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Structures built by *Solenopsis geminata* (Fabricius,1804) near fern nectaries

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ABSTRACT

Some species of ants build structures away from the nests using soil particles and plant debris. This peculiar building behavior can be displayed near plant food sources, such as extrafloral nectaries, in which the structures apparently work as shelters that protect ants from competitors and parasitoids. Here we report similar structures observed near the nectar-secreting glands of croziers of the fern *Pteridium caudatum* in a field study plot. Workers of the tropical fire ant *Solenopsis geminata* were seen moving between these aggregates and feeding on nectaries. We also observed structures composed of soil aggregates and plant debris apparently used as shelters by *S. geminata* workers which went in and out from them. We suggest that this building behavior might be an opportunistic strategy of *S. geminata* to monopolize the exploitation of these energy-rich sources facing the sympatric ant *Pheidole radoszkowskii*, a frequent visitor of the nectaries and a highly aggressive competitor.

Keywords: Ant behavior, Ant-constructed shelters, Ant-plant interaction, Nectar glands, *Pteridium*, Tropical fire ant.

Introducción

Among ants, there are species that build physical structures away from their main nest to cover foraging trails or food sources. Some of them, for instance, can build shelters using bits of dead vegetal material and soil particles (Anderson and McShea 2001 and references therein). This building behavior is considered a protection strategy of foraging ants against competitors, predators or desiccation (Blüthgen and Feldhaar 2010). Several cases of structures built away nest have been reported among fire ants in the genus *Solenopsis*. For instance, Clarke *et al.* (1989) observed that *Solenopsis invicta* (Buren, 1972) constructed shelters for tending honeydew-producing hemipterans. A similar behavior was also observed in *Solenopsis geminata* (Fabricius, 1804) by Moya-Raygoza and Larsen (2008). These authors found that shelters had a positive effect in the number of leafhoppers and foragers, suggesting that these structures provided both trophobionts and ants with a refuge from which to escape high temperatures and parasitoids. In addition to the construction of shelters involved in mutualistic relationships, it has also been reported that *S. geminata* foragers may cover plant exudates with soil particles furnishing a canopy under which workers feed (Travis 1941).

In this note, we report observations on the building behavior exhibited by workers of *S. geminata* near extrafloral nectaries (EFN) of the bracken fern *Pteridium caudatum* (L.) Maxon in the Andean mountains of

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Venezuela. In addition, we documented aspects of the foraging behavior of this fire ant and its interaction with other ant species in the study area.

The tropical fire ant *S.geminata* is a one of the most serious worldwide pest ants (Wetterer 2011). Originally from the Neotropics, it spread to other continents due to the earliest stages of global commerce (Gotzek *et al.* 2015). The workers of this omnivore ant are important predators of arthropods and seeds (Risch and Carroll 1982; Lai *et al.* 2018). As well as be attracted to honeydew-producing hemipterans, they also feed on others carbohydrate-rich sources such as EFN (Vergara *et al.* 2007).

EFN are glands located in vegetative parts of plants that secrete a sugary water-based nectar (Nepi *et al.* 2018). They are widespread in angiosperms and in ferns, in which having no flowers, are simply named nectaries (Koptur *et al.* 2013). EFN are thought to provide protection to vascular plants by attracting arthropods that prey on herbivores (Bentley 1977, Koptur 2005, Marazzi *et al.* 2013). Being an important energy source for many ant species, EFN play a key role in shaping an ample variety of ant-plant interactions (Koptur 1992, Heil and McKey 2003, Rico-Gray and Oliveira 2007).

EFN in the croziers (the first growth stage of ferns) of the bracken *Pteridium* spp. occur as one pair of rounded protuberances found at the junction of the main stem with the first pair of pinnae (Rumpf *et al.* 1994). During the active life of bracken nectaries, which is estimated from about 6 to 10 days, the nectar can be observed like a drop of a colorless liquid (Page 1982). After this period, the secretion decreases to tiny drops and bracken nectaries turn dark brown. The exudation ceases when the fern pinna become fully unrolled (Tempel 1983).

So far, few studies have documented the ocurrence of stuctures built by ants near nectaries. Our observations seek to shine new light that could contribute to understand the adaptive significance of the ant-construct structures observed near EFN.

Materials and Methods

Observations of structures built by ants in fern nectaries.

The occurrence of workers of *S. geminata* associated with certain intriguing structures around bracken nectaries were casually observed in May 6th 2010 in a 182 m^2 experimental plot in Cerro La Bandera, near Mérida city (lat 8º38'4" N, long 71º9'15" W) at 1 980 m of elevation. This area had been cleared of vegetation and coarse woody debris three weeks before as preparation for a study on fern growth. At the time of the first observation, we noted the presence of one nest of *S.geminata* within the plot. The vegetation was mostly made of young sprouts of *P. caudatum* (52 croziers) and scattered growing grasses. During the first and subsequent days of observation ((May 10th, 13th and 20th), we also noted that the nectaries of many others croziers, which had no structures around them, were visited by workers of other ant species.

We collected ant workers from ferns and nest, and stored in 75% ethanol for species identification. In the case of *S.geminata*, we compared the collected specimens with reference specimens identified by K. Jaffe (Universidad Simón Bolívar, Venezuela). For the identification of the other ant species collected, we followed to Palacio and Fernández (2003), Longino (2003) and Serna *et al.* (2019). Ant vouchers were deposited at insect collection of Laboratorio de Ecología de Insectos, Departamento de Biología, Universidad de Los Andes, Venezuela.

Observations of the feeding behavior of *S. geminata.*

During June-July 2018, we came back to the study area which had been cleared as in the previously referred experience and we monitored the ant foraging activity in 62 croziers of *P. caudatum*. In addition, to obtain more information about the feeding behavior of *S. geminata* in this area, we offered in each of three nests one honey drop on fresh leaves sections placed at ground level as bait. All observations were done between 7:30 am and 10:30 am during six days, and filmed using Sony Cybershot® digital cameras DSC-T9 and DSC-T200.

Results and Discussion

Observations of structures built by ants in fern nectaries.

On the first day of observation, we noted that three croziers of *P. caudatum* (5,8% of population) had some scattered particles of soil and vegetable debris near the nectaries (Figure 1a). Three to five workers of *S.*

geminata visited the nectaries while others workers of the same specie moved the particles around these glands. In the second and third day of observation, the same croziers showed two kinds of structures near nectaries presumably built with the remains observed the first day. In two croziers, nectaries were surrounded and/or covered by these fragments (Figure 1b). The third crozier showed a set of fragments stacked in an elongate form. In all cases, ant workers (3, 3 and 5, respectively) visited nectaries, walked around them or crawled below the structure that seemed to function as a shelter (Figure 1c). On the fourth day of observation, only one of the croziers showed remains of the previously described structures and three workers of *S. geminata* moved near the nectaries. During all days of observations we also noted that nectaries of many others croziers, which had not structures around them, were visited by workers of *Pheidole radoszkowskii* (Mayr,1884) .

Structures built by *Solenopsis* near plant secretions have been scarcely documented. Travis (1941) pointed out that foragers of *S. geminata* covered plant exudates and other moist materials with soil particles and plant debris, under which ants then feed. Longino (personal communication) observed that *S. geminata* workers built a soil pavilion covering EFN in leaf petioles of a *Passiflora* vine touching the ground. The behavioral plasticity involved in activities such as shelter building away from the nest also has been reported in *S. invicta*, another highly invasive ant, which builds satellite nests at the base of plants when harvesting EFN (Koptur *et al.* 2017).

Anderson and McShea (2001) defined buildings made by ants away from their nests as functional adaptive units, or intermediate-level parts, elaborated by a set of workers of the colony. These authors refer to those structures built to exploit EFN as "shelters" used temporarily to maintain easy and exclusive access to this rich food source. In our study, it is likely that the nectaries of *P. caudatum* were the closest and most abundant carbohydrate source in the disturbed area.

We suggest that the two kinds of structures observed near the nectaries of *P. caudatum* represent two different

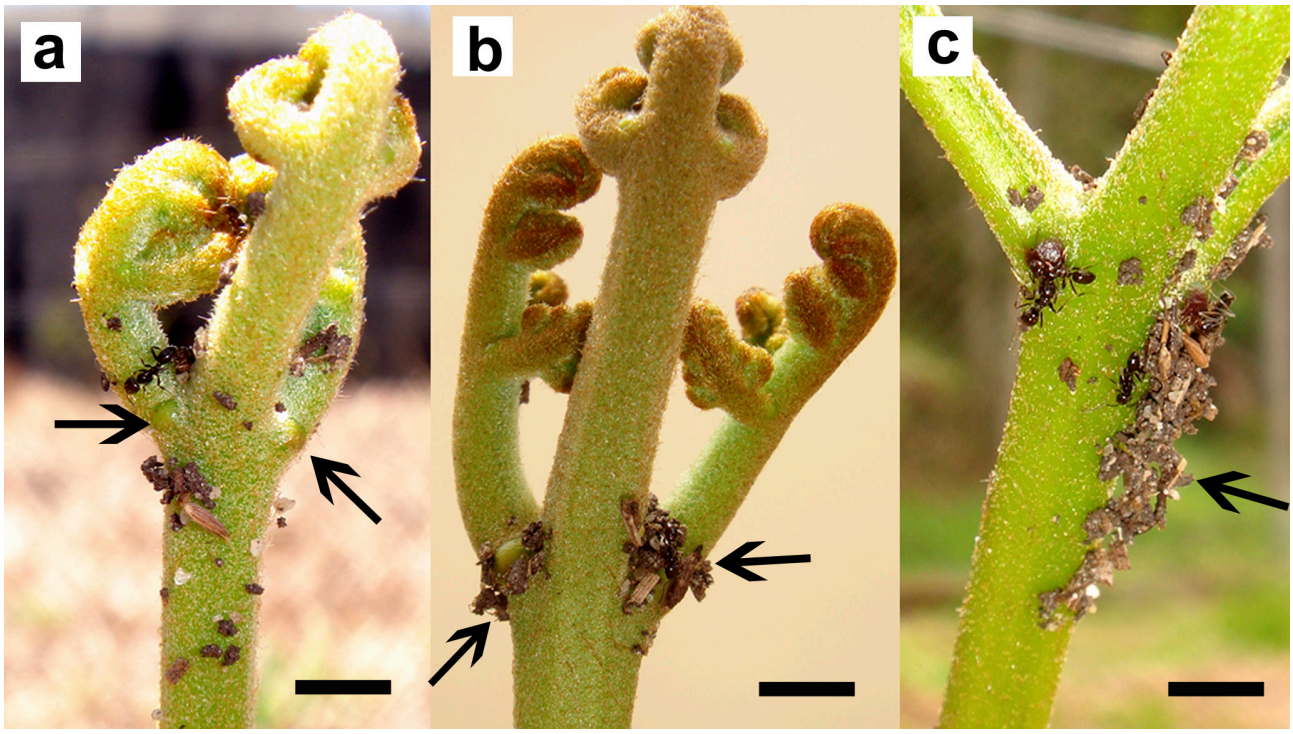

Figure 1. Structures built by *Solenopsis geminata* near nectaries of the fern *Pteridium caudatum*. (a) Scattered particles of soil and vegetable debris near the nectaries (arrows). (b) Nectaries covered with soil particles and plant debris (arrows). (c) A structure built near the nectaries (arrow). All the images show *S. geminata* workers moving around the structures and visiting the nectaries. Scale 5 mm.

ways used by *S. geminata* to gain exclusive access the resource. One way could be the construction of a structure simple, with lesser time and energy cost to colony-specific territorial marking (Figure 1b). Site fidelity would increase foraging efficiency, because ants would recognize with least effort where a rich food source is (Hölldobler and Wilson 1990). The other mechanism could involve construction of structurally more complex shelter to harbor a set of foraging and/or patrolling workers, while nectaries were producing sweet secretion (Figure 1c).

In relation to the apparent temporal nature of these structures, we were not able to ascertain if these structures were disassembled by ants themselves or by a fortuitous event.

Observations of the feeding behavior of *S. geminata*.

During our observations on 62 croziers of *P. caudatum* carried out in 2018, we could not see similar structures such as described previously nor workers of *S. geminata* visiting nectaries. As in previous experiences, we observed that many croziers were visited by workers of *P. radoszkowskii*. In the experiments using bait, workers of *P. radoszkowskii*, were able to rapidly find and monopolize one honey drop near the foraging area of *S. geminata* (Figure 2a). In one case, we were able to observe that following their exclusion, workers of *S. geminata* dug a burrow under the leaf section which contained the honey drop (Figure 2b) from which major workers emerged to fight with the hostile *Pheidole* workers, repelling them from the resource. Some of them were observed throwing plant debris and soil particles on the honey drop. A few minutes later, the opening of the burrow was covered with the excavated soil particles setting up a structure similar to a roof. It seemed work as a shelter from which workers emerged for feeding on the honey drop and / or face the constant attempts of *P. radoszkowskii* to visit it (Figure 2c). This subterranean foraging behavior is a remarkable feature in *S. invicta* and *S.geminata* (Markin *et al.* 1975, Chang and Ota 1976). In fact, we also noted (unpublished observations) that *S. geminata* workers buried dead grasshoppers with soil and plant debris when they were provided as bait.

These observations suggest that the two kinds of structures observed near fern nectaries may work as defensive strategies of *S. geminata* against the sympatric

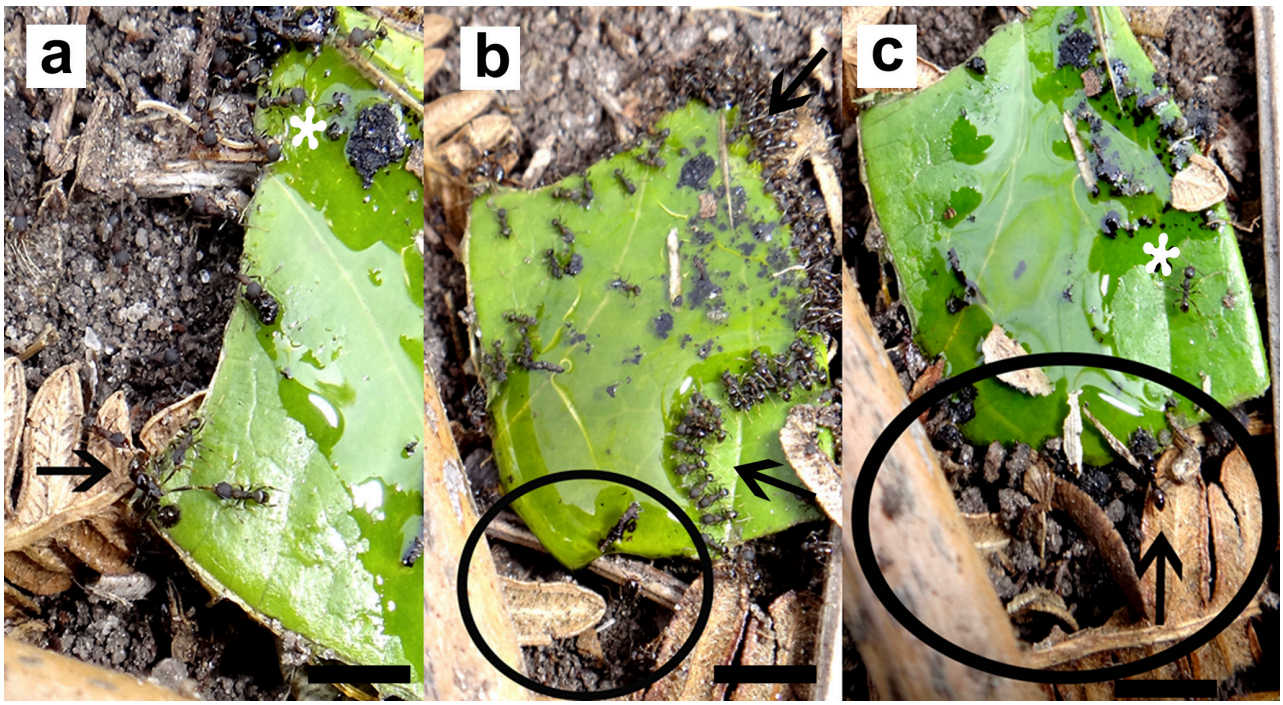

Figure 2. *S. geminata* building a shelter to face *P. radoszkowskii*. (a) Foragers of *P. radoszkowskii* rapidly found (asterisk) the honey drop and attacked *S. geminata* foragers (arrow). (b) While workers of *P. radoszkowskii* fed on honey drop (arrows), *S. geminata* workers built a subterranean shelter with debris (circle). (c) Workers of *S. geminata* emerged from the shelter (circle) to deter *P. radoszkowskii* intruders (asterisk). Scale 5 mm.

ant *P. radoszkowskii*. In studies done in the same study area, it was found that *P. radoszkowskii* was the most frequently collected species on croziers of *P. caudatum*, while *S. geminata* was collected in very low frequency (Ávila-Núñez and Otero 2013, Ávila-Núñez and Otero 2019). Competitive interactions of the ground-foraging ants *S. geminata* and *Pheidole* spp. are frequent in neotropical ecosystems (Perfecto and Vandermeer 2011). For example, foraging experiments performed in coffee monocultures, where the ant community was reduced to two dominant species, showed that *P. radoszkowskii* was more efficient at finding food sources, whereas *S. geminata* was better at defending the resources once they were encountered (Perfecto 1994).

Conclusions

As far as we know, this is first case documented for *S. geminata* building structures on nectaries, adding another trait of behavioral plasticity to the wide set of strategies that allow to invasive ant species to dominate plant-derived resources (Koptur *et al.* 2017).

We suggest that the building of structures near fern nectaries by *S. geminata* in our study area seemed be an opportunist strategy to face the competition from *P. radoszkowskii* in a recently perturbed enviroment, likely with limitations of feed resources.

However, further work needs be done to demonstrate what our observations suggest. For now we will concentrate on increasing the number of observations on the structures that *S. geminata* builds near fern nectaries and examine more deeply the role of *P. radoszkowskii* as possible competitor in this ant-plant interaction.

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