysis”). All reference searches (including other media below) were carried out between April and June of 2020.

Social media search

We used the social media platforms YouTube (youtube.com), Facebook (facebook.com), and Twitter (twitter.com) to collect additional evidence (accounts and videos) of predation events on wasp individuals and colonies. Non-naturally occurring predation events (e.g. artificial set-ups such as arenas) were excluded from our data.

YouTube: Using the YouTube video database, we initially combined the search terms “predator of”, “predation on” or “attack on” with the common names for social wasps (e.g., “hornets”, “hover wasps”, “paper wasps”, “social wasps”, “wasps”, and “yellowjackets”). We then conducted a focused search using the common names for specific predator taxa (based on data from the literature search) + predation terms + common name of social wasp (e.g. “badger attack on social wasps”). This facilitated the database’s search mechanism, while normalizing the amount of data obtained for predators which are reported less often or lack empirical evidence in the literature (Supp. Table S1). For each search, we scanned the first hundred results, though the most relevant were usually shown within the first 10-20 results. That means, even though we found abundant videos of other arthropods being preyed upon, we sometimes found videos of wasps as prey being mislabelled as bees or other insects, despite never including “bee” or the other descriptor as a search term.

Facebook and Twitter: We posted our request for evidence of wasps being preyed upon to two Facebook “groups”: “Enthusiasts of Social Wasps” ([URL 1]) and “Ecology of Vespinae” ([URL 2]) on 17 April, 2020 (Supp. Fig. S2a), and posted a general call on Twitter (tagging those authors with a Twitter account) on 16 May, 2020 (Supp. Fig. S2b). For both posts, we included an image of a *Vespula* queen on a pink *Grevillea* flower. This image allowed us to avoid biasing responses (e.g., an image of a bird eating a wasp might have drawn the attention from those with other examples of bird predation), while also increasing the exposure of the post, given that the image was clear and brightly colored.

Direct Email to Wasp Researchers: We contacted wasp researchers directly or via wasp-focused listservs (Supp. Fig. S3). All responses that included unpublished observations of individual or colony level predation were categorized as ‘unpublished accounts.’

Organization of evidence

Taxonomy of predators. Predation records were classified as direct or indirect evidence, as well as media type (literature, social media, video, or unpublished accounts). Direct evidence is represented by both “Empirical” studies (experiments or systematic observations where quantitative data were collected) and “Observations” (a description, image, or video of a direct observation of a predator attacking a wasp or colony) records. “Indirect Evidence” refers to predation claims, common lore, or instances where predation was inferred through evidence left behind following a predation event. Predators were categorized by Phylum, Class and Order, and compared across the four tribes of Polistinae, one tribe of Vespinae, and Stenogastrinae.

Social wasp subfamilies (and Polistinae tribes) were further categorized by colony size, nest architecture, colony cycle, and coordination of colony response. We discuss patterns in predation based on these colony characteristics.

Biogeography of predators. When location of direct evidence of colony predation was provided, records were grouped by continent. We included Central America as a separate ‘continent’ since the social wasp fauna in the area differs greatly from the rest of North America (Hunt, 2007); and used “Oceania” instead of “Australia” to allow the grouping of records made in western Pacific areas (combining Australia, New Zealand, and Guam). Each record was counted once for each area cited by an observer; for example, we counted D. Santoro’s personal observation on the predation of humans on *Vespula* in Japan and China as two distinct observations in Asia.

Evolution of predators. Using the results from the literature and social media searches, we mapped the evolutionary origins of vertebrate predators with the most records of predation attempts of social wasp colonies: three Classes (Aves, Mammalia and Reptilia), and the top two Orders in the

Classes Aves (Accipitriformes and Passeriformes) and Mammalia (Carnivora and Primates). Among invertebrate predators, we mapped the evolutionary origins of Hymenopteran Family Formicidae (ants) and Genus *Vespa* (hornets, Family Vespidae). Along this evolutionary map, we also plotted the evolutionary origins of Aculeata (stinging wasp, bee, and ant ancestor), Vespidae, the common ancestor of Polistinae and Vespinae (the hypothesized evolution of eusociality in those groups), and the origins of the three social wasp subfamilies in Vespidae (Vespinae, Polistinae, and Stenogastrinae).

RESULTS & DISCUSSION

Search results

Our sampling efforts yielded a total of 720 records of direct evidence (“Observation” and “Empirical Studies” data; n=376, 52.2%) and “Indirect Evidence” (n=344, 47.8%) of predation events on social wasps (summarized in Table 1; Supp. Table S4). Most events were obtained from the literature search (n= 509, 70.7%), followed by video data (n= 119, 16.5%), unpublished accounts (n= 72, 10.0%), and social media reports (n= 20, 2.8%). Although most of the data were published in scientific literature, our diverse methods of data collection increased our sample size and allowed the inclusion of previously unpublished predator observations (e.g. predation of Ropalidiini wasps by macaques, A. Brahma pers. comm.), and surprising new observations (e.g., attack on a Stenogastrine wasp by a predatory nematode, S. Turillazzi pers. comm.).

Although empirical studies were the least common reference type (n= 61, 8.5%), all were published in the scientific literature (Table 1). “Observations” (n= 428, 59.4%) and “Indirect evidence” (n= 231, 32.1%) dominated the reference types reported. This shows a clear opportunity for future empirical research on predation on social wasps.

Predation on wasp colonies was recorded most often in Polistinae (52.7%), while predation on individual wasps was recorded most often in Vespinae (42.0%). This is likely due to the fact that Polistinae nests are often exposed (Figure 1c) when compared to Vespinae, which often build nests in cavities or underground (Spradbery, 1973; see “Patterns of predator variation with regards to social wasp traits” below).

Taxonomy of predators

Predator type varied across the subfamilies within Vespidae, and by whether they preyed upon individuals or colonies (Table 2). Direct evidence on individual polistine and vespine wasps shows they were primarily preyed upon by arthropods (Class Araneae and Insecta) and birds (Class Aves). Amphibians, carnivores, and reptiles were also observed eating individual wasps. Only one observation of predation on a Stenogastrinae individual was observed, and it was particularly unusual.

Stefano Turillazzi reported an observation of a predatory nematode consuming (not parasitizing) a stenogastrine wasp.

At the colony level, direct evidence of predation on Polistinae consists mostly of records of hymenopteran predators (Figure 3); ants were most often observed preying upon Polistinae wasps (Strassmann, 1981; Jeanne, 1972; O'Donnell and Jeanne, 1990), followed by *Vespa* hornets (Matsuura, 1991; Matsuura and Sakagami, 1973). *Vespa* will attack and collect adults as well as brood as prey items to bring back to the colony; *Vespa mandarinia* can recruit nestmates to join them in the attack on the colony (Ono et al., 1995). Passeriformes (e.g., crows) had the second highest record of colony predation (Figure 3; Raw, 1997). In spite of collecting the most direct evidence of Hymenoptera as predators, indirect evidence of Hymenoptera as predators of Polistine wasps in the literature were over-presented, whereas Passeriformes predators were never identified (indirectly) as predators of polistine colonies (Figure 3).

Carnivores were the most common predators of colonies of Vespinae, followed by Accipitriformes (eagles, hawks, and kites; Figure 3). The highly specialized *Pernis* honey buzzard can individually raid vespine colonies for brood combs, seemingly unaffected by the wasps' aggressive response (Huang et al., 2004; Gamauf, 1999). Among the Carnivore predators, we found the most direct evidence of badgers and weasels (family Mustelidae; Blackith, 1958; Lanszki and Heltai, 2007) preying upon vespine wasps, followed by bears (family Ursidae; Mealey, 1980). These carnivores possess strong paws with long claws, effective in digging up and tearing apart the wasp nest envelope (in the case of *Vespula*), undoubtedly playing a role in the success of carnivores as colony predators. Indirect evidence of Carnivora predators in the literature were slightly over-represented; whereas indirect evidence of Accipitriformes predation were slightly under-represented relative to the direct evidence we found (Figure 3).

There were only nine records of direct evidence of predation on Stenogastrine colonies (Table 2). Among these, *Vespa* hornets were identified as the most common predator ($n = 6$), followed by ants ($n = 2$) and one record of a reptile consuming a Stenogastrine colony. Additionally, Hymenoptera were also the only taxonomic group reported in indirect evidence as predators on Stenogastrine colonies.

We compared traits characteristic of the three subfamilies of Vespidae, and four tribes of Polistinae (colony cycle, colony size, nest building patterns, and climate) with the primary colony predator taxon (Figure 2). Social wasps varied in terms of colony cycle (seasonal and perennial), colony size ($2-10^7$ adults produced in a colony), and the types of nest that were constructed. Most subfamilies and tribes were primarily preyed upon by Hymenoptera, and this seemed most closely linked to the fact that those groups were predominantly located in tropical climates. Vespinae tend to be found in temperate climates, and they were preyed upon mostly by Carnivora. Polistini are found in both temperate and tropical climates, yet Epiponines (exclusively tropical) had more direct evidence of predation by mammals among the Polistinae tribes.

How does predation pressure across these taxonomic groups vary geographically?

We found direct evidence of predation on social wasp colonies in every inhabited continent (all except Antarctica; Figure 4). Predation on polistine colonies was recorded in every continent, while predation on vespine colonies was only recorded in North America, Europe, and Asia. Stenogastrine wasps are only found in Asia, and that is where its predation events were recorded (Turillazzi, 1991).

Evidence of colony predation in Africa and Oceania was limited to 6 and 5 records respectively, compared to >30 records for each of the remaining continents. This small amount of evidence suggests our findings probably do not represent the full picture of prey-predator relationships in those regions. For instance, despite the presence of Vespinae wasp populations in Africa and Oceania (Lester, 2018), along with predator clades that are widely reported to prey on wasps elsewhere in our data (e.g. *Pernis apivorus* honey buzzards in Africa, Bijlsma, 2002); weasels in Oceania, King, 2017), we could find no evidence of these predation events occurring in such areas. The same bias can be observed by separating records by countries, which also varied in terms of predation records. For example, Brazil, Costa Rica, French Guiana, and the USA each had at least 15 records, whereas the remaining countries had few or none.

Africa: In the African continent, ants were the primary predators of polistine colonies. Of note, we also uncovered a record of predation of *Belonogaster petiolata* (Polistinae: Ropalidini) by *Hoplostomus fulgineus* (Insecta: Coleoptera: Scarabaeidae). Although there are Vespinae in Africa (Tribe and Richardson, 1994) we found no direct evidence of colony predation events.

Central America: In Central America, ants and passeriform birds were the main predators of polistine colonies. *Eciton* army ants comprised two thirds (67%) of the hymenopteran examples. Army ant colonies can raid entire wasp colonies without facing significant opposition. Birds are also reported predators of Central American Polistinae, though with fewer direct observations. Records of predation by non-Accipitriformes, non-Passeriformes birds (*Ibycter americanus*) and Passeriformes (especially in the family Corvidae) on Epiponini colonies were common. Central America also had the most predation on wasp colonies by non-human Primates, all in the family Cebidae (capuchin monkeys).

North America: In North America, Passeriformes were the most common predator of polistine colonies. Still, the taxonomic diversity of polistine predators in North America was the highest for all continents (which may be linked to the higher number of predation events recorded in this region). Along with other insects (including ants) and various chordates, we also found direct evidence of a black widow spider (*Latrodectus mactans*) preying upon a colony of *Polistes apachus* (Gibo and

Metcalfe, 1978). Carnivora, namely bears (Ursidae), skunks (Mephitidae), and badgers (Mustelidae), were the primary predators of vespine colonies in North America.

South America: In South America, ants were the primary predators of polistine colonies, although non-passeriform/ non-accipitriform birds were also commonly recorded. Bird predation in South America was mostly recorded for non-Accipitriformes, non-Passeriformes birds, with consistent records of predation of the red-throated caracara (*Ibycter americanus*) upon Epiponini, Polistini and Mischocyttarini (McCann et al., 2013; McCann et al., 2015; McCann et al., 2010). In South America, we found the only record of predation by bats, *Phylloderma stenops* (Mammalia: Chiroptera), upon *Polybia sericea* (Polistinae: Epiponini; Jeanne, 1970b), and by bees, *Trigona hypogea* (Hymenoptera: Apidae), upon *Agelaia flavissima* and *Polybia emaciata* (Polistinae: Epiponini; Mateus and Noll, 2004). Among the ant predators, *Eciton*, *Camponotus*, and *Crematogaster* were common predators of wasp colonies in South America. Like Africa, although vespine populations have established in the temperate regions of Chile and Argentina (Masciocchi and Corley, 2013), we did not find evidence of predation on Vespine colonies in South America.

Asia: Asia is the only continent where all three social wasp subfamilies are present, and where predation on each was recorded. Ants are common predators of polistine colonies in Asia, but here, two of the most seemingly specialized groups of social wasp predators emerged: *Vespa* hornets and *Pernis* honey buzzards. Predation by *Vespa tropica* is one of the foremost causes of colony failure in *Polistes chinensis* in Japan, and hornets may play a significant role in controlling Asian polistine populations (Miyano, 1980). Although we only found seven records of direct evidence for Stenogastrine colony predation, *V. tropica* was the primary predator of these colonies. Still, it is worth noting that an unidentified gecko (Reptilia: Gekkota) was recorded preying upon a colony of *Parischnogaster mellyi*. It is likely that predators of Stenogastrinae are largely unreported in the literature; however, predation on stenogastrine colonies has been described as remarkably rare in nature (S. Turillazzi, pers. comm.). Finally, vespines were almost only recorded being preyed upon by mammals (Primates, all Hominidae; and Carnivora), with a smaller proportion of Hymenopteran predators recorded (including *Vespa*). Notably, human consumption of wasps was the primary cause of vespine predation in Asia, showing a unique prey-predator dynamic as well as an important cultural relationship between human societies and social wasps compared to other continents (Nonaka, 2010; see “Humans as predators across continents” below).

Europe: In Europe, similarly to Asia, ants, *Vespa* hornets, and the European honey buzzard (i.e., “specialized predators”) were the primary predators of polistine wasp colonies. Honey buzzards were also a major predator of Vespinae. The European badger *Meles meles* was the most common

carnivore predator on European vespines, consistent with the carnivore predation data in North American on vespine colonies.

Oceania: In Oceania, ants were the primary predators of polistine nests, and Ropalidini colonies were the only tribe to be repeatedly recorded with direct evidence of predation. As in Asia and North America, Oceania had one record of geckos attacking Polistinae colonies (DS, pers. obs.). Similarly to South America and Africa, despite vespine wasp colonies having established in this region, we found no evidence of colony level predation.

Humans as predators across continents: Human predation on social wasps was recorded in North America and Asia (not including nest removal for the purpose of population control or other non-consumption related purposes). Insects are recognized as an important food source for early hominids (Arnold, 2017). In fact, contemporary consumption of edible insects by humans is still common amongst one third of the world's population (Raheem et al., 2019). In the specific case of social wasps, researchers have documented long traditions of harvesting wild nests to eat larvae and pupae. Moreover, collectors have also developed practices that can be understood to some extent as domestication, such as the rearing and keeping of wasps in human-made enclosures for their entire life cycle (Payne and Evans, 2017; Saga, 2019). Wasp brood is highly nutritious also for humans, being rich in proteins and containing essential amino acids (Ying et al., 2010). Wasps are notably appreciated as food in parts of Asia, being commercially available at high prices depending upon their species (Nonaka, 2010). Another aspect of human exploitation of social wasp products can be seen in the use of nests in medicine recipes since ancient times (Chinese Pharmacopoeia Commission, 2010). Referred to as *Nidus vespae*, contemporary science has investigated the therapeutic use of nests for human health, suggesting medical significance for the treatment of rheumatoid and psoriatic arthritis, dental disease, respiratory disorders, cervical erosion, and other disorders (Wang et al., 2013).

The co-evolution of predators and their social wasp prey

Stinging aculeate Hymenopterans evolved approximately 200 million years ago (mya; Huang et al., 2019; Peters et al., 2017; Tang et al., 2019). These solitary stinging ancestors to social insects likely used their stings to immobilize prey before carrying it back to the nest to feed their larvae. Vespidae evolved ~166mya, which is also when Stenogastrines split from the rest of the Vespidae wasps (Huang et al., 2019). There were two separate origins of eusociality in Vespidae (Huang et al., 2019; Hines et al., 2007), once in the common ancestor of Vespinae and Polistinae (~75-80mya; Huang et al., 2019; Tang et al., 2019) and once in Stenogastrinae (between 166 and 29mya; Huang et al., 2019). Vespinae and Polistinae originated ~62 and 55mya, respectively (Huang et al., 2019).

Among the five main predators of social wasps, the ants (Family: Formicidae) originated before either origin of eusocial evolution in Vespidae (135-115mya; Huang et al., 2019; Brady et al.,

2006). Primates (74mya) and Carnivora (63mya; Class: Mammalia) originated before the three social subfamilies radiated (Figure 5; Springer et al., 2003) and Passeriformes (47mya) and Accipitriformes (44mya; Class Aves) originated after Vespinae and Polistinae (Oliveros et al., 2019; Nagy and Tökölyi, 2014). In other words, the coordinated response to low levels of carbon dioxide or vibrations – both indicators of a vertebrate predator – likely evolved before these extant predator lineages did.

Coordinated defensive behavior towards vertebrates may have evolved in the early social vespine ancestor in response to predation pressure from small mammals (225mya; Kemp, 2005), birds (116mya; Lee et al., 2014) and possibly lizards (>300mya; Laurin and Reisz, 1995) and other reptiles, many of which may be extinct today. This predation pressure may have driven the evolution of the response of 10s or 100s of individuals to leave the nest and attack an intruding predator, and the prevalence of defensive strategies with varied degrees of aggressiveness employed throughout Vespidae, and not limited to one subfamily or tribe. Those wasps that responded fast enough and with strong enough venom would have succeeded in deterring the potential predator.

Individual stinging insects can be consumed by a variety of predators (e.g., Table 2). Some of these predators have evolved strategies to avoid the harmful effects of toxic venoms. Although they were not found to be a common colony predator, reptiles were observed to prey upon individuals and/or colonies of all three subfamilies of social vespids. Horned lizards have evolved an innate resistance to harvester ant venom, one of the most toxic mammalian venoms, through a combination of a factor in their plasma (Schmidt et al., 1989), and a slippery and viscous mucus that lines their mouth and digestive system (Schmidt, 2016). In spite of being able to avoid the painful or lethal effects of venom, this resistance does not protect the lizard from a colony response (Schmidt, 2016). In other words, in the coevolutionary arms race of predator and prey, small predators may have evolved tolerance to an attack from a single stinging insect, but the evolutionary response of coordinated defensive attack (e.g. harvester ant attack en masse by biting) means that small vertebrate predators could be quickly overwhelmed by their potential prey.

Among the predators identified here, two orders of birds (Passeriformes and Accipitriformes) and two orders of mammals (Primates and Carnivora) originated after eusociality evolved in Polistine and Vespine wasps (Figure 5). These large, robust creatures would have stumbled across a social wasp nest, filled to the brim with proteinaceous larvae, and tried their luck at having a treat. For instance, the observations of hawks attacking vespine colonies suggests that the birds are somewhat aware of the wasps' retaliation, but overall unphased and undeterred (van Bergen, 2019; video 39, Supp. Table S5). Similar observations of carnivore predators also show that these mammals can withstand multiple stings to obtain their prize (video 33, Supp. Table S5). Social wasps' defensive response may have evolved alongside predation: as colonies became larger, they attracted more, larger and more sting-tolerant predators, and experienced greater predation pressure. This, in turn, may have selected for stronger defensive responses by wasp colonies, which had greater numbers of workers to allocate towards defense. This positive feedback may explain the wide variation in defensive response across

species: while most social wasps can sting in response to a threat, many species, particularly with small colonies, often flee rather than defend (*Mischocyttarus* spp., *Metapolybia* spp.; Hermann and Chao, 1984; KJL, pers. obs.), or mount a relatively weak defense (*Vespula consobrina*; Akre et al., 1982; Gaul, 1952). However, their close relatives produce impressive defensive responses (e.g., *Vespula germanica*; Jandt et al., 2020; *Synoeca*; de Castro e Silva et al., 2016). The *Vespa* colonies, with their large workers, strong venom, and terrifying aggressiveness may be the ultimate evolutionary response to attacks on vespine colonies.

CONCLUSION

Wasp colonies are preyed upon by a diverse variety of natural enemies. Social wasps have evolved various primary (nest construction) and secondary (coordinated behavior) responses to defend the colony and avoid predation. The most common predators of social wasps tend to be other Hymenoptera (specifically ants and hornets), carnivores (Order Carnivora), primates (Order Primates), perching birds (Order Passeriformes), and hawks (Order Accipitriformes) are commonly observed preying upon wasp colonies. The prevalence of these different predator groups varied across different geographic regions, and we highlight gaps in some regions where colony predation has not been recorded, despite the presence of social wasps. The specialized behavior of some predators (e.g., honey buzzards) may be a good starting point to deepen our understanding of the coevolutionary relationships between predators and social wasp prey.

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FIGURE LEGENDS

Figure 1. Evidence of social wasp predation, and defensive strategies to prevent colony level predation. (A) A direct observation of an Otago skink (*Oligosoma otagense*) capturing a *Vespula germanica* (Vespinae) queen in New Zealand (Oceania). Photo by Ricardo Rocha Mello 2019. (B) A *Vespula vulgaris* (Vespinae) nest (left) after being excavated from underground (by JMJ, not included as a predation event), and (right) after peeling away the paper envelope to reveal the combs full of brood. Photos by JMJ 2018. Nesting underground (out of reach) and/or building nest envelope that blends in with the bark/stems of the tree in which it is built (crypsis) are examples of primary defensive strategies to avoid colony level predation. (C) A *Polistes major major* (Polistinae: Polistini) foundress, on her nest, displaying a warning posture. Photo by KJL 2014. Visual behavioral displays are examples of secondary defensive strategies to deter nearby predators from attacking the colony.

Figure 2. Colony characteristics (colony cycle, size, nesting site, architecture and climate) of the three social subfamilies of Vespidae wasps (broken into the four tribes for Polistinae). Data are not provided for the three solitary subfamilies (Euparagiinae, Masarinae, or Eumeninae), as they were not included in the data presented in this study. The primary colony predator taxon is based on data shown in Table 2.

Figure 3. Direct vs indirect evidence of predation on social wasp colonies by the top five predators (see Table 2), and all other predators combined (“Other”). Percentage of direct evidence of predation is shown with filled bars (grey = predation on Polistine colonies, dark grey = predation on Vespine colonies, light grey = predation on Stenogastrine colonies); and percentage of indirect evidence is shown with dashed bars. There was no indirect evidence of Passeriformes predation on Vespinae colonies. Percentages are calculated based on the total evidence (direct or indirect percentages calculated separately) for each subfamily.

Figure 4. Relative frequency of direct evidence of predation events on the three social subfamilies of Vespidae wasps across the six continents where Vespidae are found. A separate pie chart was made for each subfamily in each of the continents where colony predation was recorded and the predator was defined. Pie charts are linked to the continent where its data was recorded by black lines. The most common Orders of predator are shown with solid colors, remaining Orders are combined and represented by “Class: Other” as striped colors. A gray gradient was used to differentiate continents with shared borders. Continent map was modified from original template from © George the Geographer 2014.

Figure 5. Evolutionary origins of predators and prey. (Top) The evolutionary origins of the top three Classes of Chordates (Reptilia, Mammalia, and Aves), and the top four Orders (from Mammalia and Aves) of colony predators. Ants and *Vespa* hornets are shown separately to represent evolutionary origins of the top Hymenopteran predators. (Bottom) Evolutionary origins of Aculeata, Vespidae, and the three main subfamilies of Vespidae (Polistinae, Stenogastrinae, and Vespinae). It is hypothesized that eusociality evolved twice in the Vespidae family, once in Stenogastrinae (sometime between 166 mya and 29 mya) and once in the common ancestor of Vespinae + Polistinae (approximately 80-75 mya).

TABLE LEGENDS

Table 1. Summary of records collected on individual- and colony-level wasp predation (combined). Direct Evidence is split into empirical studies and direct observations of predation events. Indirect evidence includes common lore or inferred predator based on post-predation damage. Values represent total number of references for each data collection type (literature search, social media campaign, video, and unpublished observations).

Table 2. Summary of direct evidence of **(A)** individual-level and **(B)** colony-level predation on the three social subfamilies of Vespidae (Polistinae, Stenogastrinae, and Vespinae). Direct evidence includes instances when predation was directly observed and reported in the literature, social media, or other sources. Columns listed as “Unknown” represent wasp prey that could not be confirmed from video or was described vaguely in text as “social wasp” or “Vespid wasp”. “Paper wasps” were categorized as “Polistini”, as that is the accepted common name for *Polistes* wasps, and “Yellowjackets” and “Hornets” were categorized as “Vespini”, as those are common names for *Vespa*, *Vespula* or *Dolichovespula*. Data are presented for predator Phylum (grey rows), which are broken into Class and most commonly observed Orders (white rows).