

— Novel Ideas and Pilot Projects —

FLORAL LARCENY BY THE STINGLESS BEE *TRIGONA AMALTHEA* ON GRANADILLA (*PASSIFLORA LIGULARIS* JUSS)

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Abstract—Floral larceny (robbery and thievery of nectar and/or pollen) by some species of stingless bees in the genus *Trigona* has been long reported for several plant species, although the consequences for plant reproduction are unknown for many cultivated species. Here we i) describe the behaviour of *Trigona amalthea* Olivier in relation to flowers of granadilla (*Passiflora ligularis* Juss), ii) provide a preliminary assessment of fruit set in six experimental plots, one exposed to attacks by *T. amalthea* only (infested) and the other plots without attacks from any species (control plots), and iii) discuss potential strategies for preventing damage from *T. amalthea* based on species traits such as foraging range. We observed *T. amalthea* chewing styles and stigmas of both flower buds and mature flowers while primarily extracting pollen. Destruction of floral structures prior to ovule fertilization probably accounts for the significant reduction in fruit set in the infested plot compared to control plots, although replicated infested plots are required for robust confirmation. Moreover, negative effects may be intensified by the small size of the experimental plot. Further studies are needed to assess impacts on commercial plantations, including investigations into a potential dilution effect in larger crop fields, as well as plant mechanisms to cope with consumer damage (resistance and tolerance). Legitimate pollinators were found to cover larger distances than *T. amalthea*. Therefore, locating crop fields at optimal distances from bee nesting habitat might reduce damage by balancing bee services and disservices.

Keywords: Floral robbery, florivory, ecosystem disservices, passion fruit, crop pest, crop pollination management, Colombia

INTRODUCTION

Reproduction of most flowering plant species is mediated by animal pollinators, which are attracted by the flowers through advertising signals (e.g., colours, shape, or scents) and food rewards (i.e., pollen and nectar) (Willmer 2011). However, some flower visitors do not contribute to plant pollination, because they extract rewards but transfer little or no pollen. In some cases, this is caused by a mismatch between the morphology or size of the flower and that of the flower visitor. Hence, despite the fact that such visitors collect pollen and/or nectar through the flower opening, pollen is hardly transferred. These types of visitors are considered “thieves”. In other cases, visitors damage floral structures by making holes in buds, mature flowers or anthers, in order to extract pollen or nectar without entering the flower. Such visitors are known as “robbers” (Inouye 1980). Robbery and thievery of nectar and pollen are collectively referred as floral larceny (Irwin et al. 2001, 2010) and often reduce plant reproductive success, although neutral and positive effects have also been documented (Hargreaves et al. 2009; Irwin et al. 2010).

Although bees participate in the pollination of most wild and cultivated plants (Klein et al. 2007; Ollerton et al. 2011), they are also common robbers and thieves of nectar and pollen (Hargreaves et al. 2009; Irwin et al. 2010). Particularly in the Neotropics, some species of stingless bees in the genus *Trigona* (subgenus *Trigona* s. str.) have long been reported as floral larcenists in wild plants (Roubik 1982; Renner 1983; Roubik et al. 1985; Boiça Jr et al. 2004; Gélvez-Zúñiga et al. 2017), as well as in a wide variety of crops such as citrus (*Citrus* spp), macadamia (*Macadamia integrifolia* Maiden & Betche), banana (*Musa* sp.), soursop (*Annona muricata* Linnaeus), blueberry (*Vaccinium ashei* Reade), Mangosteen (*Garcinia mangostana* Linnaeus), yellow passion fruit (*Passiflora edulis* Sims, f. *flavicarpa* Degener) and purple passion fruit (*Passiflora edulis*, f. *edulis*) (Wille 1965; Henigman 1975; Silva et al. 1997; Sobrinho et al. 1998; Sacramento et al. 2007; Silveira et al. 2010; Ramírez et al. 2012). Larcenist behaviours of *Trigona* bees targeting flowers are diverse. They include chewing and piercing anthers to collect pollen (Wille 1965; Renner 1983; Ramírez et al. 2012), and making holes through the calyx and corolla to access the nectar chamber, both in mature flowers and flower buds (Roubik 1982; Roubik et al. 1985; Silveira et al. 2010; Gélvez-Zúñiga et al. 2017). Effects of larcenist behaviours of *Trigona* bees on plant reproduction, however, have not been studied for many plants, and the results are diverse. In the

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tropical wild plants *Quassia amara* and *Pavonia dasypetala*, seed production was indirectly reduced by *T. fulviventris* and *T. ferricauda* respectively, due to attacks on, and consequent deterrence of, effective pollinators (Roubik 1982; Roubik et al. 1985). In contrast, reduced pulp percentage of the cultivated *Passiflora edulis* was directly linked to the behaviour of *T. spinipes* of removing pollen from the stigmas (Silva et al. 1997). However, no effect on fruit set was observed in this plant species from calyx perforations made by *T. spinipes* (Silva et al. 1997). The wide variation in bee behaviours and their consequences for plant reproduction will be better documented as more *Trigona*-plant interactions are studied.

Granadilla (*Passiflora ligularis* Juss) is a passion fruit species mainly produced in Colombia and Peru for local consumption and global markets (Agronet 2017; SIEA 2017). Similar to other commercial passion fruits (Junqueira & Augusto 2017), granadilla is a crop highly dependent on bee pollination. The heavy and sticky pollen is primarily transferred by large-bodied bees (Arias-Suárez et al. 2016). Experimental studies have shown that fruit set is significantly higher when flowers are naturally exposed to bees than when pollinators are excluded (Arias-Suárez et al. 2016). The positive effect of bees on granadilla production has long been recognized in handbooks for producers (although measured only recently), along with the damage caused by *Trigona* stingless bees to granadilla flowers (Rivera et al. 2002; Bernal & Cabrera 2006; Melo 2007; Mora & Benavides 2009). However, detailed information such as the species involved, type of damage and effects on pollination is largely lacking. In this study, we aimed to i) describe the behaviour of *Trigona amalthea* Olivier in granadilla flowers in an experimental plot in Colombia, ii) compare fruit set between plots differing in the presence of *T. amalthea* (i.e. present – absent), and iii) discuss potential preventive and control strategies for *T. amalthea* based on information on foraging ranges (as compared to effective pollinators of granadilla) and floral preferences.

MATERIALS AND METHODS

Study region and experimental plots

The study region was located in the department of Quindío, Central Andes of Colombia (4°N, 75°W) between 1900 and 2000 m a.s.l. Mean annual rainfall is 2817 mm, and mean monthly temperature ranges between 16 and 24°C (Fagua et al. 2013), matching the optimal growing conditions of *P. ligularis* (Fischer et al. 2009). The landscape is predominantly a mosaic of pasture for cattle grazing (62%) and subandean forest (31%). We studied six experimental granadilla plots (belonging to a larger pollination experiment, Gutiérrez-Chacón et al. *unpublished data*), each with 12 one-year-old granadilla plants. All plots were located on cattle grazing pastures equally distant from any forest area (20 m); distances between plots were at least 1 km. One plot showed attacks from *T. amalthea* to floral structures (infested plot, 'I') whereas the other plots did not show attacks from *T. amalthea* (control plots, 'CI – C5'). We could not include replicates of the infested condition as *Trigona*-caused damage was observed in just one of the experimental plots.

Behaviour of *Trigona amalthea*

Surveys were conducted from 23rd November to 14th December 2015, between 07:00 and 13:00, which is the period of maximum stigmatic receptivity and nectar and pollen presentation (Rivera et al. 2002). To describe the behaviour of *T. amalthea* in the infested plot, we made observations of individual bees damaging flowers during 15-minute observation periods on six different days (for a total of 90 min of sampling effort). To assess the potential effectiveness of *T. amalthea* as a pollinator of granadilla, we calculated the percentage of visits in which *T. amalthea* individuals made contact with floral reproductive structures in undamaged flowers. For this, we observed three flowers for 10 minutes each on six different days (in total 18 flowers), and calculated the percentage of touches to stigma only, anthers only, or both simultaneously in a single visit. We further estimated the percentage of damaged flowers by counting the total number of open flowers from all plants in the plot, and the number of flowers showing injuries in floral structures on three different days.

Fruit set

We compared fruit set from flowers exposed to natural pollination (left open for free access to flower visitors) from the infested and the control plots. Flowers of only four plants (out of 12) in each plot were assessed; the other plants were assigned to pollination treatments not part of this study. In each plant, we randomly marked 4 – 6 open flowers (which are functional for just one day) on six different days, for a total of 27 – 30 flowers per plant. Fruit set was assessed 5 – 7 days after flower opening by inspecting the ovary of each marked flower, which starts swelling within the first two days after fertilization (Hammer 1987). We estimated percentage of fruit set (marked flowers that had swollen/total marked flowers × 100) per plant in each plot. In the infested plot, we included damaged and non-damaged flowers as a random sample of all flowers exposed to bee effects, including those produced by *T. amalthea*.

Abundance of flower visitors

We estimated the abundance of flower visitors in each plot in order to account for differences in fruit set between plots due to differences in pollinator density. For this, we scanned 100 open flowers while walking slowly along the plot for a maximum of 15 minutes (scanning round) and recording flower-visitor species (Vaissière et al. 2011). In each plot, we carried out a total of 21 scanning rounds during seven days (three rounds per day); 12 rounds in the early morning (7:00–10:30) and nine rounds in the late morning (10:30 – 13:00). Bees were identified based on a reference bee collection of the study area (Gutiérrez-Chacón et al. 2018). Identification of *T. amalthea* was confirmed by V.H. Gonzalez (University of Kansas).

Foraging ranges of flower visitors and nest location of *Trigona amalthea*

We estimated foraging ranges of bee species visiting granadilla flowers using the distance between the two insertion points (tegula) of the wings ('inter-tegular distance', ITD), which is an indicator of the flight musculature (Cane, 1987)



FIGURE 1. Damage caused by *Trigona amalthea* to granadilla flowers. Petals of flower-buds are perforated and cut away with the mandibles to extract mainly pollen (a, b). From open flowers, *T. amalthea* obtain nectar and pollen but can also continue damaging floral structures (c), causing loss of flower functionality as stigmas and styles can be totally destroyed (d).

and a strong predictor of foraging ranges (Greenleaf et al. 2007). An ITD average per species was obtained by measuring 10 specimens. Following relationships proposed by Greenleaf et al. (2007), we used ITD and bee family to predict the 'typical homing distance' (THD, distance at which 50% of bees return when moved away from the nest), the 'maximum homing distance' (MHD, distance at which 10% of bees return when moved away from the nest), and the 'maximum feeder distance' (MFD, maximum distance reached after progressive movements of artificial feeders, once bees have been trained) in the R package BeeIT (Cariveau et al. 2016). To determine the distance between *Trigona* nests and the infested plot, and to describe some of their characteristics, we located nests by observing flying directions (arrival and departure) and following *T. amalthea* individuals to their nest (D. Melo, pers. communication).

Statistical analyses

Mean percentage of fruit set (calculated across four plants per plot) was compared between plots with a one-way ANOVA, followed by a Bonferroni's post hoc correction of multiple pair-wise comparisons on means. To compare abundance of flower visitors between plots, we pooled bee abundance across the three scanning rounds in a single day, and compared mean abundance (across seven days) using a

one-way ANOVA. All analyses were conducted in the software R 3.3.2 (R Core Team 2016).

RESULTS

Behaviour of *Trigona amalthea*

We observed individuals of *T. amalthea* injuring both flower buds and mature flowers (Fig. 1). In buds, *T. amalthea* cuts away petals and corona filaments to create holes through which individuals extract mainly pollen. Holes (usually one or two) were located either in the centre or toward the tip of the petals, at the level of the anthers (Fig. 1a, b). In mature flowers, they collected both nectar and pollen, but also chewed stigmas, anthers and styles (Fig. 1c, d). From the total visits performed by *T. amalthea* to undamaged flowers, there was no contact with any of the floral reproductive structures (anthers or stigma) in 76% of the visits; contact with anthers or stigma only occurred in 16% and 5% of the visits, respectively, and both structures were touched in a single visit only in 3% of the visits. From all open flowers in the infested plot (assessed during three days), 47% (SD = 8%, $N = 3$) showed damage by *Trigona* bees.

Fruit set

Percentage fruit set differed significantly among plots ($F_{5,23} = 5.13$, $P < 0.01$). The Bonferroni post hoc test showed

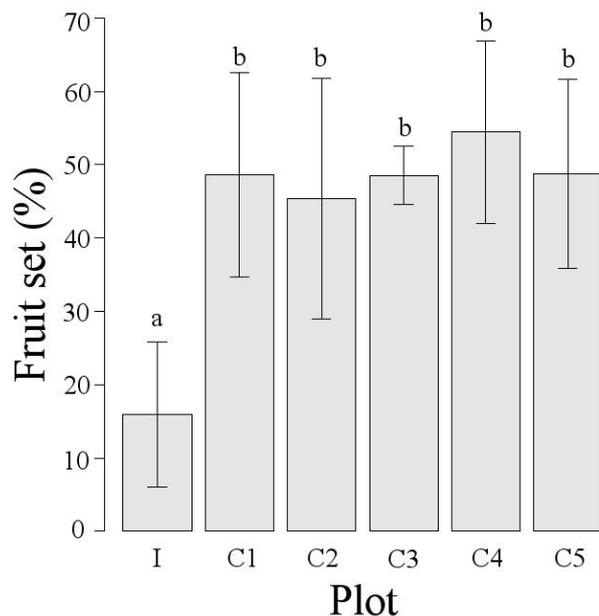


FIGURE 2. Comparison of the percentage of fruit set (Mean \pm SD) between plots whose flowers were attacked by *T. amalthea* (I = infested plot) and plots without attacks from this species (C1 – C5 = control plots). Bars with different letters are significantly different according to the Bonferroni post hoc adjustment for multiple comparisons $P < 0.05$ (See data in Supplementary Table S1).

that percentage of fruit set was significantly lower in the infested plot (Mean = 16%, SD = 10%) compared to each of the control plots, where mean percentage of fruit set ranged

between 45% (SD = 17%, plot C2) and 54% (SD = 13%, plot C4) ($P < 0.05$, Fig. 2).

Abundance of flower visitors

Abundance of flower visitors, which were mainly bees (Tab. 1), did not differ among plots ($F_{5,41} = 0.43$, $P = 0.83$). *Trigona amalthea* was absent from most of the control plots (except in C2 where two individuals were observed), but was the most abundant species in the infested plot (Tab. 1), where we observed 0.73 ± 0.3 (mean \pm S.D.) individuals of *T. amalthea* per flower.

Foraging ranges of flower visitors and nest location of *Trigona amalthea*

The predicted maximum foraging distance of *T. amalthea* was 0.87 km (MFD), while the smallest of the three foraging distances of large pollinators such as *Xylocopa lachnea* and *Epicharis rustica* was 6.92 km (THD, Tab. 1). In our study, the *Trigona* bees attacking granadilla flowers originated from two different nests, located at 200 and 300 m from the infested plot. Both nests were built in the intersection of tree branches and at the base of epiphytic roots of Bromeliaceae plants, at 2.5 and 5 m high, respectively. The trees were located in pastures at 5 and 60 m, respectively, from forest areas.

DISCUSSION

Given the damages inflicted by *T. amalthea* to flower buds and mature flowers of granadilla, as well as the low frequency of contacts with reproductive structures when visiting mature

TABLE 1. Abundances and predicted foraging ranges of bee species observed in granadilla flowers in the infested plot (I) and the control plots (C1 – C5). Foraging distances were predicted using ITD and bee family following relationships proposed by Greenleaf et al. (2007), in the R package BeeIT (Cariveau et al. 2016).

Species	Plot						Foraging distances (km)		
	I	C1	C2	C3	C4	C5	THD ^a	MHD ^b	MFD ^c
Bees									
<i>Apis mellifera</i>	638	1784	1788	1530	1658	1375	0.56	1.20	1.70
<i>Epicharis rustica</i>	12	1	0	4	4	34	6.92	16.41	10.27
<i>Eulaema cf. meriana</i>	0	1	0	0	0	0	4.62	10.86	7.42
<i>Eulaema cingulata</i>	2	4	0	2	2	1	6.54	15.47	9.86
<i>Paratrigona rinconi</i>	0	2	0	0	2	5	0.05	0.09	0.30
<i>Partamona cf. peckolti</i>	5	19	47	40	2	259	0.10	0.19	0.49
<i>Pseudaugochlora graminea</i>	1	3	0	2	2	1	0.34	0.72	1.18
<i>Thygater aethiops</i>	0	2	0	2	23	11	0.99	2.18	2.56
<i>Thygater sp.</i>	1	2	3	0	0	2	1.45	3.23	3.36
<i>Trigona amalthea</i>	1314	0	2	0	0	0	0.22	0.46	0.87
<i>Xylocopa lachnea</i>	17	33	4	15	21	36	9.95	23.94	13.29
Wasps									
<i>Synoeca sp.</i>	0	0	0	0	5	0	-	-	-
Scoliid wasp	0	0	0	0	4	0	-	-	-
Total	1990	1851	1844	1595	1723	1724			

flowers, this species of stingless bee can be considered both as a robber and thief of *P. ligularis*. Injuries to floral structures were mainly produced to collect pollen. In buds, *T. amalthea* did not make holes in the calyx, as is done by nectar robbers such as *T. fulviventris* and *T. ferricauda* (Roubik 1982; Roubik et al. 1985). Instead, they cut in at the level of the anthers, indicating their pursuit of pollen. In both buds and mature flowers, *T. amalthea* severely chewed anthers and stigmas where pollen grains were available. Pollen removal from stigmas of yellow passion fruit by *T. spinipes* has been observed in Brazil (Silva et al. 1997). Among *Trigona* species, colonies of *Trigona* s. str. are the largest in size, comprising thousands of individuals. Such colonies naturally demand high amounts of food for their larvae (Renner 1983).

Fruit set was significantly lower in the infested plot than in plots free from *T. amalthea*. Because the abundance of overall flower visitors was similar between plots, we discount differences in fruit set due to differences in the abundance of pollinators. Pollination of granadilla was likely diminished by *T. amalthea* due to the destruction of styles and stigmas preceding ovule fertilization. Comparable flower injuries were also observed in granadilla fields in the Eastern Andes of Colombia (Melo 2007). Our results differ from findings in yellow passion fruit (*P. edulis* f. *flavicarpa*), where perforations of the calyx caused by *T. spinipes* did not affect fruit set (Silva et al. 1997). *Trigona amalthea* can thus exert a direct effect on granadilla by damaging structures related to potential reproductive output, contrasting to the indirect effects of *T. fulviventris* and *T. ferricauda* on seed production, which include attacking and deterring effective pollinators (Roubik 1982; Roubik et al. 1985). As any type of consumer-caused damage to developing floral buds or mature flowers before the development of the seed coat is considered florivory (McCall & Irwin 2006; Irwin et al. 2010), *T. amalthea* could therefore be also considered as a florivore in granadilla. However, florivorous behaviour of bees seems uncommon, with beetles and moths being the most frequent florivores (Althoff et al. 2005; Penet et al. 2009; Cardel & Koptur 2010; Söber et al. 2010; McCall & Barr 2012; Eliyahu et al. 2015; Carper et al. 2016). In previous studies, bee-caused damage to flower parts have been mostly related to pollen and nectar robbery (Irwin et al. 2010); floral structures such as ovaries and styles are usually sequentially or simultaneously damaged while the animal is collecting pollen (McCall & Irwin 2006).

Due to the small size of our experimental plots, our findings should be considered with caution. One nearby colony of *T. amalthea* can devastate a small plot, but negative effects can be diluted in large fields such as those found in the main producing regions in Colombia (of several hectares). Therefore, the impacts of *Trigona* bees on granadilla production need to be evaluated on commercial plantations, and should include investigation on the main strategies of plants to cope with consumer damages: resistance and tolerance. To resist attacks, plants can reduce the frequency or intensity of damage by producing secondary metabolites, which act as repellents or inhibitors (Wink 2003). Although secondary metabolites may help *Passiflora* species to resist herbivory attacks (Wheeler & Bennington 2001; Patil et al. 2015), empirical data on the induction of these compounds in response to floral larceny is largely lacking (Irwin et al.

2010). Tolerance, on the other hand, refers to the maintenance of fitness after consumer damage (Irwin et al. 2010). The production of surplus flowers in response to high rates of floral larceny has been reported in the wildflower *Ipomopsis aggregate* Pursh (Irwin et al. 2008). Similarly, granadilla produce many more flowers than can be developed to mature fruits (Gutiérrez-Chacón et al. *unpublished data*), but whether this is a mechanism to cope with florivory is matter of further research.

Damages caused by *T. amalthea* in granadilla were directed toward flower buds and mature flowers. The behaviour of *T. spinipes* in *Passiflora coccinea* was similar, except that only mature flowers (not buds) were damaged (Boiça Jr et al. 2004). However, we did not conduct observations during the fruit production period, and damages to fruits caused by *T. spinipes* have been reported in yellow passion fruit (Rodrigues Netto & Berlote 1996). Other plant structures such as leaves, branches and floral peduncles have been reported to be damaged by *Trigona* bees in broccoli (*Brassica oleracea* Linnaeus), physic nut (*Jatropha curcas* Linnaeus) and yellow passion fruit (Boiça Jr et al. 2004; Rasmussen et al. 2009; Santos et al. 2012). In those cases, bees mainly extracted fibers and resins, likely to be used as materials for nest construction, in contrast to food resources exploited in granadilla plants.

Given the potential negative effect that *Trigona* bees can exert on crop production, preventive and control strategies may be desirable. Crop fields in highly forested landscapes may be more susceptible to attacks, since stingless bees are positively associated with forests (Brosi 2009). Although we found the nests of *T. amalthea* within pastures, they were located in large trees, which are common in forests but not in pastures. Thus, a primary preventive measure could be a minimum distance between the crop field and the forest habitat. Although 900 m was the predicted maximum flight distance at which it is still energetically profitable for *T. amalthea* to forage, legitimate pollinators such as *Xylocopa lachnea* Moure, *Epicharis rustica* Olivier, and *Apis mellifera* Linnaeus are able to cover much larger distances. Future investigations are needed to identify crop locations with a suitable balance between bee pollination services and disservices by *Trigona* bees. In terms of control strategies, although destruction of *Trigona* nests is a widely recommended practice for producers (Aguiar-Menezes et al. 2002; Sacramento et al. 2007; Mora & Benavides 2009), locating nests is not always possible and may be incompatible with environmentally friendly practices (Santos et al. 2012). Instead, the use of attractive trap plants that divert *Trigona* bees from the target crop species (Ratnadass et al. 2012), is a potential solution and a topic that awaits further research. Plants in the family Cucurbitaceae can potentially serve as trap plants (Melo 2007). However, empirical data on appropriate plant species across regions, planting densities of the target crop, and cost-benefit analysis are required to validate the use of trap plants as a control management for *Trigona* spp. Successful development and implementation of preventive and control strategies for *Trigona* bees will depend on more accurate assessments of the impacts on commercial passion fruit plantations.

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APPENDICES

Additional supporting information may be found in the online version of this article:

APPENDIX I. Raw data on fruit set per plant per plot

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