

Research Article

Observations on Forced Colony Emigration in *Parachartergus fraternus* (Hymenoptera: Vespidae: Epiponini): New Nest Site Marked with Sprayed Venom

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Five cases of colony emigration induced by removal of nest envelope and combs and a single one by manipulation are described. The disturbance was followed by defensive patterns, buzz running, and adult dispersion. An odor trail created by abdomen dragging, probably depositing venom or Dufour's gland secretions, connected the original nest to the newly selected nesting place and guided the emigration. The substrate of the selected nesting place is intensely sprayed with venom prior to emigration, and this chemical cue marked the emigration end point. The colony moves to the new site in a diffuse cloud with no temporary clusters formed along the odor trail. At the original nest, scouts performed rapid gaster dragging and intense mouth contacts stimulating inactive individuals to depart. Males were unable to follow the swarm. Individual scouts switched between different behavioral tasks before and after colony emigration. Pulp collected from the old nest was reused at the new nest site.

1. Introduction

According to Sennott and Jeanne [1], three organizational challenges must be faced when swarms disperse. The first is that a subset of the population, the scouts, must find and agree upon a suitable nest site. Second, the scouts induce the rest of the colony to leave for the new site. Finally, scouts guide the emigrating swarm to the new site. A division of labor during the swarming and new nest initiation also has been described [1–4].

West-Eberhard [5] described, for Epiponini, a pattern of aggregation called clumped swarms. These consist of temporary, compact clusters formed at intervals along the swarming route while searching for potential nesting sites. Clumped swarms have been described for *Polybia ignobilis*, *P. raii*, *P. occidentalis*, and *Parachartergus apicalis* [6]. According to Hunt et al. [7], *Apoica pallens* also forms temporary clusters during its emigration.

Scent marking behavior is of great importance to signal the route followed by swarms. Jeanne [8, 9] experimentally confirmed Naumann's conclusion [10] that swarming wasps

follow a scent trail made by secretions of abdominal glands applied to surfaces. According to Howard et al. [11], *Apoica pallens* individuals were observed flexing their terminal gaster segments dorsally while clustering in leaves during an absconding event. This posture exposed the bases of the 5th and 6th sternites, suggesting that the wasps were releasing a pheromone from the sternal glands on these segments. In this way, they would communicate via aerial signaling, rather than by gaster dragging on substrate. Smith et al. [12] suggested that wasps use diverse pheromones to coordinate the swarm. Although gland identity has not been confirmed for most cases, it seems safe to conclude that the gastral ones are often involved.

Several Neotropical genera of epiponines, including *Parachartergus*, lack Richard's gland, and some lack the van der Vecht's gland as well [12]. In several species of these genera, scouts still display the gastral rubbing and trail-following behavior. Sternal glands are also absent in the Paleotropical genus *Polybioides*. However, these wasps use Dufour's (*Po. tabidus*) and the venom gland (*Po. raphigastrea*) as sources of trail pheromone [12–14].

Here, for the first time, the behavior of *Pa. fraternus* scouts during forced emigration is described. I show that *Pa. fraternus* wasps spray venom on the substrate of the newly selected nesting site prior to emigration. Individual behavioral flexibility displayed by scout wasps during the emigration process is also described.

2. Material and Methods

I observed six swarming events in colonies of *Pa. fraternus* over four years (2001–2004) during the months of February to June. Four colonies (C1, C2, C3, and C4) were studied on a private property at Pedregulho, São Paulo State (20°15'S 47°27'W). Two colonies (C5 and C6) were relocated from the same municipality to the University of São Paulo, at Ribeirão Preto Campus. The relocations occurred after sunset to ensure that all adult wasps remained inside the nest. Five colonies were induced to emigrate by removing their envelope and combs (C1, C2, C3, C4, and C6). Workers and queens were individually marked with different color dots on the thorax. While the majority of the individuals were color-coded at the original nest, some scouts were marked while walking at the new nest site, and others were collected and coded while gaster dragging in leaves nearby.

Queens were recognized by their characteristic behavioral syndrome, in which their movement on the substrate was slower than workers, their wings were always half-opened, and the gaster was curved laterally (about 30 degrees) towards every approaching wasp (similar to the gaster-bending display of *Metapolybia* queens mentioned by West-Eberhard [15]). Queen status was confirmed through oviposition observations in the new nest site after colony establishment. Individual wasps observed dragging their abdomens at the original nest substrate, on leaves or prominent objects on the chemical trail or dragging and venom spraying at the new nest site, were considered to be scouts. A total of 11, 10, 29, 15, 10, and 12 queens were color-coded in C1, C2, C3, C4, C5, and C6, respectively. For the workers, 38, 51, 40, 36, 198, and 37 individuals were marked for each colony, respectively.

Relative age and ovary development data were taken for individual wasps only from colony C3. For this, a haphazard sample of color-coded workers was collected after emigration, while laying an egg, or directly from inside the nest when they arrived carrying pulp or water. Relative age was estimated by the extent of pigmentation of the transverse apodeme across the hidden base of each sternite. In this way, following Richards [16], West-Eberhard [17], Forsyth [3], and Mateus et al. [18], females were assigned to the following progressively older age classes: (1) no pigmentation; (2) light brown; (3) dark brown; (4) black. Pattern of ovarian development was checked only for scouts on this colony. Scouts ovaries were categorized into five developmental types following the methods described by Mateus et al. [18]. Type 1 consisted of filamentous ovarioles bearing no visible oocytes. Type 2 possessed slightly developed oocytes, while type 3 consisted of small well-defined oocytes. Type 4 were those

with at least one near-mature oocyte, while type 5 possessed one or more well-developed oocytes.

Except for colony 5, which had been observed and videotaped before the pre-emigration process, all colonies were periodically videotaped beginning from the time envelope and combs were removed until nest re-establishment at the new nest site. Chemical trail deposition and the process of a new nest site selection by scouts was observed and recorded. At the new site, scouts were also periodically videotaped. On the day after the nest structure removal, a video record of the wasps clustered on the original nest substrate was used to estimate the population for each colony. The cluster was recorded early in the morning (i.e., about 07:00) before the wasps started flying.

Swarming behavior comprises the entire sequence of events from removal of the nest structures up to new nest site settlement. Pre-emigration period was measured as the time between removing the nest structures and the start of the emigration process. The start point of the emigration process was considered to be when large numbers of wasps started to fly around the original nest and then departed.

Foragers from colony C5 were color-coded and its observations in the video tape showed that returns to the nest with clearly distended abdomens and in general exchanging the liquid at the nest entrance referred to water foraging; while foragers presenting abdomens near to the normal size, exchanging the resources inside the nest, and spending long time outside the nest were supposedly nectar foragers. Prey and pulp could be observed in the foragers mandibles and were clearly distinguished by color and shape.

3. Results

3.1. Chronological Account of the Swarming of Pa. fraternus. Nest envelope and comb removal from five of the six studied colonies (except colony C5), described above, was followed by similar behavior in all studied colonies.

Removal of the nest structures provoked aggressive defensive behavior including venom spraying directly into the observer's eyes through the mesh of the bee-suit veil, buzz running, and dispersion. The buzz running executed by this specie is similar to the one described by Sonnentag and Jeanne [1] for *Polybia occidentalis*, in which the wasp runs rapidly on the surface of the original nest buzzing its wings and performing quick stops followed by another running event. Many of the disturbed wasps landed on nearby leaves either alone or in small groups. After 20 to 30 minutes, the dispersing individuals returned to the original nest site and crowded on the remaining nest substrate fiber. As soon as the returning wasps landed on the substrate, intense buccal and antennal contacts were observed.

During and immediately after envelope and comb removals, all six colonies displayed brood cannibalism. Many wasps were observed removing large larvae from cells, chewing them for a while and then dropping them on the comb margin or after carrying them in the mandibles in flight. In colony C5, when the envelope was partially

removed to promote intranest observations, similar brood cannibalism occurred involving medium-sized larvae.

During pre-emigration, some individuals were observed dragging their abdomens on the substrate of the original nest before flying. Although the queens and some workers remained inactive, other workers were walking faster than usual. A few foragers returned with water, nectar, or prey and rapidly transferred them to other adults. Some scouts were observed to perform a slow hovering flight while facing the nest 0.3 to 1.0 meters away, followed by landing on the nest substrate or flying away. This type of flight corresponds to that described by West-Eberhard [5] as a looping flight, and it will be subsequently referred to this way.

Upon landing, scouts often antennated the substrate while walking. Scout wasps visited leaves, tree trunks, fence posts, walls, and prominent objects in different directions within 50 meters from the nest. As the looping flights activity increased, some scouts started gaster-dragging runs, which consisted of rapid walking shaking its abdomen side to side with the gastral sternites pressed and rubbed against the substrate. Dragging runs are typically fast and followed by flights. Scout wasps continually returned to the original nest where they landed on the substrate walking faster than usual, making many buccal contacts which were followed by dragging and a new flight event. Over time, scout numbers gradually increased. The increase in the number of scout wasps could clearly seem in the video record of the individuals on the leaves and other marked places along the chemical trail.

At the end of the day, the individuals returned to the original nest site and formed 3 to 5 overnight resting clusters separated by 5 to 10 cm. The next morning, scouts began flying soon after sunrise, and the number of scouts gradually increased throughout the day.

The new nest site was found by following the flight direction of scouts which had been dragging on peripheral leaves and other prominent objects. At the new nest site, groups of individuals were gaster dragging on the surface and performing looping flights in front of the selected place (colonies C1, C2, and C3). After landing on the new nest site, the scouts usually antennated and pressed their mouthparts against the substrate while walking. After that, they performed gaster dragging and flight. These behaviors were usually repeated many times by the same individuals and followed the same sequence in every observation (Figure 1).

Following the return of the first scouts to the original nest site, many unmarked individuals were observed following the chemical trail, and landing on the new nest site adopting the same behavior described for the scouts. About one hour before the start point of the emigration, additional behavioral changes were observed. On the original nest site, speed and intensity of dragging behavior increased as well as the number of individuals performing these behaviors. Meanwhile, on the new nest site, as observed for colonies C1, C2, and C3, scouts were performing fast gaster-dragging runs and bending their abdomen downwards, then, after a quick stop, they sprayed venom on the substrate (Figure 2). Close inspection of the videotaped instances revealed extruded stings during venom spraying. No vapor



FIGURE 1: Cluster of scouts of *Pa. fraternus* from colony C2 visiting a selected new nest site and gaster-dragging on the substrate surface during pre-emigration.



FIGURE 2: Scouts of *Pa. fraternus* from colony C2 spraying venom on the substrate at the new nest site prior to population departure from the original nest.

clouds were observed after this venom spraying, nor could liquids be found on the substrate although an intense smell of venom was perceivable, and it was enough to cause allergic reactions in the eyes and nose of the observer.

Trail followers arrived at the new nest site in a diffuse cloud, and they flew in wide looping arcs before landing. Early in the new nest initiation phase, a circle of individuals formed surrounding the area containing queens and inactive wasps and where the new nest structures were being built.

A few males were counted (6, 4, 5, 9) on the substrate of the original nests after population departure in colonies C2, C3, C4, and C6, respectively. No males were found at the new nest site.

3.2. Individual Colony Emigration Details (Table 1). In colony C1, one hour before departure, 22 scouts were present at the new nest site, dragging and spraying venom. About 20 minutes before the beginning of the emigration process, the population size in the original nest was estimated to be 280 wasps. Emigration itself was characterized by a high number of wasps leaving the original nest and following the chemical trail made by scouts. Several wasps hovered in

TABLE 1: Data relating to emigration events for the six colonies of *Parachartergus fraternus* studied in Brazil. See text for additional details.

Colony number	Pre-emigration initiation (date and time)	Pre-emigration duration (hours)	Cluster of scouts found prior to emigration	Duration of emigration (minutes)	Date and time of emigration	Emigration distances (meters)	Population estimate
C1	02/25/01 10:35	50	02/26/01 15:00 12 scouts	30	02/27/01 11:30	28	290
C2	03/22/01 9:00	74.5	03/25/01 10:00 24 scouts	25	03/25/01 11:30	30	270
C3	03/03/03 11:30	48	03/05/03 11:00 40 scouts	35	03/05/03 11:23	28	350
C4	03/03/03 14:30	49	not found	not observed	03/05/03 between 12:15–13:35	75	360
C5	06/14/03 8:00	55	not found	25	06/16/03 15:00	26	340
C6	03/23/04 18:30	67	not found	not observed	03/26/04 between 12:50–13:45	33	320

front of the scent-marked leaves or landed on them, often antennating the substrate while walking. One hour after the start of the emigration process, 260 individuals were estimated in the new site area. Some scouts continued gaster dragging and spraying venom on the substrate at this point. Emigrating wasps landed on the place where scouts had sprayed venom. After most wasps reached the new nesting place, some color-coded scouts returned to the original nest using the chemical trail and stimulated the remaining wasps to leave through buccal contacts and gaster dragging. Some marked wasps were observed to collect pulp from the original nest before and after emigration. The whole emigration event lasted about 30 minutes.

In *colony C2*, one hour before emigration, 24 scouts wasps were counted gaster dragging and spraying venom on the new nest site substrate. Four minutes before the beginning of population departure, one scout landed in the new site with a small pulp ball in its mandibles. Two minutes after the emigration started, 73 individuals were estimated at the new nest site and, after ten minutes, about 100 individuals could be found there. The large number of wasps spraying venom in the substrate produced a strong smell of venom around the new nest site. The first peduncle construction started 36 minutes after the emigration process had begun. Some wasps were observed returning to the original nest to collect vegetal pulp.

A cluster of scouts from *colony C3* followed the same behavior pattern mentioned above. The number of scouts at the new site and alighting on the chemical trail gradually increased. At the beginning of the emigration process, about 30 wasps were flying around the new site, and 108 individuals were estimated at the original nest site. Just prior to the start of the emigration, some wasps shared pulp at the new nest site, and two peduncles were initiated almost simultaneously. Wasps also were observed returning to the natal nest to

collect pulp. The duration of migration in colony C3 was around 35 minutes.

In *colony C4*, two hours before emigration, 24 scout wasps were observed in a house wall 22 meters from the natal nest; they were gaster dragging on the substrate. About the same time, another group of scout wasps was observed following a chemical trail tracking in a different direction. In the natal nest, the population was agitated, buccal contact was frequent, and arriving scouts performed gaster dragging and flew away almost immediately. The number of scouts in the wall cluster gradually decreased over the next two hours. Unfortunately, the spot selected for the new site could not be found before the emigration. Again, many scouts returned to the natal nest and collected pulp. On the day after, we found the new nest site 75 meters from the natal nest. Four small combs and a partial envelope had already been built.

Colony C5 wasps were observed after the repeated envelope removals over the days prior to emigration. Striking behavioral changes occurred, including a notable reduction in foraging activity, with most of the adult population remaining inside without any external activity. Part of the envelope previously removed to enhance inner observations (see Section 2) was not reconstructed, and a few large larvae were dropped from the colony entrance. Scout wasps were seen visiting leaves 40 meters from the original nest, and thereafter, their activity increased. Some scouts were performing gaster dragging and hasty running over leaves nearby, while others executed the same dragging on the nest entrance before departure.

The pre-emigration pattern for this colony was similar to the ones observed for the other colonies in which the nest structures were actively removed. All queens remained inside the nest, mostly hidden below the combs. During the second and third day, the number of scout wasps increased on the chemical trail. Some marked wasps started to display

TABLE 2: Examples of different behavioral roles displayed by selected individual scouts of *Pa. fraternus* from colony C5 which were the most active foragers and scouts during pre-emigration and nest initiation. Previous role, forager activity: Fn = forager nectar; Fw = forager water, Fpr = forager prey; Fpu = forager pulp. During pre-emigration, individual number of gaster-dragging events on the substrate near natal nest entrance, and number of trips to the new nest site. Nest initiation, forager activity, and number of trips per individual.

Individual	Previous role Forager activity and number of trips observed	During pre-emigration		Nest initiation Forager activity and number of trips observed
		Number of gaster draggings	Number of trips	
1	Fn-1	2	2	Fpu-6
2	Fn-5	4	5	
3	Fn-1	11	14	Fpu-3
4	Fn-2	2	6	Fpu-5
5	Fn-5	1	1	
6	Fn-4	3	10	Fpu-1
7	Fn-9	2	6	Fpu -1
8	Fw-2	2	13	Fpu-2
9	Fpr-8	1	4	Fpu-2
10	Fpu-1	1	5	
11	Fw-5	2	10	Fpu-5
12	Fn-2	1	13	Fpu-4
13	Fn-5	3	10	Fpu-5
14	Fn-1	1	2	
15	Fn-1	2	2	
16	Fn-1	6	4	Fpu-1

scout behavioral patterns. The number of wasps in the nest entrance increased as the number of wasps gaster dragging on the substrate in front of the nest entrance increased.

Emigration was initiated after a large number of wasps started leaving the original nest and flying around. A diffuse but continuous movement of wasps formed a “cloud” 2 to 4 meters wide and 3 meters high until reaching the new nest site. At the new nest site, scouts continued gaster dragging and spraying venom on the substrate throughout the swarm movement and even after the population arrived at the new nest site. At the end of the chemical trail, a great number of wasps performed looping flights around the new site before landing on it. Nest construction started almost immediately after population arrival, with a comb peduncle and a piece of envelope being built simultaneously. Foraging activity for pulp and water increased, and many wasps returned to the original site to collect nest material.

In *colony C6*, two hours before emigration, a large number of scouts were flying around the original nest and landing on leaves nearby. Individual scout behaviors were similar to others mentioned above. Emigration start point was not recorded; however, the duration of pre-emigration was about 67 hours. The new nest was found the next day, 33 meters from the original one, and 12 meters high.

3.3. Individual Task Flexibility of Scout Wasps. Patterns of scout wasp behaviors for the six observed colonies were similar. During nest initiation, color-coded scouts from *colonies C1* and *C2* built cells, shared pulp, and foraged for water and pulp. In the day following colony initiation, marked scouts were the most active builders and foragers.

In *colony C3*, before emigration, a scout removed pulp from the substrate in the natal nest. At the new nest site, two scouts shared pulp and applied it to an initial peduncle. During nest initiation, scouts were active builders and foraged for water. A single color-coded scout was captured immediately after laying an egg in one of the first cells built in the new nest on 03/05/03. Dissection revealed it had developed ovaries and was uninseminated. However, none of 26 marked scouts collected on the following day while returning with water, pulp, or while building envelope or cells, were young individuals or had any ovarian development [18].

In *colony C5*, we verified that some active foragers became active scouts during pre-emigration. Although the cluster at the new nest site was not found before the emigration event, behavioral patterns during nest establishment were observed. Table 2 summarizes the division of labor among color-coded individuals whose behaviors were previously videotaped during a study aiming to analyze foraging activities, and behaviors during the worker production phase, pre-emigration, and nest initiation processes. Color-coded scouts observed gaster dragging on the substrate in front of the natal nest entrance were subsequently monitored, revealing individual task flexibility and division of labor, as these same individuals had been observed foraging for water, nectar, pulp, and prey before pre-emigration. Remarkably, during the pre-emigration phase, they turned into active scouts, depositing the chemical trail and stimulating the inactive population to emigrate. During the new nest initiation, these same wasps foraged for pulp and shared it with nest-mates.

4. Discussion

Venom spraying to mark the new nest site prior to colony emigration has not been reported for any other epiponine species. For *Pa. fraternus*, venom spraying was previously described exclusively as having a defensive function [19, 20], also observed for other species in the genus, *Pa. aztecus* [21] and *Pa. colobopterus* [20].

The results of the induced swarming showed that the duration of the pre-emigration stage varied from 2 to 3 days in *Pa. fraternus* (Table 1). This duration is similar to that described for *Agelaia areata* [22] but was longer than that described for *P. occidentalis* [6]. According to Jeanne [22], the pre-emigration phase of an absconding swarm of *Agelaia areata* lasted about 4 days. Bouwma et al. [6] induced colonies of *P. occidentalis* to emigrate by dismantling their nests; the swarming process occurred on the same day for eight colonies and on the next day for one other experimental colony. However, for both species, the pre-emigration period was not precisely determined since it was not the main objective of those investigations. The results described here also differ somewhat from other studies [1, 5, 6, 11], probably due to methodological differences in swarm triggering (e.g., entire nest translocation [1, 6, 9] or natural swarm observations [5, 22]).

The duration of the pre-emigration phase suggests that adults of *Pa. fraternus* were not prepared for the obligatory departure. For *Pa. fraternus*, in all cases, after the disturbance associated with the nest structures removal, the colony population gradually returned to the original nest site and regrouped on the substrate covered by the remaining pulp fibers that defined the natal nest. No temporary clusters of wasps were observed to form along the emigration route. In studies of *P. occidentalis*, when a swarm was induced, scouts typically formed small aggregations near the old nest along the eventual emigration trail being marked [1, 6, 23]. Chadab [24] observed regrouping off the nest in various Neotropical epiponine species attacked by army ants. Howard et al. [11] observed regrouping in *Apoica pallens* following absconding. After a failed attempt to collect the entire population of a nest of *A. thoracica*, all individuals left the nest and regrouped in a bush four meters from the original nest (S. Mateus unpublished observation).

Immediately after the removal of nest structures, buzzing runs or breaking behavior were displayed by many individuals in the substrate of the original nest. This behavioral pattern was similar to one described by Sonnentag and Jeanne [1], who noted that wing buzzing may be associated with pheromone release and dispersion. Excited buzz running by a few or many individuals is the most characteristic behavioral response observed when absconding is provoked by a sudden event [5, 8, 10, 23]. Ezenwa et al. [25] suggest that buzz running is a pre-emigration behavior, associated with brood removal and occasional cannibalism.

The observed brood cannibalism during envelope removal in this study was similar to that reported for *Metapolybia aztecoides*, *Protopolybia acutiscutis*, and *Synoeca surinama* [5]. Disturbed colonies of *Chartergellus communis*

and *Pa. smithii* displayed similar behavior (S. Mateus unpublished observation).

“Dragging behavior” for trail marking, as well as repeatedly rubbing the ventral surface of the gaster on substrates between new and old nest sites, was first reported by Naumann [10] and since observed in many species of swarm-founding wasps [3, 5, 9, 12, 26]. Gaster-dragging behavior was previously observed in *Pa. fraternus* [12, 26] both before and during emigration.

The observations of scouts of *Pa. fraternus* marking the chemical trail by dragging their abdomens on leaves or other prominent objects along the emigration route suggest that the wasps may use venom or possibly products from the Dufour’s gland as sources of trail pheromone since Richard’s Gland is absent in this species. This secretion would be spread on surfaces by the gaster-dragging behavior. The African ropalidiine *Polybioides tabidus* also lacks sternal glands, and Francescato et al. [13, 14] suggest that in this species, the trail pheromone is produced in the Dufour’s gland.

Consistent with studies on some other epiponine species (e.g., *P. occidentalis*) [6], we found that *Pa. fraternus* males were not able to follow the emigration swarm, as they remained on the substrate of the original nest after all the females had emigrated. However, *Apoica* males can follow the swarm [11, 19, 27]. Males have also been observed in emigrating populations of *Apoica thoracica* and *Synoeca virginea* (S. Mateus unpublished observations).

Colony C5 was under observation for other purposes when its spontaneous swarming took place. Similar to other epiponine species [3, 5, 25], the first signs suggesting imminent nest abandonment were buzz running and a reduction of foraging and building activities.

During pre-emigration, no group or clusters of wasps were present on the nest envelope. However, many individuals stayed around the nest entrance performing intense buccal contacts with incoming scouts.

Following site selection and spray marking, many scouts returned to the natal nest where they performed gaster dragging and intense buccal contacts with inactive wasps before returning to the new nest site. According to Sonnentag and Jeanne [1], the increased bumping stimulates previously inactive individuals to become active and follow the pheromone trail to the new nest site. After contact interactions with scouts, the previously inactive individuals gradually started flying around the natal nest, and within a few minutes, most departed. West-Eberhard [5] reports similar observations.

Reuse of pulp from original nest in early stages of new nest establishment was observed in all colonies and has also been previously reported by O. W. Richards and M. J. Richards [28] and Sarmiento-M [29] for *Pa. fraternus*. In one case (colony C3), construction of the new nest began before the swarm arrived. Nest initiation prior to emigration has also been observed in *P. velutina* [24], *P. sericea* [9], and *Apoica pallens* [10].

During the new nest initiation, a group of wasps encircled the selected nesting spot, facing outward, apparently defending the site. Queens and many inactive wasps clustered

in the upper part of the circled area. Forsyth [3] estimated that about 80 percent of a swarm's population serve as guards, while the remainder become actively engaged in foraging and building activities.

Pa. fraternus queens' only observed activity was oviposition in cells newly built by workers. According to Herman et al. [30], queens of *Pa. colobopterus* are rarely involved in any interactions with other colony members, and no evidence that queens regulate worker activity was found.

For reproductive swarms of epiponine wasps, distances from the natal to the new nest are difficult to obtain. However, absconding swarms typically re-establish the new nest within a few meters of an abandoned site [5, 6, 31] (but an absconding swarm of *Agelaius areata* traveled 319 meters over four days [22]). For the six studied colonies of *Pa. fraternus*, average emigration distance was 36.16 meters (Table 1). For six emigrating colonies of *P. sericea*, the new nest was located 15 to 172 m (mean = 85 meters) from the natal nest [9]. According to Bouwma et al. [6], the distance for 102 induced swarms of *P. occidentalis* colonies ranged from zero to 115 meters. Forsyth [23] suggested that the upper limit for emigration distance might be the foraging range of the foragers who act as scouts. For reproductive swarms, the dispersal distance is important since it potentially affects population "viscosity" and inbreeding. In addition, distance of swarm dispersal can potentially impact competition for resources between the parent and daughter colonies [3].

Division of labor is the division of the work force among the range of tasks performed in the colony, whereas task partitioning is the splitting of a discrete task among workers [32, 33]. For *Pa. fraternus*, both were observed at different phases of the emigration event—during pre-emigration, emigration, and nest initiation. Scouts selected the new nest site, deposited the chemical trail, and stimulated inactive nest mates to leave. At the new nest site, some marked wasps switched to become active builders and foragers. Flexible behavior was striking in colony C3, where one scout was first observed building cells and then ovipositing during nest initiation. Dissection confirmed that this individual fit the definition of an "intermediate" worker, which O. W. Richards and M. J. Richards [34] refer to as an unseminated female bearing some kind of ovary development. Such individuals are commonly found in nests of *Pa. fraternus* [18, 19], where their abundance varies at different stages of the colony life cycle.

4.1. How Do the Emigrating Wasps of *Pa. fraternus* Recognize the End of the Chemical Trail? According to Jeanne [9], for *P. sericea*, the new nest site is recognizable by the presence of a large number of gaster-dragging wasps. In *P. occidentalis*, in which temporary clusters are formed along the emigration trail, the clusters may serve as visual cues to attract the emigrating wasps [3]. The population ultimately aggregates on the last cluster, probably attracted by pheromone release [11]. A remarkable finding in this study is that *Pa. fraternus* does not form clusters along the emigration route. Instead, emigrating wasps form a diffuse swarm, and since scout wasps abundantly spray venom on the substrate of the new

nest site, the venom could be the cue that indicates the end point of the chemical trail. This hypothesis is also supported by the fact that no venom spraying has been observed while scouts were marking the chemical trail, occurring only at the end point. Additionally, the strong venom concentration at the new nest site could serve to deter potential enemies, such as ants, at a vulnerable stage of the nesting cycle.

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