Psyche

Hymenopteran Collective Foraging and Information Transfer about Resources 2012

Guest Editors: F. A. L. Contrera, M. J. Couvillon, and J. C. Nieh

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Editorial Board

Contents

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Editorial

Hymenopteran Collective Foraging and Information Transfer about Resources 2012

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1. Introduction

Foraging in social insects is a complex behavior, as it must balance the decisions made by individual foragers, which typically have limited information, against overall colony needs and the unpredictability of a changing environment. Even solitary insects must deal with the changing spatial and temporal availability of resources. Thus, social and solitary insects have evolved different foraging strategies, some of them studied in this special volume. The studies are divided in three sections: (1) the role of different types of information on nestmate activation during foraging (2) the role of recruitment and interference competition on foraging, and (3) the role of bee behaviors relevant for effective pollination.

2. Information-Based Activation of Nestmates

Social insect colonies can activate their constituents based upon new information during foraging. In this special issue, two papers, respectively, examine how this activation works for information about food competition and information about a profitable nectar source.

Within the same species, different colonies can compete for the same food sources. In their study on the effects of interference food competition in the ant, *Lasius niger*, Fourcassié and colleagues placed a conspecific competitor (an invader) from an alien colony in a foraging arena being exploited by a resident colony. Although the resident colony did not defensively recruit to the invaded foraging site, they responded locally. Resident foragers attacked the alien forager, and the number of resident foragers significantly increased through local recruitment to the vicinity of fights. The residents therefore responded locally, but the colony did not respond at a larger spatial scale to the presence of a competitor.

However, social insect colonies can also mobilize their efforts on a larger spatial scale. For example, they can mobilize nestmates to explore their environment for food and convey a range of information, from the simple existence of food (bumble bees [1]) to its presence and location (honey bees [2]). In their study on wasps, *Polybia occidentalis*, Schueller and Jeanne demonstrate that experienced foragers trained to a feeder could activate foraging for a food source and attract feeder-naïve nestmates (newcomers) to a feeder based upon its scent. These newcomers preferred visiting a feeder with the same scent as that brought back by experienced foragers over a feeder with a different scent. However, experienced foragers did not communicate food source location because newcomers did not significantly prefer the location visited by experienced foragers. This demonstrates that *P. occidentalis*, like bumble bees [3], can be activated to forage based upon food scent and follow an individual-based search strategy, not a group foraging strategy in which food location is also communicated.

3. Foraging Activity Regulation

The seasonal changes in the environment, as well as the presence of invasive species, are factors known to influence the foraging behavior of social insects [4, 5], which developed several strategies to deal with these constraints. The contributions in this section deepen our understanding of the role of environment and invasive species on the foraging regulation in two species of ants and in a bee species. In their paper, Gúzman-Mendoza and coauthors show that in high productivity environments, the niche breadth of the ant, *Pogonomyrmex barbatus*, increases when the resources diminish (dry season) and it decreases when the environmental conditions are better (rainy season). However, in naturally poorer environments, the niche breadth is similar in both seasons. Their results show that *P. barbatus* colonies have different strategies of foraging in different environments, as related to local productivity and seasonal influences.

In another study, Paris and Espadaler showed that the richness of foraging native ants and the time they spent foraging in forest fragments are negatively affected by the presence of the invasive ant, *Lasius neglectus*, and also that trunks in isolated trees may act as dispersal stepping stones for this species. Lastly, Nascimento and Nascimento showed that the stingless bee *Melipona asilvai*, a species from a semiarid region, experiences a strong decrease in the foraging activity and honey storage in the rainy season, suggesting a seasonal diapause in this species.

4. Bee Behaviors Relevant for Effective Pollination

A majority of our commercial crops are insect pollinated [6–8]. However, as we are now all increasingly aware, both wild [9–11] and managed [11, 12] pollinators are experiencing declines in some parts of the world. This situation has focused our attention, as demonstrated in the last two papers, on current and possible future players on the pollinator stage.

The Japanese hornfaced bee *Osmia cornifrons* Radoszkowski (Hymenoptera: Megachilidae) was introduced into the United States in 1977, specifically as a pollinator of rosaceous fruit crops like apples and pears. However, *O. cornifrons* remains a relatively unstudied species. McKinney and Park analyzed trends in daily activity and found that behaviors correlated with temperature, rain, and time of day. These data may be useful for management practices, particularly in finding ways to minimize the impact of pesticides and suggestions for when best to move bees into crop blooms.

Kleinert and Giannini take a broader perspective in their paper. By building a bee-plant interaction matrix, the authors evaluate the bee-plant interactions in different locations within Brazil. They find that *Apis mellifera*, an introduced species to Brazil, and *Trigona spinipes*, a native Brazilian stingless bee species, are the most generalist species. Additionally, both *A. mellifera* and *T. spinipes* are distributed widely, possess a broad diet niche, and contain high levels of individuals per colony.

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Research Article

Cue-Mediated Recruitment in a Swarm-Founding Wasp: Successful Foragers Induce Nestmates to Search off Nest for a Scented Carbohydrate Resource

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The ability of social insect colonies to recruit nestmates to profitable resources increases colony-wide foraging efficiency by providing individuals with information that narrows their search for resources. Here we ask if for the Neotropical swarm-founding wasp *Polybia occidentalis* naïve nestmates are able to use food-scent cues from rich carbohydrate resources brought to the nest by successful foragers to orient to off nest resources. Foragers were allowed to freely visit a training dish containing a scented sucrose solution. At a second location, in a different direction from the nest, two sucrose-filled dishes were offered, one with the training scent and one with an alternate scent. Naïve foragers preferentially chose the training scent over the alternate scent, indicating that natural rates of resource inflow to the nest are sufficient to induce nestmates to forage at resources with a specific scent. Naïve foragers did not forage more often at the location at which the active foragers were foraging, an indication that directional information is not communicated in this species. The total number of foraging trips made by a colony's foragers was not determined by the size of the foraging force, but rather by the average individual foraging rate for the colony.

1. Introduction

Recruitment in social insects has been variously defined as communication that brings individuals to where work is needed [1], "(a)ny behavior that results in an increase in the number of individuals at a particular place" [2, page 115], and "the local increase of workers cooperating at a particular place" [3, page 29]. Recruitment to food enables foragers to exploit patchily distributed resources more efficiently than is possible by independent searching, because it allows them to make use of information that reduces the uncertainty of finding the resource [4, 5]. For species that store excess food reserves in the nest, recruitment allows the colony to more quickly and fully exploit bonanzas that temporarily exceed immediate demand [6, 7].

Although recruitment is often narrowly defined as exclusively signal mediated [8–10], it may also be mediated by social cues [2, 3, 6, 7, 11–14]. Thus, one may distinguish between "signal-based recruitment" and "cue-based recruitment." The waggle dance of the honey bee and pheromone trails of ants are examples of the former, whereas the social wasps' use of food odors brought to the nest and local enhancement at feeding sites are examples of cue-based recruitment to food resources [2, 15]. Although most ant and many bee species have evolved signals used in recruitment to food, they no doubt also make use of social cues [3, 15–19]. In contrast, the social wasps appear to lack signal-based recruitment to food and to rely exclusively on cue-based mechanisms [6, 7, 14, 20–23] (with the exception of the hornet *Vespa mandarinia*, which uses a pheromone signal to recruit nestmates to assist in attacking honey bee colonies [24]).

Foraging and recruitment to food have been little studied in the over 230 species of Neotropical swarm-founding wasps in the polistine tribe Epiponini [14]. This group is known for its broad range of colony sizes, complex social structure,

and striking ecological dominance [25, 26]. Several studies of *Polybia occidentalis* provide insight into the foraging process in this group. *P. occidentalis* is characterized by moderately large colony size and by the ability to store nectar in the nest [26, 27]. During the founding stage, foraging rates are directly correlated with the number of cells in the nest and with the number of larvae in later developmental stages, both of which are indications of colony demand [28].

The coordination of colony-level foraging in *P. occidentalis* occurs without the use of food-source scent-marking [29]. Instead, naïve foragers use cues encountered both in the nest and at the food site to help locate food. Direct introduction of a scented sugar solution into the nest causes an increase in the number of foragers departing from the nest [30]. At least some of these site-naïve individuals learn the food-associated scent and use it as a cue to help locate the source in the field [7]. In a study showing the importance of local enhancement as a cue, foragers bringing a rich, unscented sugar solution to the nest caused an increase in the number of new individuals arriving at a feeding station, where they overwhelmingly chose the food dish at which conspecifics were feeding over an identical dish without conspecifics [6].

In two later studies on this species [7, 30], done at the same field site as the present study, large amounts of scented sugar solution were added directly to the nest, rather than letting foragers bring the resource to the nest from a dish to which they were trained. This approach has two advantages: (1) the large influxes of food stimulated a foraging response that rose enough above background rates to be quantifiable and (2) the output response could be precisely quantified in terms of the known amount of resource input. These studies also demonstrated that the recruiting effects occur independently of the behavior of returning foragers in the nest.

However, these prior studies leave several questions unanswered. Schueller et al. [7] added 40 mL of a 2.0 M sucrose solution to the nest, an amount equivalent to more than 6,000 crop loads (average forager crop size is approximately 6.6 μL) [31]. This translates to a foraging rate equivalent to over 100 loads/min during the 60 minutes of the study. As this rate is more than 35 times the maximum foraging rate documented for this species [32], it leaves open the question of whether the much smaller amounts of scented solution brought back by a few foragers can have the same inducing effect. Although Hrncir et al. [6] let trained foragers return to the nest from a distant dish, because they used unscented sugar solutions, no inferences could be made about the wasps' use of odor cues. Finally, none of these studies directly addressed the question of whether returning foragers provide information about the direction of the resource. In many swarm-founding wasp species, during the dispersal of a swarm from its parental nest, scout wasps lay scent spots on vegetation between the old nest and the new site they have chosen [26, 33, 34]. Although some *Agelaia* spp. have been shown not to use this system to recruit nestmates to a rich protein source [20], whether or not in *P. occidentalis* uses this type of recruitment system for either protein or carbohydrate resources has not been tested.

Here, we address three questions. Firstly, we ask whether the influx of a profitable, scented carbohydrate resource brought to the nest by active foragers is sufficient to induce inactive foragers to begin foraging and searching for a resource with the same scent. Secondly, we ask whether more foragers arrive at the resource being exploited by the active foragers than at an identical resource in a different direction, which could indicate that directional information is being conveyed at the nest. Finally, we ask whether the magnitude of the colony's response to the influx of high-quality food is correlated with colony demand, as measured by number of adults and/or brood, and how the colony-level response is parsed at the individual level.

2. Methods

The investigation was conducted on the private property of the Hagnauer family and the adjacent grounds of Hacienda La Pacifica, near Cañas, Guanacaste, Costa Rica (10.450N, 85.125W), during June and July 2010, shortly after the beginning of the rainy season. Historically, this area was dry forest. Now the Hagnauer property is predominantly pastureland with scattered trees, whereas the grounds of Hacienda La Pacifica have wooded patches with openings planted to lawns and ornamentals. *P. occidentalis* nests are abundant in such disturbed areas; the wasps often construct nests in trees and shrubs along fence lines or roadsides. Colonies were sought within a radius of approximately 1 km from the study site and then moved to locations convenient for conducting the experiment, typically into isolated trees in pastures or yards. We conducted thorough searches of potential nest sites in the area to be sure that no other *P. occidentalis* colonies were close enough for their foragers to interfere with our experiments. Because these wasps are unable to fly in the dark, nests were moved at night to ensure that all colony members were present in the nest during the relocation process. At their new locations, nests were attached to branches about a meter high using metal binder clips, wire, or plastic zip ties. The proximal ends of the branches were coated for approximately 2.5 cm with Tanglefoot (Tanglefoot Co., Grand Rapids, MI, USA) to prevent predation by ants.

Two feeding stations were used during this investigation. The training station was used to mark foragers and, after marking was completed, was used to supply a sucrose solution scented with the training scent to trained foragers. The testing station offered a choice of scented sucrose solutions, one with the training scent and another with an alternate scent. Both stations consisted of Plexiglas tabletops (43 cm $\times$ 30 cm) attached to tripods and adjusted so that the dishes were approximately 0.75 m above the ground and clear of nearby vegetation. The training and testing stations were located 5 m apart and 5 m downwind from the colony (Figure 1). A 2.0 M sucrose solution, either unscented (during training and marking) or containing a 2% scent extract (during testing), was used in all dishes. The sucrose solution was placed in glass feeder dishes (6.5 cm diameter, 1.75 cm deep)—one placed in the center of the training station, and two placed approximately 11 cm apart at the

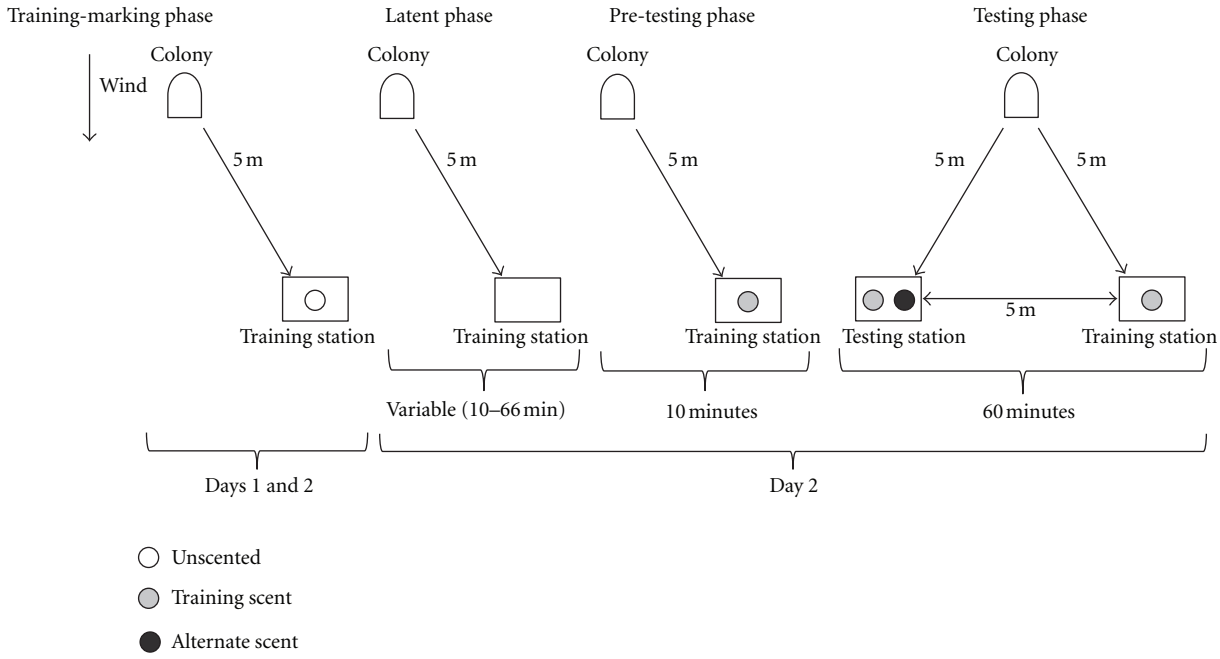

Figure 1: Experimental set-up and procedure. Prevailing wind direction is indicated.

testing station. For the scented solutions, extracts of pure vanilla and imitation cherry (McCormick & Co, Inc., Hunt Valley, MD, USA) were used. Throughout the investigation, the criterion of a "visit" to a dish required that the forager land on the dish and imbibe some of the sucrose solution.

Each of seven colonies was used for one experimental trial (Table 1), consisting of a two-day training-marking phase, a latent phase, a 10 min pretesting phase, and a 60 min testing phase (Figure 1). During the training-marking phase, a large pool of foragers were trained to forage at a dish containing an unscented sucrose solution at the training station and were marked so that they could be identified during the pretesting and testing phases (Table 1). The training procedure began by placing the dish against the nest, allowing workers to feed from it, and then incrementally moving it to the final experimental location (procedure described in detail in von Frisch [35] for honey bees and Schueller et al. [7] for *P. occidentalis*). By the time the training dish was moved to the final location, 5 m downwind of the nest, many foragers were foraging from it.

For marking, each forager was caught by grasping her around the petiole with reverse-action forceps as she landed on the training dish. She was then immediately marked on the thorax with a unique color code (with Decocolor paint pens) and released. The total numbers of individuals marked during both training-marking phase days are given in Table 1. On day one marking continued until, for a period of 10 min., all foragers arriving at the dish were already marked; in other words until there were no longer any unmarked foragers arriving. At the beginning of day two of the training-marking phase, additional unmarked foragers arrived at the dish. These, too, were marked until there were no more unmarked foragers arriving at the training station. The ultimate location of the training station was the same for all phases of the experiment. For each colony the training-marking sessions were carried out on consecutive days, except for colonies 10014 and 10004, when rain intervened (Table 1).

When marking on day two was complete, the training dish was removed from the table at the training station, defining the beginning of the latent phase. With a reward no longer present, the rate of forager arrivals at the station waned. The latent phase ended when no foragers arrived for a period of 2 min. The duration of the latent phase ranged from 10 to 66 min (Table 1). The purpose of the latent phase was to allow foraging on the unscented solution to cease before the colonies were exposed to the training scent.

At the end of the latent phase, the 10-min. pretesting phase was initiated by placing a feeder dish containing 2.0 M sucrose solution, now scented with the training scent, atop the training table. For each colony, one scent was randomly assigned as the training scent and the other as the alternate scent (Table 1). The purpose of this phase was to allow marked foragers to resume foraging, only now they were bringing the training-scented sucrose solution to the nest. Their identities and numbers of visits to the training dish were recorded. All unmarked foragers arriving at the training dish were counted and then captured by placing a 15-dram plastic collection vial over them when they landed on the dish or table. They were placed on ice until the end of the experiment, then released. This was done to ensure that the identity of each forager arriving at the training dish was known and that no forager foraged at both the training and testing dishes.

At the end of the pretesting phase, the 60-minute testing phase was initiated by placing two dishes (henceforth

Table 1: Colony information. For each colony the following are indicated: the colony identification number, dates on which foragers were marked and tested, training scent used, number of combs in the nest, number of adults present at collection (within 36 hrs of end of experiment), total number of foragers marked during the training-marking phase, and the duration of the latent phase. Colony 10028 absconded before it was collected, so it was not possible to count the number of adults on the nest.

Colony	Dates	Training scent	Number of combs	Number of adults	Total marked	Latent phase (min)
10052	June 25-26	cherry	7	2120	93	16
10048	June 28-29	vanilla	7	409	68	10
10029	July 2-3	cherry	7	710	33	25
10014	July 8, 10	vanilla	6	1322	62	24
10028	July 11-12	vanilla	12	NA	66	15
10018	July 15-16	cherry	7	572	36	66
10004	July 21, 23	vanilla	6	462	20	45
Total					378	

referred to as "testing dishes") containing a 2.0 M sucrose solution on the table at the testing station. The testing dishes were placed 11 cm apart and crosswind from each other. One dish was scented with the training scent and the other with the alternate scent. All three dishes—the dish at the training station and the two at the testing station—remained in place throughout the testing phase. At the training station, marked foragers were free to make repeated visits to the dishes; their identities and the number of trips each made were recorded. At the testing station, we recorded the identity, time of arrival, and dish choice (scent and position—left or right, as seen from downwind) of each forager. After each arrival by a forager at a testing dish, the position (left versus right) of the training-scented dish was randomly assigned using a random number table. To ensure that each naïve forager arriving at the testing station made only one visit and had not previously foraged at the training dish during the pretesting and testing phases, as well as to prevent the alternate scent from being brought to the nest, all foragers, marked and unmarked, arriving at either of the testing dishes were captured in 15-dram plastic collecting vials and placed on ice until the end of the experiment. Foragers were defined as "naïve" if they had not visited the training station while the scented dish was present (i.e., during the pretesting and testing phases), and so had no experience with the training scent other than potential exposure to it on the nest. By the end of the testing phase, ample sucrose solutions remained in all dishes.

Within 36 hrs after the conclusion of its testing phase, each colony was collected after sundown by enclosing it in a plastic bag and snipping the supporting branch. The bagged nest was placed in a freezer for at least 12 hours to kill the adult wasps, and then counts were made of the number of adults present, the number of combs in the nest, the number of brood cells, the number and approximate stages of the larvae, and the number of pupae. The adults from colony 10028 absconded before collection, so the adults could not be counted.

Analysis of forager choice at the testing station was performed using a one-factor ANOVA model. We used the proportions of landings at the two dishes at the testing station, rather than absolute counts of landings, because the colonies differed in size and therefore it was not meaningful to compare absolute counts. The proportion of landings on the dishes depended both on what scent was used and whether or not the scent was the one to which the wasps were trained. In order to isolate the effect of training, particularly with a different number of trials conducted with each scent as the training scent, our analysis had to account for both factors. To do so, we define Y_{ij} as the proportion of landings on the dish containing vanilla, whether or not it was the training scent. The model underlying our analysis can be written as

$$Y_{ij} = \mu + T_i + e_{ij}, \tag{1}$$

where $i = 1, 2$ corresponds to the training scent (1 = vanilla, 2 = cherry); j indexes the trial number for each level of i; μ is the overall mean; T_i is the treatment effect; e_{ij} is the random error. We used a weighted ANOVA (with weights proportional to total number of arrivals at the testing station), recognizing that a trial with more landings will result in a more precise measure of the proportion. Because the response variable is a proportion, we used the "arcsine square-root" transformation to achieve homogeneous variance [36].

We predicted that if marked foragers are communicating directional information back at the nest, significantly more naïve foragers would arrive at the training station. A paired t-test was used to compare the number of naïve foragers arriving at the training station to the number arriving at the testing station.

Our analysis of foraging-rate patterns during the pretesting and testing phases explored the relationships between various pairs of the variables: total forager arrivals, average number of trips per forager, number of marked foragers at the training stations, total number of adults, number of larvae, and latent phase. Where appropriate, simple linear regression analyses were performed to quantify the relationships.

Five additional experimental trials were performed, but results were excluded from the forager-choice analysis and/or foraging-rate analyses. For three of these colonies, the total number of arrivals at the testing station was one or none, and thus the colonies provided insufficient data for either analysis. During another trial, the marks on the majority of

Table 2: Arrivals at the training and testing stations during the pretesting and testing phases. Column 2: number of marked foragers making one or more trips to the training station. Columns 3–11: numbers of arrivals. Only the marked foragers visiting the training station (column 3) were allowed to make repeated visits. All others were captured and held on ice upon arrival; therefore, columns 4 and 6–11 represent both numbers of arrivals and numbers of individuals arriving.

		Training station			Testing station					
		Number of arrivals			Number of arrivals					
		Training scent			Training scent			Alternative scent		
(1) Col	(2) Number mk'd indiv	(3) Mk'd	(4) Unmk'd	(5) Total	(6) Mk'd	(7) Unmk'd	(8) Ttl	(9) Mk'd	(10) Unmk'd	(11) Ttl
04	6	197	16	213	3	0	3	1	0	1
18	7	360	8	368	1	6	7	1	1	2
29	8	270	3	273	0	3	3	0	0	0
14	11	204	5	209	1	2	3	1	1	2
28	14	266	16	282	3	3	6	0	3	3
52	22	185	1	186	3	6	9	2	4	6
48	33	179	10	189	1	3	4	0	3	3
Ttl	101	1661	59	1720	12	23	35	5	12	17

Table 3: The relationship between the total number of arrivals to the training station and the average number of foraging trips/forager to the training station, the number of adults in colony, the number of marked foragers foraging at the training station, the number of larvae in the colony, and the duration of the latent phase, using a simple regression analysis.

Source	Slope	Adjusted R^2	*df*	*P*
Average number of trips/forager	3.71	0.84	6	0.0009
Number of adults	0.030	−0.13	5	0.594
Number of marked foragers foraging at training station	−5.56	0.27	6	0.108
Number of larvae	0.044	−0.023	6	0.395
Latent phase (min)	2.22	0.34	5	0.095

foragers arriving at the testing station indicated that they were members of a nearby, newly relocated swarm and not from the colony being tested. The fifth trial (colony 10052) was excluded because its results appeared to have been biased by a previous trial using the same colony. This colony was tested on June 26 with cherry as the training scent and again on July 1 with vanilla as the training scent. Sixty-seven percent of the foragers coming to the testing dishes on July 1 chose the cherry-scented solution. Since *P. occidentalis* colonies store nectar [6, 27], it was likely that colony members had been exposed to the scent of cherry for five days and thus were apt to search for the cherry rather than the newly introduced vanilla. Although this trial was not used for the forager-choice or latent phase analysis, it was included in foraging-rate analysis because nectar storage is not expected to affect foraging rates. Colony 10028 was excluded from regression analyses involving total numbers of adults because the colony members absconded before it could be collected and censused.

3. Results

3.1. Training Station. One-hundred-one marked foragers from the seven colonies made a total of 1,661 trips to the training dish during the pretesting and testing phases (mean = 16.4, SD = 17.3, max/min = 65/1) (Figure 3; Table 2). In addition, fifty-nine unmarked foragers arrived at the training dish during the pretesting and testing phases (Table 2).

Table 4: Relationship between the total number of foraging trips to the training dish/forager and latent phase (min), the number of adults in the colony, and the number of larvae in the colony, using a simple regression analysis.

Source	Slope	Adjusted R^2	*df*	*P*
Latent phase (min)	0.74	0.80	5	0.0039
Number of adults	0.0050	−0.17	5	0.726
Number of larvae	0.012	−.029	6	0.404

The distributions of the numbers of foraging trips made by marked foragers from each nest to the training station for each colony during the pretesting and testing phases are shown in Figure 3. The total number of arrivals to the training station, a measure of colony foraging effort, is correlated with the average number of foraging trips/forager, but not with the number of marked foragers foraging at the training dish, the total number of adults in the colony, or the number of brood in the second larval instar and above (Figure 4, Table 3). The number of foraging trips to the training dish per forager is correlated with the duration of the latent phase, but not the number of adults in the colony, or the number of larvae in the colony (Figure 5, Table 4).

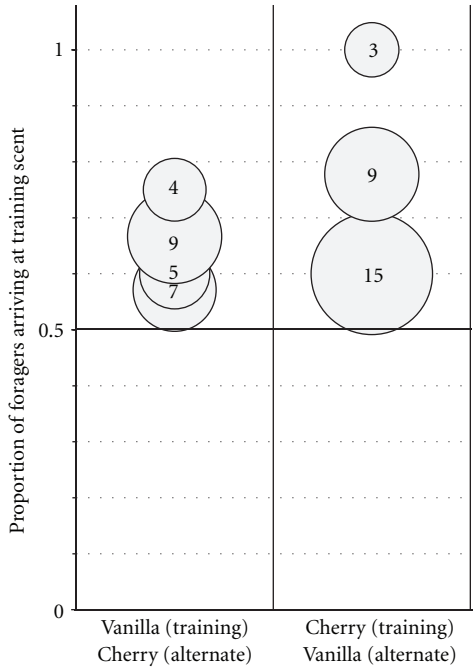

Figure 2: Arrivals at the testing station. Training and alternate scents are indicated. Each circle represents one colony. The center of the circle indicates the proportion arriving at the training scented dish for the colony. The area of the circle is proportional to the total numbers of unmarked foragers arriving at either of the dishes at the testing station; this number is indicated by the number inside the circle.

3.2. Testing Station. Fifty-two foragers from the seven colonies arrived at the one or the other of the two testing dishes during the testing phase (Table 2). Of those, thirty-five were unmarked, so had not previously foraged from any of the dishes (Table 2). Across all colonies, two-thirds of the foragers that arrived at the testing station chose the training scent over the alternate scent $F1, 5 = 7.32$, $N = 7$, $P = 0.0425$ (Figure 2).

The average time between forager arrivals at the testing station was 373 seconds, SD = 531, max/min = 2741/21 seconds, $N = 45$ (7 foragers were the first arrivals so could not be used for this analysis). None arrived while another was at the station.

The number of unmarked foragers arriving at the training station (59) did not differ significantly from the total number of naïve foragers arriving at the testing station (52) (paired t-test: $df = 6$, $T = -0.327$, $P = 0.755$), or the number of unmarked foragers arriving at the testing station (35) (paired t-test: $df = 6$, $T = -1.149$, $P = 0.294$). No marked forager foraged at both the training and testing stations during the testing phase. Only 118 (31%) of the 378 foragers that were marked during the training-marking phase arrived at the stations during the pretesting and testing phases (Tables 1 and 2).

4. Discussion

In this investigation, naïve foragers learned the scent of a carbohydrate solution brought to the nest by successful foragers and used the food-scent cue to locate a sucrose solution at a novel location off nest. Foragers brought the scented sucrose solution to the nest in amounts many times smaller than those added artificially to nests in a previous study [7] and represented a naturally attainable rate of food influx into the nest.

Newly-activated foragers arrived in equal numbers at the training and testing stations, suggesting that these foragers searched for a familiar resource off nest without obtaining directional information at the nest. This result also fails to provide any evidence that *P. occidentalis* lays scent-marks to rich food sources, as it does to new nest sites [26, 33, 34]. Because there was never a wasp present when a forager arrived at the testing station, foragers could not have been using local enhancement to make a choice between the dishes. We conclude, therefore, that naïve foragers relied upon olfactory cues to locate the scented solution off nest. This is the first demonstration that *P. occidentalis* foragers are activated to visit a novel feeder location in response to foragers bringing a scented resource to the nest, without having been trained to arrive at that specific location [6, 7] or using local enhancement cues [6].

The strength of volatiles characterizing natural carbohydrate sources utilized by *P. occidentalis* no doubt varies. Honeydew and extrafloral nectars may provide relatively weak olfactory cues, whereas floral nectars and ripe and rotting fruits no doubt provide strong cues that are detectable from some distance downwind [37]. It is likely that both olfactory cues emanating from a fruit and the visual cue of conspecifics already foraging on it are both utilized by searching foragers, but their relative importance may vary depending on a number of variables, including wind strength and direction and line-of-sight visual distance.

How effective were the active foragers in bringing naïve wasps to the resources? Across all colonies, the 1,661 trips to the training dishes by marked foragers resulted in 111 foragers arriving at the training and testing stations. Thus, it took 1,661/111 = 15.0 forager loads of 2.0 M sucrose to bring each new forager to the resources. By comparison, when Taylor et al. [30] applied 4 mL, or approximately 600 forager loads [30, 31], of the same resource (2.0 M sucrose) directly to the nest, it resulted in approximately 36 additional foragers exiting the nest. By the same calculation, it required 600/36 = 16.7 forager load equivalents to stimulate one extra departure. Taylor et al. [30] counted new foragers as they left the nest, whereas in our investigation the new foragers were counted as they arrived at the resources 5 m downwind from the nest. Since it is unlikely that all naïve foragers departing in search of the scented resource experienced in the nest succeed in finding the resource, the fact that the two figures are so similar suggests that foragers returning with a rich resource (this study) may provide some form of alerting signal that stimulates more to leave the nest than would in response to the resource alone [30]. Although this comparison of the

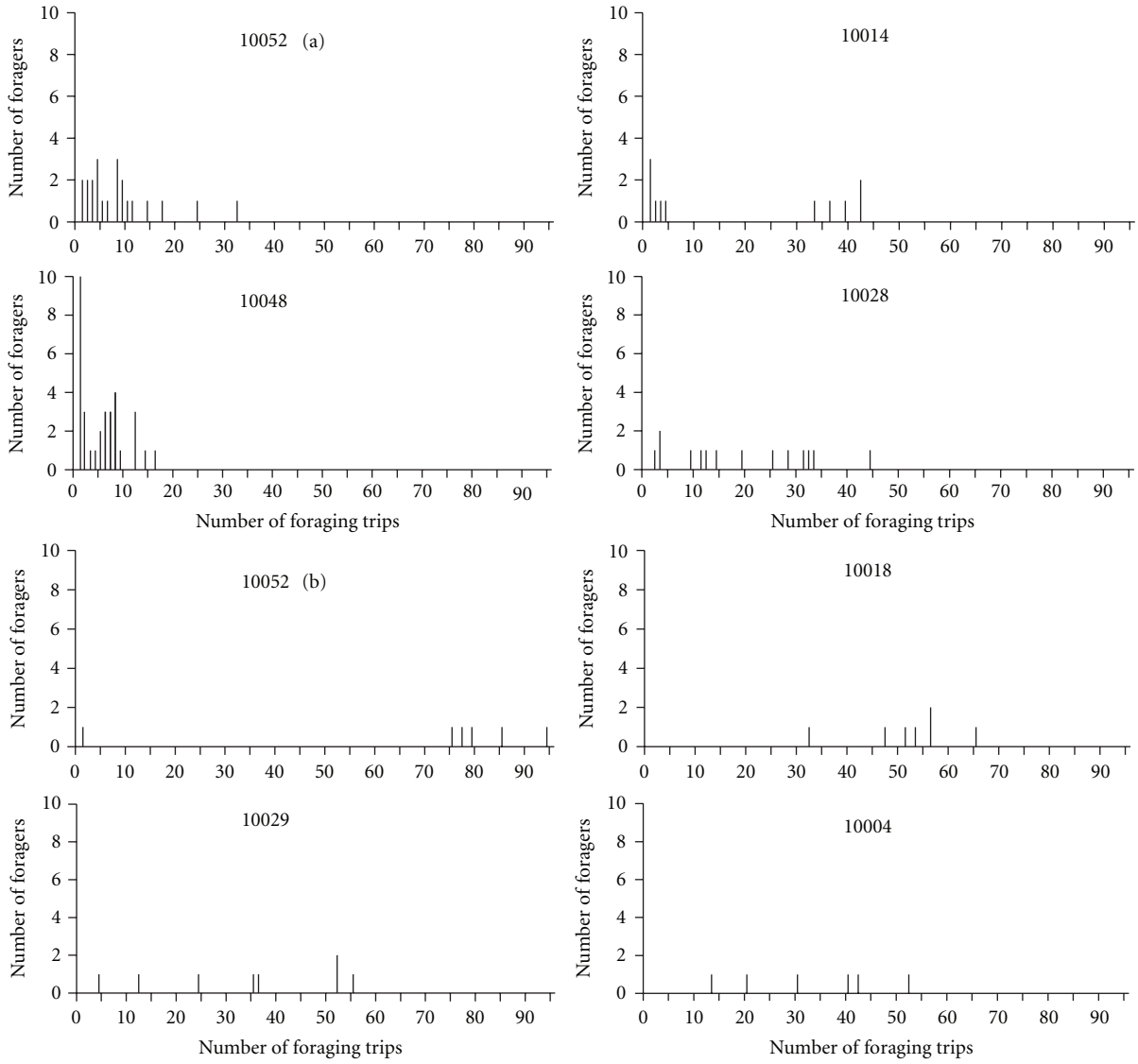

Figure 3: Distribution of numbers of foraging trips each marked forager made to the training station during both the pretesting and testing phases. The x-axis represents the number of trips by each forager and the y-axis represents the number of foragers making the indicated number of trips. 10052 (a) refers to colony 10052 when it was tested on June 26 and 10052 (b) refers to colony 10052 when tested again on July 1.

results of the two studies is rather crude, it is nonetheless worth making for the experiments it may suggest.

Foraging effort, measured as the total number of foraging trips made by marked foragers, did not correlate with colony demand, as measured by either the number of adults or the number of larvae in the colony. This result contrasts with that of Howard and Jeanne [28], who found a strong correlation between foraging rate and colony demand in the same species. The difference may be attributable to differences in the methods used. Howard and Jeanne measured ongoing foraging rates in unmanipulated colonies [28], whereas we trained a set of foragers to make repeated visits to a rich resource. Foraging rates vary tremendously among individuals [38] for reasons that are not well understood. The overall rate at which each colony exploited the resource may have been a function of the individual rates of those foragers in the subset that happened to have been trained to our dishes, independently of the demands of the colony.

Given that colony-level foraging effort bore no relation to colony demand, nor to the number of active foragers in the colony, measured as the number of marked individuals arriving at the testing station, one might then expect a positive correlation between the number of foragers making repeat visits in each colony and the total number of visits to the dishes made by each colony. In contrast to expectation, the relationship trended negative, although not quite significantly so. Although the regression of total trips per colony on the number of active foragers was not significant, there was a positive correlation between total trips and the average number of foraging trips/forager for each colony.

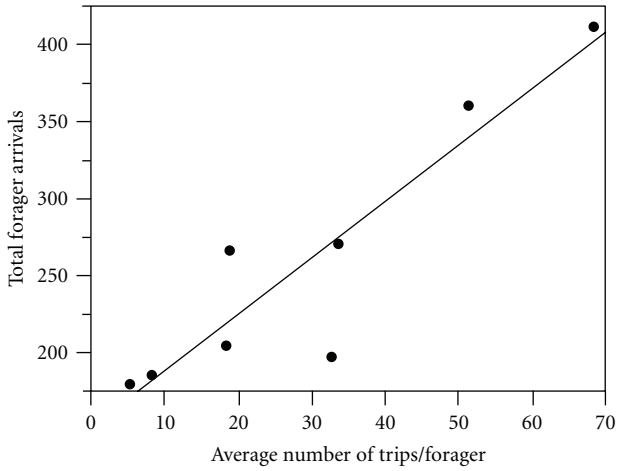

Figure 4: The total number of arrivals of marked foragers, a measure of colony-wide foraging effort, at the training station during the pretesting and testing phases as a function of the average number of trips per forager.

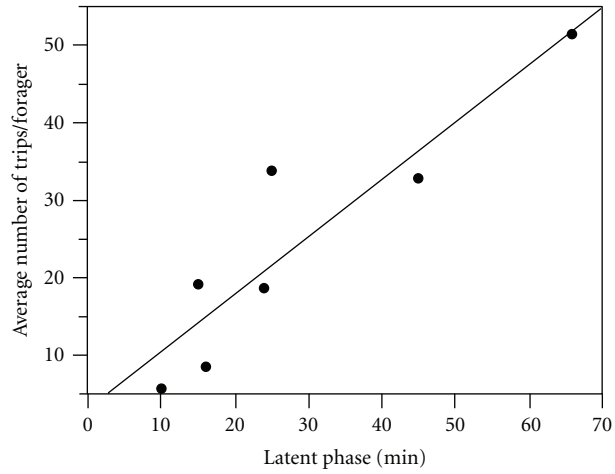

Figure 5: Average number of trips/forager for marked foragers arriving at the training station during the pretesting and testing phases as a function of the duration of the latent phase.

That is, in the colonies that employed the largest number of foragers, those foragers performed the fewest foraging trips, on average. In fact, this relationship was so strong that in colonies employing the fewest foragers, not only did each forager make more trips than in large-group colonies, but the total number of trips made by these colonies was almost double those in the large-group colonies. This is a counterintuitive pattern. A reasonable a priori assumption would be that samples of 6–33 foragers (Table 2) would have similar mean per-capita foraging rates, and therefore that the overall number of trips made by those samples would be in direct relation to the number of foragers in the sample. That this was not the case suggests the existence of some kind of group-size-related dynamic.

One possibility for the observed pattern is that, compared to colonies with small numbers of foragers, in colonies with a large number of foragers returning to the nest, each forager received a less-than-enthusiastic reception by nectar receivers, or a longer unloading-delay, causing them to wait longer before making the next trip. Another possibility is that colonies with the highest overall foraging rates had a higher proportion of "elites" actively foraging than the colonies with lower overall rates. Elite foragers make a disproportionate number of trips [39]. Although the presence of elite nectar foragers has not been documented in *P. occidentalis*, they have been shown to exist in *Vespula germanica* [39], and it has been shown that some *P. occidentalis* make disproportionately more of the foraging trips for nest building materials [40].

Interestingly, the number of foraging trips per forager was also positively correlated with the length of the latent phase, which may be a reflection of the average persistence and foraging rate of the colony's foragers. During the latent phase, the training dish was removed from the training station, disrupting any foraging reinforcement until foragers were no longer arriving at the station. Colonies with the most active and persistent foragers would, therefore, have the longest latent phase. This pattern might also be explained by different proportions of actively foraging elites across colonies. If elite foragers, in general, not only make relatively more foraging trips than nonelites, but also tend to persist longer at the task [40], then one would predict that the latent phase for colonies employing more elites would be longer than those with fewer active elites, the pattern observed during this investigation.

Results of the present investigation demonstrate that the social wasp *P. occidentalis* uses a cue-based form of food recruitment whereby the arrival in the nest of foragers with a rich, scented carbohydrate resource induces naïve nestmates to forage at an off nest resource with the same scent. Many groups of social insects employ this simple mechanism [41]. In choice experiments, naïve *Vespula vulgaris* and *V. germanica* foragers chose resources with the same scent as the ones that were brought to the nest by successful foragers [22, 42]. When a scented carbohydrate solution was added directly to the nest, naïve foragers also preferentially chose the resources with the same scent off nest [23]. Similarly, bumble bee (*Bombus terrestris*) foragers preferentially chose resources with the same scent as those stored in honey pots inside the colony [17, 41]. Honey bee foragers use scent cues experienced at the nest, in addition to the waggle dance, to help locate food sources off nest [4, 15, 35, 43–45]. Cue-based recruitment to food sources has the advantage of allowing foragers to home in on particularly profitable resources, thus, expending less energy than independent searching would require [5, 45]. Recruitment is especially advantageous for species such as *P. occidentalis* that live in the tropics, where resources are more patchily and ephemerally distributed than in temperate regions [45, 46].

In light of the results from this and several other recent investigations, a good picture of carbohydrate foraging and recruitment for *P. occidentalis* can now be drawn. Foragers learn to associate visual and olfactory cues with a carbohydrate resource and use these to aid them in relocating the resource on return visits [7, 47]. They do not mark

the resource with a pheromone signal [31]. Meanwhile, the influx of carbohydrates from successful foragers incites inactive foragers to leave the nest and search off nest. They obtain no directional information from the successful foragers, but they do learn the olfactory cues of the food brought to the nest and search for a resource with the same scent ([6, 30], present investigation). Local enhancement is a second site-based cue that attracts nestmates visually to a specific resource [6]. Both kinds of cues are likely to shorten search time, thereby decreasing energetic expenditures and mortality, by allowing foragers to home in on high quality resources more quickly than by uninformed random searching ([7, 30, 48, 49], present investigation). This mechanism of activating previously inactive foragers may aid in rapid exploitation of resources when they become available [30].

One of the lingering questions about foraging in *P. occidentalis* is whether or not signals play a role in the recruitment process. Taylor et al. [30] observed an increase in rapid running across the envelope when a carbohydrate resource was added to the nest. This behavior was described as being much like the wing fanning and animated running signals used by successful *Bombus* spp. foragers that induce nestmates to begin foraging [50–53] and may indicate that *P. occidentalis* uses an alerting signal as well as a cue-mediated recruitment mechanism [30]. This has yet to be confirmed [30] but, if used, may serve to enhance the efficacy of cue-based recruitment by activating more individuals than is possible via cues alone.

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Research Article

Foraging Activity and Trophic Spectrum of Red Ant *Pogonomyrmex barbatus* Smith, 1858, in Productivity-Contrasted Microenvironments

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Foraging strategies can be influenced by many factors such as abundance, availability, and toxicity of the resources. In arid zones, the distribution and productivity of plants also act as additional factors that affect foraging strategies. Twenty colonies of *Pogonomyrmex barbatus* ants were studied in an arid zone of central Mexico to evaluate the trophic niche breadth in two sites with contrasting productivities in terms of their diversity and amount of resources during two seasons. The results suggest that when the resources are abundant as in the rainy season, the trophic niche breadth is reduced in sites with high productivity and, in the same sites, the trophic niche breadth increases when the resources are limited as in the dry season. In contrast, the trophic niche breadth is similar in both conditions of resource availability (i.e., rainy and dry seasons) at sites with low productivity. During the dry season, populations of *P. barbatus* showed a similar foraging behavior in sites with high and low productivity. Thus, the particular characteristics of a site can significantly affect the foraging strategies of the ants in those environments.

1. Introduction

Food options for organisms are often influenced by several resource characteristics such as availability, distribution, toxins content, palatability, and acceptance, and by the behavior and biology of the organisms, including life cycle, tolerance to environment changes, and feeding habits restrictions [1, 2]. Gordon [3] enumerated the mechanisms behind diet modification in ants in relation to changes in the foraging area: an increase in territory results in higher levels of resources, cost in territory defense, risk of predation, and energy used for gathering and transporting the resources [1, 3]. Other factors that may affect the availability or not of the resources in ant foraging areas include localization, because physical conditions can be very important in the colony development; food availability; intensity of biotic interactions such as inter- and intraspecific competition [4, 5].

According to the optimal foraging theory (OFT), organism must develop cost-effective strategies to obtain more resources and energy by using mechanisms favored by natural selection, resulting in a positive impact on the species fitness [2]. In the case of ants, which are highly diverse and abundant [6], foraging mechanisms involve three general patterns: hunting (including predation and granivory), rewards (e.g., exploitation of extrafloral nectaries, elaiosomes, and homopteran secretions), and defense for discovered resources [7]. Depending on the ant species,

cognitive plasticity (learning) and the use of visual signals are important foraging mechanisms, as observed in *Ectatomma ruidum* (Roger, 1860) and *E. tuberculatum* (Olivier, 1792) [8], and in *Pogonomyrmex* sp., whose learning is related to site fidelity [7].

In arid ecosystems, primary production occurs in pulses attributable to rainy seasonal patterns [9] that produce a high environmental heterogeneity as result of the unequal distribution of humidity in time and space [10]. These seasonal patterns are relevant because little modifications in the ecosystem's components, such as precipitation, can influence variations in other elements, thus generating various microhabitats with different productivities, composition and abundance of primary producers, primary consumers, and predators [11–13].

Resource abundance is an indicator of productivity in terms of energy availability. Organisms modify their feeding behavior in relation to food availability in the habitat. In the case of resource scarcity, several important coincidences in the diet of species have been recorded, increasing the competition for food [14]. In contrast, feeding specialization occurs under conditions of food abundance [2, 15].

Although the arid zones have been regarded as sites with low ant diversity, recent investigations have revealed a remarkably high diversity and abundance [6, 16, 17], together with highly variable interactions and trophic habits, as influenced by time. These reports indicate that ants play relevant roles in various ecosystem processes, including nutrient recycling and redistribution of resources [18].

The aim of the this study was to examine the foraging strategies of *Pogonomyrmex barbatus* (Smith, 1858) in relation to habitat productivity by attempting to answer the following question: how does the trophic spectrum of *P. barbatus* influence habitat productivity in a semiarid zone? We assumed that productivity would be directly related to the diversity and abundance of food [11, 19, 20], allowing a direct relationship between productivity and resources diversity and abundance. Our hypothesis was that, under relatively high productivity, the feeding habits of *P. barbatus* would be more specific, whereas in habitats with relatively low productivity, the feeding habits would follow a generalist behavior. High and low productivities in a habitat are defined in this study as a function of the plant species richness and food abundance.

2. Materials and Methods

2.1. Study Sites. The study was performed at the "Helia Bravo" Botanical Garden (18°27′30″N, 97°24′50″W) at 1678 m a.s.l., located in the Zapotitlán Salinas Valley, into the physiographic region of Tehuacán-Cuicatlán, in Puebla and Oaxaca States, Mexico. The weather is generally dry with a rainy period from May to October each year and 400 mm of annual average precipitation, and a dry season from November to April. The annual average temperature ranges from 18 to 22°C. The dominant vegetation consists of xerophytic shrub, as reported by Rzedowski [21], with physiognomic variations related to the local environmental conditions, resulting in different vegetation types [22].

Two sites in the Botanical Garden, each with contrasting productivities based on plant cover, species richness, and productivity, were selected. The first site was named Jardín (18°19.78′N, 97°27.45′W) and showed the highest values of plant cover (116.36%) and species richness ($S = 25$), when compared to those of the second site named Llano (18°19.54′N, 97°27.26′W), which is located in a zone with high erosion (plant cover = 45.54%; species richness = 16). The distance between the sites, estimated with a Garmin 60 C GPS, was 600 m in a linear direction, although a hill was located between the two sites. Species similarity between the two plant communities was estimated as 12.2% by using the Renkonen similarity index. The availability of resources at the Jardín site, according with a preliminary study by Guzmán-Mendoza [23] was 2,252 seeds of different species, 175 remains of vegetal material (branches, leaves, and parenchymal tissue of leguminous pods), and 1,379 objects of animal material (insects, exuviae, spiders, and caterpillars) per 600 m^2. At the Llano site, the available resources included 12,760 seeds, 470 plant material remains, and 1,004 animal materials per 600 m^2. The amount of resources differed in relation to the site; thus, the Llano site possessed a greater variety of resources (Jardín: $\chi^2_{0.05,12} = 634.46$, $P < 0.0001$; Llano $\chi^2_{0.05,12} = 5663.86$, $P < 0.0001$), and season (rainy season: $\chi^2_{0.05,12} = 1141.14$, $P < 0.0001$; dry season: $\chi^2_{0.05,12} = 4805.67$, $P < 0.0001$). The composition of resources (i.e., seeds types and animal composition) was similar in both sites and seasons.

2.2. Foraging Activity of Pogonomyrmex Barbatus. To establish the intensity of foraging activity, the number of ants engaged in searching and gathering resources for an approximated duration of 8 minutes was counted. In each site (Jardín and Llano) were studied ten colonies for a total of 20 colonies studied in the area. In each observation, the colony disk was divided into four quadrants with directions NE, SE, SW, NW, and each quadrant was observed for 2 minutes. The ants leaving or joining the colony was recorded for each quadrant, counting only those that crossed the disk border. All data were analyzed using two-way analysis of variance (ANOVA) to compare the number of ants engaged in foraging between sites and seasons. Significant differences were tested using the least significant differences (LSDs) multiple comparison test [24].

Trophic niche breadth was estimated from the recorded number of ants returning to the nest with objects in their mandibles. Observations were performed for approximately 20 minutes. The objects carried by the ant using their mandibles were removed using entomological forceps and were assigned to one of the categories previously mentioned. To measure niche breadth, Levins index [25] was used to estimate the width, which was used as a measure of distribution of individuals uniformity among resources. The index value is highest when individuals are observed in all resources, and the minimum value is observed when the individuals are present in only one resource [25]. We estimated the diversity

Table 1: Results of two-way ANOVA test for the effect of site, season and interaction on the foragingintensity of *Pogonomyrmex barbatus* at the "Helia Bravo" Botanical Garden, Puebla, Mexico. Significant level $\alpha = 0.05$.

Variation source	Square sum	F value and probability
Sites	3971.0	$F_{0.05(1)1} = 1.135$; $P = 0.293$
Seasons	68967.4	$F_{0.05(1)1} = 19.719$; $P = 0.001$
Site ∗ season	18409.1	$F_{0.05(1)1} = 5.263$; $P = 0.027$

Table 2: Results of multiple comparison LSD tests for ant foraging during dry and rainy season in two sites, Jardín and Llano. $\alpha = 0.05$. LlR: Llano rainy; LlD: Llano dry; JR: Jardín rainy; JD: Jardín dry. Distinct letters indicate significant differences.

Site-season	Difference average	Probability	Confidence intervals (95%)	
LlD_a				
LlR	120.09	<0.05	171.05	69.12
JD_a	21.90	>0.05	72.87	29.05
JR	60.18	<0.05	111.14	9.21
LlR				
JD	98.18	<0.05	47.21	149.14
JR	59.90	<0.05	8.94	110.87
JD_b				
JR_b	38.27	>0.05	89.23	12.69

of resources by using the Shannon index and compared the results obtained in both communities [25]. The comparisons were made between sites and seasons. Data analyses were performed using SPSS 12.0 software (SPSS INC. 2003 SPSS for Windows rel. 12.0, Chicago IL, USA).

3. Results

3.1. Foraging Intensity. There were differences in the number of ants engaged in foraging in both sites and seasons. During the rainy season, the Llano colonies showed a higher number of foraging ants (average ± se = 53.5 ± 22.73) than the Jardín colonies (20.65 ± 18.96). During the dry season, the observed pattern was reversed: the Jardín colonies were more active (15.07 ± 9.73) than the Llano colonies (6.59 ± 7.17; Table 1). The results of ANOVA test showed significant differences in the site and season, and the LSD multiple-comparison test, LSD reveled that ants were more active during the rainy season, regardless of site (Table 2). The lowest values in activity for both sites (Figure 1) were recorded during the dry season. However, the foraging activity in Jardín was similar during both seasons (MD = 38.2, $P = 0.137$). Nevertheless, in Llano, the season significantly influenced the foraging ant activity (Table 2).

3.2. Trophic Niche Breadth. Similar to the study by Guzmán-Mendoza [23], the heterogeneity of available resources was similar in both sites ($t_{0.05,17.97} = 0.66$, $P = 0.52$), despite the greater abundance of seeds recorded in Llano. The

Table 3: Trophic niche breadth of *Pogonomyrmex barbatus* at two semiarid sites with contrasting productivities during the rainy and dry season. JR: Jardín rainy; JD: Jardín dry; LlR: Llano rainy; LlD: Llano dry.

Site-season	Levins standardized index	Shannon diversity index	t value and probability
JR	0.31	0.95	
LlR	0.17	0.81	$t_{0.05(44)} = 4.96$, $P < 0.0001$
JD	0.16	0.76	
LlD	0.14	0.73	$t_{0.05(34)} = 0.713$, $P = 0.48$

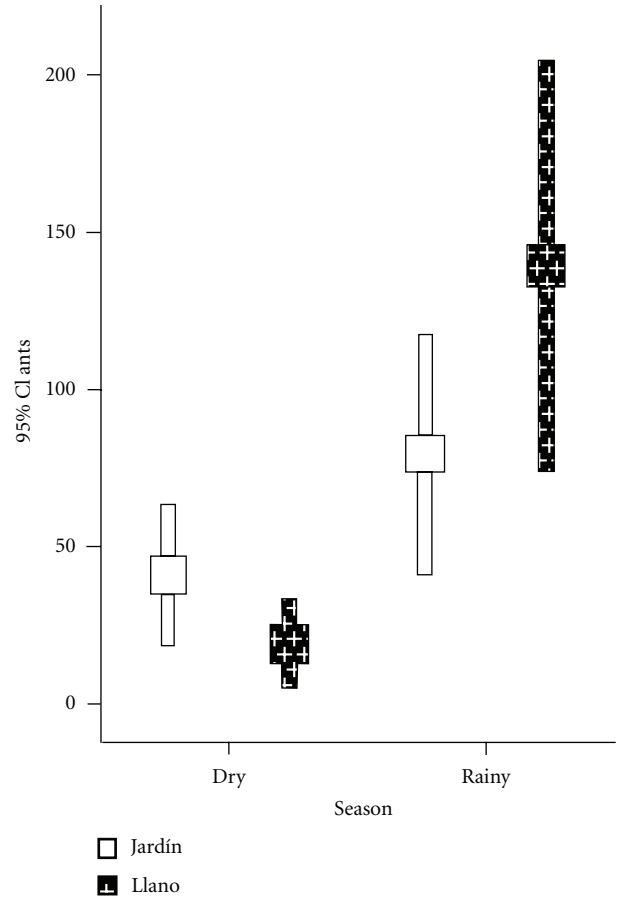

Figure 1: Average foraging activities of active ants at two sites at the Zapotitlán Valley, Puebla, Mexico, with contrasting productivities during two seasons.

comparison of trophic niche breadth showed that the Jardín colonies exhibited a stronger generalist approach than the Llano colonies ($t_{0.05,44} = 4.96$, $P < 0.0001$, Table 3). However, both sites showed that more seeds were used as a major resource on the basis of the observed number of ants physically carrying this specific resource (Figure 2).

Despite the variety of resources available to the colonies, the ants of Jardín mainly foraged on seeds, arthropods, floral structures, leaves and excreta, whereas the Llano ants

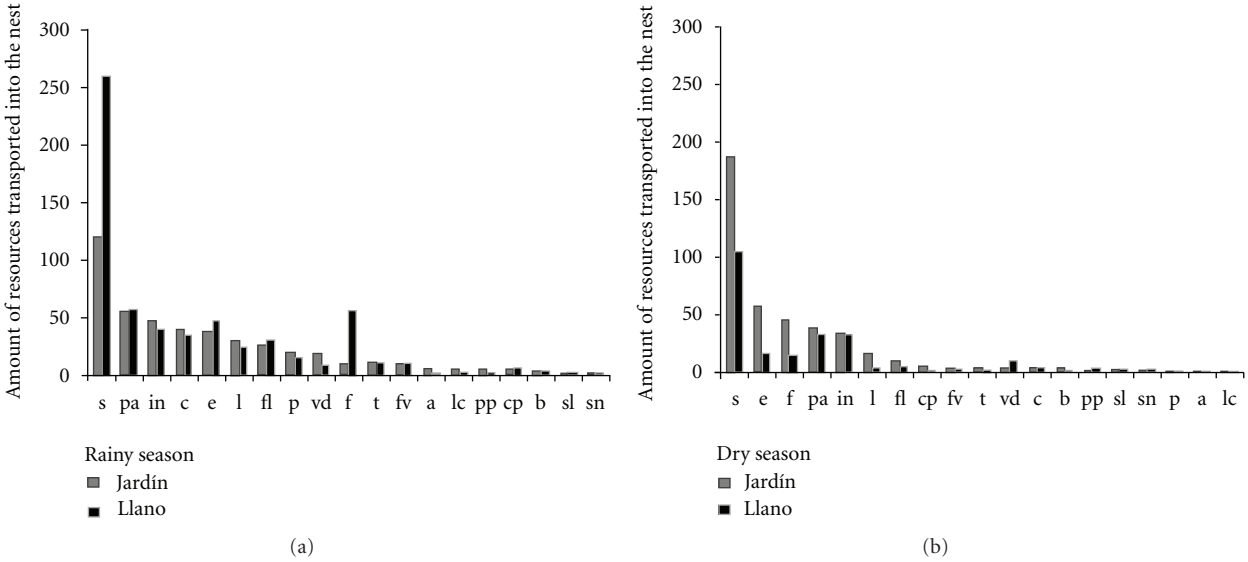

Figure 2: Resources removed from the ant mandibles during the rainy and dry season in two contrasting sites at the "Helia Bravo" Botanical Garden at Zapotitlán de las Salinas, Puebla, Mexico. a: algae; b: buds; c: capitate; cp: caterpillars; e: excretes; f: fruits; fl: flowers; fv: fleshy vegetal tissue; in: insects; l: leaves; lc: lichen; p: peels; pa: pieces of arthropods; pp: pupae; s: seeds; sl: soil; sn: snails; t: twigs; vd: vegetal debris.

were more actively focused on seeds, fruits, arthropods, and excreta.

During the dry season, the amount of resources differed at both sites. More resources and heterogeneity were recorded at Jardín than at Llano ($t_{0.05,17.97} = 44.43$, $P < 0.0001$). The comparison between trophic niches breadth values showed no significant differences during this season ($t_{0.05,34} = 0.713$, $P = 0.48$, Table 3).

4. Discussion

Results from counting the number of foraging ants in relation to trophic niche breadth suggest a direct and positive relationship between both variables. A high number of foraging ants indicated a wider range of choices diet, as observed in the Llano site during both rainy and the dry seasons. When resources were limited, some foraging ants invested less time searching for resources, and instead, focused on the most common resources in the area, such as seeds, insect fragments, excreta, and fruits, as shown in Figure 2. This pattern is related to the season, humidity, and temperature conditions. However, other ant species can search for complementary food sources to increase their trophic spectrum and foraging efficiency [7]. On the basis of these results, our study does not completely agree with the optimal foraging theory (OFT) that predicts wide-range diets in low productive environments, as compared to limited-range diets in high productive environments [2]. Although that theory has been tested in different cases [14, 26, 27], evidence for granivory systems are limited [28], and it seems that the behavioral peculiarities of ants related to patterns of foraging for resources, make them to perform somehow away from the predictions of OFT [29].

The number of foraging ants is related to trophic niche breadth, but the patterns of increase or decrease in the number of foraging ants depend on the environmental conditions related to the season, as shown by the recorded humidity and temperature values. Seasonality is an important factor for niche breadth of *P. barbatus* at the two studied sites, and attributable to the availability of resources and time of foraging, which are directly related to the humidity and temperature of the soil surface. In other arid zones, ants belonging to other species of *Pogonomyrmex* genus showed differences in their foraging habits in response to an environmental gradient; some of them preferred the highest temperatures during the day, whereas others showed peak foraging activity during the coldest hours of day [27]. At the Jardín site, the changes number of foraging ants were attributable to abundance of resources, whereas the diversity of resources at the Llano site showed a modified niche breadth; here, a wider trophic niche was observed with higher diversity levels and more forager ants. Thus, ants at the Jardín site under conditions of high abundance and diversity of resources reduced their trophic niche breadth and activity and were more generalists to a greater extent when the diversity of resources was limited. These results suggest that trophic niche breadth is not influenced by resource abundance alone, contrary to the assumption of the OFT [2].

Although differential abundance of resources can modify the niche breadth, as reported in other organisms such as fishes [14], tadpoles [30], and several butterflies species, and other animals present at a site that was in its first stages of succession after perturbation events and in which food was limited [15, 31], these conditions promote species superposition of diets and strong competition for food. Thus, the abundance and diversity of resources can play an

important role in the establishment of variations in trophic niches. On the basis of the results of this study, it is possible to identify particularities in resource use according to inherent features of each site.

The results obtained in this study may increase knowledge on the feeding scheme of ants, which are important species because of their abundance and diversity but have been poorly studied in terms of their feeding relationships [32]. Nevertheless, it is necessary to conduct more observations and field experiments to quantify the influence of other parameters on ant diet, such as age, species diversity, and predation, to understand the role of the ants in the food web of arid ecosystems [32, 33].

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Research Article

Foraging Activity of Native Ants on Trees in Forest Fragments Colonized by the Invasive Ant *Lasius neglectus*

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Our aim was to investigate the foraging activity of native ants on tree trunks in accordance with their location in forest fragments and the presence or absence of the invasive ant *Lasius neglectus*. Trees were categorized as isolated, edge, or core trees according to their location in forest fragments. In invaded fragments, *Lasius neglectus* had the highest spatial-temporal tree visitation. Isolated trees were visited more and for a longer time by this invasive ant. Invaded fragments had low native ant activity on trees compared to fragments without *L. neglectus*. The few encountered native ant species showed a lower frequency of visitation and for less time in comparison with their spatial-temporal visitation in control fragments. *Crematogaster scutellaris* and *Temnothorax lichtensteini* visited all tree categories in both fragments (invaded or control) but *Lasius grandis* stayed for longer on isolated trees from control fragments. We conclude that in fragments invaded by *Lasius neglectus*, the richness of native ant foraging on trees was negatively affected. Isolated trees close to roads could act as dispersal stepping stones for *Lasius neglectus*.

1. Introduction

In ants, daily and seasonal foraging activity is mainly modulated by the interaction of abiotic and biotic variables [1–4]. Temperature of soil surface and relative humidity has been reported as the most relevant variables that influence ant foraging [5]. However, other abiotic variables such as sunlight, rainfall, wind intensity, atmospheric pressure, and light intensity may influence the activity of some ant species [6–9]. Foraging activity determined by physical variables is modulated by biotic variables such as interspecific competition and habitat structure [3], resource productivity [10], food type, and colony needs [11] and physiological constraints such as heat tolerance [7]. Additionally, the activity of dominant species (*sensu* [12]) may determine the foraging patterns of less dominant species [13]. In this regard, invasive ant species become dominant because of their aggressive behavior and the major abundance that their unicolonial social structure and polygyny (many queens per colony) allow them to achieve in a short time. In consequence, invasive ants monopolize food sources, mainly honeydew-producing insects, negatively affect native arthropods and even small vertebrates, and disrupt and develop mutualisms in native communities [14]. In short, ant-aphid interactions may have strong and pervasive effects extending across multiple trophic levels [15].

The invasive ant *Lasius neglectus* [16] has been proposed by Tsutsui and Suarez [17] as a candidate to become a similar problem to the Argentine ant *Linepithema humile*. Like other invasive ant species, *L. neglectus* relies on honeydew for its main food source and, but for a single instance in a grassland without trees in Tiflis [18], known food sources come exclusively from insect prey and honeydew-producing insects on trees [19]. Thus, here we limit our observations to that particular habitat: trees. *L. neglectus* modifies the arthropod community [20] and does not build elaborate nests. Instead, *L. neglectus* usually nests under flat stones [21], in the topsoil under leaf litter and even

in trash piles (authors pers obs). In human habitats, *L. neglectus* tends to nest inside electrical devices [22]. In Spain, the distribution of *Lasius neglectus* comprises 20 localities. Depending on the locality, its distribution may comprise an area of several hectares where no other ant species are found or there are only a few trees that are eventually shared with other ant species (http://www.creaf.uab.es/xeg/Lasius/Ingles/distribution.htm, last update December 2011). Up to now, this invasive ant species has never been recorded in natural sites in Spain. However, in 2007 several individuals were found foraging in a natural reserve at Argelès-sur-Mer, France (http://www.creaf.uab.es/xeg/Lasius/Ingles/argelessurmer.htm). This highlights the ability of *L. neglectus* to establish in natural areas.

The distribution of invasive ant species is usually shown by placing dots on a map or by painting an entire area [23]. However, a closeup view shows that not all places are equally occupied by an invasive ant species. In this regard, understanding how changes in the spatial-temporal foraging of an invasive species may help to invest control efforts only in hotly invaded areas at the right time. For two years, we have been estimating the attention and abundance of tended aphids for the invasive ant *Lasius neglectus* on oak trees in forest fragments in a suburban area of Catalonia, Spain. Our first impression was that not all trees were equally visited by *L. neglectus* and that some trees are shared or even visited only by native ants. We, therefore, wondered how the spatial-temporal foraging of native ants varies on trees in forest fragments colonized or not by the invasive ant *Lasius neglectus*. During the activity season, we surveyed how many and for how long native ant species foraged on trees in forest fragments colonized or not by this invasive ant. Additionally, we investigated whether the foraging activity of *L. neglectus* varied according to tree location (isolated, edge, or core trees) because invasive ants are mainly associated with disturbed areas as noted by Majer et al. [24] and Suarez et al. [25]. We hypothesized that the native ant species *Lasius neglectus* would occupy more trees located in more disturbed areas (isolated trees) and for a longer time in comparison with native species. Considering the general evidence of the effect of invasive ants on local ants [14], we expected a richer ant community in forest fragments not colonized by *Lasius neglectus*.

2. Material and Methods

2.1. Study Area. This study was performed on the campus of the Autonomous University of Barcelona (41°30′ N, 2°6′ E), an area of 263 ha. Given its biogeographic location, relief and climatic conditions, this area is considered typical Mediterranean mixed holm oak forest. However, this original mixed forest was fragmented due to the agricultural and forest activities performed over the last two centuries. In the late sixties, when the university was built, the campus area was covered by 51.4 ha of fragmented forest [26]. At that time, in Catalonia, land use changed due to the abandonment of agricultural activities and the replacement of firewood with new sources of energy. In consequence, the forest recovered and nowadays 81 ha of the campus is fragmented into the original holm oak (*Quercus ilex* L.) forest, mixed forest (*Pinus* spp. plus *Quercus* spp.), and pine forest (*Pinus halepensis* Mill. or *Pinus pinea* L.). In the first two forest categories, the understory comprises *Asparagus acutifolius* L., *Crataegus monogyna* Jacq., *Rubia peregrina* L., *Rubus ulmifolius* Schott, *Ruscus aculeatus* L., *Smilax aspera* L., *Viburnum tinus* L. and *Hedera helix* L, and in more open forest areas *Spartium junceum* L., *Juniperus communis* L, and *Rosmarinus officinalis* L. In pine forest, the understory is scarce, with *Brachypodium sylvaticum* (Huds.) Beauv. and *Ulex parviflorus* Pourr.

The climate is Mediterranean, with a wet spring and fall and a dry winter and summer. Mean annual temperature is 16.5°C and mean annual rainfall is 575 mm.

In 1997, *Lasius neglectus* was first recorded in a pile of rubble close to one of the University's railway stations. Nowadays, this ant occupies 15% of the campus area including forests, shrubland, gardens, and pavements (Figure 1).

2.2. Forest Fragment Traits and Surveys. We chose as large an area as possible within different fragments of mixed forest in order to survey all trees. We were constrained by the presence of dense understory mainly composed of *Smilax aspera* and *Rubia peregrina* and *Rubus ulmifolius* and by ravines. In April 2005, we chose three areas of 0.14 ha, 0.032 ha, and 0.103 ha occupied almost exclusively by *Lasius neglectus* (Figure 1). In previous years, we noticed that in invaded fragments some trees were regularly visited by native ant species. These invaded areas were separated by roads (distance range: 80–220 m). Two of the chosen areas border grassland (0.094 ha and 0.248 ha) where there were isolated trees. In forest sites, tree density varied between 364 and 844 trees/ha. Meanwhile on grassland, tree density was 46–53 trees/ha.

In April 2006, we added to the study four areas of forest fragments of 0.12 ha, 0.084 ha, 0.04 ha, and 0.057 ha that were not occupied by *Lasius neglectus*. The distance between them was 220 to 2600 m while the distance from forest fragments invaded by *Lasius neglectus* ranged from 720 to 2370 m. Tree density was 298–575 tree/ha.

In all forest fragments, holm oaks represented 20–94% of the surveyed trees. The other tree species included in the fragments were *Quercus humilis* (20–38%), *Pinus halepensis* (20–60%), and *Populus alba* (17–31%).

We measured tree diameters at breast height (DBH) and differentiated trees according to their location in the forest. We considered three categories of tree: isolated trees (I) when the tree trunk was located more than 5 m from the forest and their crown did not contact the forest canopy, edge trees (E) when they bordered fields or roads, and finally, core trees (C) when the trunk was located 5 m from the forest edge and more than 60% of their crown was in contact with the crown of other closer trees. Isolated trees close to invaded forest were considered part of the invaded area.

In this study, on each sampling date, we considered a tree to be visited by a given ant species when we saw a trail on the tree trunk with workers moving downwards with their gasters full of honeydew or a few workers climbing to

Figure 1: The University campus is composed by three main units. The first unit comprises all the university and transportation infrastructure like buildings, parkings, railway stations, roads, and paths. The agroforestal unit is composed by natural areas such as mixed and pine forests, shrubland, grassland and reedbed. Finally, the gardened unit included grass areas with several isolated trees and bushes. The area of the campus invaded by *L. neglectus* is surrounded by a black line. On the right side, areas (a, b, and c) of the chosen invaded (dotted line) and control (continuous line) forest fragments have been enlarged. Isolated trees are shown with small white circles. The arrow, in figure (b) points a roundabout where there are five isolated trees colonized by *L. neglectus*.

explore the crown. Between late April and mid October, we recorded all ant species that were observed climbing all tree trunks, comprising in total 120 trees in invaded fragments and 78 trees in control fragments. We identified ant species foraging on tree trunks in the field, when possible, or we took samples for identification in the laboratory. Trees were observed between 9 h and 13 h (solar time) every 25 ± 2 days, (mean $\pm$ SE). Invaded fragments were surveyed in both years (2005 and 2006), while control fragments were surveyed in one year (2006).

2.3. Statistical Analysis. The size and shape of the chosen areas of fragment types (invaded or not) were compared using a t-test. Tree abundance of each tree category (isolated, edge and core trees) and tree diameter were compared separately using a two factor ANOVA. We considered fragment type and tree category as factors.

The analysis of foraging activity was divided into spatial tree visitation, that is, how many trees of each category were visited and temporal tree visitation, that is, for how long trees of each category were visited. We expressed foraging activity as a percentage of visited trees from each tree category and fragment type. For example, in invaded fragment #number 2, there were 14 core trees. In May, 11 trees were visited by the invasive ant *L. neglectus*. So, the tree visitation score was 78.5% (11/14). Prior to analysis, percentages were subjected to the arcsin transformation although raw data are presented in the text.

2.4. Foraging Activity and Richness of Native Ants. We compared ant species richness using a t-test considering fragment type (invaded or control) as the grouping variable.

Spatial tree visitation by native ants was compared using two-way ANOVA repeated measures including fragment type, tree category, and date of survey as fixed factors and the percentage of visited trees as the dependent variable. Temporal tree occupancy was compared using a two way ANOVA considering fragment type and tree category, as fixed factors and the number of months that a given tree was visited by native ants as the dependent variable.

When significant differences were found ($P < 0.05$) Tukey post hoc comparisons were run. All analyses were performed using Statistica 6.0 [27].

2.5. Foraging Activity of L. neglectus and Its Effect on Native Ants. In invaded forest fragments, spatial tree visitation of *L. neglectus* was analyzed using two-way repeated measures ANOVA including ant type (invasive or native), tree category (isolated, edge, core trees), and date of survey (repeated measure) as fixed factors and the percentage of visited trees as the dependent variable. In this study, we will report only those results related to the main effect of the factors or only their interaction, because at this stage we are not specifically interested in seasonal patterns. Temporal tree occupancy was compared using a two-way ANOVA considering ant type and tree category as fixed factors and the number of months

Table 1: Mean (SE) of forest fragment size, tree abundance and tree diameters at fragments occupied by the invasive ant *Lasius neglectus* (LN) or native ants (NA). Trees were categorized as: isolated trees (I), edge trees (E), or core trees (C). Total abundance of each category is after (SE). Different letters showed significant differences of post hoc comparisons of the interaction between tree category x fragment type (Tukey, $P < 0.05$).

Fragment type	Area (ha)	Edge (m)	Abundance			Diameter (cm)		
			I	E	C	I	E	C
LN	0.092 (0.031)	81.67 (6.74)	2.33 c (1.45) 7	14.67 ab (2.33) 44	23.0 a (4.51) 69	29.49 (2.78)	31.58 (4.00)	28.47 (2.57)
NA	0.075 (0.017)	53.30 (23.98)	1.75 c (0.85) 7	12.75 ab (3.66) 51	5.0 bc (1.08) 20	25.75 (5.12)	28.62 (2.13)	21.51 (2.68)

that a given tree was visited by invasive or native ants as the dependent variable.

3. Results

3.1. Forest Fragment Traits. Both fragment types (invaded or control) had similar size and shape characteristics (area: $t = 0.49$, $df = 5$, $P = 0.646$; edge: $t = 0.88$, $df = 5$, $P = 0.421$; edge/area: $t = 1.26$, $df = 5$, $P = 0.264$, Table 1). The interaction between tree category and fragment type was significant (ANOVA, fragment type x category interaction, $F_{2,15} = 5.74$, $P = 0.014$, Table 1). This was due to less abundance of isolated trees in both forest types (Tukey, $P < 0.05$). On the contrary, core trees were significantly more abundant in invaded fragments (Tukey, $P < 0.05$). However, edge trees did not differ between forest types (Tukey, $P > 0.05$). Tree diameters were similar for both fragment types, (ANOVA, $F_{2,192} = 1.14$, $P = 0.320$) and for all categories (ANOVA, $F_{2,192} = 0.79$, $P = 0.455$, Table 1). Given the general similarity of those characteristics and the common origin of the forest fragment, we assumed that possible differences in ant foraging in trees in invaded and noninvaded fragments are attributable to the presence of the invader, and not to any environmental gradient.

3.2. Foraging Activity and Richness of Native Ants. Richness of native ants foraging on trees was significantly higher in control than in invaded fragments (2006, $t = -6.35$, $df = 5$, $P = 0.0014$, invaded: 6.67 ± 0.31, control: 9.25 ± 0.27) (Table 2). Relative frequencies of native ants diminished markedly in invaded fragments (Table 2).

The spatial foraging of native ants in both fragment types (invaded or control) was the same for all tree categories (repeated measures ANOVA, interaction of forest type x tree category, $F_{2,13} = 2.08$, $P = 0.164$, Figure 2(a)) but in control forest fragments they foraged significantly more than in invaded fragments (repeated measures ANOVA, $F_{1,13} = 43.28$, $P < 0.001$, control: 57.63 ± 3.88% visited trees, invaded: 13.75 ± 4.59% visited trees).

Native ants, in control fragments, remained in all tree categories for a similar time but in invaded fragments they remained significantly more on edge than core trees but some isolated trees were eventually visited (ANOVA, $F_{2,192} = 4.06$, $P = 0.019$, Tukey $P < 0.05$, Figure 2(b)).

Invaded and control forest fragments shared three native ant species whose frequency enabled statistical analysis of their spatial-temporal foraging on trees depending on the fragment type (invaded or control). They are *Lasius grandis*, *Crematogaster scutellaris*, and *Temnothorax lichtensteini* (Table 2).

Spatial tree foraging of *Crematogaster scutellaris* (Cs) and *Temnothorax lichtensteini* (Tl) was similar for both forest fragments (repeated ANOVA measures, Cs, $F_{1,13} = 0.93$, $P = 0.352$; Tl: $F_{1,13} = 0.22$, $P = 0.647$). The interactions between fragment type and tree category were not significant (repeated ANOVA measures, Cs, $F_{2,13} = 0.41$, $P = 0.672$; Tl: $F_{2,13} = 1.04$, $P = 0.382$). In invaded fragments, *Lasius grandis* appeared in only one fragment, so it was not possible to analyze its spatial tree visitation.

Temporal tree foraging of *Crematogaster scutellaris* and *Temnothorax lichtensteini* was similar in both forest fragments (ANOVA, Cs, $F_{1,192} = 0.78$, $P = 0.379$; Tl: $F_{1,192} = 0.58$, $P = 0.446$) but the permanence of *Lasius grandis* differed between fragment types (ANOVA, $F_{1,192} = 64.37$, $P < 0.001$). Post hoc comparisons showed that *Lasius grandis* in control fragments remained for significantly ($P < 0.05$) more months on isolated trees (2.43 ± 0.30 months) than on edge or core trees (edge: 1.22 ± 0.11 months, core: 0.65 ± 0.18 months) while in invaded fragments it remained for a similar time ($P > 0.05$) on edge (1.36 ± 0.12 months) and core trees (0.03 ± 0.1 months). There were no isolated trees in the only invaded fragment where *Lasius grandis* was found.

3.3. Foraging Activity of L. neglectus and Its Effect on Native Ants. In both years, the invasive ant *Lasius neglectus* (LN) visited significantly more trees than native ants (NA) (repeated ANOVA measures, mean ± SE, year 2005, LN: 35.67 ± 3.11% visited trees, NA: 7.71 ± 3.11% visited trees; year 2006, LN: 29.21 ± 3.87% visited trees, NA: 13.75 ± 3.87% visited trees, Table 3). The interaction between ant type and tree category (isolated, edge, or core trees) was significant in both years (Table 3). Post hoc comparisons showed that in both years the invasive ant foraged significantly more on isolated trees than core trees (Tukey, $P < 0.05$) but edge tree visitation did not differ significantly from the other two categories (Tukey, $P > 0.05$, year 2005, isolated trees: 54.36 ± 6.10%, edge trees: 33.75 ± 4.98%, core trees: 18.91 ± 4.98%; year 2006, Figure 3(a)). Native ants in 2005 only visited edge (13.26 ± 4.98%) and core trees (9.86 ± 4.98%, $P > 0.05$) while in 2006 all tree categories were visited in similar percentages (Figure 3(a)).

In both years, *Lasius neglectus* remained on a given tree for significantly more months (year 2005: 2.78 ± 0.19 months; 2006: 2.15 ± 0.16 months) compared with native ants (year 2005: 0.60 ± 0.19 months; 2006: 0.98 ± 0.16

Table 2: Relative frequency (absolute frequency/number of observations) of tree visitation by each ant species at invaded (I) or control (C) forest during the activity period (7 months; in 2006). In brackets are shown absolute frequency that is the number of times each ant species was found along the seven censuses (number of observations: 840 at invaded fragments, 546 at control fragments). Ants were discriminated according to their nesting site: soil (S), arboricolous (A), or arboricolous-under bark (U).

Ant specie	I	C	Nesting site
Lasius neglectus	0.173 (145)		S
Lasius grandis	0.021 (18)	0.176 (96)	S
Lasius emarginatus	0.001 (1)	0.101 (55)	S
Crematogaster scutellaris	0.095 (84)	0.148 (80)	A
Camponotus aethiops		0.064 (35)	S
Camponotus cruentatus	0.008 (7)	0.035 (19)	S
Camponotus piceus		0.002 (1)	S
Camponotus truncatus	0.005 (4)	0.060 (33)	A
Formica rufibarbis		0.002 (1)	S
Myrmica spinosior		0.015 (8)	S
Pheidole pallidula	0.001 (1)	0.002 (1)	S
Plagiolepis pygmaea	0.004 (3)	0.031 (17)	S
Temnothorax lichtensteini	0.026 (22)	0.038 (21)	U
Native ant species richness	8	12	

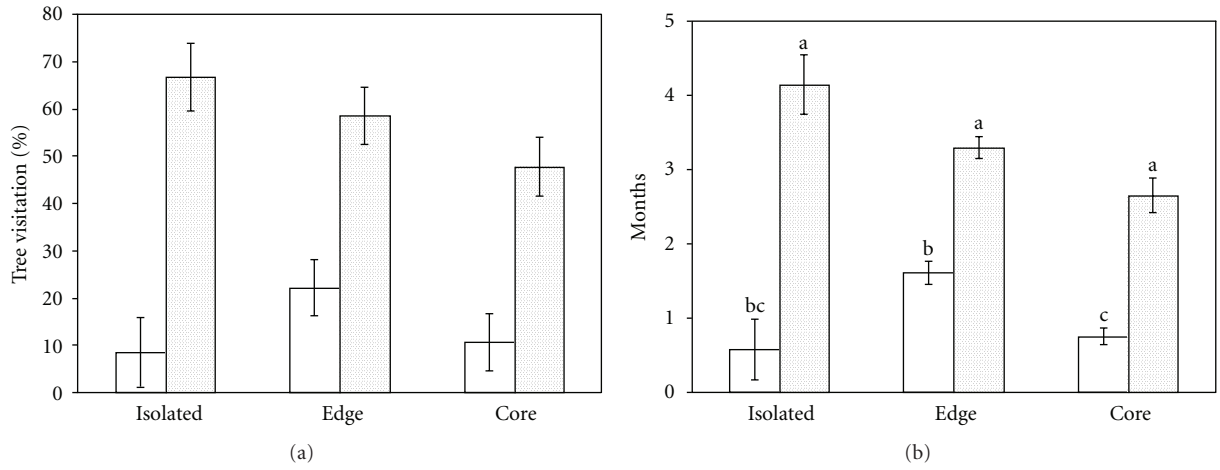

Figure 2: Foraging activity of native ants on trees is shown as the percentage (mean ± SE) of visited trees (a) and the months they remain visited (b) per tree category in 2006 at invaded fragments (bars in white) or at control fragments (dotted bars). Different letters showed statistical differences of the tree category x ant type interaction ($P < 0.05$).

months, ANOVA, year 2005: $F_{1,232} = 66.29$, $P < 0.001$; year 2006: $F_{1,234} = 20.67$, $P < 0.001$). The interaction between ant type and tree category was significant in both years (ANOVA, year 2005: $F_{2,232} = 15.27$, $P < 0.001$; year 2006: $F_{2,234} = 15.45$, $P < 0.001$). In both years, the invasive ant remained on isolated trees for significantly more months (year 2005: 4.67 ± 0.50 months) in comparison to the permanence on the other two tree categories ($P < 0.05$, year 2006, Figure 3(b)). The permanence on edge or core trees of the invasive ant differed significantly ($P < 0.05$) only in 2005 (year 2005, edge: 2.41 ± 0.19 months, core: 1.26 ± 0.15 months; year 2006, Figure 3(b)). Native ants in 2005, a year in which they did not visit isolated trees, remained for the same time on edge (1.02 ± 0.19 months) and core trees (0.77 ± 0.15 months, $P > 0.05$), whereas in 2006 the permanence of native ants was higher on edge trees ($P < 0.05$, Figure 3(b)).

4. Discussion

The consequences of ant invasions on native ant biodiversity has been widely explored. The invasive Argentine ant, *Linepithema humile*, has competitively displaced native ant species as it has spread in its introduced range [28, 29]. Similarly, the red imported fire ant, *Solenopsis invicta*, devastated native fauna as it expanded its range across the southeastern United States [30]. In monsoonal Australia, high abundance of the big-headed ant, *Pheidole megacephala*, corresponded with a 42–85% decrease in the abundance

Table 3: Repeated measures ANOVA of tree visitation (%) at invaded fragments, depending on ant type (invasive or native) and tree category (isolated, edge or core trees). Significant effects ($P < 0.05$) are shown in bold.

	2005			2006		
Source effect	*df*	*F*	*P*	*df*	*F*	*P*
Ant type	1	36.72	**<0.0001**	1	7.43	**0.021**
Tree category	2	1.17	0.349	2	2.79	0.108
Ant type x Tree category	2	9.67	**0.005**	2	7.48	**0.010**

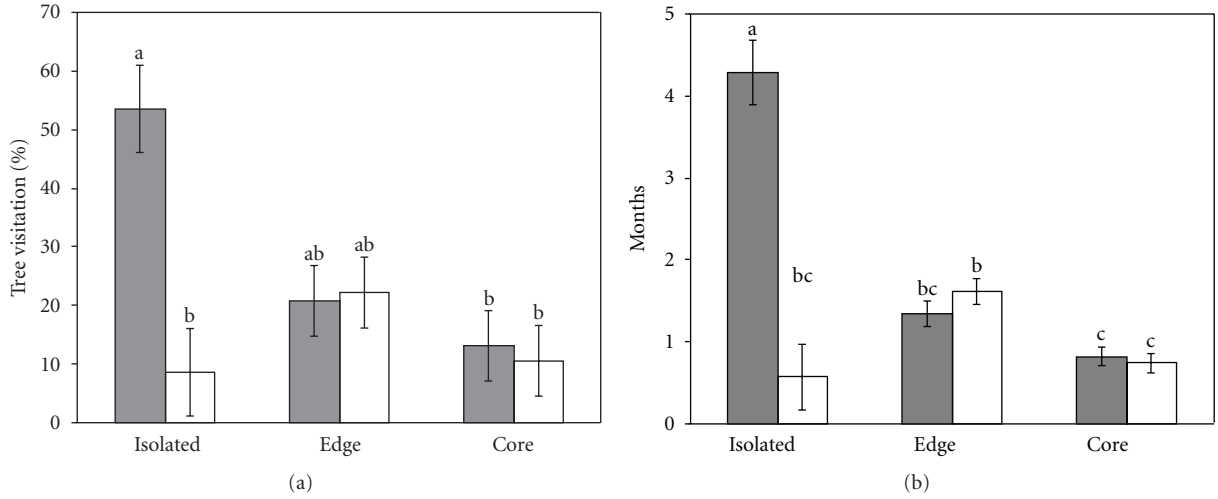

Figure 3: Foraging activity at invaded forest fragments is shown as the percentage (mean ± SE) of visited trees (a) and the months they remain visited (b) per tree category in 2006. Bars showing trees visited by *Lasius neglectus* are in grey and visited by native ants are shown in white. Different letters showed statistical differences of post hoc comparisons (tree category x ant type effect) ($P < 0.05$).

of other native invertebrates [31], and the yellow crazy ant, *Anoplolepis gracilipes,* displaced other ant species as its activity increased and boundaries expanded on Christmas Island [32]. According to Andersen [33], only those native ant species with specialist foraging times or microhabitat preferences are the most resistant to elimination.

4.1. Foraging Activity and Richness of Native Ants. In our study site, the richness of ants foraging in trees in invaded forest fragments was significantly lower in comparison with control forest fragments. The strongest effect of the presence of *L. neglectus* is for the congeneric *L. grandis* and the weakest effect is for smaller and cryptic species. This general finding was already reported by Ward [34] in an Argentine ant invasion in natural habitats of the lower Sacramento River Valley. This effect of *L. neglectus* on the ant community has been reported by other authors at sites with a higher density of this invasive ant [18, 35]. The native ants *Lasius grandis*, *Crematogaster scutellaris,* and *Temnothorax lichtensteini,* were encountered in both fragment types (control or invaded) (Table 3) but showed a lower frequency in invaded fragments. All these native species collect honeydew and small insects. In the invaded fragments, the few trees on which *Crematogaster scutellaris* and *Temnothorax lichtensteini* were able to forage were visited with the same spatial-temporal tree visitation as in the control fragments. *Lasius grandis* was found in only one invaded fragment so comparison was not possible with the situation in control fragments where it remained for more months on isolated trees at the highest tree visitation frequency. This could be the consequence of its nesting habit. The native ant *Lasius grandis* is able to nest in open areas that are associated with isolated trees and dig burrows at the base of visited trees from where workers climb to tend aphids (Paris pers. observ.). The other two native ant species that appeared in all fragments, *Crematogaster scutellaris* and *Temnothorax lichtensteini*, have their own ecological particularities that may enable them to coexist with *L. neglectus*. In mixed forests, *Crematogaster scutellaris* is considered a dominant ant species or codominant with *Pheidolle pallidula* [36, 37]. This native ant is an arboricolous polydomous nesting ant that changes its nesting location frequently and is highly aggressive. These traits may enable *Crematogaster scutellaris* to coexist with *Lasius neglectus* in invaded fragments. Marlier et al. [36] observed, in a fig plantation (*Ficus carica* L.) with the presence of *Lasius neglectus*, that the presence of *Crematogaster scutellaris* did not influence invasive ant activity. Instead, the opposite effect is probably certain although this should be specifically tested. The frequency of tree visitation suggests that in invaded forest fragments *Lasius neglectus* negatively affected the presence of *Crematogaster scutellaris*. In fact, in Doñana National Park, *Crematogaster scutellaris* colonies were successfully displaced from cork oak trees by another invasive ant: *Linepithema humile* [37]. The other native ant species found in all invaded fragments, *Temnothorax lichtensteini*, is a cryptic

species that nests under bark and its small size and low abundance likely diminished the probability of encountering *Lasius neglectus*. Other authors have also reported that some native ant species are able to coexist with invasive ants. On Christmas Island, *Paratrechina minutula* and *Paratrechina longicornis* were commonly found in the same area as the invasive ant *Anoplolepis gracilipes* supercolony [32]. In Japanese urban parks, *Paratrechina sakurae* and *Camponotus vitiosus* coexisted with the invasive ant *Linepithema humile* [38].

Although our monthly surveys were conducted between 9 and 13 PM, we do not expect the situation for native species found in invaded fragments to change over the course of the day because of their foraging patterns. Previous data on *Lasius neglectus* activity showed that this invasive ant has a 24 hr activity cycle (http://www.creaf.uab.es/xeg/Lasius/Ingles/gr2dailyactivity.htm). Concerning *Lasius grandis*, we do not have a detailed 24 hr activity cycle and no information was found in the literature. But a survey performed in the invaded fragments at 6 hour intervals in previous years showed that *L. grandis* was active all day. In fact, other *Lasius* (s.str.) ant species also showed a 24 hr activity period. *Lasius lasioides* in northern Tuscany, Italy (Figure 1 [39]), showed continuous activity between May and July. In Maryland, USA *Lasius alienus* in a woodlot of a second-growth forest composed mostly of oaks (*Quercus* spp.), and Virginia pines (*Pinus virginianus*) also showed an activity period of 24 hrs (Figure 3 [40]). According to Redolfi et al. [41], the maximum foraging pattern of *Crematogaster scutellaris* occurs mainly between 9AM and 16 PM. Concerning *T. lichtensteini*, which is one of the most abundant ant species in Catalonian forests [42], we found no information about its daily foraging pattern. However, considering that this ant species nests under the bark, that its nest comprises less than 200 individuals, and also that is a timid ant species that forages alone and avoids competition, its presence was probably not perceived by *L. neglectus*.

Some field observations lead us to speculate on how *Lasius neglectus* may displace native ants. First, the abundance of *Lasius neglectus* in trees and soil is higher compared with native ants [35]. This higher abundance increases the possibility of finding and monopolizing food resources to the detriment of native ants [12]. Second, on tree trunk trails, when *Lasius neglectus* workers find a native ant worker, they try to capture it or show highly aggressive behavior towards it by pulling their legs or antennae. This behavior should disrupt native ant foraging on the canopy, diminishing the food supply for native colonies. The aggressive behavior of *Lasius neglectus* towards native ants has recently been observed in laboratory aggression tests with *Lasius neglectus* and other *Lasius* native ants: attacks by *Lasius neglectus* were performed faster and most frequently against *Lasius grandis*, were intermediate against *Lasius emarginatus*, and delayed in time and less frequent against *Lasius cinereus* [43]. Finally, recently fertilized native queens of *Messor* sp and *Lasius grandis* that landed on invaded forest fragments were captured immediately by *Lasius neglectus* workers (Paris pers. observ.). Hence, the invasive ant may directly interfere with the establishment of new native colonies.

4.2. Foraging Activity of L. neglectus and Its Effect on Native Ants. In both years, spatial-temporal tree visitation by the invasive ant *Lasius neglectus* was higher than that of the native ants found in invaded fragments. In particular, isolated trees were more visited and for a longer time by the invasive ant in comparison with other tree categories and with native ant foraging on trees. The polydomous colony structure of *L. neglectus* enables them to move freely among trees with a higher aphid abundance. On the contrary, the native ants may deal with territorial constraints that inhibit them from foraging for a long time on trees previously occupied by other native ants. The Argentine ant *Linepithema humile* is also prone to relocate its nest close to food sources on trees and move away when sources are exhausted or workers do not have access to climb the tree [44]. This strategy enables invasive ants to monopolize honeydew sources in order to maintain the large worker activity for community dominance. On the other hand, the fragmentation of the forest also plays an important role in modifying, at the edges, the availability of honeydew sources, the environment, and the ant community. These factors may interact to favor the foraging of *L. neglectus* and some native ants in the case of control fragments. In fact, several studies have recorded increased abundance of tended phytophagous insects such as aphids and treehoppers, on isolated and edge trees from patches of scrubland, neotropical savanna and tropical and temperate forest fragments [45–47]. This edge effect appears to be the result of the interaction between two adjacent ecosystems when they are separated by an abrupt limit [48]. The response may differ depending on the group. In rainforests, some insect groups respond positively to edges while others are negatively affected. Certain termites, leafhoppers, scale insects, aphids, aphid-tending ants [46], and light-loving butterflies [49] increase near edges. In particular, ant-tended aphids increase on isolated trees [47]. On the contrary, numerous bees, wasps [46], ants and butterflies [49] respond negatively to edges. Additionally, at forest edges, ant richness diminishes, ant community composition is modified [50, 51], and a variety of ecosystem processes [52], such as seed dispersion by ants, may change [53]. In a previous study in the same area, we found no differences in aphid abundance tended by *L. neglectus* or the native ant *L. grandis* on holm oaks located at the edge and isolated [19]. However, not all trees were surveyed due to their height and the slope of the area. Therefore, we cannot discount the possibility of there being a gradient in the abundance of tended-aphids from the core of the forest fragment to the edges.

5. Conclusions

In invaded fragments, spatial-temporal foraging of native ants and their richness on trees was strongly diminished in comparison with control fragments. However, the native ants *Crematogaster scutellaris* and *Temnothorax lichtensteini*, both arboricolous, were able to coexist with the invasive ant but showed a lower frequency of foraging on trees and remained for less time in comparison with their permanence in control fragments. The mechanisms that may enable coexistence

between native and *L. neglectus* were a combination of small body size, arboreal nesting habits, and cryptic behavior. Additional sampling approaches (pitfall trap captures, presence in baits, leaf litter sampling) are needed to ascertain the generality of those mechanisms. Some uncoupling of ground foraging and tree foraging levels has been detected in Argentine ants [54].

Forest fragments with high edge-to-interior ratios or disturbance-induced edges are highly susceptible to ant invasion, which can reach natural areas using roads and forest edges as dispersion paths [14, 25, 26]. Isolated trees are usually found on paths and roadsides and have been proposed as spreading corridors for *Lasius neglectus* [55]. In fact, isolated trees were visited more and for a longer time by *Lasius neglectus* than by native ants. Preventing the abundance of aphids on isolated trees or making it difficult for ants to climb trunks should help prevent this invasive ant from reaching other sites. Additionally, monitoring of road edges that pass through an invaded area will help with the early detection of new propagules of *L. neglectus*.

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Research Article

Extreme Effects of Season on the Foraging Activities and Colony Productivity of a Stingless Bee (*Melipona asilvai* Moure, 1971) in Northeast Brazil

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This study reports the influence of season on foraging activities and internal colonial parameters of *Melipona asilvai* in an Atlantic forest area of northeast Brazil. We used video cameras connected to a PC to monitor all departures and returns of foragers and the types of materials they carried. Foraging activities decreased almost 90% from dry to rainy seasons, but temperature and humidity were not the main factors influencing departures. Observed honey storage and an extreme cutback in activities during the rainy period suggest a seasonal diapause in this species.

1. Introduction

Foraging activities in social insects are influenced by unpredictable environmental variables in terms of timing and location of food [1]. According to Biesmeijer and de Vries [2], there are two main features which govern foraging activities of bees: (1) internal factors, such as individual memory and threshold response to react to the foraging stimuli, and (2) external factors, such as environmental and colony conditions which determine the level of exposure to stimuli associated with the decision [3–8]. Colonies of honeybees and stingless bees can allocate more foragers to collect nectar and pollen in response to the amount of food in storage and availability of resources in the field [7, 9–12].

Stingless bee colonies consist of several hundred to tens of thousands of individuals, and information exchange among the workers is a key feature to colony foraging efficiency and indirectly to colony growth and reproductive success [13]. The influence of weather on foraging activities has been studied in several eusocial bee species [14–25]. These studies report that weather conditions, light intensity, humidity, food availability, competition, colony state, and physiological conditions of individuals are important factors that influence the foraging activities of *Melipona* species.

In this study we report an extreme effect on foraging activity and colony production in response to environmental variables for colonies of *Melipona asilvai*. For this purpose, we used a novel observational approach in order to monitor all daily departures and entrances of foraging bees.

2. Material and Methods

2.1. Study Site. The experiments were performed at the Campus of Universidade Federal de Sergipe (UFS), São Cristóvão (10°55′S, 37°03′W, altitude 2 m). The study area is characterized as a subhumid area of Atlantic Rain Forest or "Zona da Mata." According to Amâncio [26], two distinct seasons are found in this region: a rainy season happening from April to August (pluviosity between 1.100 mm and 1.500 mm) and a dry season taking place from September to March. The air temperature cycle is close to uniform with no significant seasonal thermal variation.

2.2. Species. Three queenright colonies of *Melipona asilvai* were collected for this study. The colonies, originally from

Nossa Senhora da Glória, Sergipe state, were transferred to the UFS Entomology Laboratory. Each colony was housed in a wooden box covered with glass to facilitate observation. A plastic tube connected the colonies to the outside environment, thus permitting the bees to forage freely. The temperature in the hives was controlled at 28°C by means of a thermostat.

2.3. Data Collection. This study was carried out on March 10–28th 2009 (rainy season) and on June 10–28th 2009 (dry season). We used security microcameras (model CCD Sony 480L Day 0.1 Lux Color) which were placed on small glass-covered boxes (5.0 × 3.0 × 3.0 cm) connected to each entrance tube. Video recordings were programmed to start at 05:00 h, before the first foraging departure, and the recording concluded at 19:00 h, after the termination of outside activities. The cameras were linked to a computer using an AVerMedia EZmaker frame grabber (Avermedia, Milpitas, CA) and VirtualDub software, http://www.virtualdub.org/. This setup allowed the observer to identify the corbiculae load, such as mud (irregular-shaped brown material), resin (brighter rounded material), pollen (whitish to yellowish opaque load), and liquid load (water and nectar). Incoming foragers with liquid presented expanded abdomens compared to other unloaded foragers. Nectar and water loads were not individually determined.

To investigate how seasonality affects food storage and colony conditions, we daily counted honey and pollen pots, brood cells in construction, and the relative number of individuals in the colony (workers on the brood combs). All parameters were registered around 18:00 h after video recording. Data on temperature and relative humidity were measured with a digital thermohygrometer kept outside the laboratory.

2.4. Data Analyses. The data were analysed with a general linear model (GLM) where colonies, season, and time of day were entered into the analysis as the independent variables and number of bees entering or exiting as the dependent variables [27]. The Kruskal-Wallis test and the Mann-Whitney U test were used to verify whether the type of load collected by foragers occurred at distinct periods of the day and to compare colony productivity between seasons, respectively. A Kendau Tau correlation test was also used to estimate the relationship between abiotic factors and the frequency of flights. All analyses were made with Statistica 7.0 (Statsoft inc.).

3. Results

3.1. Foraging Activities and Seasonality. General linear mixed models showed that foraging activities were significantly affected by almost all parameters tested (Table 1). Variance between colonies was not significant, meaning that the number of foraging departures and returns between the three colonies were not different. Footage analyses of 73,375 flight returns showed conspicuous differences in activities between rainy and dry seasons. Season, time, and time × season showed significant effects on the frequency of foraging activities.

Table 1: Results of GLM of foraging activities related to dry and rainy seasons, time of day, and studied colonies.

	D.F.	Deviance	F	P
Model	1	932658.2	320.35	0.003
Season	1	805939.7	1019.69	<0.0001
Time	12	9770.8	12.36	0.001
Colony	2	1911.7	2.78	0.06
Season∗time	12	8351.4	10.56	<0.0001
Error	5851	790.4		

There was not a strong correlation of air temperature and relative humidity with the frequency of foragers' exiting (Figure 1; dry season: temperature: $\tau = -0.20$, $P = 0.83$ and humidity: $\tau = 0.34$, $P = 0.73$; rainy season: temperature: $\tau = 2.71$, $P < 0.05$ and humidity:$\tau = -0.03$, $P = 0.37$). On the other hand, a comparison of pooled data showed a positive tendency between temperature and number of bees exiting the nest ($\tau = 13.94$, $P < 0.001$).

3.2. Foraging for Resources, Time of Day, and Season. The onset of nest departures during the dry season occurred around 5:30 h. During the rainy season, the first exiting trips started between 6:00 and 9:00 h, with an exceptional initial foraging exit occurring at 13:00 h. In both seasons, foraging trips ended around 18:00 h. During the dry season, the activity peak of departures occurred between 7:00 and 8:00 h (mean ± S.D. = 38.46 ± 30.64 bees; Figure 1(a), while the observations took during the rainy season did not produce a clear peak of activity due to the small number of exiting individuals (Figure 1(b)). Liquid foraging changed in intensity throughout the time of day during the dry season but not in the rainy season where liquid foraging was significantly reduced (dry season: $H_{12} = 195.17$, $P < 0.001$; rainy season: $H_{12} = 104.77$, $P < 0.001$; Figures 3(a) and 3(b)). Foraging for liquid during the dry season began around 6:00 h, with a peak activity at 7:00 h (mean ± S.D = 97.5 ± 12.4 bees) and decreased after 11:00 h. A total of 43,228 bees were observed returning with liquid loads. During the rainy season, the activity of liquid collection showed no significant peak (Figure 2(b)). In this period of observations, 1,959 liquid foragers were recorded.

Collection of pollen, resin, and mud also differed among seasons and time of day (Figures 3(a) and 3(b)). Pollen collection showed a significant variation with relation to the time of day in both seasons (dry season: $H_{12} = 225.26$, $P < 0.001$; rainy season: $H_{12} = 66.65$, $P < 0.001$; Figures 2(a) and 2(b)). 5,198 bees were observed returning with pollen during the dry season and 340 bees during the rainy season. Resin collection peaked at 7:00 h in the dry season and from 8:00 to 10:00 h during the rainy season (dry season: $H_{12} = 80.07$, $P < 0.001$; rainy season: $H_{12} = 32.21$, $P < 0.001$). During the dry and rainy seasons, 6,213 and 118 bees were observed returning with resin, respectively.

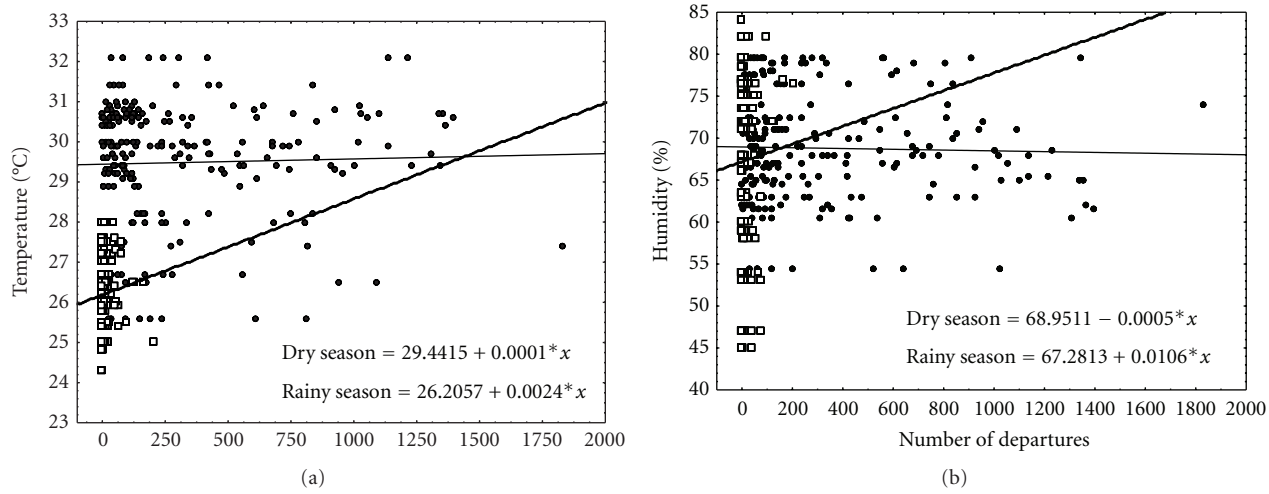

Figure 1: Relationship between temperature (a) and humidity (b) and the number of returning *Melipona asilvai* bees (• dry season; □ rainy season).

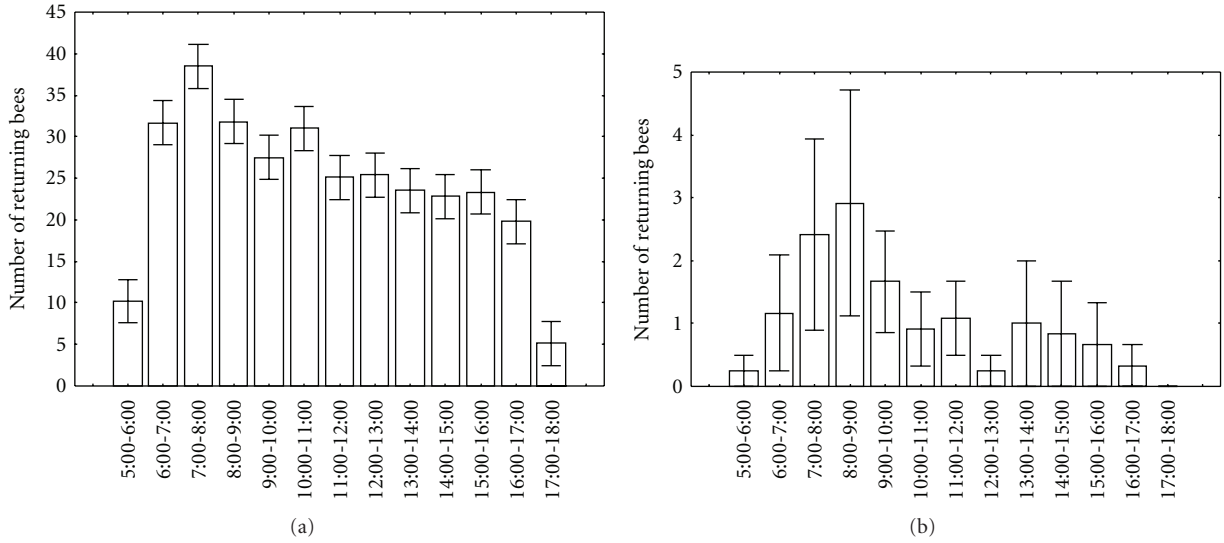

Figure 2: Daily frequency (mean ± SE) of returning *Melipona asilvai* foragers during the 38 days of observations. (a) Dry season and (b) rainy season.

Mud collection was collected throughout the day and exhibited no specific peak activity (Figures 3(a) and 3(b)). This difference was significant for both periods of study (dry season: $H_{12} = 86.19$, $P < 0.001$; rainy season: $H_{12} = 28.68$, $P = 0.004$). 16,106 and 213 returning bees were observed with mud in both seasons, respectively.

3.3. Colony Productivity. The analyses of relative colony productivity showed that all parameters significantly varied between dry and rainy seasons (Figure 4). More nectar pots were observed during the rainy than the dry season (Mann-Whitney U test = 9.10, $P < 0.001$). On the contrary, the number of pollen pots was smaller during dry season (Mann-Whitney U test = 5.15, $P < 0.001$). Brood production nearly suspended during the rainy season, so the number of cells being provisioned was significantly smaller in this season (Mann-Whitney U test = 2.67, $P < 0.05$).

4. Discussion

4.1. Foraging Activities and Seasonality. Our results showed that during the 19 days of study in the rainy season, foraging departures of *M. asilvai* foragers for food resources (liquid and pollen) decreased over 20 times. Collection of resources seems not to be independently influenced by single factors such as temperature or humidity. Another factor that can also affect the foraging activity of stingless bees is the variation in the quantity and quality of food resources between days or seasons [10, 28]. Biesmeijer et al. [9] observed higher concentrations of sugar from nectar

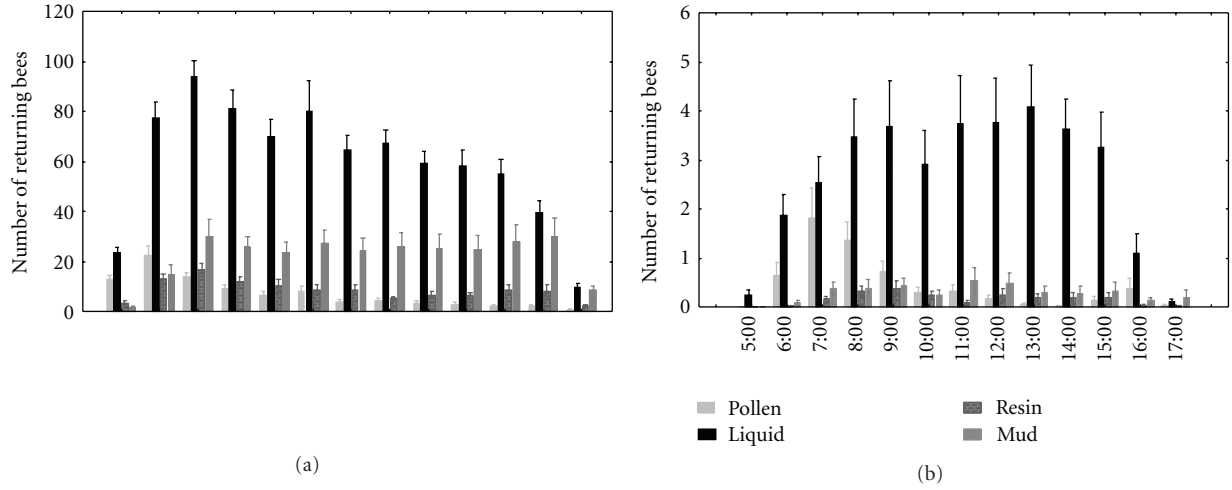

Figure 3: Daily frequency (mean ± SD) of returning bees from three *M. asilvai* colonies bringing different types of loads during dry season (a) and rainy season (b).

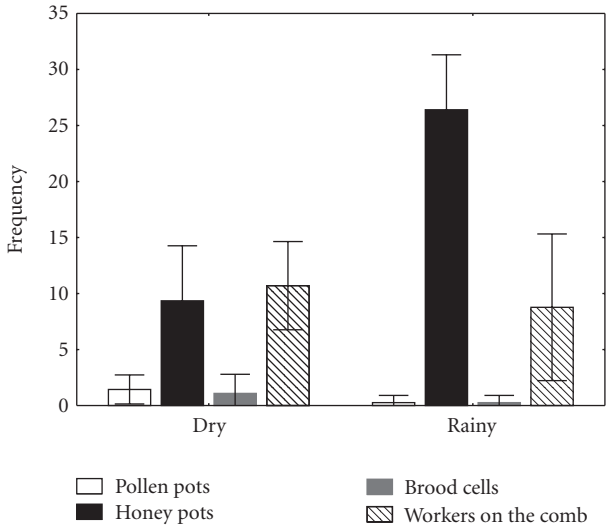

Figure 4: Colony productivity (mean ± SD) patterns recorded during dry and rainy seasons.

collected by bees in dryer environments. Indeed, foraging organization is a result of individual foragers responding to environmental changes.

A previous study carried out with the same species in a drier area of Northeast Brazil registered a similar relationship between abiotic factors and foraging activities [29]. Other studies made in higher latitudes verified that temperature and relative humidity are the most limiting factors affecting the peaks of flight activity of stingless bees [17, 21, 23].

4.2. Foraging for Resources, Time of Day, and Season. Our studies showed that pollen collection in *Melipona asilvai* peaked during the first hours of the morning and decreased by the afternoon. This pattern has been seen in other *Melipona* species as well [30, 31]. Hilário et al. [21] observed that in *M. bicolor bicolor* an intense incoming of pollen took place in the early morning, when relative humidity was higher and temperature and light intensity were more moderate. Roubik [10] stated that pollen harvesting in the first hours of day coincides with a higher availability of this resource in the flowers.

Collection of liquids occurred throughout all activity periods in *M. asilvai* colonies. Although a 90% reduction of departures flights had been observed during the rainy season, there was a regular distribution of incoming liquid during the day in both seasons. Pierrot and Schilindwein [31] recorded higher rates of nectar foraging in the afternoon periods for *M. scutellaris*, which could be related to the gradual increase of sugar concentration in insolated flowers [32]. A similar pattern was found in an experiment carried out with *M. rufiventris* in southeast Brazil [24].

Collection of liquid was remarkable during the dry season (see Figure 3(a)). The number of bees returning with liquid loads was around 70% higher than other loads. These results, associated with both a decrease in flight activity and the number of honey pots registered in the rainy season, suggests that *M. asilvai* colonies experience a kind of seasonal diapause. In southern states where seasons are more defined, flight activity of *M. bicolor schencki* and *M. marginata obscurior* was more intense during summer and spring than autumn and winter [33, 34]. Reproductive diapause has been observed in other southern species of stingless bees, such as *Plebeia remota* and *P. droryana* [28, 32].

4.3. Colony Productivity. Season had a significant effect on the relative parameters of colony production in *M. asilvai*. It is known that food resources are critical for the production of workers, queens, and males in stingless bees [35–37]. Although we did not record brood production in this study, it is reasonable to speculate that caste production and colony fission in this species occurs during the dry season when the rhythm of activities is higher.

5. Conclusion

We conclude that the dry-rainy seasonal variation strongly affects external and internal biological parameters of *Melipona asilvai*. Foraging activities decrease by almost 90% from the dry to the rainy seasons, but temperature and humidity were not the main factors influencing departures. Honey storage and a sharp decline in activities during the rainy period suggest a seasonal diapause in this species.

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Research Article

Impact of Interference Competition on Exploration and Food Exploitation in the Ant *Lasius niger*

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Competition acts as a major force in shaping spatially and/or temporally the foraging activity of ant colonies. Interference competition between colonies in particular is widespread in ants where it can prevent the physical access of competitors to a resource, either directly by fighting or indirectly, by segregating the colony foraging areas. Although the consequences of interference competition on ant distribution have been well studied in the literature, the behavioral mechanisms underlying interference competition have been less explored. Little is known on how ants modify their exploration patterns or the choice of a feeding place after experiencing aggressive encounters. In this paper, we show that, at the individual level, the aphid-tending ant *Lasius niger* reacts to the presence of an alien conspecific through direct aggressive behavior and local recruitment in the vicinity of fights. At the colony level, however, no defensive recruitment is triggered and the "risky" area where aggressive encounters occur is not specifically avoided during further exploration or food exploitation. We discuss how between-species differences in sensitivity to interference competition could be related to the spatial and temporal predictability of food resources at stake.

1. Introduction

Competition is generally considered as the major force structuring patterns of distribution and abundance in ant communities [1–4]. Both competition by exploitation and competition by interference can be found in ants. Exploitative competition is defined as the capacity for one species, one group, or one individual to find and exploit rapidly a potentially limited resource, thereby making it unavailable to competitors. Competition by interference on the other hand is defined as the capacity to prevent physical access to a resource, either directly by disturbing or attacking other foragers or indirectly, by delimiting a territory and excluding competitors from foraging sites [5]. Interference competition is particularly widespread in ants. Indeed, many ant species show some forms of territoriality [6, 7], and workers from one colony readily attack intruders from other colonies of the same [3, 8] or of a different species [9, 10].

The level of aggression displayed during interference encounters in ants can be tuned according to a variety of factors, including the species to which the competitor belongs [11, 12], the degree of familiarity with the competitor [7, 13–17], and the number of contestants [18–21] as well as the incurred risks in terms of energy/time loss, injury or even mortality [22]. Moreover, the location at which encounters occur [23, 24], the type [20], and quality [25] of resources at stake determine the intensity of aggressive displays. Encounters with intruders can give rise to immediate and overt attacks, accompanied or not by the emission of alarm pheromone, vibrational stimuli, or specific motor displays [26] whose role is to attract nearby nestmates for assistance in excluding competitors. In some cases, individuals instead of attacking, can retreat and recruit nestmates to the location of the encounter (*Oecophyla* [27]; *Pheidole* [12, 28–30]; *Atta* [31]).

Over longer time scale, competition by interference can modify the exploration pattern of ant workers which avoid the location of aggressive encounters [32]. Likewise, ants can tune their food recruitment behavior according to the risk of injury or mortality associated with a feeding place [33, 34]. As regards the aphid tending ant *Lasius niger*, it is known that previous experience with food can influence their exploration behavior [35] but one does not know whether this behavior, as well as the dynamics of food exploitation, can be affected by previous experience with competitors. In this paper we studied therefore the response of *Lasius niger* workers to the presence of a conspecific intruder on their colony home range. First, we tested whether a defensive recruitment is triggered during heterocolonial encounters, that is, whether the workers contacting an intruder recruit nestmates, either locally, in the vicinity of the confrontation or inside the nest, to assist in subduing the intruder. Second, we investigated whether ant colonies subsequently modify their exploration and food exploitation behavior in order to avoid the locations at which encounters with an alien conspecific took place.

2. Material and Methods

2.1. Species Studied and Rearing Conditions. Experiments were run on three colonies of *Lasius niger* collected in September 2010 on the campus of the University of Brussels (50.5°N et 4.2°E, Belgium). All four *L. niger* colonies collected were queenless and contained between 1,000 and 2,000 workers with brood. Colonies were placed in plastic boxes whose walls were coated with Fluon; they nested in test tubes with a water reservoir plugged with cotton at one end. Ants had also *ad libitum* access to test tubes filled with pure water or 0.6 M sucrose. In addition, they were fed every two days with pieces of mealworm larvae (*Tenebrio molitor*). The temperature in the experimental room was maintained around 22°C, and the room was lighted according to a 12 : 12 L : D regime.

2.2. Experimental Setup. During the experiments, the boxes containing the colonies were connected by a T bridge (width: 2 cm, length of each branch: 10 cm) made of foam cardboard to two foraging areas (squared platforms of 6 cm side). The foraging areas were surrounded by Plexiglas walls (height: 2 cm) coated with Fluon to prevent ants from falling off during the experiments. The bridge and foraging areas were covered with pieces of white paper that could be easily replaced so that ants could not be able to use the chemical marks left in previous trials.

2.3. Experimental Protocol. The experiment was divided into four successive phases (Figure 2). The first phase of the experiment lasted 15 minutes and consisted in the spontaneous exploration of the bridge and foraging platforms by the ants. This phase was followed by a 30-minute confrontation phase in which a worker from an alien colony (always belonging to the same colony) was introduced either on the left or the right platform (the position was alternated between replicates). As for most ant species [36], nestmate recognition in *L. niger* is based on cuticular hydrocarbons [37], and workers generally strongly react when contacting a worker from an alien colony. At the end of the confrontation phase, all ants remaining in the setup were captured with a forceps and were placed back in their nest box. We then removed the pieces of paper covering the bridge, replaced them by new ones, and proceeded with a new 15-minute exploration phase. This way, ants could only rely on their spatial memory of the location where they encountered the worker from an alien colony. The second exploration phase was followed by a 30-minute phase of food exploitation in which a bottle cap containing 1 mL of a 0.6 M sucrose solution was placed in the middle of each foraging platform. All phases of the experiment were recorded with a Panasonic WV-BP250 camcorder placed centrally above the bridge, at the level of the bifurcation leading to the two areas. The colonies were starved for two days before the beginning of each experiment. The pieces of paper covering the bridge were not changed between the different phases of an experiment. Walking workers of *L. niger* mark their colony home range passively, by laying cuticular compounds from footprints during exploration [38]. The bridge could thus be marked during the exploration phase. Such an area marking is known to potentiate the attack of conspecifics from other colonies by resident workers. The pieces of white paper however were changed between experiments so that ants could not be influenced in their choice of a branch by any odor left during previous experiments. Three colonies were tested and seven replicates of the experiment were run for each colony.

2.4. Data Acquisition and Statistical Analysis. We counted the flow of ants travelling towards the foraging areas on each branch of the bridge for each minute of the four phases of the experiment. In addition, we counted the number of ants on each foraging area for all phases of the experiment every 3 minutes.

To study the effect of our experimental procedure on the flow of ants on the bridge over the four phases of the experiment, we used a Generalized Linear Mixed Model (GLMM), [39] with the mean flow of ants per minute over the duration of each experimental phase as response variable and experimental phase as a fixed factor. Variation between colonies in the different phases of the experiment and variation between replicates within colonies in the flow of ants on the bridge were accounted for by considering colony and replicate nested within colony as random effect factors, respectively. We used treatment contrast to compare the flow of ants observed during the first exploration phase to those observed during the three other phases of the experiment. The statistical model was fitted with the penalized quasi-likelihood method using the glmmPQL function of the MASS R package with a gamma distribution error.

In order to test whether ants had a significant preference for one of the two branches of the bridge we used a binomial test on the cumulated flow of ants on each branch (expected probability = 0.5) for each replicate of the experiment. To compare the choice of the ants in the different phases of

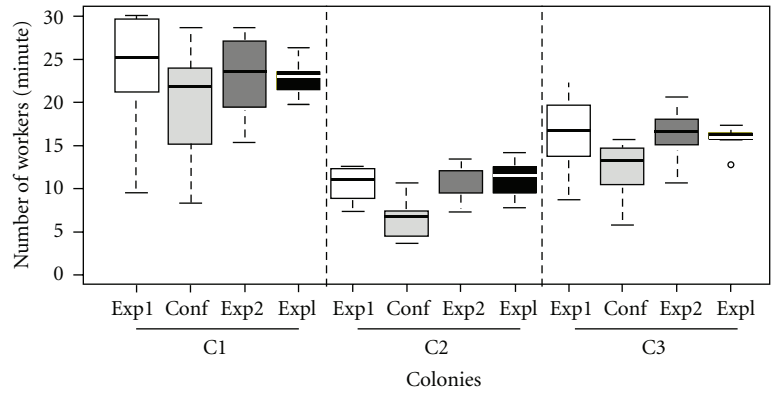

Figure 1: Mean flow of workers exiting the nest per minute for the different phases of the experiment and the different colonies (Exp 1 = first exploration phase, Conf = confrontation phase, Exp 2 = second exploration phase, Expl = food exploitation phase) and the different colonies (C1, C2, C3). $N = 7$ replicates per colony.

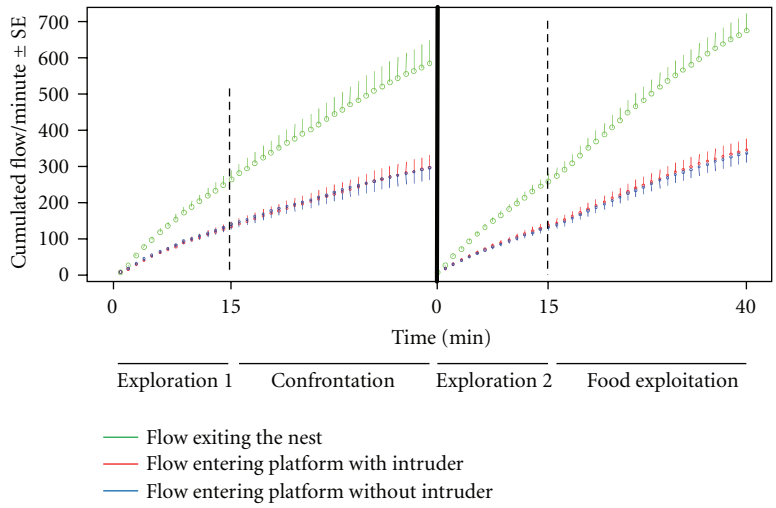

Figure 2: Cumulated flow of ants exiting the nest and on each branch of the bridge as a function of time (mean + SE for the flow exiting the nest and the branch where the alien worker was introduced in the confrontation phase, mean − SE for the other branch) $N = 21$ replicates.

the experiment we computed for each phase the number of replicates in which a given percentage of the total flow of ants was observed on the branch of the bridge leading to the platform where the alien ant was introduced in the confrontation phase. A χ^2 test for heterogeneity was then used to compare the distributions. Finally, we examined the sign of the change in the proportion of the total flow of ants exiting the nest towards the risky platform following the exposure to an alien worker. To do so we used a Student's paired t-test to compare, within each replicate of the experiment, the proportion of ants choosing the "risky" branch (leading to the platform where the alien worker was introduced in the confrontation phase) between the first exploration phase and each other phases of the experiment.

All statistical analyses were run with R version 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org/).

3. Results

There was an effect of both the phase of the experiment and of the colony on the activity level of the colonies. The mean flow of ants per minute exiting the nest was indeed different among the four different phases of the experiment (Figure 1): the flow observed during the first exploration phase was significantly higher than that observed during the confrontation phase ($t = 3.885$, df $= 60$, $P < 0.001$), but not significantly different to that observed during the second exploration phase ($t = 0.261$, df $= 60$, $P > 0.05$) or the food exploitation phase ($t = 0.377$, df $= 60$, $P > 0.05$). Variation between colonies in the different phases of the experiment was more than four times as important as variation between replicates within colonies. As can be seen in Figure 1, the flow of ants observed in colony 2 was always lower, whatever the phase, than in colony 1 or 3.

In 12 out of 21 replicates, ants did not express a significant preference for one of the branch of the bridge (binomial test, $P > 0.05$) during the first exploration phase. In the nine replicates where they expressed a significant preference for a branch, the right branch of the bridge was always chosen. However, this did not induce a systematic orientation bias for the other phases of the experiment since the branch where the alien worker was introduced was alternatively positioned on the right or left side.

The introduction of an alien worker on one platform during the confrontation phase induced neither an increase nor a decrease in the mean flow of ants per minute towards this "risky" area (Figure 2). In 11 out of 21 replicates, ants expressed a significant preference for one branch of the bridge (binomial test, $P < 0.05$). The branch leading to the platform where the alien worker was introduced was chosen in 6 replicates out of these 11 replicates. Overall, the frequency distribution of choice observed during the confrontation phase did not differ from that observed in the first exploration phase ($\chi^2 = 5.46$, df = 3, $P = 0.14$). Within each replicate, however, there was a slight but significant decrease in the proportion of ants choosing the branch leading to the risky platform ($t = -2.718$, $P = 0.013$).

During the second exploration phase that followed the confrontation phase, ants did not attempt to avoid the branch where the alien worker had been introduced. The mean flow of ants per minute on the two branches of the bridge was about the same as in the first exploration phase (Figure 2). Ants chose preferentially one branch of the bridge in six replicates out of 21 (binomial test, $P < 0.005$). Only in 2 replicates out of these 6 replicates ants chose the branch where the alien worker had been introduced. Overall, the frequency distribution of choice observed during the second exploration phase did not differ from that observed in the first exploration phase ($\chi^2 = 1.59$, df = 3, $P = 0.66$). Compared to the choice of the ants in the first exploration phase, there was no significant difference in the percentage of ants choosing the branch leading to the risky platform ($t = -1.303$, $P = 0.207$). Therefore, the choice of a branch in the second exploration phase was not influenced by the location where the agonistic encounter with an alien worker occurred.

Finally, during the last food exploitation phase, the mean flow of ants per minute on each foraging platform increased in a similar way on the two branches of the bridge (Figure 2). In 17 replicates out of 21, ants expressed a significant preference for one branch, in eight replicates they preferred the branch where the alien worker was previously introduced, and in nine replicates they preferred the other branch. Collective choices of one branch were more frequently observed during food exploitation than during the other phases of the experiment: this is an expected outcome of the amplifying properties of trail recruitment towards a food source [40]. Overall, the frequency distribution of choice observed during the exploitation phase did not differ from that observed in the first exploration phase ($\chi^2 = 56.07$, df = 3, $P = 0.11$). Compared to the choice of the ants in the first exploration phase, there was no significant difference in the percentage of ants choosing the branch leading to the risky platform ($t = 0.683$, $P = 0.502$).

As regards to the occupancy level of foraging areas, it deeply varied with the phase of the experiment (Figure 4). The number of ants on each area increased rapidly at the beginning of the first exploration phase, up to the 10th minute where it began to slightly decrease. During the confrontation phase, while the number of ants remained stable on the "safe" area, it increased steeply on the area where the alien ant was introduced and peaked at the 6th minute. On average, ants were more numerous on the risky platform than on the safe one during the confrontation phase. Actually, when an alien ant was present, a local recruitment was launched: while the intruder was seized by a few resident ants, it was attacked several times by other nestmates. During the second exploration phase, the same level of occupancy as during the first exploration phase was observed for both areas. Finally, the introduction of a food source initially induced a slight increase of the number of foragers which was similar over the two foraging areas and remained stable until the end of the experiment.

The frequency distribution of replicates as a function of the proportion of their foragers on the risky platform (Figure 5) was significantly different between the first exploration phase and the confrontation phase ($\chi^2 = 24.22$, df = 7, $P = 0.001$) due to the local defensive recruitment induced by the presence of an intruder. On the other hand, the frequency distribution of area occupancy was not significantly different between the first and the second exploration phase ($\chi^2 = 5.77$, df = 5, $P = 0.33$) and between the first exploration phase and the exploitation phase ($\chi^2 = 3.91$, df = 5, $P = 0.56$).

4. Discussion

Physical contact or interference with an alien conspecific resulted in a decrease in the flow of *Lasius niger* ants exiting the nest, the latter orienting themselves equally towards the risky or the safer locations (Figure 3). Therefore, workers having encountered a single alien individual on their home range did not recruit additional workers from the nest for assistance. Although *L. niger* workers did not launch a long-range recruitment, they did react at a local scale by increasing their number in the vicinity of agonistic encounters (Figure 4): as soon as an ant entered the risky area, it began trying to subdue the intruder. This temporarily prevented it from returning to the nest to recruit nestmates. The extended staying time of the ants on the risky area may therefore explain the absence of long-range defensive recruitment. One could argue, however, that such a defensive recruitment would be useless since the alien ant was outnumbered by resident ants, right from the beginning of its introduction on the foraging area. It would be interesting to know whether recruitment occurs in *L. niger* when cooperative defense is really useful, that is, when resident ants are outnumbered by intruder ants or when resources that can be monopolized by intruders are at stake.

After the confrontation phase, ants did not avoid the area where the encounter with the intruder took place. Unlike

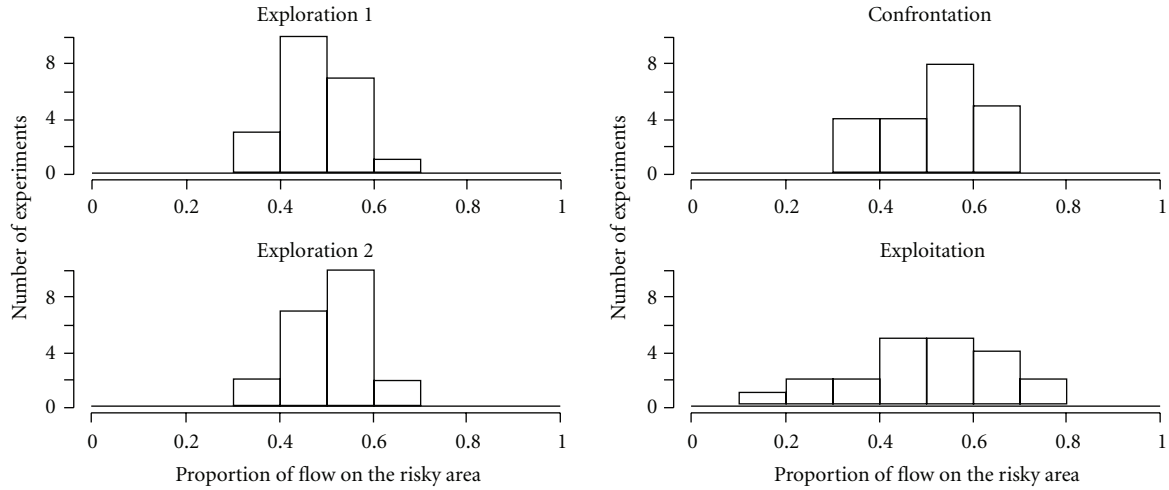

FIGURE 3: Distributions of all replicates as a function of the proportion of ants that were heading towards the area where the alien ant was introduced. The proportion values were calculated over the cumulated flows of ants observed at the end of each phase of the experiment. $N = 21$ replicates.

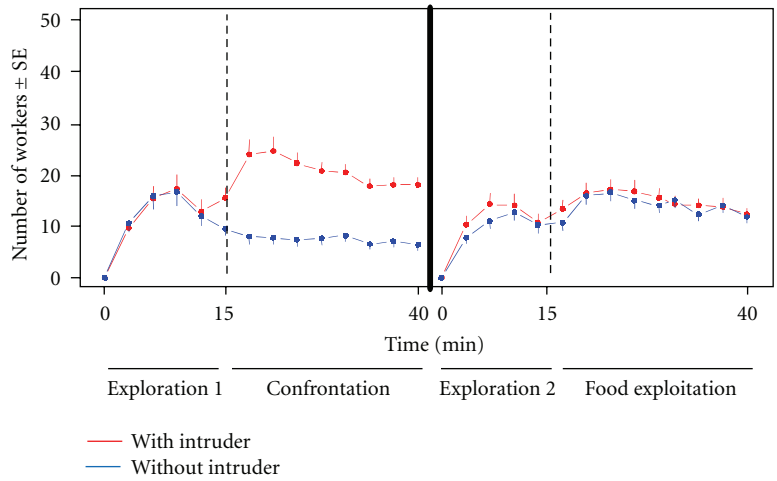

FIGURE 4: Number of ants (mean + SE for the platform where the alien worker was introduced, mean − SE for the other platform) observed every 3 minutes on each platform of the bridge as a function of time. $N = 21$ replicates.

Formica xerophila workers that avoid a location where they have had a negative experience [32], *L. niger* colonies showed the same dynamics and pattern of exploration before and after experiencing agonistic interactions. Likewise, they did not avoid or reduce recruitment intensity towards a food source discovered on a potentially risky location where they had previously experienced aggression.

It would seem logical for ant colonies to avoid potentially dangerous areas. Therefore, one may wonder why in our experiment *L. niger* colonies failed to specifically alter their level of exploration and food exploitation after being exposed to interference competition.

First, one could argue that a single alien worker did not represent a threat high enough or that the exposure time to the threat was not long enough to elicit an avoidance response. However, in the Argentine ant *Linepithema humile*, a single 3 min encounter with a heterocolonial conspecific is enough to produce a long-lasting effect, increasing the propensity to fight in encounters up to a week later [41]. In the same way, in *Lasius pallitarsis,* a short encounter with a single potentially lethal enemy is enough to induce the avoidance of associated food patches even 18–24 h after the encounter occurred [33]. Thus, in our experiment, *L. niger* ants had ample time to perceive interference competition interactions: the intruder was not immediately killed but was physically attacked by several resident workers during the 30 minutes of the confrontation phase.

Second, one could object that ants did not have enough time to develop a spatial memory of the location where the aggressive encounter took place. *L. niger* workers, however, are known to have a well-performing spatial memory [42, 43]. For instance, using a T-bridge similar to our experiment, Grüter et al. [44] showed that after one single visit to a food source, most *L. niger* workers were able to orient to

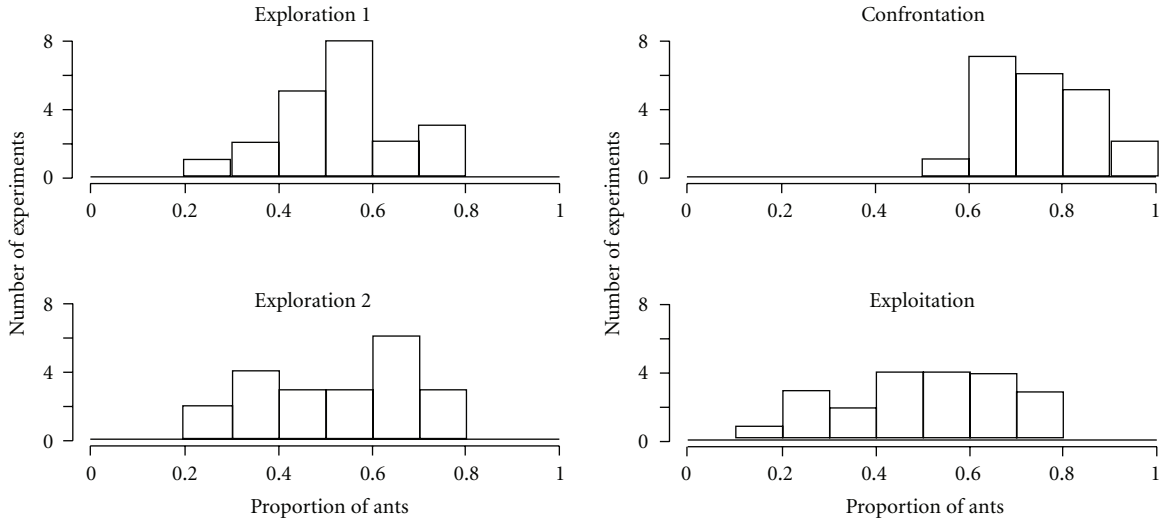

Figure 5: Distributions of all replicates as a function of the proportion of workers on the area where the alien ant was introduced (among all foragers present on the two areas). $N = 21$ replicates.

the branch associated with the food source, only on the basis of visual landmarks.

Third, the ability of an ant species to adjust its exploratory, foraging, and defense strategies to match the surrounding competitive risks is likely to be under natural selection pressure and thus strongly correlated to its ecology [24]. Specifically, interference competition interactions may lead to distinct territorial and foraging strategies according to the characteristics of the food resources at stake. For example, temporally and spatially variable food sources such as prey or seed patches are exploited by several ant species. The ephemeral availability of such resources makes the maintenance of absolute territories costly and difficult to achieve. Therefore, a high sensitivity to competition pressure seems well suited for those ants exploiting ephemeral resources allowing them to adjust in a flexible way their exploratory/food exploitation behavior and thereby to reduce the overlap of feeding areas between competing neighbor colonies. In contrast to prey or seed patches, aphid colonies provide stable and renewable resources. Since ants continually require carbohydrates from honeydew to sustain their daily activities, aphid-tending ants such as *L. niger* must maintain access to such resources, even when there is an associated risk of competition. Aphid tending ants thus may prioritize the stabilization of foraged areas by being poorly sensitive to punctual interference competition interactions. Since *L. niger* lives in environments where contacts with competitors are inevitable, defense of aphid resources could be achieved through a local enhancement of agonistic behavior at key locations, such as the vicinity of aphid colonies or the foraging trails. When the competitive pressure becomes higher, the active recruitment of defenders from within the nest will then determine the colony ability to dominate and displace competitors or to abandon the food resource.

Since aggressive behaviours can be costly in terms of energy, time, and physical injuries, any information regarding competitive pressure should be integrated at the colony level to shape the exploratory and foraging strategies of the colony. However, our study reveals that the integration of such information can vary among ant species, *L. niger* being weakly sensitive to previous exposure to a limited interference competition. To fully understand the decision-making process of ant colonies, species-specific responses to agonistic stimuli will have to be investigated in different contexts, such as when the resources at stake are of different quality. Indeed, since in nature food sources vary in their spatiotemporal availability, as well as in their associated risk, colonies may have to make complex decisions: this should involve tradeoffs between the monopolization of rewarding areas under normal competition conditions and the avoidance of dangerous areas through a high spatial flexibility of their home range.

Disclosure

The authors declare that they do not have any direct financial link with any of the commercial identity mentioned in this paper.

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Review Article

Generalist Bee Species on Brazilian Bee-Plant Interaction Networks

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Determining bee and plant interactions has an important role on understanding general biology of bee species as well as the potential pollinating relationship between them. Bee surveys have been conducted in Brazil since the end of the 1960s. Most of them applied standardized methods and had identified the plant species where the bees were collected. To analyze the most generalist bees on Brazilian surveys, we built a matrix of bee-plant interactions. We estimated the most generalist bees determining the three bee species of each surveyed locality that presented the highest number of interactions. We found 47 localities and 39 species of bees. Most of them belong to Apidae (31 species) and Halictidae (6) families and to Meliponini (14) and Xylocopini (6) tribes. However, most of the surveys presented *Apis mellifera* and/or *Trigona spinipes* as the most generalist species. *Apis mellifera* is an exotic bee species and *Trigona spinipes*, a native species, is also widespread and presents broad diet breath and high number of individuals per colony.

1. Introduction

Bees are important keys to global diversity providing vital ecosystem services such as pollination [1]. For bees, plants species are basically their main food sources, where they collect pollen and nectar and eventually other resources, such as oil. Plants are those which have interest on bees' skills to achieve successful reproduction. They have to deal with different foraging techniques employed by bees [2–4] to reach their main reward, reproduction.

In Brazil, until the end of 1960s, information about bee-plant interactions came mostly from observations made by naturalists of the early 20th century. However, the study of [5] proposed a standardized methodology to perform bee surveys that was subsequently applied to most of them, allowing further comparisons between the different surveyed localities.

The studies of [6–8] made previous synthesis of Brazilian surveys. The first one only compared information about species richness found in different biomes. The other two studies used only data from eusocial Apidae found on the surveys. Until now, no attempt was made to determine the generalist bee species in interaction networks of different localities using all Apoidea species found on them.

Interaction networks are built as a matrix of interacting species and have been justified mainly because networks involving plants and pollinators are generalists and form complex systems bringing additional challenges to their study [9].

In plant-pollinator interactions, species are commonly seen as generalists when they interact with many species of different taxa, and specialists if they interact with one or a few closely related species [10]. Reference [11] showed that in pollination systems the most generalized species are usually network keystone species. Since they interact with most plant species, they play an important role to maintain the whole network.

The main goal of this study was to determine the most generalist bee species on bee surveys conducted on different localities in Brazil.

2. Material and Methods

We searched the academic literature for bee surveys on flowering plants on different localities of Brazil, aiming to

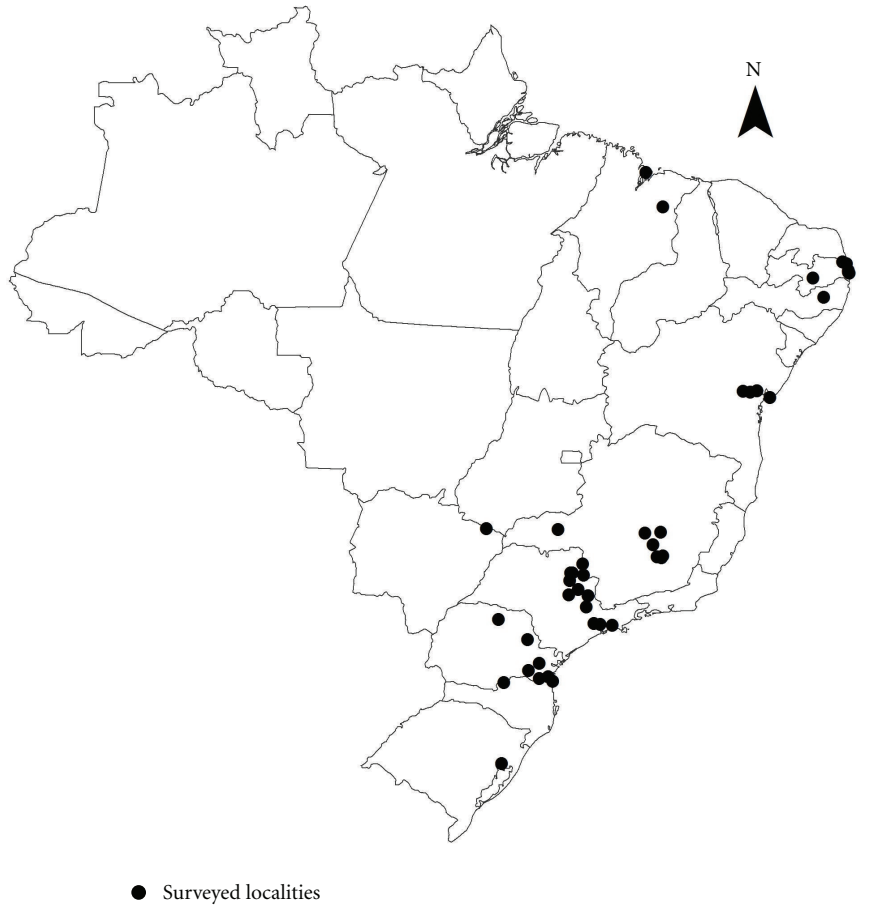

Figure 1: Brazilian localities where the bee surveys were conducted.

build a matrix of bee-plant interactions to each locality. We considered the surveys that used the standard procedure suggested by [5] and whose observations were made for at least one year. In this procedure a fixed amount of time is spent at each flowering plant (or patch) and the coverage of transects is randomized in time, order, and direction. On most of these surveys, the interactions were not detailed and could include effective pollination and/or nectar, pollen, or oil foraging.

Many survey datasets have been published only in M.S. or Ph.D. thesis and are only available to the public at their universities. When these works were subsequently published as a paper, both datasets were compared and both were cited on the reference list.

The bee taxonomic names were updated according to [12]. We discarded the observations that were taxonomically unresolved.

We used the bipartite package [13] for R 2.11.1 (The R Foundation for Statistical Computing) to analyze each matrix. Each cell of the matrix represents a single bee-plant interaction and can have a value of 0 if the interaction is not observed, or 1, if observed [14]. With this tool we determined the first three bee species with the highest number of interactions.

The declared coordinate point of each survey was also used to build a map with ArcGIS 10 software (Esri Inc.).

3. Results

We found 47 localities whose surveys fulfilled the requirements previously quoted on the methodology section. Most surveys were done on South, Southeast, and Northeast regions of Brazil, either on urban areas, on seasonally dry areas of Tropical Dry Forest (Brazilian Caatinga) and Tropical Shrublands (Brazilian Cerrado), or on Tropical Moist Forest (Brazilian Atlantic Forest) biomes (Figure 1, Table 1). We did not find any bee survey on the North region and only one on the Midwest region of Brazil.

The first, second, and third most interacting species on each surveyed locality are found on Table 1. We found a total number of 39 different species. Most of them belong to Apidae (31 species) and Halictidae (6) families, and to Meliponini (14) and Xylocopini (6) tribes (both from Apidae family). The genus with the highest number of interacting species was *Xylocopa* (5 species). The genera *Trigona, Exomalopsis,* and *Augochloropsis* presented each three interacting species.

Table 1: Number of times bee species were quoted as the first, second, or third most interacting species on the Brazilian bee surveys.

Family	Tribe	Species	1st	2nd	3rd	Biome (*sensu lato*)	References
Andrenidae	Oxaeini	*Oxaea flavescens*		1	1	Tropical Shrublands	[15, 16]
Apidae	Apini	*Apis mellifera*	20	15	2	Various	[15, 17–56]
	Bombini	*Bombus morio*		1		Tropical Shrublands	[26]
		Bombus pauloensis	2	4	3	Tropical Shrublands, Tropical Moist Forest and Urban Area	[26, 33, 36, 57–62]
	Centridini	*Centris klugii*			1	Tropical Shrublands	[26]
		Centris leprieuri			1	Tropical Shrublands and Tropical Moist Forest	[45, 46]
		Melissoptila cnecomala		1		Tropical Shrublands	[26]
	Euglossini	*Eulaema nigrita*	1			Tropical Moist Forest	[27]
	Exomalopsini	*Exomalopsis analis*			1	Dune	[22]
		Exomalopsis auropilosa	1			Urban Area	[62]
		Exomalopsis fulvofasciata	1		1	Tropical Shrublands	[41, 63, 64]
	Meliponini	*Cephalotrigona capitata*		1		Tropical Moist Forest	[65]
		Melipona scutellaris			1	Tropical Moist Forest	[51–53]
		Mourella caerulea	1			Tropical Shrublands	[61]
		Paratrigona lineata	2			Tropical Dry Forest and Tropical Shrublands	[32, 57]
		Paratrigona subnuda	1	1	1	Urban Area and Tropical Moist Forest	[34, 35, 42, 43, 55, 56]
		Plebeia droryana		1	1	Urban Area and Tropical Shrublands	[50, 66]
		Plebeia emerina		1	1	Tropical Moist Forest	[39]
		Scaptotrigona bipunctata			1	Tropical Shrublands	[66]
		Scaptotrigona tubiba			1	Tropical Moist Forest	[67]
		Tetragona clavipes			1	Tropical Shrublands	[38]
		Tetragonisca angustula		1	6	Various	[17, 27, 28, 40, 48, 50, 54, 63, 64]
		Trigona fulviventris			2	Tropical Moist Forest	[37, 39]
		Trigona pallens	1			Tropical Shrublands	[44]
		Trigona spinipes	16	14	11	Various	[15–21, 24–56, 61, 63–67]
	Tetrapediini	*Tetrapedia rugulosa*			2	Tropical Shrublands	[23–25, 30]
	Xylocopini	*Ceratina maculifrons*			2	Urban Area and Tropical Shrublands	[16, 62]
		Xylocopa carbonaria	1			Dune	[22]
		Xylocopa cearensis			1	Urban Area	[49]
		Xylocopa grisescens			1	Tropical Dry Forest	[29]
		Xylocopa ordinaria			1	Urban Area	[49]
		Xylocopa suspecta			1	Tropical Moist Forest	[47]
Halictidae	Augochlorini	*Augochlora esox*			1	Tropical Dry Forest	[57]
		Augochloropsis callichroa		1		Tropical Moist Forest	[67]
		Augochloropsis crassiceps			1	Tropical Moist Forest	[65]
		Augochloropsis illustris		1		Urban Area	[62]
		Ceratalictus theius		1		Tropical Shrublands	[58–60]
	Halictini	*Dialictus opacus*		3		Urban Area, Tropical Dry Forest and Tropical Shrublands	[18–21, 49, 58–60]
Megachilidae	Anthidiini	*Hypanthidium divaricatum*			1	Tropical Moist Forest	[39]

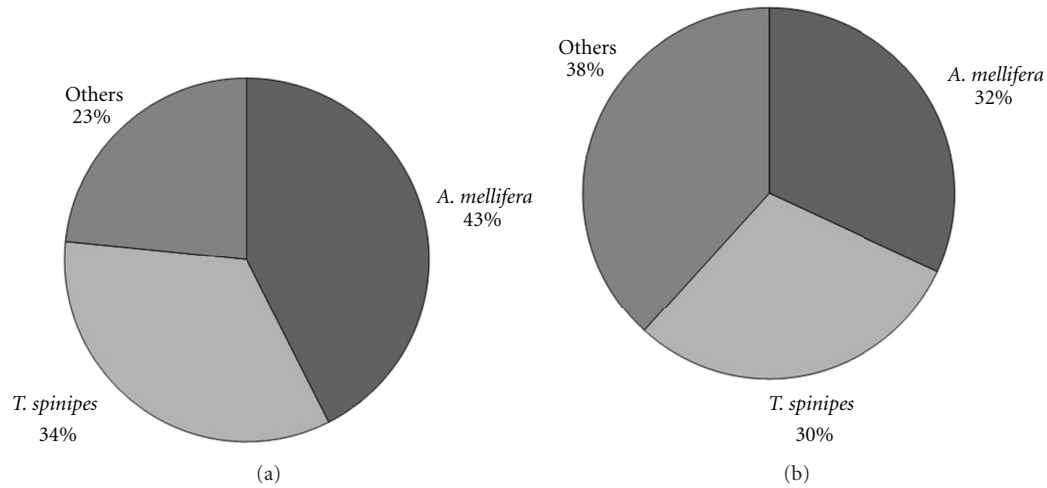

Figure 2: Percentage of Brazilian bee surveys presenting *Apis mellifera* or *Trigona spinipes* as (a) the first species with highest number of interactions and (b) the second species with highest number of interactions.

On most surveys *Apis mellifera* and/or *Trigona spinipes* were the most interacting species (Table 1). Considering the first and second species with the highest number of interactions, *A. mellifera* was present on 75% of the Brazilian surveys and *T. spinipes* on 64% (Figure 2).

Other important interacting species were *Bombus pauloensis* that was quoted nine times on the different localities and on different ranks (first, second, or third interacting species), *Tetragonisca angustula* (7 times), *Dialictus opacus,* and *Paratrigona subnuda* (3 times each) (Table 1).

Halictidae and Xylocopini species as well as *A. mellifera* and *T. spinipes* were found on different biomes (Table 1). Most of Meliponini species were found on Tropical Moist Forest and on Tropical Shrublands.

4. Discussion

Apidae is a large family of bees, whose species are mostly generalist foragers. It is widely distributed, occurring on different biomes under different environmental characteristics [68]. Bee species from the Meliponini tribe live in tropical and subtropical regions of the world and are considered to be important pollinators of plant species on different environments [69].

T. spinipes, one of the most generalist stingless bee species according to our results, presents colonies with a huge number of individuals and wide diet breath, and it shows widespread distribution over the Brazilian territory. Moreover, they build aerial nests, being independent of any kind of holes to nidify. Independence of holes and the great availability of workers may determine the degree of dispersion over the countryside and the generalist interacting behavior [70].

A. mellifera is an exotic bee species also widespread in different biomes. It is well adapted to different climatic conditions and presents a generalist foraging behavior. Despite the potential negative impact on native pollinator species [71], it was already recognized as the most important pollinator of natural environments and also of agricultural crops [72].

Although we are not aware of any study comparing *A. mellifera* and *T. spinipes* pollinating performance, they are probably important resource competitors, due to their similar colony size and widespread distribution. The efficient communication system exhibited by *Apis mellifera* and the aggressive behavior on flowers, already reported to *T. spinipes*, complete this scenario [73, 74].

Recent reports of the colony collapse disorder syndrome of *Apis mellifera* species arouse the awareness of the importance of this species [75], especially due to its importance to agriculture. At the same time, it also brings the attention to the native pollinators and their importance to local crops, and international initiatives have been suggested to protect them [76].

Far from the number of interactions found for the two main species, two other generalist bee species were *B. pauloensis* (9 interactions) and *T. angustula* (7 interactions). Both species were found in distinct biomes, including urban areas, thus suggesting a broad ability to survive at different environmental conditions. But unlike *T. spinipes* both depend on cavities to nidify and do not present an efficient communication system as *A. mellifera* and its ability to leave for other places when conditions become hard [77], or the aggressive behavior on flowers reported to *T. spinipes*. Besides, their colonies are much smaller than those of these two species. All these factors together are responsible for the lower number of interactions presented by them in comparison to the two main species.

In summary, we demonstrated the importance of a native bee species (*T. spinipes*) and of an exotic one (*A. mellifera*) to interaction networks on surveys conducted in Brazil. As already mentioned, their populous colonies, broad distribution, and aggressive behavior probably are the most important contributors to these results. Comparisons involving their pollinating performance and resource

partitioning are suggested as important lines for further research.

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Research Article

Nesting Activity and Behavior of *Osmia cornifrons* (Hymenoptera: Megachilidae) Elucidated Using Videography

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Osmia cornifrons Radoszkowski (Hymenoptera: Megachilidae) is utilized as an alternate pollinator to *Apis mellifera* L. (Hymenoptera: Apidae) in early-season fruit crops. This study was conducted to investigate nesting activities and associated behaviors of *O. cornifrons*. *Osmia cornifrons* nesting activity was recorded by using a digital video recorder with infrared cameras. Nesting behavior of ten female *O. cornifrons* was observed, and the number of nesting trips per hour was recorded. Trends in daily activity were determined with regression analysis, and chi square analysis was used to determine if *O. cornifrons* spent a greater amount of time performing certain activities. The percentage of time required to gather nesting resources and complete nest construction activities was recorded from the video footage. Results of this study showed that pollen gathering was the most time-consuming gathering activity, requiring 221.6 ± 28.69 min per cell and cell provisioning was the most time-consuming intranest activity, requiring 28.9 min ± 3.97 min. We also found that *O. cornifrons* activity was correlated with time of day, temperature, and precipitation. Various nesting behaviors, including cell provisioning and partitioning, oviposition, grooming, resting and sleeping, nest-searching, and repairing behaviors, are described in this paper.

1. Introduction

Pollination services are both economically valuable [1] and essential to many crop production systems [2]. With colony collapse disorder and various pests threatening the honeybee [3] and issues such as habitat fragmentation and pesticides threatening wild pollinators [4], considerations for alternate pollination strategies by effectively managing solitary bees have become more relevant to agricultural production [5].

The Japanese hornfaced bee, *Osmia cornifrons* Radoszkowski (Hymenoptera: Megachilidae), is an important pollinator of rosaceous fruit crops such as apple and pear. Historically, *O. cornifrons* has been managed in Japan for apple pollination since the 1940s and was introduced into the United States for pollination in 1977 [6]. Additionally, *O. cornifrons* is being used for orchard pollination in Korea and China [7, 8]. *Osmia cornifrons* has been shown to be up to 80 times more effective at pollinating apples than *A. mellifera* [9] and has several benefits over *A. mellifera* such as flower constancy and consistent anther contact [10]. Despite these benefits, *O. cornifrons* remains an underutilized pollinator in the United States.

Understanding the nesting biology of *O. cornifrons* is important for management of the bees for growers, population managers (i.e., those who sell the bees to growers), and researchers. For example, by understanding *O. cornifrons* nesting biology, one can select release sites where *O. cornifrons* has access to adequate resources. Understanding the limiting factors of *O. cornifrons* activity, such as temperature thresholds, allows one to predict if *O. cornifrons* will be pollinating on a given day of the blooming season. In addition, knowing the nesting biology of *O. cornifrons* provides growers and researchers with insights into the biology of other *Osmia* bees such as *O. lignaria*, a managed solitary bee pollinator in the United States.

Observing nesting behavior of solitary bees such as *O. cornifrons* can be challenging because it is difficult to observe bees inside their nests. Despite this challenge, several aspects of *O. cornifrons* nesting biology have been described previously. Yamada et al. [11] described nesting behaviors of

O. cornifrons including cell provisioning, mud wall partitioning, and the time required to gather pollen and mud by utilizing glass tubes wrapped in paper as artificial nests. The paper could be removed from these glass tubes after the bee entered, which permitted *O. cornifrons* nesting activities to be observed. A major disadvantage of using glass tubes is that *O. cornifrons* could be disturbed by a sudden and un-natural increase in light levels in the innermost portion of the tube when the paper is removed from the glass tube; Lee et al. [12] noted that luminance is an important factor affecting *O. cornifrons* activity. In addition, the presence of visible observers has been found to alter the frequency of activities in some insects, such as damselfly nymphs [13].

This study investigated the nesting biology of *O. cornifrons* and described in detail the behaviors associated with nesting activities. There were four objectives in this study: (1) developing an unobtrusive and novel method to observe the nesting behavior of solitary bees, (2) investigating the factors that affect *O. cornifrons* activity levels, (3) determining how much time is allocated to gathering nesting resources and constructing the nest, and (4) describing the behaviors that occur during nest construction.

2. Materials and Methods

2.1. Experimental Insects. *Osmia cornifrons* used in this experiment were acquired from a population that had been successfully established and managed for several years prior to the experiment on a blueberry farm in Independence, WV (N 39.46992, W 79.934651). In early November 2009, the bees were brought into the laboratory at West Virginia University (Monongalia County, WV) and placed into cold storage at 5°C for overwintering. On 9 May 2010, the bees were released in a residential area in Morgantown, WV, USA (N 39.666871, W 79.965523), where a power source for prolonged video recording of bee nest was readily available. Wilson et al. [14] stated that *O. cornifrons* could be successfully released and propagated on landscape plants in a city.

2.2. Developing a Protocol for Observing O. cornifrons In-Nest Activity. To effectively record in-nest activities of *O. cornifrons*, three camera housings were constructed from white pine and Masonite boards (Figure 1). An opening was cut into the front of the box to allow six observation nest blocks [15] to sit below the camera (Figure 2). A Masonite board roof with a 3.5 cm × 4 cm × 1.5 cm block of white pine attached to the center held an infrared camera (The Hawk Eye Nature Cam, West Linn, OR, USA) with the lens 44.3 cm from the bottom of the release box. The camera emits infrared light allowing for continuous observation without disturbing *O. cornifrons*. Cameras were connected to a 4-channel digital video recorder (DVR) (Falco Model LX-4PRO, Falco Pro Series, Taiwan) to record continuously for the entire duration of *O. cornifrons* nesting activity. The three camera housings were placed next to a building facing south and were covered with plastic to help shelter the nests from rain. A fourth camera was set outside the three camera housings facing the nest entrances. This camera was used to observe *O. cornifrons* searching behaviors and to record the weather. Nesting activities of *O. cornifrons* were recorded from 9 May 2010–1 June 2010.

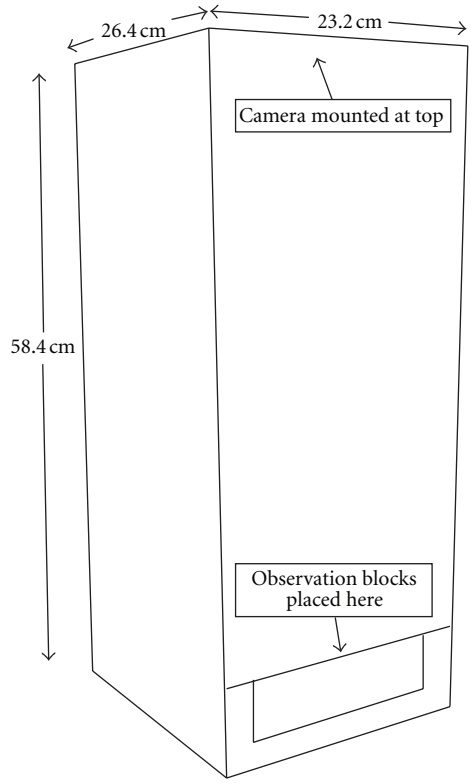

Figure 1: Diagram of camera housings for recording intranest behavior of *O. cornifrons*. The frame was made of white pine timber, and the walls were made from Masonite boards. The camera was mounted to the lid and faced down toward the observation blocks. A small groove was cut into the back of the frame to allow space for the camera cord.

Figure 2: An example observation nest block with *O. cornifrons* cocoons. The nest block was designed for videotaping nesting behavior of *O. cornifrons* by covering the top of the block with transparent plastic film.

2.3. Determining Factors Affecting O. cornifrons Activity. To determine the daily activity pattern of *O. cornifrons*, the number of trips from observation nest blocks initiated per

hour was recorded for ten bees from 15 May 2010–21 May 2010. Data were taken from the start of nesting to six days later. Only those trips where *O. cornifrons* gathered nesting materials (i.e., pollen or mud) were used to determine daily activity levels. The relationship between the number of trips *O. cornifrons* initiated and the time of day was determined using nonlinear regression analysis (SigmaPlot 11, Systat Software, Inc., San Jose, CA, USA).

To determine the effect of temperature on *O. cornifrons* activity levels, hourly climate data were obtained from a National Climate Data Center (NCDC) weather station located ca. 3.3 km from the study site. The weather station (i.e., MGTN RGNL-W L B HART FD AP located at N 39.642867, W 79.919947) is an automated surface observing system weather station which reports NCDC version 3 climate data. Bee activity data (i.e., number of trips initiated per hour) from 18 May 2010 (sunny day) were used to correlate temperature with activity. Correlation between precipitation and bee activity from 16-17 May 2010 (rainy days) was analyzed to determine the effect of precipitation on *O. cornifrons* activity. Because the weather station reported trace precipitation (<0.25 mm rain) without a numerical value, hours of trace precipitation are considered to be 0.025 mm of rain. Correlations of bee activities with temperature and precipitation were analyzed with Pearson's product moment correlation using SigmaPlot 11.

2.4. Intranest Activity of O. cornifrons. To determine the amount of time spent by *O. cornifrons* on different in-nest activities, video data were logged for ten bees from 15 May 2010–21 May 2010: three bees from camera 1, three bees from camera 2, and four bees from camera 3. Intranest activities included nest scouting, construction of preliminary plugs, cell provisioning, oviposition, cell partitioning, resting, grooming, sleeping, fighting, and other activities. For each activity, duration was measured as follows: (1) the start time was taken from the point at which the bee reached the area of the nest being constructed, (2) the stop time was taken from the point work activity ceased, (3) if the bee stayed in the nest for >20 s after building activity ceased, this extra time was recorded along with noting after work activities. A chi-square test determined if the time requirements of intranest activity differed significantly using SigmaPlot 11.

2.5. Gathering Activity of O. cornifrons. To determine the amount of time *O. cornifrons* requires for gathering nesting materials, time away from the nest was recorded for ten bees during every trip made. Trip times were recorded from the start of nesting (15 May 2010) until six days later (21 May 2010). Only trips in which nesting materials were brought back to the nest were used in data analysis. A threshold of 1 h was set for pollen gathering trips and 30 min for mud gathering trips. Any trips exceeding these thresholds were excluded from the data used in calculating the time requirements of gathering activities. The thresholds were not used to calculate the number of trips that *O. cornifrons* took to complete one part of a cell. This was done to account for trips in which *O. cornifrons* engaged in both gathering and nongathering activity (e.g., resting), while still being able to report an accurate number of trips required to complete the provisioning and partitioning of a cell. A chi-square test determined if time requirements of gathering activity differed significantly using SigmaPlot 11.

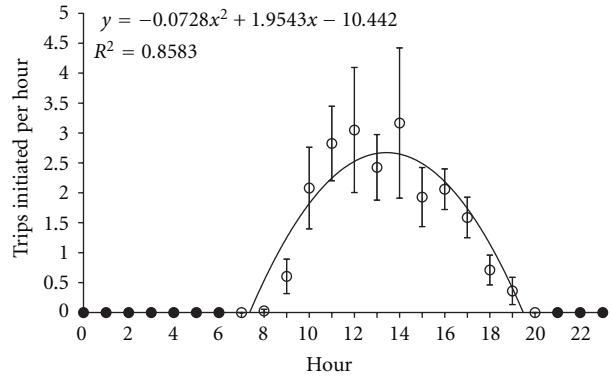

Figure 3: The average number of trips taken per hour by *O. cornifrons*. Hour 0 is 12:00 am and hour 23 is 11:00 pm. Error bars indicate standard error. Only the open circles were used to determine the regression equation.

2.6. Description of O. cornifrons Behaviors. To describe *O. cornifrons* behaviors, 30 *O. cornifrons* were observed from the time nesting was initiated (15 May 2010) until nesting ceased or six days later (21 May 2010), whichever came first. Behaviors were divided into nesting behaviors and nonnesting behaviors. Any behaviors performed during nest constructing activities were considered nesting behaviors and all other behaviors were considered nonnesting behaviors. Nesting behaviors included scouting behavior, preliminary plug behavior, cell provisioning behavior, oviposition behavior, and cell partitioning behavior. Nonnesting behaviors included grooming behavior, resting behavior, sleeping behavior, fighting behavior, nest-searching behavior, nest repair, and nest supersedure. Additionally, other behaviors that did not fall under any of the listed categories were also recorded and described.

3. Results

3.1. Factors Affecting O. cornifrons Activity. Data of daily nesting activity of *O. cornifrons* was fitted with a second-order polynomial trend (Figure 3): $y = -0.0728x^2 + 1.9543x - 10.442$ (d.f. $= 2, 13$; $F = 33.30$; $P < 0.0001$; $r^2 = 0.86$), where y is the number of trips initiated per hour and x is time of day. Daily activity was tested for normality using the Shapiro-Wilk normality test and was found to be normally distributed ($W = 0.9053$; $P = 0.1346$; $\alpha = 0.05$). Variance of daily activity data was constant when disregarding the time of day based on the constant variance test ($P = 0.3642$). All nesting activities of *O. cornifrons* occurred between 7:00 am and 8:00 pm, and the most trips initiated per hour occurred between 10:00 am and 6:00 pm. *O. cornifrons* was not active on days when it rained (Figure 4).

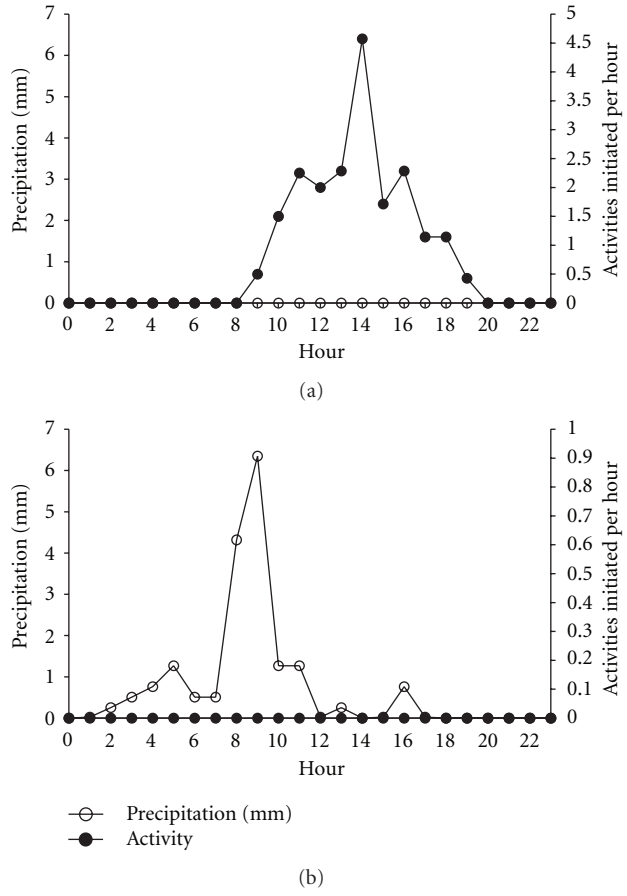

Figure 4: Relationship between *O. cornifrons* activity and precipitation on a day without rain (16 May 2010) (a) and a day with rain (17 May 2010) (b). Hour 0 is 12:00 am and hour 23 is 11:00 pm.

Individuals responded to rain by staying in their nests and occasionally walking to the nest entrance and looking out, but not exiting the nest.

Results of the Pearson product moment correlation test showed that activity and temperature were significantly correlated ($n = 24$; $\rho = 0.856$; $P < 0.0001$). The positive correlation coefficient indicates that *O. cornifrons* activity increased with temperature (Figure 5). *O. cornifrons* were not active below 13.9°C.

3.2. Intranest and Gathering Activities of O. cornifrons. The average total duration of labor required for cell completion (i.e., pollen provisioning, oviposition, and mud wall partitioning) was 51 min ± 6.5 min, and average time to complete the preliminary plug was 27 min ± 2.5 min. Provisioning the cell took most of the total time, requiring 29 ± 4.0 min (i.e., 57% of the total time to complete a cell). Building the mud-wall partition required 20 ± 1.8 min (i.e., 40% of the total time to complete a cell). Oviposition required only 3% of the total time to complete a cell, requiring 2 ± 0.7 min. Cell provisioning was the most time-consuming intranest activity, requiring 28.9 min ± 3.97 min.

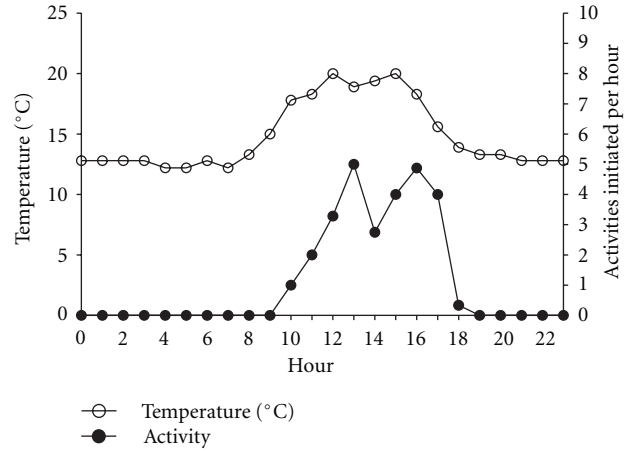

Figure 5: Relationship between *O. cornifrons* activity and temperature. Hour 0 is 12:00 am and hour 23 is 11:00 pm.

The total time required for *O. cornifrons* to gather pollen and mud for one cell was 255 ± 36.8 min, and gathering mud for a preliminary plug required 45 ± 13.7 min. Gathering pollen took 222 ± 28.7 min with an average of 19.8 trips. Gathering mud for the cell partition took 33 ± 8.1 min with an average of 11.5 trips.

3.3. Nesting Behaviors of O. cornifrons. Most nesting behaviors were distinct and consistent throughout the recorded video. Scouting behavior was the most variable behavior observed. When *O. cornifrons* searched for nests, they entered empty nests and moved to the back of the nest. Then they performed a series of forward and backward movements accompanied by turning upside down and left to right, inspecting the nest thoroughly. Finally, they turned and left the nests, occasionally coming back and performing these behaviors again.

During preliminary plug activity, *O. cornifrons* focused on plugging the upper edges of the nest, where the transparency film was attached to the observation block. During many of these trips, *O. cornifrons* moved back and forth repeatedly. This is likely a method used by the bees to measure distance [11]. They used their middle legs for support by holding them out perpendicular to their bodies and grasping the sides of the nest. Then, while holding mud with their mandibles, they bent their abdomen up until the apex of the abdomen was nearly in contact with the mandibles. Moving backwards, the mud ball was spread like a paste onto the nest surface. Use of the abdomen for nest building usually occurred during the preliminary plug activity and most often when the corner formed by the nest and the transparency film was being plugged. Although the use of abdomen during preliminary plug construction may be an artifact of the transparency film in this study, such behavior was observed in *O. lignaria* during mud gathering [16, 17] and mud wall construction [17].

Cell provisioning started when *Osmia cornifrons* females approached the rear of the nest where the pollen ball was being made. They then manipulated the pollen ball with their

mandibles by either pecking at the pollen ball or pushing the pollen ball with the mandibles, using them like a shovel. During this time nectar from the crop was added to the pollen ball. After mandibulating the pollen ball, they turned in the nest and backed up so that their abdomen was over the pollen ball. Then they scraped the pollen from their scopa with their hind legs.

Oviposition behavior looked deceptively similar to cell provisioning behavior. Before oviposition *O. cornifrons* mandibulated the pollen ball, and then turned to oviposit. The primary difference in behavior between oviposition and provisioning was that the abdomen moved vigorously during nest provisioning, but it was very still during oviposition.

Osmia cornifrons females started building a mud wall partition by creating a mud ring around the inner circumference of the nest. Building the ring usually took several trips, and the abdomen was occasionally used to spread mud around the ring in concentric circles. Once there was just a small opening left in the ring they placed mud in the hole and then rotated their entire body several times with their face seemingly directly in contact with the mud wall.

3.4. Nonnesting Behavior of O. cornifrons. Grooming behavior and resting behavior were the most commonly observed nonnesting behaviors. An *Osmia cornifrons* female often groomed itself right after provisioning a cell. Grooming entailed using the front legs to clean off the antennae as well as shaking the abdomen back and forth and rubbing it with the hind legs, seemingly to clean the scopa before the next pollen load was gathered. Frequently *O. cornifrons* would groom itself as it made a hasty exit from the nest. Usually the process did not take more than 20 s to complete and did not slow down nest building activity. When grooming took more than 20 s, it was often followed by resting activity. *Osmia cornifrons* was considered resting when it was in the nest but was not performing any noticeable activity.

Sleeping behavior was defined as all activity that occurred between the final trip of one day and the first trip made the following day. Most frequently, after the final activity of the day, *O. cornifrons* would move about the nest, seemingly giving the nest a thorough inspection. After inspection, activity would cease for several minutes at a time, and if *O. cornifrons* moved, it was only ca. 4 cm. Finally activity would cease for several hours at a time, and if the bee moved, it would most often simply turn sideways. The bees often slept sideways or upside down inside the nest. Many bees did not sleep in the nests at all but returned the next day. If it rained on the morning after a bee had been sleeping outside its nest, the bee did not return to its nest during the rainy day but did return the following day. Some *O. cornifrons* also slept in empty nests. In the morning, as light entered the nest entrances, *O. cornifrons* would begin to move again. Most often, *O. cornifrons* moved ca. 4 cm then ceased movement again for some time. Eventually *O. cornifrons* would go to the nest entrance and look outside. Sometimes they left immediately, but more frequently they moved back into the nest and waited. On a few occasions a bee took flight only to return a few minutes later and resume a resting state.

There was only one observation of an attempt to repair a damaged nest. The nest became damaged when one corner of the transparency film cover became detached from the nest, and when that occurred, one individual attempted to repair the uncovered area. First it spent a great deal of time inspecting the damaged area, then it began gathering mud and trying to patch the open area at the back of the nest. It made 13 trips and patched a large area of the opening but was unable to successfully close it. After the bee's unsuccessful attempt to repair the nest, it seemed to abandon the nest.

4. Discussion

Solitary bee activity levels might be affected by time of day, temperature, or precipitation. *Osmia cornifrons* has previously been observed foraging as early as 6:10 am and as late as 6:00 pm [18]. The earliest time *O. cornifrons* became active in our study was 8:00 am and activity continued until as late as 8:00 pm, a result similar to that recorded by Matsumoto and Maejima [18]. Lee et al. [12] reported that temperatures above 20°C caused an increase in *O. cornifrons* activity. Our study showed that the minimum temperature for *O. cornifrons* to be active was 13.9°C, and bee activity increased with temperature. Matsumoto and Maejima [18] observed *O. cornifrons* activity at temperatures as low as 10.7°C. The difference in the observed minimum temperature for *O. cornifrons* activity in our study and Matsumoto and Maejima's [18] observations may be due to temperature tolerance differences between populations of *O. cornifrons*. In our study, *O. cornifrons* did not fly on rainy days, though this might be attributed to low temperatures on those days; the maximum temperature on the rainy day analyzed in this study was 14.4°C which is 0.5°C above the determined minimum temperature threshold for activity. *O. cornifrons* was most active on warm, sunny days. Therefore, *O. cornifrons* can be expected to be most active from 10:00 am to 6:00 pm on warm days (>13.9°C) without precipitation.

The majority of time that *O. cornifrons* spent performing nesting activities was used for gathering pollen and provisioning the nest, which agrees with information reported by Lee et al. [12]. The average number of cells in *O. cornifrons* nests is 9.5 [15], and results of this study showed that the average number of trips to complete a cell was 31.3. This means that it takes an average of 297 trips for *O. cornifrons* to complete a nest, though this could vary as the nesting season progresses. Comparatively, *O. lignaria* was found to require an average of 32.4 trips to provision a cell and 6.9 trips to construct a mud wall [17] and was found to construct 3.64 cells per nest on average [19].

In addition to observing *O. cornifrons* behaviors described previously, two unusual behaviors were observed that have not been described in detail previously. First, one case of nest supersedure was observed in this study. An *O. cornifrons* female had oviposited in the back of its nest and began building a mud wall. For an unknown reason the bee seemed to abandon the nest but may have been a victim of predation. Two days later, another bee entered the nest, destroyed the original egg, laid a new egg, and finished the mud wall.

Second, *O. cornifrons* females sometimes seemed to have difficulty relocating their nests. Many times a female would enter a nest and immediately turn around and leave, then enter an adjacent nest. Sometimes a bee would enter two or three nearby nests before finally entering its own nest. When *O. cornifrons* entered a nest occupied by another female *O. cornifrons*, fighting took place. During fighting, *O. cornifrons* utilized its mandibles to fight off intruding *O. cornifrons*. Also during fighting, *O. cornifrons* would bend its abdomen forward putting its body in a C-shape. It was difficult to observe from the video footage if the abdominal behavior was being used for offensive or defensive purposes. The duration of fighting was usually several minutes, and most often the original bee displaced the intruder. On some occasions nest constructing activity was interrupted by intruding bees. When an interruption like this occurred, the bee failed to complete the activity it had been working on prior to the interruption and instead inspected the back of the nest and began the behavior all over again.

Osmia cornifrons behaviors described by Yamada et al. [11] were found to be similar to those observed with the video in our study. This indicates that *O. cornifrons* is likely not disturbed by using glass tubes to view their nesting behaviors. Still, the video method has advantages over using glass tubes which make it a valuable tool for studying solitary bees: (1) it does not require the physical presence of the researcher, (2) it can gather data on activities nonstop for weeks at a time which is nearly impossible to do otherwise, (3) video footage can be rewound, sped up, or slowed down as needed to analyze the data, and (4) video footage can be archived and used in other studies. The biggest disadvantages of using the video are the power requirements to run the equipment, the time-consuming nature of watching video footage, the cost of the equipment, and the possibility of technological failure.

This study showed that *O. cornifrons* was most active between 10:00 am and 6:00 pm, and they spent most of their active time gathering pollen and provisioning their nests. It also showed that temperature and precipitation have strong effects on the activity of *O. cornifrons*. This information is important as it can be used to avoid pesticide application during *O. cornifrons* peak activity. Our results indicate that pesticide application should be avoided between the hours of 11:00 am and 4:00 pm to reduce direct contact with foraging *O. cornifrons*.

Ideally, pesticide application should not occur between 7:00 am and 8:00 pm, but this is an impractical recommendation for most growers. Furthermore, observations of *O. cornifrons* sleep habits indicate that they frequently sleep outside the nest, which means that it may be impossible to completely avoid affecting *O. cornifrons* with pesticide sprays. Previous management practice has been to place *O. cornifrons* in the field seven to ten days before crop bloom [10]. From the data gathered it is recommended that growers wait for several days of temperatures above 13.9°C so that the bees can maintain activity after emergence. Releasing *O. cornifrons* in colder weather than this will hinder their ability to perform pollination duties and may cause the bees harm as they cannot forage in the cold temperatures. Additionally, this type of data would be useful in investigating seasonal age differences in the time to provision a brood cell and determining the effect of pesticides on *O. cornifrons* behavior by comparing video footage of *O. cornifrons* in treated and untreated fields.

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