

# Chapter 3

## The Foraging Behaviour of Neotropical Social Wasps



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**Abstract** The evolution of eusociality among the Hymenoptera is related to the development of colonies with big populations, which in turn presented these social insects with the need for a constant intake of nutrients necessary for their collective survival. Taking a closer look on how the social wasps (Hymenoptera: Vespidae) manage to provide their colony with resources is of great value to understand the evolution of social life, but also the impact insect societies have on the environments they live in. Here, we attempt to explore the foraging behaviour of vespids, summarizing its general aspects and defining historically established key concepts. We build on previous reviews while bringing updated references and focusing on the literature on Neotropical social wasps (Polistinae). In this chapter, we define and investigate a series of topics, including the foraging activity of colonies, the flight range of foragers, the intricacies of the trophallaxis behaviour, the search and obtainment of different types of resources, and their storage inside nests. Finally, we attempt to diagnose the issues and challenges faced by Neotropical wasp researchers and suggest a few ways investigations may take for the advancement of the field when studying the foraging behaviour.

**Keywords** Activity · Paper wasps · Polistinae · Predation

### 3.1 Introduction

Among the diversity of behaviours shown by the social wasps, foraging is probably the most popular topic in specialized literature. Through their foraging activity, wasps form a network of interactions that is ultimately responsible for their value in providing ecological services (such as pest predation, pollination or seed dispersal).

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There is a great deal of importance in investigating the foraging behaviour, for it leads to understanding the social wasps' evolutionary history, basic biology and the ecological context in which they are inserted.

“Foraging activity” can be defined for social wasps as the functional group of behaviours of collecting environmental resources essential for survival at the colony level. These resources can be used either in the nourishing of adult wasps and their offspring or in the construction and maintenance of nests. Since the Polistinae social wasps are opportunistic and generalist predators, collected resources vary in nature and origin. This allows wasps to explore a wide array of ecological interactions. The foraging behaviour of social vespids has been detailed in literature review papers (Raveret-Richter 2000) and chapters in books dedicated to the group (Spradbery 1973; Carpenter and Marques 2001; Jeanne and Taylor 2009). In this chapter, we attempt to summarize and describe the general aspects of social wasp foraging, building on those previous studies by updating the references to reflect the state of the art. Furthermore, while previous literature reviews have been mostly skewed towards temperate-zone organisms, we here focus our efforts on the Neotropical Polistinae, aiming to bring a fresh perspective to the field of social foraging research.

## 3.2 Activity Schedule and Rhythm

The Polistinae clade is almost exclusively made of diurnal species (Spradbery 1973). A flow of individuals committed to the foraging activity coming in and out of the nest are often visible during daytime. At night, nests are usually more cryptic, since most of their inhabitants inside the nest, showing low levels of activity. Even in colonies of the Epiponini tribe, which sometimes keep guards around nest openings during the night (e.g. Chavarría-Pizarro and West-Eberhard 2010), such individuals will remain mostly motionless unless disturbed. The remarkable exception to this rule within the Polistinae is the wasps from the genus *Apoica* Lepeletier, which is exclusively comprised of nocturnal species and therefore presents foraging activity that differs from the rest of the subfamily (Hunt et al. 1995; Warrant 2008).

Diurnality is the main trend among insects, especially in tropical zones. This is partially due to a stimulation of their activity by environmental factors that are typically higher during the day, such as luminosity and temperature (Huffaker and Gutierrez 1999). Indeed, foraging activity in Neotropical social wasps is normally positively correlated to environmental temperature and negatively correlated to the relative air humidity across different genera (e.g. Ribeiro-Júnior et al. 2006; Santos et al. 2009; Cavenazzi and Noll 2011; Castro et al. 2011; Detoni et al. 2015; Jacques et al. 2018). The influence of wind speed in the process is not as clear, although there is consensus that strong winds discourage foraging by hindering the wasps' ability to fly (Elisei et al. 2005, 2013). Luminosity regulates the foraging activity through physioethological thresholds (Spradbery 1973; Ribeiro-Júnior et al. 2006), which are required since wasps rely heavily on visual orientation during their foraging bouts. Furthermore, there is evidence that artificial light sources may attract

large amounts of wasps around sunset, when foragers are usually returning to their nests (Barbosa et al. 2016). This argument reinforces the group's positive phototropism and its relation with foraging light thresholds.

The diurnal habit of the social wasps may, however, be explained by more than only their stimulation by abiotic factors. Firstly, the localization of their prey and other alimentary resources is oriented to a good extent by visual clues, thus requiring a source of light (as seen in Jeanne 1972). Secondly, most of the prey captured by Polistinae wasps (especially caterpillars) are also active during the day (Heinrich 1979), which makes prey-predator encounters more likely and is therefore essential for the wasps' success in protein foraging.

One of the main research interests in the social wasp foraging schedule is how does the foraging fluctuate in intensity through the day, a process that can be called "foraging activity rhythm". A colony's rhythm can be measured by counting how many foragers leave and return to the nest per time unit, generating a flow that varies according to the time of the day (Giannotti et al. 1995; Jacques et al. 2018). Spradbery (1973) has described a general pattern of foraging rhythm for diurnal social wasps: the activity begins around sunrise, being limited by the availability of solar light, and reaches its daily peak around noon and decreases through the afternoon until it ceases around sunset.

In theory, social wasp larvae will require a greater amount of energetic resources during the morning, after a period of deprivation during the night. That would explain why foraging tends to be more intense during the first half of the day, even if the amount of light available is similar to that in the afternoon (Gaul 1952). Alternatively, studies show that in many different species, the foraging activity peaks at the warmest hours of the day, which would also explain that positive correlation (Resende et al. 2001; Lima and Prezoto 2003; Elisei et al. 2005; Ribeiro-Júnior et al. 2006; Rocha and Giannotti 2007; Castro et al. 2011; Detoni et al. 2015).

There is a great difference between the foraging rhythm of the independent-founding social wasps (Mischocyttarini and Polistini) and the swarm-founding social wasps (Epiponini), the latter usually being more active. Colony size, as observed by Edwards (1980), is likely a variable that plays a role in that difference: while a *Mischocyttarus* or *Polistes* colony has a few dozen workers on average, nests of the Epiponini tribe commonly host hundreds, thousands or even millions of foragers (that last case being true for some nests of the extremely populous *Agelaia* colonies). Still, the difference in adult populations alone does not seem to explain rhythm differences across species. For example, *Polistes simillimus* Zikán (1951) (Polistini) and *Protopolybia sedula* (de Saussure, 1854) have similar colony sizes, yet the rhythm of the swarm-founding *Pr. sedula* (average 105.4 forager departures and 108 returns per hour; Detoni et al. 2015) is clearly much more intense than that of *Po. simillimus* (average 18.4 forager departures and 20.9 returns per hour; Prezoto et al. 1994). A possible explanation for such phenomenon is that, due to the lower worker:brood ratio in Epiponini populations, the colony's metabolic needs are higher and, therefore, an intense foraging rhythm is required. In fact, the worker:brood ratio seems to be a central element in the social biology of the Polistinae (London and Jeanne 2003).

Unlike diurnal Neotropical social wasps, the *Apoica* genus is distinguishable from other swarm-founding wasps (and social wasps, in general) for their nocturnal habits. Hunt et al. (1995), when studying *Apoica pallens* (Fabricius, 1804) in Venezuela, noted the complete absence of foraging activity during daytime, a period which workers spent by ventilating the nest and guarding the colony against threats. After sunset, the workers start foraging; the activity begins at a slow pace, but then an “explosive departure” occurs, with hundreds of foragers leaving the nest in few minutes, in which “the air was filled with wasps” (Hunt et al. 1995). The intense flow is normalized in a few instants and remains stable through most of the night time, decreasing in the hours prior to dawn. Similar events were observed in the species *Apoica flavissima* (Vecht, 1972) by Nascimento and Tannure-Nascimento (2005), which also verified the typical influence of temperature and humidity on the species’ foraging, as well as possible relationship to the phase of the moon. This exceptional pattern of activity has likely arisen as a strategy to avoid losses caused by direct competition (Smith et al. 2017).

### 3.3 Flight Range

Foraging behaviour shares dynamics across different groups of social insects. The need to not only locate and obtain food but also to bring it back to the nest is a challenge faced by all social foragers. The exploration of natural resources must, therefore, have the nest as its geographical reference. Studying the flight range of social wasps allows us to better understand the geographical reach of colonies when interacting with their ecosystems, especially regarding their impact as predators.

By looking at predator ants as an example, it is clear how social foraging is related to the nest site. Camponotini ants create trails that run for several dozen meters, on which they mark their progress through pheromones so that nestmates may easily find the way between nest and food. The species *Camponotus sericeiventris* Guérin, for example, usually builds one or more foraging trails radiating from the nest and reaching up to 86 meters in length, either vertically or horizontally (Elisei et al. 2012).

A major biological difference between ant foragers and wasps resides in the latter’s ability to fly. Flight makes dispersion easier, if not more effective, especially when regarding the vertical exploration of ecosystems. On the other hand, the lack of attachment to the substrate while foraging means that a reliable pheromone-marked trail, as seen in ants, is not possible for wasps. That is undoubtedly one of the main drives for the wasps’ strong dependence on visual orientation (Raveret-Richter and Jeanne 1985). As a result, there is a cost-benefit relationship regarding exploration: the further away from the nest a forager flies, the smaller the chance that it will be able to find its way back, which can lead to worker loss in the colony. A colony set in a poor environment, where its workers must increase their foraging flight range in order to obtain food, is therefore at severe disadvantage (Prezoto et al. 2016b).

“Flight range” is defined as the maximum distance a forager is able to fly with significant chances of returning to the nest and, therefore, being successful at foraging. By obtaining the flight range value, it is possible to deduct an effective radius in which foragers will be active around the colony (equal to  $\frac{1}{2}$  flight range, since that includes the flights from the nest and back) (Gobbi 1978; Santos et al. 1994).

Studies on the flight range of Brazilian social wasps are few and restricted to few taxa (Table 3.1). The method used to assess a species’ flight range is consistent among publications and is made by following these steps: (1) intercepting social wasp workers from colonies in the pre-emergence stage; (2) marking the workers to allow individual distinction; (3) releasing the workers at multiple distance intervals

**Table 3.1** Social wasp foraging flight range across studies

Taxon			Flight range (m)	Study
<b>Vespidae</b>				
<b>Polistinae</b>				
	<b>Polistini</b>			
		<i>Polistes</i>		
		<i>Polistes canadensis</i>	250	Santos et al. (1994)
		<i>Polistes lanio</i>	> 200	Giannotti et al. (1995)
		<i>Polistes simillimus</i>	100	Prezoto and Gobbi (2005)
		<i>Polistes versicolor</i>	300	Gobbi (1978)
	<b>Epiponini</b>			
		<i>Angiopolybia</i>		
		<i>Angiopolybia pallens</i>	48	Cruz et al. (2006)
		<i>Polybia</i>		
		<i>Polybia emaciata</i>	76	Galé et al. (2015)
		<i>Polybia fastidiosuscula</i>	81	Souza et al. (2011)
		<i>Polybia occidentalis occidentalis</i>	126	Santos et al. (2000)
		<i>Polybia occidentalis venezuelana</i>	50	Hernández et al., (2009)
		<i>Polybia rejecta</i>	<210	Dejean et al. (2017)
		<i>Polybia scutellaris</i>	150	Machado and Parra (1984)
		<i>Polybia sericea</i>	75	Bichara Filho et al. (2010)
		<i>Protopolybia</i>		
		<i>Protopolybia exigua</i>	75	Ribeiro Júnior et al. (2008)

The 70% return rate suggested by Santos et al. (2000) was used as criteria to set the values displayed here

from the nest; and (4) assessing the proportion of workers that returned to the nest from each distance (Santos et al. 1994). Although this method allows the assessment of the maximum distance from which a worker can return to its nest, a return rate of at least 70% is used as a valid estimator of a species' effective flight range (Santos et al. 2000). Following that assumption, most species would have an effective flight range within 300 meters (Gobbi 1978).

### 3.4 Trophallaxis

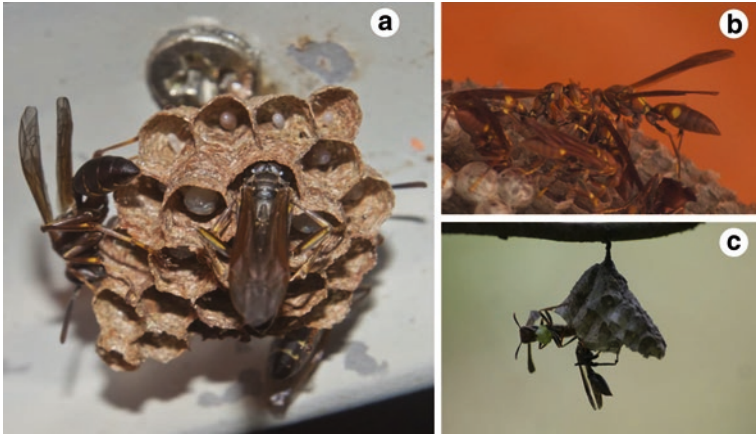
Thus far we focused on how external factors influence on a colony's foraging activity, especially those linked to external environmental variables. In addition, social wasps are also capable of an internal and social behavioural control of foraging. Of these behaviours, the most fascinating – and possibly, the most relevant for the group's natural history – is trophallaxis.

The term trophallaxis was coined by author William Wheeler in 1918 to describe the reciprocal exchange of liquids between two insects through their respective mouths. The term's definition has been updated and broadened to include unidirectional exchanges as well (Hunt and Nalepa 1994). This behaviour has implications for various aspects of social life other than just foraging; trophallaxis has been studied in the context of establishing social cohesion and the hierarchy of social wasp colonies (Roubaud 1916; Jeanne 1991).

According to Spradbery (1973), social wasp trophallaxis is divided into two distinct categories according to the life stage of its participants: *adult-larva trophallaxis* and *adult-adult trophallaxis*. We will explain each of these individually, as they present distinct effects on a colony's foraging behaviour.

To initiate adult-larva trophallaxis, a reproductive wasp or worker will approach a larva, usually observable when the adult inserts its head inside a nest cell containing brood (see Fig. 3.1a). The adult wasp stimulates the larva by antennating its mouth parts (and also possibly by beating its gaster against the nest in *Polistes*). The wasp larva will then secrete saliva, which is transferred into the adult's gastric tract. Pioneer studies on adult-larva trophallaxis showed that larval saliva is highly attractive to adults (Du Buysson 1903; Janet 1903); later, chemical analysis allowed the characterization of saliva as mainly composed of sugars and amino acids. Indeed, Hunt and colleagues (1982) describe larval saliva as being nutritionally much superior to wasps than the richest floral nectar.

At first impression, this scenario seems to escape the logic of social foraging. Since wasp larvae are in constant need of nutritional intake in order to grow and develop, what would be the biological rationale behind giving away such a highly caloric resource to adult wasps, which are able to forage for self-sustenance? Researchers tried to solve this enigma by addressing the question from different perspectives. Ishay and Ikan (1968a, b) showed through radioactive marking that the sugary substances in larval saliva do not derive from the nectar collected from foragers but instead from proteolytic enzymes. This finding led to the conclusion



**Fig. 3.1** (a) An adult *Mischocyttarus* sp. wasp inserts its heads inside a cell containing a larva; (b) a group of adult *Polistes* wasps engaged in trophallaxis; (c) an adult paper wasp (to the left) holds a mass of maxillated prey in her mandibles

that larvae provide rewards for adults feeding them, generating a positive feedback. However, other studies suggest that the process is not that simple. First, trophallaxis in *Polistes* seems to be not always reciprocal but rather a one-way exchange; this prevents larvae from rewarding foragers immediately after being fed (Suryanarayanan & Jeanne 2008). In addition, larva saliva provision seems to increase in frequency when colonies show minimal foraging activity (Ikan and Ishay 1966). In other words, larvae will dispense more resources despite being fed less often. Indeed, *Mischocyttarus* wasps seem to have higher sugar concentration in their saliva during the pre-emergence stage of the colony cycle, when worker populations are smaller and foraging is costlier when compared to post-emergence (Hunt 1988). In conjunction, these findings come together in the hypothesis that trophallaxis plays a major role in the social cohesion of a colony: in times when food is scarce or foraging is otherwise energetically costly, larvae will provide attractive resources to avoid being cannibalized by adults, a common strategy during periods of nutritional stress (Gadagkar 1991). Nevertheless, it is still possible that adult-larva trophallaxis has a role in foraging during periods of regular activity, and these nutritional interindividual dynamics constitute a cornerstone in the evolution of eusociality in Hymenoptera.

The second category, adult-adult trophallaxis (see Fig. 3.1b), is somewhat less studied than when immature wasps are involved in the process and its biological significance has been less explored by researchers. There is evidence for some groups that adult-adult trophallaxis is a mediator in determining the social hierarchy in social insects. In Polistinae, foraging load partitioning between adult nestmates seems to also play a role, or at least reflect, the hierarchical organization of a colony (O'Donnell 1995a; Tindo and Dejean 2000; Sinzato et al. 2003).



It has been suggested for some swarm-founding species that trophallaxis between adults could result in recruitment for foraging within the colony (Taylor et al. 2012). Conversely, a study with *Agelaia multipicta* (Haliday, 1836) does not support this hypothesis (Jeanne et al. 1995). Food recruitment in social wasps is a somehow elusive topic, and we recommend the reading of Jeanne and Taylor's (2009) discussion about this phenomenon. Since trophallaxis is often observed immediately after a forager returns to its nest with sugary substances, it has also been used as a non-invasive behavioural indicator to distinguish the forager's load (Giannotti et al. 1995).

### 3.5 Searching for Resources

A detailed narrative on the challenges faced by a social wasp worker when leaving the nest to forage is provided by Raveret-Richter and Jeanne (1991). The first step is locating the resource in the environment, whether it is sugary food, water, nest material or a prey. For the latter, the forager must still subjugate its prey, and, if it is too big to be carried back in one piece, it must be fragmented before the wasp can return to its nest. In this case, the wasp still needs to memorize where she left the remaining fragments, so it can return to claim them later – and potentially fight off opportunists to do so. The whole process involves a diverse series of behaviours, of which the most instigating include orientation during flights and the ability to locate resources.

Most behaviours linked to the foraging activity in social wasps are intrinsically connected to a learning process. Prior to being able to fly out in the open, young foragers-to-be make short trips around the nest in order to memorize the surrounding landscape. These visual cues will be used to find the colony upon returning from a foraging trip. Gaul (1951) suggests that temperate-zone vespids make a series of three flights, in which the forager executes progressively wider loops around the nest opening, culminating in a sudden departure for the actual foraging during the third flight. This behavioural display is named *orientation flight* (Spradbery 1973).

After their departure, foragers must be able to detect resources in the environment using sensorial stimuli. Authors attribute different weights to the importance of different cues for the localization and identification of food sources, but there is a consensus on the conjoined relevance of visual and olfactory cues (Raveret-Richter 2000). Pioneer studies on resource identification in social wasps stressed the role of olfactory cues (Iwata 1976), and evidence has been added to the case of chemical perception in wasps over the years. A good example is how wasps are able to detect leaves that were damaged by chewing herbivores (especially by caterpillars, which they usually prey upon) and choose to land on those instead of healthy leaves as a substrate in order to maximize prey encounters (Saraiva et al. 2017). Furthermore, olfactory cues seem to be especially important for the detection and obtainment of sugary substances. Some wasps may consider a site's scent more than its colour when choosing where to land (Mcpherson and Mills 2007) and are able to detect honeydew from long distances (Gaul 1952). Finally, carrion-feeding species



(such as those in the tropical genus *Agelaia*) are likely to use mainly chemotactic cues to locate their food (F.P., pers. obs.).

Resources may also be located visually, which is especially true for prey. Wasps may even misdirect predation behaviours towards shapes that resemble prey (Jeanne 1972). Some researchers defend that visual orientation may be more important than olfactory, especially for the capture of highly active prey, since the wasp's sight may rely heavily on the perception of movement (Spradbery 1973; Jeanne and Taylor 2009).

Overall, a forager may use visual cues to search for prey in a larger scale, chemical cues as it approaches the prey in a smaller scale to choose a landing site. This integration of different stimuli was suggested and described in detail for *Polybia* wasps by Raveret-Richter and Jeanne in 1985.

After identifying and capturing their prey, foragers must bring the food back to their nests. Prey will often have a much larger body mass than foragers, and so wasps need to cut their prey in fragments and carry them in multiple trips. Sometimes, wasps will execute orientation flights around the fragmented prey to memorize its location (Takagi et al. 1980).

Inter- and intraspecific interactions between social wasps will often take place at a food source. Forager aggregates in *Agelaia* sp. may be evidence that local enhancement (use of social cues to facilitate the finding of good foraging sites) is being used to a colony's benefit (Forsyth 1978). Other species may use local enhancement to exploit a competitor's efforts. *Mischocyttarus immarginatus* (Richards, 1940) wasps have been observed to attract foragers of three other different species (*Polistes instabilis*, *Polybia diliguetana* and *Polybia occidentalis*) that quickly robbed prey fragments after the original predator left the site (Raveret-Richter 1990). Conversely, niche overlap between species may not affect their direct survival in some environments (Jacques et al. 2018). When wasps compete with ants for food, they might show exceptional behaviours to overcome direct competition; a notable example is the reported removing of ants from sites by dropping them from heights (Ricioli et al. 2017). These are only some of the examples on the ways the social wasp's search for resources might generate multi-level ecological interactions, constituting one of the group's most relevant traits.

### 3.6 Items Foraged

Social wasps are notably generalist and opportunistic in their foraging behaviour. This implies that wasp foragers are able to explore a wide range of resources while showing varied behavioural strategies to do so. These habits were probably developed in the group in the answer to the evolution of sociality, which requires a nutritional and energetic income much higher to that of individual life. Greater foraging behavioural plasticity, in contrast with specialization, could allow colonies to survive periods of food shortage and extend their lifespans (Jeanne and Taylor 2009).

These traits add to the complexity of social foraging and must be taken into account when studying social wasp diet and prey preferences.

The items foraged by wasps are usually divided into four groups (West-Eberhard 1969; Raveret-Richter 2000): (1) water, (2) nest-building materials (often called “vegetal fibre”), (3) sugary substances (also called “carbohydrates” or even “nectar”) and (4) protein (also called “prey”). These groups have different functions for the maintenance of the colony, as discussed below. Raveret-Richter (2000) has reviewed the foraging of each of these items in detail for social wasps, and a good part of the literature on them has remained untouched for Neotropical paper wasps. We here provide a summarized description of these behaviours and discuss more recent findings for the Polistinae and advise the reader to refer to Raveret-Richter’s work for a more extensive review.

### **3.6.1 Water**

Social wasps imbibe water droplets during foraging activity, which is done from water bodies such as lakes and puddles or from accidental/temporary containers such as morning dew (Jeanne 1986). Wasp foragers may display unusual behavioural alternatives to avoid competition while foraging for water. For instance, wasps may choose to perform a short nimble landing on the water’s surface to drink from it instead of joining other wasps on the water’s edge (Prezoto et al. 2016a).

After its collection, water may be used in more than one way in the colony. In addition to being ingested by adults or larvae for metabolic purposes (Kasuya 1982), water is also added to vegetal fibre during nest construction and repair (Akre 1982). Workers will also place droplets on nest walls or inside cells. In conjunction with fanning (wing beating) behaviour, it makes up a behavioural strategy to thermoregulate the colony on hot days (Wilson 1971).

### **3.6.2 Nest-Building Materials**

Vegetal fibre is the main construction material used by Polistinae, which has rendered them the popular name “paper wasps”. Fibre is collected from natural vegetal structures such as branches or trunks, but may also be obtained from untreated, unpainted wood worked by man such as old furniture (Wenzel 1991). Foragers land on the substrate and cut a shred of the fibre using their mandibles, which are then maxalated and mixed with saliva into a rounded shape. At least for one species, foragers will regurgitate water on the original source before cutting of the fibre – probably making its removal easier and helping in keeping the material’s cohesion (Jeanne 1986).

### 3.6.3 *Sugary Substances*

Sugary substances, or simply carbohydrates, are collected by foragers and used as a main source of energy by adult wasps, which feed almost exclusively on it (Jeanne and Taylor 2009). Carbohydrates are usually collected in the form of plant nectar or the honeydew exuded by homopterans (Evans and West-Ebehrard 1970; Moller et al. 1991). This resource is shared at the nest to both adult and immature wasps via trophallaxis.

Nectar can be collected from both extrafloral nectaries and flowers, although many of the latter are not accessible to wasps due to their morphology (Spradbery 1973; Köhler 2008). The flowers visited by wasps reflect the group's generalist/opportunistic habits: favoured species vary as different flowering seasons coincide with a need for high carbohydrate intake at the colonies (Köhler 2008). Additionally, it is during flower visitation that wasps may act as pollinators.

One of the most studied alternatives for plant nectar as a carbohydrate source is the collection of honeydew. This substance is a metabolic by product secreted by aphids and scale insects after the ingestion of sap. Homopteran families such as Aphidae, Psyllidae and Coccidae are often visited by wasp foragers for the collection of honeydew and may even benefit from wasp protection against predators (Letourneau and Chloe 1987; Moller et al. 1991).

Other alternatives for carbohydrates exploited by wasp foragers include tree sap (Jeanne and Taylor 2009), bee honey robbing (Edwards 1980) and ripe fruit. The latter seems to be especially attractive to foragers when at the over-ripe or rotting stage: wasps have been observed foraging at Brazilian cherries (Souza et al. 2013), Brazilian grapes (De Souza et al. 2010), cactus fruits (Santos et al. 2007), cashews (Santos and Presley 2010), grapes (Hickel and Schuck 1995), guavas (Brugger et al. 2011), mangoes (Barbosa et al. 2014) and prunes (Prezoto and Braga 2013).

### 3.6.4 *Protein*

Protein foraging in social wasps is the main interest in a myriad of studies on the group's ecology. In addition to its role in the social cohesion of a colony (see "Trophallaxis), protein foraging in Neotropical social wasps is the key behaviour behind the growing interest in exploiting the group as agents of pest control (Prezoto et al. 2019).

Even though adult wasps may eventually consume portions of prey, these are largely destined to larval nourishment. In addition to ingesting sugary substances, larvae require a constant protein intake in order to fully develop into adults. For that reason, it is generally expected that protein foraging intensifies during stages when the proportion of brood in a colony is higher (London and Jeanne 2003).

The main source of protein foraged by wasps comes from prey, namely, terrestrial arthropods (Prezoto et al. 2019). The standard method for assessing social wasp

prey preference is the interception of foragers as they return to the nest and physically removing the load from their mandibles for analysis (Giannotti et al. 1995). This method is limited, however, because most wasps chew prey fragments prior to their transport (Fig. 3.1c). Visual taxon identification performed on prey matter is therefore restricted to higher taxonomical levels, such as families (Jeanne and Taylor 2009). *Polybia occidentalis* (Olivier, 1791) is a notable exception: since their prey is carried back almost intact, the species stands as a good model for cost-efficient diet assessment (Hunt et al. 1987).

Despite the challenges involved, various researchers have put effort into assessing social wasp diets. Jeanne and Taylor (2009) state that wasps, although generalists, tend to choose soft-bodied terrestrial arthropods as their prey. The biggest portion of these is represented by caterpillars (Lepidoptera) and adult flies (Diptera), with a smaller amount of Dermaptera, Orthoptera, Odonata, Hemiptera, Coleoptera, Hymenoptera and Arachnida being captured. The trend for targeting caterpillars during protein foraging has been verified in many Neotropical social wasps; Table 3.2 shows species and environments for which Lepidoptera larvae constituted at least 50% of their diets.

This preference for caterpillar as prey seems to be established across different genera of both individual- and swarm-founding social wasps, especially in environments altered by man. In environments dominated by fewer species, such as in monoculture plantations, the proportion of Lepidoptera in social wasp diets can reach values as high as 95–100% (Prezoto et al. 2006; Elisei et al. 2010). This supports the claim that social wasps, although generalist, may act as facultative specialists (Raveret-Richter 1990).

**Table 3.2** Research showing species of social wasps that capture a majority (50% or more) of Lepidoptera as their prey in different Neotropical environments

Species	Environment	Study
<i>Apoica pallens</i>	Pasture areas	F. Prezoto, unpublished data
<i>Mischocyttarus cassununga</i>	Urban parks	M. Detoni, unpublished data
<i>Polistes lanio</i>	Farms	Giannotti et al. (1995)
<i>Polistes simillimus</i>	Farms	Prezoto et al. (1994)
<i>Polistes versicolor</i>	Farms; urban parks	Prezoto et al. (2006); Elisei et al. (2010)
<i>Polybia dimidiata</i>	Farms	Campos-Farinha and Pinto (1996)
<i>Polybia ignobilis</i>	Farms; urban parks	Silva et al. (1968), Gobbi and Machado (1986), Picanço et al. (1988), Marques (1996)
<i>Polybia occidentalis</i>	Farms; urban parks	Gravena (1983), Gobbi et al. (1984)
<i>Polybia paulista</i>	Farms; urban parks	Gobbi and Machado (1985), Campos-Farinha and Pinto (1996), Marques (1996)
<i>Polybia sericea</i>	Farms; urban parks	Silva et al. (1968); Marques (1996)

Nevertheless, a generalist diet still plays an important role in social wasp ecology. Diet composition may shift significantly away from lepidopterans to fit prey seasonality. As an example, research shows colonies preying on Diptera at high proportions for the species *Polybia platycephala* (Richards 1951) (Prezoto et al. 2005) and *Synoeca cyanea* (Fabricius, 1775) (Prezoto and Braga 2013).

The opportunistic aspect of social wasp foraging allows the exploitation of a range of alternatives for protein foraging. *Agelaia* wasps are notable for their carrion-feeding behaviour, a trait that sometimes is also seen in *Angiopolybia*, *Brachygastra*, *Parachartergus*, *Polybia*, *Protonectarina* and *Synoeca* (O'Donnell 1995b; Silveira et al. 2005). Wasp foragers may further act on corpse decomposition. Gomes et al. (2007) observed *Polybia ignobilis* individuals capturing flies that were laying eggs on rotting carcasses. Another usual strategy is preying on alate ants and termites during nuptial flights, when they are most vulnerable (Holfing and Machado 1985; Raveret-Richter 2000). Finally, unusual behaviours have been recorded for social wasps such as robbing prey from spider webs and other arthropod predators (Chevalier 1924; Jeanne 1972), preying on vertebrate eggs (Warkentin 2000) and capturing prey from bait traps used in insect diversity studies (Maciel et al. 2014).

### 3.7 Resource Storage

To overcome the challenge of feeding a colony for extended periods of time, some vespids have developed strategies to store resources in their nests. This behaviour is comparable to the production of honey in social bees (Seeley 1989) or the storage of vegetal matter in subterranean ant nests (Taber 1999). In Polistinae these behaviours are somewhat simpler but still reflect the importance of resource storage in the success and evolution of eusociality (Hunt 1982, 1991).

In their “Observations on the social wasps of South America (Hymenoptera, Vespidae)”, Richards and Richards (1951) performed an extensive analysis on the nests of different social wasp species and found two types of resources: liquid storages (honey-like sugary substances) and solid storages (maxalated prey fragments). Both types were found inside nest cells, although each one showed different distribution patterns through the nest. Other studies analysed liquid storages and found them to be of vegetal origin, usually nectar from flowers surrounding the colonies. These substances are sometimes called “wasp honey” or simply “honey” (Strassman 1979; Guimarães et al. 2008).

Resource storages are found in nests of both independent- and swarm-founding species, but seem to be more common in the latter (Richards and Richards 1951; Prezoto and Gobbi 2003). The nests of swarm-founding paper wasps have multiple layers of combs surrounded by an envelope, which probably provides food stocks with better protection against robbers when compared to the exposed, single-combed nests of the independent-founding *Polistes* and *Mischocyttarus*. Honey storage has been verified for the swarm-founding species *Metapolybia cingulata*

(Fabricius, 1804), *Polybia bicyttarella* (Richards, 1951), *Polybia bistrata* (Fabricius, 1804), *Polybia ignobilis* (Haliday, 1836), *Polybia occidentalis* (Olivier, 1791), *Polybia platycephala* (Richards, 1978), *Polybia scutellaris* (White, 1841), *Protonectarina* spp. and *Protopolybia emortualis* (de Saussure, 1855) (Richards and Richards 1951; Hunt et al. 1987; Corujo et al. 2010; Rocha 2011) and for the independent-founding *Mischocyttarus cassununga* (von Ihering, 1903), *Mischocyttarus drewseni* (de Saussure, 1854), *Mischocyttarus socialis* (de Saussure, 1854) *Polistes simillimus* (Zikán, 1951) and *Polistes versicolor* (Olivier, 1791) (Richards and Richards 1951; Jeanne 1972; Prezoto and Gobbi 2003; Guimarães et al. 2008; Barbosa et al. 2017). The species *Brachygastra lecheguana* (Latreille, 1824) stands out for storing honey in remarkable amounts (Richards and Richards 1951).

Rossi and Hunt (1988) described two patterns for honey storage inside nests. Honey droplets may be placed inside empty cells (Strassman 1979; Machado 1984; Hunt et al. 1987) or cells shared by eggs or first instar larvae (and rarely by second instar larvae) (Rau 1928, 1939; Heldmann 1936; Jeanne 1972). Honey placed in cells also containing immature wasps was related to providing young larvae with additional nourishment by Jeanne (1972). This claim is supported by behavioural evidence, since adults may engage in trophallaxis with larvae immediately after visiting honey storages (Jeanne 1972; Guimarães et al. 2008). When stored in empty cells, honey is usually placed in older, unproductive combs (in swarm-founding species) or in the comb's peripheral cells (in independent-founding species). These storages are possibly long-term food reserves to grant the colony its sustenance at the final phases of the cycle, which often coincide with food shortage periods (Strassman 1979). This claim is supported by the fact that honey storages seem to be more conspicuous during dry seasons (Hunt et al. 1987). Finally, from behavioural observations, when individual wasps do not interact with nestmates after visiting honey storages, it can be inferred that the reserves are purposed for individual adult nourishment (Prezoto and Gobbi 2003).

Solid resource storages, on the other hand, seem to be a more widespread behaviour in Neotropical social wasps – especially in the genus *Polybia*. Studies with *Polybia platycephala* and *Polybia occidentalis* (Richards and Richards 1951; Rocha 2011) report a high number of nest cells containing fragments of flies (Chironomidae) and alate ants (Hymenoptera) and termites (Blattodea). The high proportion of alates found in storages is further evidence of the wasp's opportunistic foraging, since reproductive ants and termites are usually available as prey in short periods but in very high densities. Furthermore, the unusual abundance of prey could be the necessary stimulus for building solid resource storages.

Investigating resource storages in social wasp nests can provide insights outside of the wasp's life history. As an example, pollen analysis performed on honey storages allows researchers to identify flowers visited by wasp foragers without needing to deal with the challenges of tracking wasps during their bouts (Corujo et al. 2010). Overall, storage analysis can be a complementary key to understand the ecological interaction webs that wasps take part in.

### 3.8 Future Directions

Due to many factors, the research on the foraging behaviour of social wasps in the Neotropical environments – especially in Brazil, where most of its research groups are based at – unfortunately lags behind studies carried out in other climatic zones, not unlike social wasp research that sometimes lags behind ant and social bee studies. Underfunding, allied to the relatively small number of researchers devoted to study the group, is probably the main factor responsible for that issue. Curiously, the general public's negative perception of wasps as organisms (Sumner et al. 2018) could be one element involved in preventing wasp research to be funded while also pushing prospective researchers away from the field during their formation. Another considerable challenge faced by researchers is the impressive diversity of social wasps in the Neotropics. Many of these species have nothing but their taxonomical description available in literature, and even abundant, widely distributed ones lack published data on their life history. This often forces investigators to focus on general biology and behaviour prior to addressing the field's trending theories, which is usually looked down by editors and funding organizations.

Yet, as research on basic biology and behavioural ecology progresses, scientists must look ahead to explore the frontiers of sociobiology. Here, we discuss what we consider promising methods and theories for the future of social wasp foraging behaviour research in Neotropical areas.

#### 3.8.1 *Biological Control*

The use of paper wasps as agents of agricultural pest control has been suggested as early as in the 1950s (Rabb and Lawson 1957). In the Neotropics, this possibility has been repeatedly brought up as the inspiration behind investigations on wasp foraging behaviour and even materialized itself in the form of experimental studies (Prezoto and Machado 1999). Hard experimental evidence obtained in controlled settings (such as pest predation rates and plant productivity in greenhouses) has only very recently been published (Southon et al. 2019), finally opening the way for exploiting social wasps in carefully designed pest control plans. Current research on the matter has been mostly limited to anecdote reports on wasps nesting or foraging within crops. The allocation of scientific resources to explore social wasp foraging in controlled experiments could be hugely beneficial to the field. Additional possibilities were recently opened as wasps have been suggested as controllers of dipterans of medical interest (Prezoto et al. 2016b). The current epidemiological relevance of *Aedes* mosquitoes, vectors of the dengue, Zika and Chikungunya fevers, could be used to motivate researchers and funding agents to invest in social wasps foraging as a control alternative.



### 3.8.2 *Molecular Analysis*

The overwhelming majority of studies in the foraging behaviour of Neotropical social wasps rely on observation data. Conversely, the so-called Omics Age brings a wide range of new ways to answer questions on sociobiology (Ghoul et al. 2017). In addition to applying well-established genetics methods to social wasps – such as searching for genes linked to foraging success (Ingram et al. 2011) or identified genetic-physiological thresholds for the perception of specific foraged items (Değirmenci et al. 2018) – we also suggest that researchers explore the innovative fields on ecogenetics in their investigations. For instance, metabarcoding the gut content of foragers and larvae (Krehenwinkel et al. 2016) is a way to overcome the challenges of tracking foragers outside their nests while obtaining reliable data on their interactions with both vegetal species and prey. If successfully done, this could reinforce arguments on the ecological services provided by social wasps.

### 3.8.3 *Collective Personalities*

Since the early 2000s, the study of animal personalities has been experiencing a sharp increase in interest among behavioural ecology researchers. Previously interpreted as statistical noise, consistent behavioural variations are now investigated for their theorized role in success and evolution of organisms (Sih et al. 2004). Moreover, the study of social behaviour and the personality of superorganisms – or collective personalities – has presented itself as an exciting new subarea in which sociobiology may be explored through research (Jandt et al. 2014; Wright et al. 2019). For foraging behaviour, relationships between personality traits and general ecology – such as aggressiveness and foraging success or parental care – could be verified for Neotropical social wasps, helping not only in the understanding of their life history but also of the evolution of social behaviour as a whole.

## 3.9 **Concluding Remarks**

The foraging behaviour of Neotropical social wasps is one of the most fascinating topics to be explored on the group's behavioural ecology. Here, we briefly presented some of the most unique aspects involved in the activity of wasp foragers and tried to show how its different particularities make up complex relationships with other traits such as nest building, pollination or social hierarchy. Studying the foraging behaviour of social wasps is one of the keys to understand the evolution of eusociality in Hymenoptera.

In our perspective, in the specific case of the Neotropical wasps, the group's diversity should transition from being a challenge to being an advantage to research-

ers. Exploring the foraging activity of different clades with both classic behavioural approaches and innovative methods will surely lead to the discovery of unheard behavioural strategies and shed a new light on the existing knowledge not only for the taxon but also for Neotropical systems as a whole.

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## References

- Akre RD (1982) Social wasps. In: Hermann H (ed) Social insects. Academic, New York, 385 pp
- Barbosa BC, Paschoalini MF, Prezoto F (2014) Temporal activity patterns and foraging behavior by social wasp (Hymenoptera, Polistinae) on fruits of *Mangifera indica* L. (Anacardiaceae). *Sociobiology* 61(2):239–242
- Barbosa BC, Detoni M, Maciel TT, Prezoto F (2016) Studies of social wasp diversity in Brazil: over 30 years of research, advancements and priorities. *Sociobiology* 63(3):858–880. <https://doi.org/10.13102/sociobiology.v63i3.1031>
- Barbosa BC, Detoni M, Maciel TT, Prezoto F (2017) Resource storage in the Neotropical social wasp *Mischocyttarus socialis* (Saussure, 1854) (Vespidae: Polistini). *Sociobiology* 64(3):356–358. <https://doi.org/10.13102/sociobiology.v64i3.1686>
- Bichara Filho CC, Santos GMM, Santos Filho AB, Santana-Reis VP, Cruz JD, Gobbi N (2010) Foraging behavior of the swarm-founding wasp *Polybia (Trichothorax) sericea* (Hymenoptera, Vespidae): daily resource collection activity and flight capacity. *Sociobiology* 55(3):899–907
- Brugger BP, Souza LSA, Souza AR, Prezoto F (2011) Social wasps (*Synoeca cyanea*) damaging *Psidium* sp. (Myrtaceae) fruits in Minas Gerais state, Brazil. *Sociobiology* 57:533–535
- Campos-Farinha AEC, Pinto NPO (1996) Natural enemies of *Chlosyne lacinia saundersii* Doubl. & hew. (Lepidoptera: Nymphalidae) in the state of São Paulo. *Anais da Sociedade de Entomologia do Brasil* 25:165–168
- Carpenter JM, Marques OM (2001) *Contribuição ao estudo dos vespídeos do Brasil (Insecta: Hymenoptera, Vespoidea, Vespidae)*, vol 2. Cruz das Almas, Universidade Federal da Bahia. Publicações digitais. 147p
- Castro MM, Guimarães DL, Prezoto F (2011) Influence of environmental factors on the foraging activity of *Mischocyttarus cassununga* (Hymenoptera, Vespidae). *Sociobiology* 58:133–141
- Cavenazzi NCS, Noll FB (2011) Environmental factors influencing foraging activity in the social wasp *Polybia paulista* (Hymenoptera: Vespidae: Epiponini). *Pysche* 2011:542487. <https://doi.org/10.1155/2011/542487>
- Chavarría-Pizarro L, West-Eberhard MJ (2010) The behavior and natural history of *Chartergellus*, a little-known genus of neotropical social wasps (Vespidae Polistinae Epiponini). *Ethol Ecol Evol* 22(4):317–343. <https://doi.org/10.1080/03949370.2010.510035>
- Chevalier L (1924) Observations sur les guêpes. *Bulletin de la Société des sciences naturelles de l'Ouest de la France* 3:66–72
- Corujo VLF, Basilio MA, Galati BJ (2010) Pollen content accumulated in nests of *Polybia scutellaris* (Hymenoptera, Vespidae). *Grana* 49:308–313. <https://doi.org/10.1080/00173134.2010.525663>
- Cruz JD, Giannotti E, Santos G, Bichara-Filho C, Rocha A (2006) Nest site selection and flying capacity of neotropical wasp *Angiopolybia pallens* (Hymenoptera: Vespidae) in the Atlantic rain Forest, Bahia, Brazil. *Sociobiology* 47(3):739–750
- De Souza AR, Venancio D, Prezoto F (2010) Social wasps (Hymenoptera: Vespidae: Polistinae) damaging fruits of *Myrciaria* sp. (Myrtaceae). *Sociobiology* 55:297–299

- Değirmenci L, Thamm M, Scheiner R (2018) Responses to sugar and sugar receptor gene expression in different social roles of the honeybee (*Apis mellifera*). *J Insect Physiol* 106(1):65–70. <https://doi.org/10.1016/j.jinsphys.2017.09.009>
- Dejean A, Rodríguez-Pérez H, Carpenter JM, Azémar F, Corbara B (2017) The predatory behavior of the Neotropical social wasp *Polybia rejecta*. *Behav Process* 140:161–168. <https://doi.org/10.1016/j.beproc.2017.05.011>
- Detoni M, Mattos MC, Castro MM, Barbosa BC, Prezoto F (2015) Activity schedule and foraging in *Protopolybia sedula* (Hymenoptera, Vespidae). *Revista Colombiana de Entomología* 41(2):245–248
- Du Buysson R (1903) Monographie des guêpes au *Vespa*. *Annales de la Société Entomologique de France* 72:260–288
- Edwards R (1980) Social wasps: their biology and control. East Grinstead, Rentokil Ltd, 398p
- Elisei T, Ribeiro-Júnior C, Guimarães DL, Prezoto F (2005) Foraging activity and nesting of swarm-founding wasp *Synoecca cyanea* (Fabricius, 1775) (Hymenoptera, Vespidae, Epiponini). *Sociobiology* 46(2):317–327
- Elisei T, Nunes JV, Ribeiro C Jr, Fernandes AJ Jr, Prezoto F (2010) Uso da vespa social *Polistes versicolor* no controle de desfolhadores de eucalipto. *Pesquisa Agropecuária Brasileira* 45(9):958–964
- Elisei R, Ribeiro Júnior C, Guimarães DL, Prezoto F (2012) Comportamento de forrageio de *Camponotus sericeiventris* Guérin (Hymenoptera, Formicidae) em ambiente urbano. *EntomoBrasilis* 5(2):170–172
- Elisei T, Nunes JV, Ribeiro C Jr, Fernandes AJ Jr, Prezoto F (2013) What is the ideal weather for social wasp *Polistes versicolor* (Olivier) go to forage? *Entomobrasilis* 6(3):214–216. <https://doi.org/10.12741/ebrasilis.v6i3.342>
- Evans HE, West-Eberhard MJ (1970) The wasps. University of Michigan Press, Ann Arbor, 265 pp
- Forsyth AB (1978) Studies on the behavioral ecology of polygynous social wasps. Doctorate thesis. Harvard University, Cambridge, 226 pp
- Gadagkar R (1991) *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, pp 151–190
- Galé YL, Morinson MV, Gracia PC (2015) Amplitud de vuelo y capacidad de carga de la avispa social *Polybia emaciata* Lucas, 1879 (Hymenoptera: Vespidae: Polistinae). *Entomotropica* 30(11):105–111
- Gaul AT (1951) Addition to vespine biology VII. Orientation flight. *Bull Brooklyn Entomol Soc* 46:54–56
- Gaul AT (1952) The awakening and diurnal flight activities of vespine wasps. *Proc Royal Entomol Soc London* 27:33–35
- Ghoul M, Andersen SB, West SA (2017) Sociomics: using Omics approaches to understand social evolution. *Trends Genet* 33(6):4048–4419. <https://doi.org/10.1016/j.tig.2017.03.009>
- Giannotti E, Prezoto F, Machado VLL (1995) Foraging activity of *Polistes lanio lanio* (Fabr.) (Hymenoptera, Vespidae). *An. Soc. Entomol. Brasil* 24(3):455–463
- Gobbi N (1978) Determinação do raio de vôo de operárias de *Polistes versicolor* (Hymenoptera: Vespidae). *Ciência & Cultura* 30:364–365
- Gobbi N, Machado VLL (1985) Material capturado e utilizado na alimentação de *Polybia (Myrapetra) paulista* Ihering, 1896 (Hymenoptera, Vespidae). *Anais da Sociedade Entomológica do Brasil* 14:189–195
- Gobbi N, Machado VLL (1986) Material capturado e utilizado na alimentação de *Polybia (Trichothorax) ignobilis* (Haliday, 1836) (Hymenoptera, Vespidae). *Anais da Sociedade Entomológica do Brasil* 15:117–124
- Gobbi N, Machado VLL, Tavares-Filho JA (1984) Sazonalidade das presas utilizadas na alimentação de *Polybia occidentalis occidentalis* (Olivier, 1791) (Hym., Vespidae). *Anais da Sociedade Entomológica do Brasil* 13:63–69

- Gomes L, Gomes G, Oliveira HG, Morlin JJ, Desuó IC, Silva IM, Shima SN, Von Zuben CJ (2007) Foraging by *Polybia (Trichothorax) ignobilis* (Hymenoptera, Vespidae) on flies at animal carcasses. *Revista Brasileira de Entomologia* 51:389–393
- Gravena S (1983) Táticas de manejo integrado do bicho mineiro do cafeeiro *Perileucoptera coffeella* (Guérin-Ménéville, 1842): I – Dinâmica populacional e inimigos naturais. *Anais da Sociedade de Entomologia do Brasil* 12:61–71
- Guimarães DL, Castro MM, Prezoto F (2008) Patterns of honey storage in colonies of the social wasp *Mischocyttarus cassununga* (Hymenoptera, Vespidae). *Sociobiology* 51(3):655–660
- Heinrich B (1979) Foraging strategies of caterpillars. *Oecologia* 42(3):325–337
- Heldmann G (1936) Über das Leben auf Wabe mi mehreren überwinterten Weibchen von *Polistes gallica* L. *Biologisches Zentralblatt* 56:389–400
- Hernández J, Sarmiento CE, Fernández H (2009) Actividad de forrajeo de *Polybia occidentalis venezuelana* (Hymenoptera, Vespidae). *Revista Colombiana de Entomología* 35(2):230–234
- Hickel ER, Schuck E (1995) Vespas e abelhas atacando a uva no Alto Vale do Rio do Peixe. *Agropecuária Catarinense* 8:38–40
- Holfing JC, Machado VLL (1985) Análise populacional de colônias de *Polybia ignobilis* (Haliday, 1836) (Hymenoptera, Vespidae). *Revista Brasileira de Entomologia* 29(2):271–284
- Huffaker CB, Gutierrez AP (1999) *Ecological entomology*. Wiley, New York, 756 p
- Hunt JH (1982) Trophallaxis and the evolution of eusocial hymenoptera. In: Breed MD, Michener CD, Evans HE (eds) *The biology of social insects*. Westview Press, Boulder, pp 201–205
- Hunt JH (1988) Lobe erection behavior and its possible social role in larvae of *Mischocyttarus* paper wasps. *J Insect Behav* 1:379–386
- Hunt JH (1991) Nourishment and the evolution of the social Vespidae. In: Ross KG, Hunt JH, Baker I, Baker HG (eds) 1982. Similarity of amino acids in nectar and larval saliva: the nutritional basis for trophallaxis in social wasps. *Evolution*, vol 36, pp 1318–1322
- Hunt JH, Nalepa CA (1994) Nourishment, evolution and insect sociality. In: Hunt JH, Nalepa CA (eds) *Nourishment and evolution in insect societies*. Westview, Boulder, pp 1–19
- Hunt JH, Jeanne RL, Baker I, Grogan DE (1987) Nutrient dynamics of a swarm-founding social wasp species, *Polybia occidentalis* (Hymenoptera: Vespidae). *Ethology* 75:291–305
- Hunt JH, Jeanne RL, Keeping MB (1995) Observations on *Apoica pallens*, a nocturnal Neotropical social wasp (Hymenoptera: Vespidae, Polistinae, Epiponini). *Insect Soc* 42:223–236
- Ikan R, Ishay J (1966) Larval wasp secretions and honeydew of the Aphids, *Chaitophorus populi* feeding on *Populus euphratica* as sources of sugars in the diet of the oriental hornet, *Vespa orientalis* F. *Isr J Zool* 15:64–68
- Ingram KK, Kleeman L, Peteru S (2011) Differential regulation of the foraging gene associated with task behaviors in harvester ants. *BMC Ecol* 11:19
- Ishay J, Ikan R (1968a) Food exchange between adults and larvae in *Vespa orientalis* F. *Anim Behav* 16:298–303
- Ishay J, Ikan R (1968b) Gluconeogenesis in the oriental hornet, *Vespa orientalis* F. *Ecology* 49:1
- Iwata K (1976) Evolution of instinct: comparative ethology of hymenoptera. Amerind, Nova Deli, 535 pp
- Jacques GC, Pikart TG, Santos VS, Vicente LO, Silveira LCP (2018) Niche overlap and daily activity pattern of social wasps (Vespidae: Polistinae) in kale crops. *Sociobiology* 65(2):312–319. <https://doi.org/10.13102/sociobiology.v65i2.2670>
- Jandt J, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A (2014) Behavioural syndromes and social insects: personality at multiple levels. *Biol Rev* 89:48–67. <https://doi.org/10.1111/brv.1204>
- Janet C (1903) *Observations sur les Guêpes*. Naud, Paris, 82 pp
- Jeanne RL (1972) Social biology of the Neotropical wasp *Mischocyttarus drewseni*. *Bull Mus Comp Zool* 144:63–150
- Jeanne RL (1986) The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. *Behav Ecol Sociobiol* 19:333–341

- Jeanne RL (1991) Polyethism. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, 678 pp
- Jeanne RL, Taylor BJ (2009) Individual and social foraging in social wasps. In: Harau S, Hrnrcir M (eds) Food exploitation by social insects: ecological, behavioral and theoretical approaches. CRC, Boca Raton, pp 53–79
- Jeanne RL, Hunt JH, Keeping MG (1995) Foraging in social wasps: *Agelaia* lacks recruitment to food (Hymenoptera: Vespidae). *J Kansas Entomol Soc* 68:279–289
- Kasuya E (1982) Central place water collection in the Japanese paper wasp, *Polistes chinensis antennalis*. *Anim Behav* 30:1010–1014
- Köhler A (2008) Floral preferences of the polistine wasp *Polistes versicolor versicolor* Olivier, 1792 (Hymenoptera: Vespidae: Polistinae, Polistini) in Santa Cruz do Sul, Southern Brazil. *Biociencias* 16(2):162–165
- Krehenwinkel H, Kennedy S, Pekár S, Gillespie RG (2016) A cost-efficient and simple protocol to enrich prey DNA from extractions of predatory arthropods for large-scale gut content analysis by Illumina sequencing. *Methods Ecol Evol* 8(1):126–134. <https://doi.org/10.1111/2041-210X.12647>
- Letourneau DK, Chloe J (1987) Homoptera attendance by wasps and ants: the stochastic nature of interactions. *Psyche* 94:81–91
- Lima MAP, Prezoto F (2003) Foraging activity rhythm in the neotropical swarm-founding wasp *Polybia platycephala sylvestris* (Hymenoptera: Vespidae) in different seasons of the year. *Sociobiology* 42(3):745–752
- London KB, Jeanne RL (2003) Effects of colony size and stage of development on defense response by the swarm founding wasp *Polybia occidentalis*. *Behav Ecol Sociobiol* 54(539):546
- Machado VLL (1984) Análise populacional de colônias de *polybia* (*Myrapetra*) *paulista* (Ihering 1896) (Hymenoptera, Vespidae). *Revista Brasileira de Zoologia* 2(4):187–201
- Machado VLL, Parra RP (1984) Capacidade de retorno ao ninho de operarias de *Polybia* (*Myrapetra*) *scutellaris* (White, 1841). *Anais da Sociedade Entomológica do Brasil* 13:13–18
- Maciel TT, Ad'víncula HL, Barbosa BC, Prezoto F (2014) Forrageio Oportunista de Vespas Sociais em Armadilhas Atrativas. *Anais do XXV Congresso Brasileiro de Entomologia*
- Marques OM (1996) Vespas sociais (Hymenoptera, Vespidae): características e importância em agrossistemas. *Insecta* 5:13–39
- Mcpheron LJ, Mills NJ (2007) Learning colour and odour in a paper wasp, *Mischocyttarus flavitarsis*. *Entomologia Generalis* 30(2):105–118
- Moller H, Tilley JAV, Thomas BW, Gaze PD (1991) Effect of introduced social wasps on the standing crop of honeydew in New Zealand beech forests. *New Zealand Journal of Zoology* 18:171–179
- Nascimento FS, Tannure-Nascimento IC (2005) Foraging patterns in a nocturnal swarm-founding wasp, *Apoica flavissima* van der Vecht (Hymenoptera: Vespidae). *Neotrop Entomol* 34(2):177–181
- O'Donnell S (1995a) Division of labor in post-emergence colonies of the primitively eusocial wasp *Polistes instabilis* de Saussure (Hymenoptera: Vespidae). *Insect Soc* 42:17–29
- O'Donnell S (1995b) Necrophagy by Neotropical swarm-founding social wasps (Hymenoptera: Vespidae, Epiponini). *Biotropica* 27:133–136
- Picanço M, Ribeiro LJ, Leite GLD, Gusmão. MR (1988) Seletividade de inseticidas a *Polybia ignobilis* (Halyday) (Hymenoptera, Vespidae) predador de *Ascia monuste orseis* (Godart) (Lepidoptera: Pieridae). *Anais da Sociedade de Entomologia do Brasil* 27:85–90
- Prezoto F, Braga N (2013) Predation of *Zaprionus indianus* (Diptera: Drosophilidae) by the social wasp *Synoeca cyanea* (Hymenoptera: Vespidae). *Fla Entomol* 96:670–672. <https://doi.org/10.1653/024.096.0243>
- Prezoto F, Gobbi N (2003) Patterns of honey storage in nests of the neotropical paper wasp *Polistes simillimus* Zikán, 1951 (Hymenoptera, Vespidae). *Sociobiology* 41(2):437–442
- Prezoto F, Gobbi N (2005) Flight range extension in *Polistes simillimus* Zikán, 1951 (Hymenoptera, Vespidae). *Braz Arch Biol Technol* 48(6):947–950

- Prezoto F, Machado VLL (1999) Ação de *Polistes (Aphanilopterus) simillimus* Zikán (Hymenoptera, Vespidae) no controle de *Spodoptera frugiperda* (Smith) (Lepidoptera, Noctuidae). *Revista Brasileira de Zoociências* 16(3):841–850
- Prezoto F, Giannotti E, Machado VLL (1994) Atividade forrageadora e material coletado pela vespa social *Polistes simillimus* Zikán, 1951 (Hymenoptera, Vespidae). *Insecta* 3:11–19
- Prezoto F, Lima MAP, Machado VLL (2005) Survey of preys captured and used by *Polybia platycephala* (Richards) (Hymenoptera: Vespidae, Epiponini). *Neotrop Entomol* 34(5):849–851
- Prezoto F, Santos-Prezoto HH, Machado VLL, Zanúncio JC (2006) Prey captured and used in *Polistes versicolor* (Hymenoptera, Vespidae) nourishment. *Neotrop Entomol* 35(5):707–709
- Prezoto F, Barbosa BC, Cappas JP, Santos ME (2016a) Water landing as a foraging strategy to water collection in a social wasp: *Polistes dominulus*. *Curr Ethol* 15(2)
- Prezoto F, Barbosa BC, Maciel TT, Detoni M (2016b) Agroecossistemas e o serviço ecológico dos insetos na sustentabilidade. In: Resende LO, Prezoto F, Barbosa BC, Gonçalves EL (eds) *Sustentabilidade: Tópicos da Zona da Mata Mineira*. Real Consultoria em Negócios Ltda, Juiz de Fora, pp 19–30
- Prezoto F, Maciel TT, Detoni M, Mayorquin AZ, Barbosa BC (2019) Pest control potential of social wasps in small farms and urban gardens. *Insects* 10(7):1–10. <https://doi.org/10.3390/insects10070192>
- Rabb RL, Lawson FR (1957) Some factors influencing the predation of *Polistes* wasps on the tobacco hornworm. *J Econ Entomol* 50:778–784
- Rau P (1928) The honey-gathering habitats of *Polistes wasps*. *Biol Bull Marine Biol Lab, Woods Hole* 54:503–519
- Rau P (1939) Studies in the ecology and behavior of *Polistes* wasps. *Bull Brooklyn Entomol Soc* 34:36–44
- Raveret-Richter MA (1990) Hunting wasp interactions: influence of prey size, arrival order, and wasp species. *Ecology* 71:1018–1030
- Raveret-Richter MA (2000) Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu Rev Entomol* 45:121–150. <https://doi.org/10.1146/annurev.ento.45.1.121>
- Raveret-Richter MA, Jeanne RL (1985) Predatory behavior of *Polybia sericea* (Olivier), a tropical social wasp (Hymenoptera: Vespidae). *Behav Ecol Sociobiol* 16:165–170
- Raveret-Richter MA, Jeanne RL (1991) Hunting behavior, prey capture and ant avoidance in the tropical social wasp *Polybia sericea* (Hymenoptera: Vespidae). *Insect Soc* 38:139–147
- Resende JJ, Santos GMM, Bichara Filho CC, Gimenes M (2001) Atividade diária de busca de recursos pela vespa social *Polybia occidentalis occidentalis* (Olivier, 1791) (Hymenoptera, Vespidae). *Revista Brasileira de Zoociências* 3(1):105–115
- Ribeiro Júnior C, Elisei T, Guimarães DL, Prezoto F (2008) Flight range extension in the swarm – founding wasp *Protopolybia exigua* (Hymenoptera, Vespidae, Epiponini). *Sociobiology* 51(1):173–180
- Ribeiro-Júnior C, Guimarães DL, Elisei T, Prezoto F (2006) Foraging activity rhythm of the Neotropical swarm-founding wasp *Protopolybia exigua* (Hymenoptera, Vespidae, Epiponini) in different seasons of the year. *Sociobiology* 47(1):115–123
- Richards OW, Richards MJ (1951) Observations on the social wasps of South America (Hymenoptera, Vespidae). *Trans Royal Entomol Soc London* 102:1–170
- Ricoli LS, Mendes G, Guillermo-Ferreira R (2017) Kick out the ants: a novel and striking behavior in ant-wasp interactions. *Sociobiology* 64(1):119–121. <https://doi.org/10.13102/sociobiology.v64i1.1199>
- Rocha MP (2011) *Biologia e ecologia comportamental da vespa social Polybia platycephala* (Richards, 1978) (Hymenoptera: Vespidae, Epiponini). Master's dissertation. Juiz de Fora, Universidade Federal de Juiz de Fora, 2011. 76 pp
- Rocha AA, Giannotti E (2007) Foraging activity of *Protopolybia exigua* (Hymenoptera, Vespidae) in different phases of the colony cycle, at an area in the region of the Médio São Francisco River, Bahia, Brazil. *Sociobiology* 50:813–831



- Rossi AM, Hunt JH (1988) Honey supplementation and its developmental consequences: evidence for food limitation in a paper wasp, *Polistes metricus*. *Ecol Entomol* 13:437–442
- Roubaud E (1916) Recherches biologiques sur les Guepes solitaires et sociales d'Afrique. *Annales des Sciences Naturelles, Zoologie* 10, 1(1):–160
- Santos GMM, Presley SJ (2010) Niche overlap and temporal activity patterns of social wasps (Hymenoptera: Vespidae) in a Brazilian cashew orchard. *Sociobiology* 56:121–131
- Santos M, Marques OM, Carvalho A (1994) Raio de ação de *Polistes canadensis canadensis* (L., 1758) (Hymenoptera, Vespidae). *Insecta* 3(2):20–24
- Santos GMM, Santana-Reis VPG, Resende JJ, Marco PD, Bichara-Filho CC (2000) Flying capacity of swarm - founding wasp *Polybia occidentalis occidentalis* Oliver, 1791 (Hymenoptera, Vespidae). *Revista Brasileira de Zoociências* 2(2):33–39
- Santos GMM, Cruz JD, Bichara Filho CC, Marques OM, Aguiar CML (2007) Utilização de frutos de cactos (Cactaceae) como recurso alimentar por vespas sociais (Hymenoptera, Vespidae, Polistinae) em uma área de Caatinga (Ipirá, Bahia, Brasil). *Revista Brasileira de Zoologia* 24:1052–1056. <https://doi.org/10.1590/S0101-81752007000400023>
- Santos GMM, Zanon JC, Pires EM, prezoto F, Pereira JMM, Serrão JE (2009) Foraging of *Parachartergus fraternus* (Hymenoptera: Vespidae: Epiponini) on cloudy and sunny days. *Sociobiology* 53(2B):431–441
- Saraiva NB, Prezoto F, fonseca MG, blasioli-Moraes MC, Borges M, Laumann RA, Auad AM (2017) The social wasp *Polybia fastidiosuscula* Saussure (Hymenoptera, Vespidae) uses herbivore-induced maize plant volatiles to locate its prey. *J Appl Entomol*. <https://doi.org/10.1111/jen.12378>
- Seeley TD (1989) The honey bee colony as a superorganism. *Am Sci* 77:546–553
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378
- Silva AGA, Gonçalves CR, Galvão DM, Gonçalves AJL, Gomes J, Silva MN, Simoni L (1968) Quarto catálogo dos insetos que vivem nas plantas do Brasil: Seus parasitos e predadores. Rio de Janeiro, Ministério da Agricultura, Depto. de Defesa e Inspeção Agropecuária, pt. 2, t.1, 621p
- Silveira OT, Esposito MC, dos Santos JN, Gemarque FE (2005) Social wasps and bees captured in carrion traps in a rainforest in Brazil. *Entomol Sci* 8:33–39
- Sinzato DMS, Prezoto F, Del-Claro K (2003) The role of males in a neotropical paper wasp, *Polistes ferreiri* Saussure, 1853 (Hymenoptera, Vespidae, Polistinae). *Revista Brasileira de Zoociências* 5(1):89–100
- Smith AR, Kitchen SM, Toney RM, Ziegler C (2017) Is nocturnal foraging in a tropical bee an escape from interference competition? *J Insect Sci* 17(2):1–7. <https://doi.org/10.1093/jisesa/ix030>
- Southon RJ, Fernandes OA, Nascimento FS, Sumner S (2019) Social wasps are effective bio-control agents of key lepidopteran crop pests. *Proc R Soc B Biol Sci* 286(1914). <https://doi.org/10.1098/rspb.2019.1676>
- Souza AR, Rocha M, Netto P, Venâncio DFA, Prezoto F (2011) Preliminary homing ability study of *Polybia fastidiosuscula* (Hymenoptera: Vespidae) workers. *Sociobiology* 56(1):133–136
- Souza GK, Pikart TG, Jacques GC, Castro AA, Souza MM, Serrão JE, Zanúncio JC (2013) Social wasps on *Eugenia uniflora* Linnaeus (Myrtaceae) plants in an urban area. *Sociobiology* 60:204–209. <https://doi.org/10.13102/sociobiology.v60i2.204-209>
- Spradbery JP (1973) Wasps: an account of the biology and natural history of solitary and social wasps. University of Washington Press, Seattle, 408 p
- Strassman JE (1979) Honey caches help female paper wasps (*Polistes annularis*) survive Texas winters. *Science* 204:207–209
- Sumner S, Law G, Cini A (2018) Why we love bees and hate wasps? *Ecol Entomol* 43(6):836–845. <https://doi.org/10.1111/een.12676>
- Suryanarayanan S, Jeanne RL (2008) Antennal drumming, Trophallaxis, and Colony development in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Ethology* 114:1201–1209



- Taber SW (1999) The world of the harvester ants. Texas A & M University Press, Austin, 213 pp
- Takagi M, Hirose Y, Yamasaki M (1980) Prey-location learning in *Polistes jadvigae* Dalla Torre (Hymenoptera, Vespidae). *Kontyû* 48:53–58
- Taylor BJ, Brus EJ, Jeanne R (2012) Introduction of a scented carbohydrate resource into the nest increases departure rate in *Polybia occidentalis*. *Insect Soc* 59(2):151–157
- Tindo M, Dejean A (2000) Dominance hierarchy in colonies of *Belonogaster juncea juncea* (Vespidae, Polistinae). *Insect Soc* 47(2):158–163
- Warkentin KM (2000) Wasp predation and wasp-induced hatching of red-eyed treefrog eggs. *Animal Behav* 60:503–510
- Warrant EJ (2008) Seeing in the dark: vision and visual behaviour in nocturnal bees and wasps. *J Exp Biol* 211:1737–1746. <https://doi.org/10.1242/jeb.015396>
- Wenzel JW (1991) Evolution of nest architecture. In: Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, 678 pp
- West-Eberhard MJ (1969) The social biology of Polistine wasps. In: Miscellaneous publications n° 140. Museum of Zoology, University of Michigan, Ann Arbor, 101p
- Wheeler WM (1918) A study of some ant larvae, with a consideration of the origin and meaning of the social habit among insects. *Proc Am Philos Soc* 57:193–343
- Wilson EO (1971) The insect societies. Belknap Press, Harvard University Press, Cambridge, MA, 548 pp
- Wright CM, Lichtenstein JLL, Doreing GN, Pretorius J, Meunier J, Pruitt J (2019) Collective personalities: present knowledge and new frontiers. *Behav Ecol Sociobiol* 73:31. <https://doi.org/10.1007/s00265-019-2639-2>