Pollination Syndrome and Nectar Protection in *Brugmansia suaveolens* (Solanaceae)

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**ABSTRACT**

Specialization between plant and pollinator species has resulted in the development of pollination syndromes in which suites of floral traits attract specific pollinators. While plants use nectar as a reward to attract pollinators, they must also defend themselves, either chemically or morphologically, against nectar robbers. *Brugmansia* (formerly *Datura*; Solanaceae) has been described as possibly sphingid, hummingbird, bee, or bat pollinated, underscoring how little is known about pollination in this genus. It is also heavily protected chemically, including the flowers. One aim of this study was to examine floral traits and compare them to known pollination syndromes to determine the most likely pollinators of *B. suaveolens*. Additionally, I looked for possible chemical protection of nectar and petals against nectar robbers. I studied the change of pollen load and the sucrose concentration in nectar every morning and night for 70 flowers in Cañitas, Costa Rica; I also did two experiments regarding ant preferences of *B. suaveolens* nectar and petals. Pollen load decreased over time and mostly at night suggesting nocturnal pollinators that were recruiting to the flowers. Sucrose concentrations in nectar also decreased over time and were higher in the morning than at night, possibly due to evaporation and condensation. My data suggest that the dominant pollinators of *B. suaveolens* are most likely bats and hawkmoths; bees may be secondary diurnal pollinators. Neither petals nor nectar deterred ants suggesting there is no chemical protection against nectar robbers in the flowers. Nectar thievery by insects, possibly including bees, appears to be especially prevalent in older flowers.

**RESUMEN**

La especialización entre las especies de plantas y polinizadores ha resultado en síndromes de polinización en los cuales los rasgos florales atraen polinizadores específicos. Mientras las plantas usan néctar como recompensa para atraer polinizadores, ellos deben también defenderse ellos mismos, tanto química como morfológicamente, contra ladrones de néctar. *Brugmansia* (Solanaceae) ha sido descrita como posiblemente polinizada por Polillas, colibríes, abejas o murciélagos, demostrando lo poco que se sabe a cerca de la polinización en este género. Esta también altamente protegida químicamente, incluyendo las flores. Uno de los objetivos de este estudio fue examinar los rasgos florales y compararlos con los síndromes de polinización conocidos para determinar el posible polinizador de *B. suaveolens*. Adicionalmente, busqué por posibles protecciones químicas de néctar y pétalos contra ladrones de néctar. Estudio el cambio en la cantidad de polen y las concentraciones de sacarosa en el néctar cada mañana para 70 flores en Cañitas, Costa Rica; también realicé dos experimentos con respecto a la preferencia de néctar y pétalos por parte de hormigas. La cantidad de polen disminuye conforme el tiempo y generalmente durante la noche sugiriendo que polinizadores nocturnos visitaron las flores. La concentración de sacarosa en el néctar disminuye también conforme el paso del tiempo y es mayor durante la mañana que la noche, posiblemente debido a la evaporación y condensación. Mis datos sugieren que el polinizador dominante de *B. suaveolens* es más probablemente murciélagos o polillas; abejas pueden ser polinizadores secundarios durante el día. Ni pétalos ni néctar espantan las hormigas sugiriendo que no hay protección química contra los ladrones de néctar en las flores. El robo de néctar por insectos, posiblemente incluyendo abejas, parece ser especialmente prevalente en flores viejas.

**INTRODUCTION**

Pollination is often specialized as this may increase the likelihood that pollen is carried to conspecifics (Nepi et al. 2010). Specialization in pollination has led to the evolution of pollination syndromes where a set of floral traits attract specific pollinators (Faegri & van der Pijl 1979). These traits can include floral morphology, scent, phenology, the quality, and quantity of specific rewards (Faegri & van der Pijl 1979). Though sometimes questioned (Hingston and McQuillan 2000; Nepi et al. 2010; Ollerton et al. 2009), the usefulness of pollinator syndromes as an approach to understanding pollination ecology is still widely supported (Kaczorowski et al. 2005; Knapp 2010; Perret et al. 2000; Raguso et al. 2003).
Beyond attracting their pollinator, plants must also defend themselves against nectar theft (Guerrant & Fielder 1981). Some floral traits, therefore, may reflect defense as well as pollination. Compounds in petals or nectar may deter aerial insect robbers, such as trigonid bees, as well as arboreal/terrestrial thieves, such as ants (Guerrant & Fielder 1981). Petal texture may also deter nectar robbers (Guerrant & Fielder 1981). That nectar must remain accessible and palatable to pollinators makes it difficult to defend against robbers. In some cases, the pollinator has evolved to deal with otherwise unpalatable substances in nectar that may make them unattractive to robbers (Adler & Irwin 2005; Johnson et al. 2006).

*Brugmansia suaveolens* (formerly *Datura*) in the Solanaceae family is a species whose floral traits may reflect both pollination and protection against nectar robbers. This plant is exceptionally chemically active and has hallucinogenic properties (Anthony et al. 2009); because of this, all studies of this plant have focused on its chemistry and left its natural history completely unexamined. The pollination biology of this species is unknown: Knapp (2010) reported that the pollination syndrome for *Brugmansia ssp.* could indicate pollination by hummingbirds, hawkmoths, or bats. Bees are reported to visit flowers as well. The goal of this study was to determine the pollination syndrome of *Brugmansia suaveolens* and to ascertain if some floral characteristics are adaptations to defend against nectar robbers. I examined *B. suaveolens* floral morphology, changes in pollen load over time, and changes in the sugar concentration of nectar as related to flower age. In addition, nectar and petals were offered to ants to assess possible traits related to nectar robbery.

**MATERIALS & METHODS**

*Brugmansia suaveolens*

This plant is native to South America but is grown as an ornamental worldwide (Zuchowski 2005). Common names are Reina de la Noche or Angels Trumpets. Flowers are large and pendulous with long, narrow corollas that flare at the mouth (Zuchowski 2005; Figure 1). Anther dehiscence occurs at night when white flowers open; these turn pink at the mouths by the following day (Anthony, 2009). Flowers also emit a strong, sweet odor at night (Zuchowski 2005).

![Figure 1. B. suaveolens blooming at night. The flower visible in the background of the photo on the right is in the early stages of wilting. Buds are also visible in the mid-ground of the photo on the right.](image)
STUDY SITE AND PLANTS
Fieldwork was conducted in the Jardín Rosewood in Cañitas, Costa Rica which is located in moist premontane habitat between 1200 and 1300 m. The site was previously cleared for pasture and has since been replanted with a variety of exotic and native species. The garden contained 37 plants of *B. suaveolens*. All *B. suaveolens* were three to five meters tall, located in full or partial sun, and were watered regularly.

FLORAL TRAITS RELATED TO POLLINATION
Pollen and nectar experiments took place over one blooming cycle from April 25th to May 4th, 2011. Flowers that bloomed on the same day were considered a set. Measurements were taken at night (6 PM – 9 PM) and in the morning (9 AM – 12 PM). 70 flowers on 24 plants were measured for five days (until wilting). All accessible (below nine feet above the ground) flowers were measured.

*Pollen Loss.*—I measured the amount of pollen on the anthers over time using a scale from zero to four. Four indicates the anthers had all of the pollen, three that the anthers had most of the pollen but were not as full as in level four, two and a half that pollen had been partially removed (the half of the anthers closest to the ovaries remained full of pollen and the other half closest to the mouth was pollen-bare), two that some pollen remained along the length of the anthers, one that there was almost no pollen left, and zero that the anthers were empty. Measurements were not used for statistical analysis if there was only one flower per set per time. Changes in pollen load during the night (night pollen amount minus the amount the following morning) and during the day (morning pollen amount minus the amount the following night) were averaged across sets. For any given time (day or night), data were combined for statistically similar sets.

*Sucrose Concentration of Nectar.*—At each measurement period I checked all the flowers for the presence of nectar. I measured the percent sucrose by weight of the nectar using a refractometer. To extract the nectar I used a microcapillary tube (various sizes were used) and flipped the flower upside-down; to fit the microcapillary tube fully down the corolla I duct taped it to another microcapillary tube. Sometimes there was too little nectar to get an accurate reading on the refractometer in which case the sucrose concentration could not be measured.

FLORAL TRAITS RELATED TO PROTECTION OF NECTAR FROM ROBBERS
*Petals.*—I placed ten stations of pink (mature) petals, white (immature) petals, and wax paper with a single drop of sugar water under trees in the garden to monitor the number of ants visiting each substrate. Stations were placed at the bases of trees in the garden to be accessible for both terrestrial and arboreal ants. Trees were located along the garden paths and were not immediately adjacent to each other. Each substrate was approximately 2 x 2 cm² and located 8 cm from the base of the tree. All petal squares were taken from a single flower (either white or pink). For each station wax paper was placed in the center with pink and white petals on either side 10 cm away (measured from wax paper edge to petal edge). One drop of sugar water (17.0% sucrose by weight) was placed on each substrate and replenished when necessary (both when ants consumed the majority of the drop and when it evaporated). After waiting ten minutes the number of ants was counted every five minutes for 25 times (two hours). Ant species were not differentiated.

*Nectar.*—I placed ten stations of sugar and nectar drops under trees to measure the number of ants visiting each. Stations were placed at the bases of non-adjacent trees located along the garden paths as with the petal experiment; trees used in the previous experiment were not used again. Sugar water and nectar drops were placed on wax paper squares of the same size as before
located the same distance apart and from the base of the tree. A single drop of sugar water (7.0% sucrose by weight) was contrasted with a single drop of *B. suaveolens* nectar. To get a sufficient amount of nectar of a consistent concentration, all nectar was collected from wilted flowers on the plants or recently fallen and mixed together. Average percent sucrose by weight of the nectar in wilted flowers is 11.91% ± 3.62% (n = 22). Both sugar water and nectar were replenished when necessary. After ten minutes I measured the number of ants every five minutes for 25 times (two hours). This experiment was spread over two days due to the constraint in the number of wilting flowers available with three stations observed the first day and seven the next. Ant species were not differentiated.

**RESULTS**

**FLORAL TRAITS RELATED TO POLLINATION**

I followed 28 buds on 16 plants from the splitting of the calyx until the first bloom. On average it took 5.2857 ± .5998 days for the flowers to bloom and turn pink. I also followed 28 flowers on 15 plants from maturation (the night they bloomed and turned pink) to wilting (easily pulled off the plant). On average it took 4.0893 ± .3348 days for the flowers to wilt. Flowers would bloom in a cycle: all the plants in the garden would bloom for about a week and then there would be no flowers at all for another week before the cycle would begin again. During the period when the garden plants were without flowers, plants outside the garden were not necessarily without blooms.

Flowers of this plant begin to bloom around 4:00 PM and start to smell strongly around 5:30 PM. Flowers remained partially closed during the day (such that it was still possible for animals could to enter the flowers). Anthers were joined but would occasionally break apart as they aged. The first night of bloom flowers do not contain enough nectar to be measureable with the refractometer.

No animals were observed entering the flowers during the night measurements. During the day bees were sometimes observed in the flowers attempting to reach the nectar. Occasionally the bees would appear to struggle to remain in the flowers and would make several attempts to enter.

I painted the pollen of three newly blooming flowers with fluorescent pollen powder paints (pollen load for all three flowers was four). The following morning pollen load was zero for all the flowers. The subsequent night I checked all the reachable flowers in the garden for fluorescent pollen grains and found none.

**POLLEN LOSS.**—The mean pollen load ranking on the anthers decreased both over time and across flower sets from earlier to later blooms (Figure 2). Pollen load decreased significantly over time (one-way ANOVA, f ratio = 66.5373, df = 26, p < .0001). This trend is visible across all sets of flowers: (all Tukey HSD tests, p < 0.05; see Figure 2). The differences between the first nights and the subsequent time measurements for all sets were the most significantly different between all times (see Figure 2). Pollen loads were equivalent across set and time after the second morning for the first set, the second night for the last set, and the first morning for the April 26th and 27th sets. The amount of pollen also decreased from the first set to the last for given times (all Tukey HSD tests, p < .05; see Figure 2).

The change in pollen was greater at night than during the day (Figure 3). The change in pollen from night one to morning one was significantly different across sets and therefore was not included in the regression lines. 6.66% of the differences in pollen load from any morning to the following night could be explained by time (regression analysis, R2 = .066587, p = .0120, n = 94, y = -0.0508x + 0.388). Although the differences in pollen load from any night to the following morning did not make a statistically significant linear line, there was a strong
decreasing trend (regression analysis, $R^2 = 0.029295$, $p = 0.0765$, $n = 108$, $y = -0.091x + 0.7381$). Less and less pollen was lost as time passed for both day and night—the slopes for day and night were not statistically different ($t$-test, Zar 1984; $df = 198$, $p = 0.373$). There was a greater amount of pollen loss during the night than the day for all times—$y$-intercepts for day and night were significantly different ($t$-test, $df = 199$, $p = 0.030$).

FIGURE 2. Changes in mean pollen load (+ SD) over time for *B. suaveolens* flowers of various bloom dates. Columns not connected by similar letters are significantly different. Pollen load decreased significantly over time and over bloom date.

FIGURE 3. Changes in the differences in pollen load of *B. suaveolens* flowers from morning to night (morning) and night to morning (night) over time. Width of the dot indicates the number of observations at that value. Slopes for day and night are not significantly different, $y$-intercepts are. Pollen loss was greater at night than during the day.
Sucrose Concentration of Nectar.—The percent sucrose by weight in nectar decreased over time (Figure 4) and ranged from an average of 22 ± 1.98% (AM1, n = 53) to 11.69 ± 3.73% (PM5, n = 22). 49.07% of the decrease in concentration can be explained by time passing (regression analysis, $R^2 = .4907, p < .0001, n = 330, y = -.0135x + .225$). The concentration of sucrose in nectar was higher in the morning than at night. Similar percentages as with the combined data of the decreases in concentration of morning and night can be explained by time (regression analyses: morning $R^2 = .49165, p < .0001, n = 157, y = -1.2306x + 22.809$; night $R^2 = .49182, p < .0001, n = 173, y = -1.4227x + 22.126$). The concentrations for morning and night decreased at the same rate—the slopes were not significantly different ($t$-test, df = 326, $p = .200$). However, the morning concentrations were significantly higher than at night—the $y$-intercepts for the best fit lines were significantly different ($t$-test, Zar 1984; df = 327, $p < .0001$).

![Figure 4](image_url)

**Figure 4.** Change in morning and night sucrose concentration of *B. suaveolens* nectar (percent sucrose by weight) over time. Slopes are not significantly different, $y$-intercepts are. Sucrose concentration was greater in the morning than at night.

Floral Traits Related to Protection of Nectar from Robbers

Insects found inside the flowers include ants (rarely), bruchid beetles (often), and small black flies (up to approximately 20 in a flower, but mostly when flowers are near wilting). All of these were clearly ingesting the nectar of the flower. Fallen flowers often contained a plethora of ants and small flies as well. Nectar was also observed dripping out of the flower. I did not observe any morphological characteristics of the flowers, stems, or leaves that appeared to be preventing access to the nectar.

Petals.—In total, 722 ants visited pink (mature) petals, 675 visited wax paper, and 533 visited white (immature) petals (Figure 5). Combining the data from all ten stations, ants significantly preferred sugar water on pink petals over wax paper, and preferred wax paper over white petals (Chi-square test, $X^2 = 30.101, df = 2$, critical value = 5.99). The average proportion of ants per station visiting a given substrate was also greatest for pink petals (mean ± SD = .3939 ± .2351; Figure 7). Unlike the combined totals, however, the average proportion of ants per station visiting wax paper was lower than for white petals (mean ± SD = .2509 ± .2216 for wax paper and .3229 ± .232 for white petals). However, the average proportion of ants per station visiting
each substrate was not significantly different between the substrates (one-way ANOVA, f ratio = 1.0827, df = 2, p = .3529). Due to low confidence in stations that received less than 20 ant visitors as choices could have been more due to chance, I removed those stations and recalculated the average proportions. Even after doing so (new n = 8), pink petals still received a greater average proportion of visitors compared to white petals which received a greater average proportion than wax paper (means ± SD = .4545 ± .2174, .3157 ± .2271, and .2298 ± .2419 for pink petals, white petals, and wax paper respectively; Figure 9). There were still no significant differences between the proportion of ants per station visiting substrate (one-way ANOVA, f ratio = 1.9614, df = 2, p = .1656).

**NECTAR.**—946 total ants visited nectar solutions whereas 1301 visited sugar water solutions (Figure 6). In total, sugar water received significantly more ants than nectar (Chi-square test, $X^2$ = 56.086, df = 1, critical value = 3.84). When comparing the proportion per station of ants visiting each solution, however nectar received more visitors (mean ± SD = .5304 ± .3238) than sugar water (mean ± SD = .4696 ± .3234; Figure 8). The average proportions of ants per station visiting a given solution were not significantly different between sugar water and nectar ($t$-test, f ratio = 1.0827, df = 2, p = .3529). Removing the stations with a low sample size (less than 20 ants per station) for the same reason as above (new n = 7) showed, like the combined data, that sugar water received more ant visitors than nectar (mean ± SD = .5756 ± .3181 for sugar water and .4244 ± .3181 for nectar; Figure 10). These average proportions were still not significantly different from each other ($t$-test, f ratio = .7918, df = 1, p = .3910).

![Figure 5](image1.png)  
**FIGURE 5.** Total number of ground-foraging ants from all ten stations visiting pink petals of *B. suaveolens*, wax paper, and white petals of *B. suaveolens*. Stations were placed at the bases of non-adjacent trees located along the garden path.

![Figure 6](image2.png)  
**FIGURE 6.** Total number of ground-foraging ants from all ten stations visiting *B. suaveolens* nectar and sugar water. Stations were placed at the bases of non-adjacent trees located along the garden path.
FIGURE 7. Mean (± SD) percent of ground-foraging ants per station visiting pink petals of *B. suaveolens*, wax paper, and white petals of *B. suaveolens*. N = 10 for each mean. Stations were placed at the bases of non-adjacent trees located along the garden path.

FIGURE 8. Mean (± SD) percent of ground-foraging ants per station visiting *B. suaveolens* nectar and sugar water. N = 10 for each mean. Stations were placed at the bases of non-adjacent trees located along the garden path.

FIGURE 9. Mean (± SD) percent of ground-foraging ants per station visiting pink petals of *B. suaveolens*, wax paper, and white petals of *B. suaveolens* after removing the stations with a low sample size (fewer than 20 ants). N = 8 for each mean. Stations were placed at the bases of non-adjacent trees located along the garden path.

FIGURE 10. Mean (± SD) percent of ground-foraging ants per station visiting *B. suaveolens* nectar and sugar water after removing the stations with a low sample size (fewer than 20 ants). N = 7 for each mean. Stations were placed at the bases of non-adjacent trees located along the garden path.
DISCUSSION

**Floral Traits Related to Pollination**

*Pollen Load.*—Pollen load decreased over time indicating the flowers in the garden are being visited by pollinators. The observations with fluorescent pollen paints suggest that pollen may be traveling to plants outside the garden. More pollen was lost the first night than any other night. As the composition of the floral essential oils changes from the first night of bloom (when the flowers are still white) to the next morning (Anthony et al. 2009), there potentially could be a correlation between early essential oil composition and the attraction of pollinators. This trend could also be related to the color change of the flowers if pollinators are more attracted to the white flowers of the first night of bloom than the later pink tinged flowers.

Flowers that bloomed earlier had more pollen than later blooming flowers for a given time period. Less pollen load on later sets of flowers is most likely due to an increase in pollinator presence over time. Considering the blooming cycle for these plants and that there were no flowers present before the first set of blooms, it could have taken several days for all the pollinators to discover the flowers were again in bloom, or early pollinators could have recruited others to increase the number of pollinators visiting the garden over time.

The loss in pollen load was greater during the night than during the day. The decrease in pollen loss was only slightly explained by time indicating that other processes are involved (probably pollination or pollen consumption). This shows that more pollinators or pollen consumers are coming at night and that *B. suaveolens* has nocturnal pollination. This is supported by the fact that these flowers open and emit odor at night, which corresponds with nocturnal pollination (Knapp 2010). As pollen was still lost during the day, it is probable that multiple species act as pollinators with the dominant pollinator (or pollinators) being nocturnal. It is also possible that the daytime pollen loss is mostly due to pollen consumption as the flowers remain mostly closed during the day.

The measurement of a two point five pollen load suggests that the visiting animal had a larger body size such that the head could only reach so far into the flower and thus removed only half of the pollen. This implies a non-insect pollinator.

*Nectar Presence and Sugar Concentration.*—The concentration of sucrose in nectar decreased over time and ranged from ~12 – 22 %. Almost half of the decline was due to time passing, but the remaining half could potentially be linked to pollination. The decline in sucrose concentration corresponded with the decline in pollen load. Pollination is known to cause chemical changes within the plant (Walles & Han 1998) and could possibly signal for a reduction in sucrose production. As nectar concentration is related to optimal foraging of pollinators (Kaczorowski et al. 2005), the greater amount of pollen being taken the first night may correspond to the high percentages of sucrose in the nectar at that time. Decreasing changes in pollen load may also correspond to lower sucrose concentrations attracting different pollinators.

The concentration of sucrose was higher in the morning than at night. Although this may be due to evaporation occurring during the morning hours, Faegri & van der Pijl (1979) found that nectar produced at the bottom of deep corollas (such as with *B. suaveolens*) is protected against evaporation. During the dry season, it is common for the plant to absorb water if it is stressed during the day, which could also account for the increase in concentration. From morning to night, however, the sucrose became more dilute. This may indicate that the flowers may be selectively reabsorbing sucrose, or producing nectar of a different composition (Corbet...
Water could also be supplied to the nectar by condensation or precipitation (Corbet 2002); even though it was the dry season, the flowers were typically watered in the mid-afternoon and could have absorbed water in this way.

**Pollination Syndromes.**—These traits can then be compared with known pollinator syndromes. Based on the literature, I have compiled a table of the floral traits known to attract the four potential pollinators for this genus—hawkmoth, bat, bee, or hummingbird—and evaluated those floral traits shared by *B. suaveolens* (Table 1).

<table>
<thead>
<tr>
<th>Pollinator</th>
<th>Color</th>
<th>Shape</th>
<th>Sucrose Concentration in Nectar</th>
<th>Odor</th>
<th>Phenology</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bees</td>
<td>Blue, purple, yellow, white*</td>
<td>Open, papilionaceous, brush form, etc.</td>
<td>~30%</td>
<td>Strong and pleasant *</td>
<td>Open during the day</td>
</tr>
<tr>
<td>Hummingbirds</td>
<td>Reddish</td>
<td>Tubular</td>
<td>~20-30%</td>
<td>Usually lacking</td>
<td>Open during the day</td>
</tr>
<tr>
<td>Hawkmoths</td>
<td>White*, cream</td>
<td>Very narrow corolla*</td>
<td>~20% *</td>
<td>Strong, sweet *</td>
<td>Open at night *</td>
</tr>
<tr>
<td>Bats</td>
<td>White*, cream</td>
<td>Wide open tube*</td>
<td>~5-15% *</td>
<td>Strong, sometimes unpleasant *</td>
<td>Open at night *</td>
</tr>
</tbody>
</table>

The white (or mostly white) *B. suaveolens* flowers open at night with a strong odor, produce nectar with a sucrose concentration from 12 – 22 %, and have a relatively narrow corolla that then opens to a fairly wide mouth, fit the pollination syndromes of bat and hawkmoth pollinated flowers. Bat or hawkmoth pollination is consistent with the nocturnal pollination. The two point five pollen load level corresponds with bat pollination as well. It is possible that nectivorous bats are only taking nectar located where the corolla begins to widen and thus not placing their heads fully in the flower; in this way, pollen would be consumed by them (should their tongue accidentally brush the anthers) and not carried (R. K. LaVal, Personal Communication). However, the two point five pollen load level suggests that the heads are being placed fully inside the flowers and the bats are consuming nectar from deeper within the corolla tube. It is also possible that both hawkmoths and bats pollinate *B. suaveolens*. Alarcón et al. (2008) found that some flowers considered bat pollinated are also secondarily pollinated by hawkmoths. As the nectar decreased in sucrose concentration, it is also possible that the flowers switch from being mainly pollinated by hawkmoths that prefer a higher sucrose concentration (Kaczorowski et al. 2005; Perret et al. 2000) to being mainly pollinated by bats that prefer a lower sucrose concentration (Perret et al. 2000; Rodríguez-Peña et al. 2007).

As bee pollinated flowers do share a few characteristics of *B. suaveolens* flowers, pollen was lost during the day, and bees were observed entering flowers, it is possible that these are
minor, tertiary pollinators. While it is possible the pollen lost during the day was consumed rather than carried off for pollination, the bees observed appeared to be interested in the nectar rather than the pollen.

**Floral Traits Related to Protection of Nectar from Robbers**

Ants did not significantly prefer pink petals, white petals or wax paper. Although the total data show a significant ant preference for pink petals over wax paper over white petals, when the variation in total ants between stations was taken into account there was no significant difference. *B. suaveolens* petals are not deterring ants from taking the nectar. Likewise, ants did not significantly prefer nectar or sugar water when taking the variation in total ants between stations was taken into account. *B. suaveolens* nectar does not deter ants from robbing it. These correspond with my occasional observations of ants in and on the blooming flowers as well as in the fallen, wilted flowers. The fact that insects too small to be likely pollinators were found consuming the nectar in the plans suggests that nectar robbery is prevalent.

Given the known chemical potency of this plant (Anthony et al. 2009), these results are somewhat unexpected. Guerrant & Fielder (1981) hypothesize that species that do not protect their nectar chemically may protect it morphologically. The ants were not deterred by the petal texture and I did not notice anything about the petals or flowers that appeared to be preventing access to the nectar. Bees, however did seem to struggle at times to remain in the flower due to the pendulous angle of the flower and the lack of a perch. Additionally, *Brugmania spp.* are commonly used as a groundhog or mole repellent in farms and gardens. This may indicate that chemical compounds in the roots, bark, or petioles are more effective at repelling ants than the petals or nectar.

Compounds that defend the plant chemically against nectar robbers may only be present at certain stages of a flower’s life (Guerrant & Fielder 1981). In my nectar experiment I used only nectar from wilting flowers; while this did not deter ants, it is possible that using nectar from younger flowers would produce a different result should the nectar of younger flowers contain ant repellant compounds that subsequently wane. This corresponds with the fact that the insects I observed tended to be more prevalent on older flowers, and ants especially were found in fallen, wilted flowers. Further research is needed to evaluate this possibility.

The blooming cycle of this plant in which there are no flowers prior to the new blooming period may make defense against nectar robbers unnecessary: if it takes a while for insects to reach the flowers and most pollen is taken the first night, it may be that it is not cost effective for the plants to invest in chemical nectar defense.

As the purpose of ant deterrence is to prevent nectar theft (Guerrant & Fielder 1981), the lack of ant deterrence found in the petals and nectar of *B. suaveolens* indicates the potential for many species to rob nectar without pollinating the flowers. Insects observed coming to the flowers, including bees (Guerrant & Fielder 1981), could be nectar robbers and not necessarily pollinators. It is possible that the bees I observed entering the flowers are exclusively robbers or that they are primary nectar robbers but occasionally act as accidental pollinators. This latter explanation also accounts for the observed diurnal pollen loss.

**Conclusions**

This study indicates that *B. suaveolens* has a pollination syndrome consistent with pollination by nocturnal bats and hawkmoths. Bees may be secondary, mainly diurnal pollinators or nectar
robbers. Neither the nectar nor the petals are protected from nectar thieves and insects are prevalent nectar robbers, especially as the flower ages.

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LITERATURE CITED


