NOTE

ANOTHER ONE BREAKING THROUGH AN ANT PLANT MUTUALISM

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ABSTRACT

Ant-plant mutualistic interactions are common and the degree of specialization varies greatly. Some *Pseudomyrmex* ants maintain an obligate mutualistic relationship with a group of plants in the genus *Vachellia*. Ants aggressively defend the resources the plants provide (food and shelter) against a wide range of herbivores and food robbers. A few arthropods successfully overcome the ant's defense, which allows them to access the resources the plant offers. We here report for the first time extrafloral nectar robbing by *Notaulacella octicola* Sabrosky, 1994 flies (Chloropidae). These flies congregate in large numbers to feed on extrafloral nectar simultaneously with *Pseudomyrmex* ants, which seem to defend the nectaries against flies. This report suggests that the extrafloral nectar of *Vachellia* represents an important food resource for *N. octicola*, particularly during the dry season when small flowers are scarce.

Keywords: *Notaulacella octicola*, *Pseudomyrmex* ants, extrafloral nectar, acacia ants.

RESUMEN

Otro más que atraviesa el mutualismo plata - hormiga. Las interacciones mutualistas entre hormigas y plantas son comunes y el grado de especialización varía mucho entre ellas. Algunas especies de hormigas en el género *Pseudomyrmex* mantienen relaciones mutualistas obligatorias con plantas del género *Vachellia*. Las hormigas defienden agresivamente los recursos que las plantas les suministra (alimento y refugio) contra un amplio rango de herbívoros y ladrones del alimento que obtienen las hormigas de la planta. Algunos pocos artrópodos son capaces de eludir la defensa de las hormigas y acceder a los recursos que la planta ofrece. Aquí reportamos por primera vez el robo de néctar extrafloral de estas plantas por las moscas *Notaulacella octicola* Sabrosky, 1994 (Chloropidae). Estas moscas se agregan en gran número para alimentarse del néctar extrafloral al mismo tiempo que las hormigas *Pseudomyrmex*, las cuales atacan las moscas para, aparentemente, defender los nectarios. Este reporte sugiere que el néctar extrafloral de *Vachellia* representa una fuente de recurso importante para *N. octicola*, particularmente durante la estación seca cuando las flores pequeñas de son escasas.

Palabras clave: *Notaulacella octicola*, hormigas *Pseudomyrmex*, néctar extrafloral, hormigas de las acacias.

Social insects gather large amount of food resources to feed the colony members, particularly the growing larvae (Seeley, 1985; Hölldobler & Wilson, 1990), and these resources are often the target of kleptoparasites (Janzen, 1975; Hölldobler & Wilson, 1990). Kleptoparasites of social insects range from closely related species (Janzen, 1975; Amador-Vargas, 2012) to phylogenetically unrelated species (Hölldobler & Wilson, 1990; Meehan *et al*., 2009); and kleptobiosis varies from occasional to obligate (Kronauer, 2004; Roubik, 2006; Wetterer & Hugel, 2008).

A group of closely related species of ants in the genus *Pseudomyrmex* maintain a tight mutualistic relationship with acacia plants of the genus *Vachellia* (Fabaceae). Plants provide shelter, nesting sites, and food resources for adult and larval ants, and the ants protect the plants from the attack by herbivores, as they defend their resources (Janzen, 1966). These plants produce Beltian bodies, a structure rich in protein, lipid, and sugar (Heil *et al*., 2004) that grow at the end of each pinnule of new leaves, and secrete extrafloral nectar from nectaries at the base of leaves (Fig. 1; Janzen, 1966). Ants collect the Beltian bodies to feed larvae and adults feed upon extrafloral nectar, which is produced continually during the day, with a peak of production around 10 am (unpubl. data SAV).

Two kleptoparasites are known to rob Beltian bodies, clipping them from the pinnules: the ant *P. nigropilosus* (Janzen, 1975; Amador-Vargas, 2012) and the salticid spider *Bagheera kiplingi* (Meehan *et al*., 2009). Both of these arthropods feed on Beltian bodies; *P. nigropilosus* uses them to feed their larvae, while the salticid uses them as a main food source. In addition, *P. nigropilosus* robs extrafloral nectar (Janzen, 1975; Amador-Vargas, 2012). Here we report for the first time the robbing of extrafloral nectar by grass flies, *Notaulacella octicola* Sabrosky, 1994 (Chloropidae

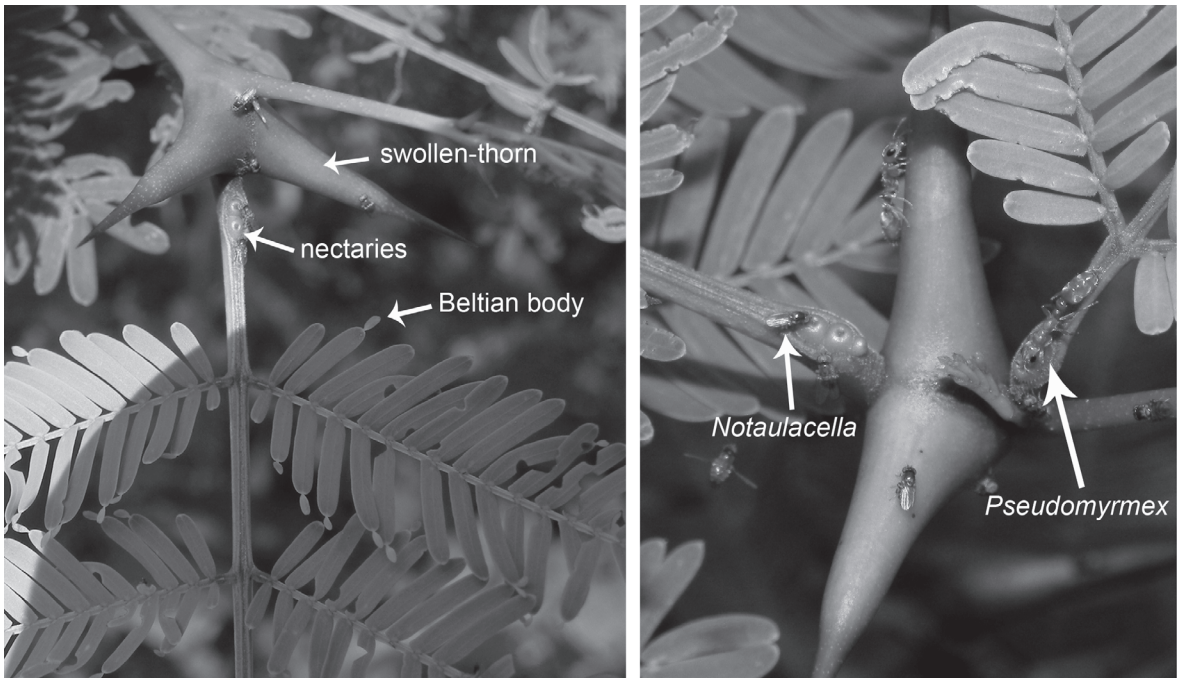

Fig. 1. *Vachellia collinsii*, *Pseudomyrmex spinicola* and the grass fly *Notaulacella octicola*. Section of a *V. collinsii* (left panel) showing the enlarged stipular thorns, extrafloral nectaries and Beltian bodies. *Pseudomyrmex* ants and *Notaulacella octicola* flies feeding on nectar.

family), on plants of *Vachellia collinsii* occupied by *Pseudomyrmex spinicola*.

We observed *N. octicola* flies, apparently feeding on extrafloral nectar of *V. collinsii*, at Santa Rosa National Park (two observers from 6:00 to 14:00 h on 20 May 2016) and Palo Verde National Park (one observer from 7:00 to 16:00 h every day on June 2012, February and May 2015, and May 2017), Guanacaste province, Costa Rica (10º50.120' N, 85º37.061 W, 298 m a.s.l.; 10º 21' N, 85º 21' W, 100 m elevation a.s.l., respectively). Both parks are located in northwestern Costa Rica and are covered primarily by deciduous forest, with tracts of evergreen forest along temporary and permanent streams (Janzen, 1986). *Vachellia collinsii* is a common treelet in second growth areas and forest edges, often forming dense clumps (Janzen, 1966). The annual mean temperature in the region is 25.8 C, and the rainy season from May or June to November averages 1372 mm in Santa Rosa (https://www.acguanacaste.ac.cr/investigacion/datos-meterologicos), and 1700 mm in Palo Verde (https://www.ots.ac.cr/meteoro/default.php?pestacion=1). Voucher specimens of *N. octicola* are deposited in the Museo de Zoología, Universidad de Costa Rica (MZUCR).

When foraging for nectar, *N. octicola* flies hover near the base of young leaves (Fig. 1). Flies then landed on or near the extrafloral nectaries, and those flies that landed near the nectaries walked toward then. Once flies were on top of the nectaries, they inserted part of their heads into the nectaries, presumably to feed on nectar (Fig. 1). *Pseudomyrmex spinicola* ants were also actively feeding on nectar of the same nectaries. The ants seemed to detect the flies because they walked directly toward them with their antennae partially raised and directed toward the flies. When ants approached the flies and nearly touched them, flies either walked backward or flew, landing on leaves, nearby twigs, or on the same twig just behind the ants, usually to return later to the same or other nectaries, sometimes walking around the ants that had attempted to attack them previously.

Larvae of most grass-fly species are known to feed primarily on stems (e.g., monocots) or other living plant tissue, or rotting wood and fungi (Stegmaier, 1966; Nartshuk, 2014). Larvae of other species feed on feces of vertebrates, or decaying animal tissue; others prey on eggs of spiders, whip spiders, and insects (Nartshuk & Pakalniskis, 2004; Víquez & De Armas, 2009; Nartshuk & Yang, 2011; Nartshuk, 2014). Information on the diet of adult grass flies is scarce, but apparently vary widely across species. Adults of many species apparently feed on mold or suck tears from some mammals (Marshall, 2012). Some species possibly feed on excrement of animals and rotten animal tissue, since they are attracted to rotten material (Mulla & Hughes, 1977), and other species prey on spider eggs, or are kleptoparasites of spiders. These kleptoparasitic species feed on fluid of

the prey that spiders are externally digesting (Marshall, 2012). With the exception of the report and distribution of some species, the biology of the genus *Notaulacella* is nearly unknown (Sabrosky, 1994).

There are only a few anecdotal reports of chloropids feeding on floral nectar (Frost, 1979; Fiel, 1997). Our observations are thus the first report of adult grass flies feeding on extrafloral nectar of plants, and besides the obligate parasite of the acacia plants (*P. nigropilosus*, Janzen, 1975; Amador-Vargas, 2012), this is the first report of a kleptoparasite robbing nectar from *V. collinsi* occupied by mutualistic *P. spinicola* ants. The extrafloral nectar of myrmecophytic acacia plants is less attractive for non-symbiotic insects, as it has mainly glucose and fructose instead of the typical sucrose solution of most flower nectaries (Heil *et al.*, 2005). How did the kleptoparasitism of *Notaulacella octicola* evolve? It is still an open question. We propose here that this kleptoparasitism could have evolved through two non-mutually different mechanisms: that either these grass-flies lost the capability to hydrolyze sucrose into glucose and fructose, as occurs in mutualistic acacia ants (Heil *et al.*, 2005), or that they are one of the few non-symbiotic insects that are attracted to the nectar of myrmecophytic acacias.

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