RESEARCH PAPER

Spatio-temporal variation of nectar robbing in *Salvia gesneriflora* and its effects on nectar production and legitimate visitors

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ABSTRACT

Nectar robbing occurs when floral visitors remove floral nectar through floral damage and usually without providing pollination in return. Even though nectar robbing may have negative, neutral or even positive effects on plant fitness, few studies have investigated temporal and spatial variation in robbing rate and their consequences, particularly in the tropics. In this study, robbing levels were estimated during 3 years in four populations of *Salvia gesneriflora*, a hummingbird-pollinated shrub endemic to central Mexico that is mainly robbed by birds, carpenter bees and bumblebees. The effect of robbing on nectar availability, flower longevity and on visitation rate by floral visitors was also evaluated. Our results indicate great variation in robbing levels across years and populations and a positive relationship between robbing level and flower abundance per population. Moreover, our results show that nectar availability is about eight times higher in unrobbed flowers than in robbed flowers, and that nectar robbers prefer younger flowers, although lifespan of robbed and unrobbed flowers did not differ statistically. Primary and secondary nectar robbers showed a higher visitation rate compared to legitimate visitors, and neither legitimate nor illegitimate floral visitors seem to discriminate between robbed and unrobbed flowers. These results suggest that robbers may respond to food availability and that no floral visitors apparently could differentiate between robbed and unrobbed flowers. Finally, results show that nectar robbers prefer the youngest flowers, which suggests that strong competition for access to nectar between pollinators and robbers might occur, mainly at the first stages of the flowers.

INTRODUCTION

Among the multiple interactions that take place between plants and animals, biotic pollination is considered a mutualistic interaction in which plants benefit from the fertilisation of their ovules by animal pollen vectors, while animals obtain some kind of reward. However, there are exploiters of mutualisms that obtain benefits without providing a reward in return (Bronstein 2001). One example is nectar robbers, which obtain nectar from a perforation or a slit in the corolla or calyx, usually without transferring pollen to the stigma (Inouye 1980). The paradigm that nectar robbing is harmful for plants began with Darwin's description of bees making holes in corolla and their probable negative effects (Darwin 1841, 1876). Indeed, empirical evidence showed that nectar robbing might damage the reproductive structures of flowers during robbing, which directly affects female plant reproductive success (McDade & Kinsman 1980; Graves 1982; Traveset *et al.* 1998). In addition, the perforation made on the flowers by primary nectar robbers facilitates nectar access for secondary robbers (Irwin & Brody 1998; Irwin *et al.* 2010), or may induce pollinators to act as secondary nectar robbers if nectar extraction is easier in robbed

than in unrobbed flowers (Lara & Ornelas 2001; Fumero-Cabán & Meléndez-Ackerman 2007). Nectar robbers may also decrease flower nectar availability, causing a reduction in the visitation rate of pollinators (Lyon & Chadek 1971; Irwin & Brody 1998; Irwin 2000). A decrease or increase in legitimate visits could affect floral duration. Indeed, many plant species close their flowers following pollination (van Doorn 1997). Hence, nectar robbing could play a key role in floral longevity and ultimately in plant reproduction (Irwin *et al.* 2010); however, this issue has been rarely addressed (*e.g.* Temeles & Pan 2002; McDade & Weeks 2004; Zhang *et al.* 2007).

Since daily nectar production in many plant species varies considerably with flower age (*e.g.* Navarro 2001; McDade & Weeks 2004; Carlson & Harms 2006), it is expected that nectar robbing will increase in the floral stage where nectar production or concentration is higher and will compete with pollinators for this resource. If robbers reduce nectar availability and pollinators could discriminate between robbed and unrobed flowers, plant reproductive success would be greatly reduced (Irwin & Brody 1998). Some nectar robbers, however, could have neutral (Guitian *et al.* 1993; Morris 1996) or even positive effects on fruit and seed production if they pollinate flowers

during robbing (Maloof & Inouye 2000; Navarro 2000; Irwin *et al.* 2001; Richardson 2004; Singh *et al.* 2014) or if they cause pollinators to travel longer distances to find nectar, which should increase outcrossing (Zimmerman & Cook 1985). The complexity of this dynamic interaction is increased when spatial and temporal variation in robbing rate is considered. For instance, spatiotemporal variation in nectar robbing has been observed in bumblebees foraging in four host plant species (Irwin & Maloof 2002). High levels of spatiotemporal variation in nectar robbing may limit the degree to which plants can respond to the selective effects of robbing (Irwin & Maloof 2002). Therefore, understanding spatiotemporal variation in nectar robbing is essential to understand the ecological and evolutionary relationship between plants and robbers. However, despite the ubiquity of nectar robbing and the potential multiple consequences on plant fitness, the magnitude and frequency of spatial and/or temporal variation in nectar robbing has rarely been explored (*e.g.* Navarro 2000; Arizmendi 2001; Utelli & Roy 2001; Irwin & Maloof 2002), particularly in the tropics, where a higher degree of specialisation in plant–pollinator interactions has been observed (Olesen & Jordano 2002; Armbruster 2006; Ollerton *et al.* 2006).

Here, we investigate the spatiotemporal variation in robbing levels and its effects on nectar availability, flower longevity and visitation rate of floral visitors in *Salvia gesneriflora*, a Neotropical hummingbird-pollinated shrub with protandrous flowers that lives between 4–6 days and are frequently robbed by bees and birds (Cuevas *et al.* 2013). In particular, we are interested in answering the following questions: (i) Do robbing levels vary among populations and years? Given the complex dynamic of plant–animal interactions mainly in the tropics, we expected large spatiotemporal variation on robbing rates. (ii) Do robbers have an effect on nectar availability for legitimate visitors and do they alter flower longevity? Because robbers may damage flowers while consuming nectar, we predicted that robbed flowers would have both less nectar for legitimate visitors and decreased flower longevity than unrobbed flowers. (iii) Do robbers prefer particular floral stages? If nectar production or concentration is higher in early floral stages (Alcalá 2010), we predicted that robbing rate would increase in younger flowers. (iv) Do floral visitors discriminate between robbed and unrobbed flowers? If robbers reduced nectar availability, we predicted that pollinators would discriminate between robbed and unrobbed flowers.

This is the first study that describes the spatiotemporal variation in robbing rate in a tropical plant. In addition, we tested the effects of robbing on flower longevity and the preference of robbers for specific floral stages, two issues that are rarely assessed.

MATERIAL AND METHODS

Study species and site

Salvia gesneriflora Lindl (Lamiaceae) is an endemic perennial shrub (0.8–4.0 m in height) of central Mexico, distributed from the state of Jalisco to Puebla (Rzedowski & Rzedowski 2005). The flowers are hermaphroditic and self-compatible; however, floral visitors are required for seed set because of herkogamy and protandry (Cuevas *et al.* 2013). *S. gesneriflora* has red, bilabiate and tubular flowers (5–6 cm long; Rzedowski & Rze-

dowski 2005), suggesting bird pollination. Indeed, our preliminary observations indicate that the hummingbird *Eugenes fulgens* visits these flowers frequently in a legitimate way, whereas the honeybee, *Apis mellifera*, collects pollen from the anthers and occasionally makes contact with the stigma. The cinnamon bellied flower piercer bird (*Diglossa baritula*) and carpenter bees (*Xylocopa* sp.) were frequently seen robbing the flowers of *S. gesneriflora* in the studied populations. *D. baritula* pierce the base of the calyx, usually damaging both the calyx and the floral tube. Carpenter bees frequently take nectar by making a slit between the calyx and the corolla. Finally, the bumblebee *Bombus ephippiatus* visited previously robbed flowers, acting as a secondary nectar robber (*sensu* Inouye 1980).

This study was carried out at Los Azufres (19° 50′ N, 100°39′W), about 80 km east of Morelia city, in the state of Michoacán, Mexico. Four populations were chosen in this area. The distance among populations ranged from 2 to 10 km, and they were within the same vegetation type and at similar elevation (2500–2800 m.a.s.l.). The climate is temperate sub-humid (mean annual temperature 12–18 °C and annual rainfall 1200–1600 mm; Carranza 1987). The vegetation is pine–oak forest with *Quercus laurina, Q. crassipes, Pinus pseudostrobus, P. teocote* and *Abies religiosa* as the dominant tree species (Carranza 1987). Understorey vegetation is represented by the genera *Baccharis, Cestrum, Lupinus* and *Salvia*, being *S. gesneriflora* a dominant species in the studied populations.

Spatiotemporal variation on robbing rate

We randomly tagged 25–35 plants per population to record total floral display (total number of open flowers) and the number of robbed flowers per plant every ~20 days throughout the flowering seasons (December–May) of 2010, 2011 and 2014. We counted the number of robbed flowers (*i.e.* flowers with holes and/or slits) and estimated the rate of robbed flowers per plant as the number of robbed flowers/total number of open flowers. To compare robbing levels and floral display among years and populations, we used repeated measures ANOVAs, with site and year as main factors, each census as the repeated term, and robbing level (arcsine-square root-transformed) and average flower production per plant (log-transformed) as the response variable. Robbing level and floral display among populations was compared with a Tukey-Kramer mean test. For each year and population we conducted Pearson correlation analysis to examine whether robbing levels were associated with flower production per plant. All statistical analyses were performed with SAS version 9.1.3 (SAS 2002) or JMP software (SAS Institute, Cary, NC, USA).

Relationship between robbing and nectar availability, flower longevity and flower age

To examine whether robbing affects available nectar for potential pollinators, nectar volume was measured once in two naturally robbed and two unrobbed flowers in ten plants per population, with calibrated micropipettes, between 09:00–11:00 h. A paired *t*-test was performed to determine whether available nectar volume (log-transformed) differs between robbed and unrobbed flowers using plant as the unit of replication. In addition, in order to know whether nectar production and concentration differs among populations, volume and

concentration was measured (from 09:00 to 11:00 h on the first day that flowers open) in two floral buds per plant in 20 plants per population that were protected with pollination bags. Nectar volume was measured with calibrated micropipettes whereas nectar concentration was estimated with a hand refractometer (Atago, Tokyo, Japan). An ANOVA was used to assess whether nectar production and concentration differs among populations, with population as the main factor and nectar production and concentration as the response variables. *A posteriori* Tukey-Kramer mean test was used to seek differences among populations.

To evaluate whether flower longevity was affected by robbing and whether time of robbing was associated with flower age, in March 2012 we recorded, in 4–13 flowers per plant (in 16 plants from population 3, $N = 152$ flowers), the day at which the flowers were robbed and the longevity (number of days) of robbed and unrobbed flowers. We placed small tags near of each selected flower and checked all flowers daily for six consecutive days. We used a *t*-test to compare flower longevity of naturally robbed and unrobbed flowers (log-transformed data). Furthermore, we used Pearson correlation analyses to explore the relationship between flower age and time of robbing.

Effect of robbing on floral visitation rate

In order to estimate robber and legitimate visitation rate and to discern whether floral visitors could discriminate between unrobbed and robbed flowers, we filmed seven plants (nine to 17 flowers per plant) with robbed and unrobbed flowers using a Sony Digital Handicam in February 2014 in population 3. Each plant was filmed for 5–7 h. Before recording, each flower was carefully examined to verify any floral damage from robbers. The pedicel of selected flowers was tagged with a small steel ring using different colours for robbed and unrobbed flowers. The identity and type of floral visitor was recorded (*i.e.* primary or secondary robber or legitimate visitor), as well as the number of flowers visited and floral condition (*i.e.* unrobbed or robbed flowers). We used a generalised linear model with a binomial distribution to determine whether robbers and legitimate floral visitors discriminate between unrobbed and robbed flowers. The model used flower condition (robbed or unrobbed) as the categorical variable and the presence or absence of visits as the dependent variable.

RESULTS

Spatiotemporal variation on robbing rate

Among years and sites, mean levels of nectar robbing per plant ranged from 4 to 78%, with a mean ($\pm$ SE) of 33.19% $\pm$ 2.7. Robbing levels in 2011 (40.91 ± 3.4) were significantly higher than in 2010 (28.67 ± 3.45) and 2014 (29.35 ± 4.18; $F_{2, 1539} = 19.49$, $P < 0.0001$). Robbing levels also differed among populations, being significantly lower during 2010 and 2014 at population 4 than in the other populations ($F_{3, 1216} = 25.52$, $P < 0.0001$; $F_{3, 276} = 5.94$, $P < 0.001$, respectively; Fig. 1). Mean robbing levels among populations ranged from 17.01 ± 1.66 at population 4 in 2010 to 47.02 ± 1.83 at population 3 in 2011 (Fig. 1).
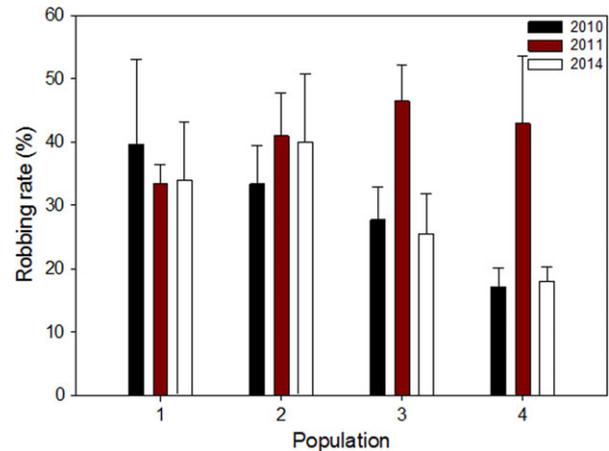

Fig. 1. Mean ($\pm$ 1 SE) robbing levels per population during 3 years in four studied populations in Los Azufres, Michoacán.

Mean flower production per plant varied from 16.6 ± 2.10 flowers at population 4 in 2010 to 51.0 ± 26.39 at population 1 in 2014. Significant differences in floral display were found among populations in 2010 ($F_{3, 640} = 5.81$, $P < 0.001$) and 2011 ($F_{3, 545} = 13.97$, $P < 0.0001$). During both years population 4 had a lower flower number per plant. We found a significant positive correlation between robbing level and flower production at all populations in 2010 and at populations 2 and 3 in 2011 ($r^2 > 0.16$, $P < 0.05$ for all correlations).

Relationship between robbing and nectar availability, flower longevity and flower age

Mean nectar production in bagged flowers did not differ among populations ($F_{3, 157} = 0.173$, $P = 0.91$). On the other hand, mean nectar concentration differ among populations ($F_{3, 152} = 16.48$, $P < 0.0001$), being significantly lower in populations 3 and 4. Mean nectar availability (*i.e.* nectar volume in exposed flowers) was around eight times higher in unrobbed flowers than in robbed flowers, and the difference was significant in all four populations (Pop. 1: $t_9 = 5.36$; Pop. 2: $t_8 = 5.7$; Pop. 3: $t_9 = 8.91$; Pop. 4: $t_9 = 6.71$; in all cases $P < 0.001$; Fig. 2). In addition, the mean lifespan of unrobbed flowers (4.3 ± 0.24 days) did not differ from that of robbed flowers (4.16 ± 0.2; $t_{46} = 0.6$, $P = 0.55$). Finally, a significant negative correlation was found between flower age and time of robbing ($r^2 = 0.75$, $P = 0.02$; Fig. 3), indicating that nectar robbers prefer younger flowers.

Effect of robbing on floral visitation rate

In 44 h of observation in 204 flowers, we recorded 13 legitimate visits by the hummingbird *Eugenes fulgens*, 17 illegitimate visits by the bumblebee *Bombus ephippiatus* and 12 by the bird cinnamon bellied flower piercer, *Diglossa baritula*. Even when the visitation rate of all illegitimate floral visitors (*i.e.* primary and secondary nectar robbers) was 2.4 times higher than that of legitimate floral visitors, the visitation rates of primary nectar robbers and legitimate floral visitors were similar (Fig. 4). There were no significant differences between the number of robbed and unrobbed flowers per plant visited by the
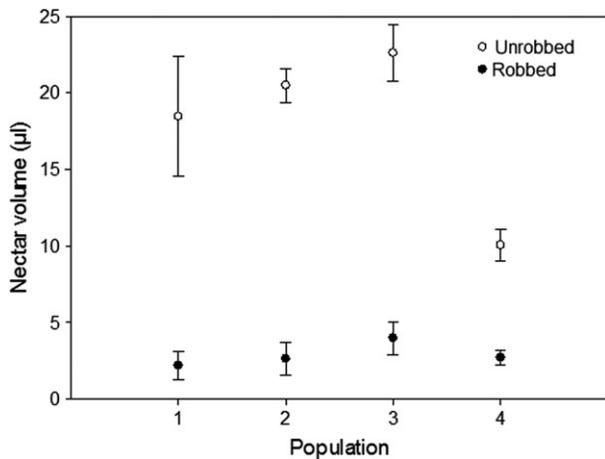
Fig. 2. Mean (± 1 SE) nectar availability from robbed and unrobbed flowers for the four studied populations. Nectar availability was, on average, eightfold higher in unrobbed flowers than in robbed flowers for all studied populations.
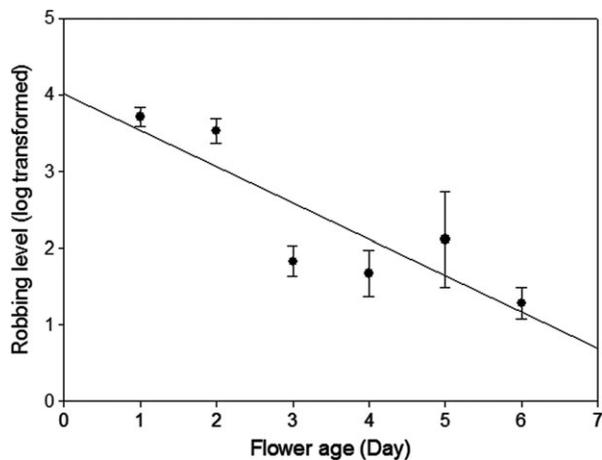

Fig. 4. Visitation rate of legitimate floral visitors (hummingbirds), and primary (*D. baritula*) and secondary nectar robbers (bumblebees) on robbed and unrobbed flowers of *Salvia gesneriflora*.

Fig. 3. Spearman correlation for the relationship between mean robbing frequency per day (log-transformed) and the age of the flower ($r^2 = 0.75$; $P = 0.02$). Best fit line is shown.

hummingbird ($\chi^2 = 1.19$, df = 1, $P = 0.276$), which always visited the flowers in a legitimate way. Similarly, no differences were found between the number of robbed and unrobbed flowers visited by either the cinnamon bellied flower piercer ($\chi^2 = 3.02$, df = 1, $P = 0.083$) or the bumblebee ($\chi^2 = 0.05$, df = 1, $P = 0.944$), which mainly act as primary and secondary nectar robbers, respectively (Fig. 4).

DISCUSSION

Our results indicate that robbing levels among years and populations is highly variable, and that there is a positive relationship between robbing level and flower production in most populations and years. Even though nectar production per flower did not differ among populations, nectar availability differed around eight-fold between robbed and unrobbed flowers. Moreover, the results presented here show that nectar robbers
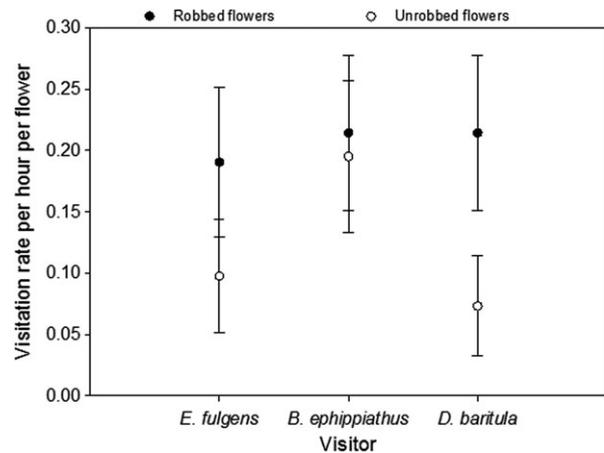
prefer younger flowers and that lifespan of robbed flower did not differ from that of unrobbed flowers. Finally, primary and secondary nectar robbers showed a higher visitation rate compared to legitimate visitors, and neither legitimate nor illegitimate floral visitors seem to discriminate between robbed and unrobbed flowers.

On average, during the 3 years of the study, we found that one-third of the flowers of *S. gesneriflora* were robbed by primary nectar robbers. In 2010 and 2014 we found consistently lower robbing levels on population 4, which had the lowest flower production per plant and the lowest nectar concentration per flower. Indeed, the positive correlation found between floral display and robbing level suggests that robbers may perceive flower abundance and associate it to food availability. In other studies, robbing level variation among years and populations has been explained by changes in robber abundances or as a decoupling between flowering and insect robber life cycle (*e.g.* Navarro 2000; Irwin & Maloof 2002).

Given that the frequency of nectar robbing was evaluated from the damage caused to flowers by primary nectar robbers, the relevance of secondary nectar robbing is unknown. However, our results obtained with camcorders indicated that the visitation rate of secondary nectar robbers was more frequent than the visitation rate of primary nectar robbers, so their impact on available nectar would be high. Indeed, we found that robbed flowers have less available nectar (around eight-fold) for legitimate floral visitors than unrobbed flowers, although we do not know to what extent this difference is caused by primary or secondary robbers. Given this marked difference in nectar availability, a higher visitor preference for unrobbed flowers would be expected; however, we found that no floral visitor seems to discriminate between robbed and unrobbed flowers. In other studies, it has been reported that pollinators are able to discriminate robbed flowers from those that are unrobbed, when robbing frequency is very high (Irwin & Brody 1998; Irwin 2000). Probably, the relatively low robbing levels recorded in 2014 (year in which visitation rate was estimated) explain the lack of discrimination by visitors. Furthermore, the lack of discrimination, in the case of robbed

flowers by carpenter bees, could be explained by the fact that these bees made a slit between the calyx and the corolla, and floral damage is frequently not easily visible.

The rate of legitimate floral visits was lower than the rate of visits of both primary and secondary nectar robbers, which might cause higher competition for nectar between legitimate visitors and robbers. Moreover, lower visitation rates of legitimate visitors could cause lower pollen deposition on flowers. Interestingly, we have not detected pollen limitation in *S. gesneriflora* in this same population in terms of fruit set or seed production (Cuevas *et al.* 2013). Hence, it seems that only a few effective pollinator visits are required to fertilise all the ovules (four per flower), as Espino (2012) found in the congeneric hummingbird-pollinated shrub *S. fulgens*, which have the same number of ovules. Similar to other studies (*e.g.* Utelli & Roy 2001; Temeles & Pan 2002; Zhang *et al.* 2007), our results indicate that floral damage caused by nectar robbers did not shorten the lifespan of the flowers. Nectar robbers, however, strongly prefer the youngest flowers, suggesting that there might be strong competition for access to nectar between pollinators and robbers at early stages of the life of flowers. The preference for younger flowers may be related to the higher nectar concentration detected during the first 2 days of life of flowers (Alcalá 2010). Given that *S. gesneriflora* is a protandrous species (Cuevas *et al.* 2013), it is probable that primary nectar robbers mainly affect male function in terms of pollen removal and seeds sired (Irwin *et al.* 2010 and references therein), whereas secondary robbers may affect more the female function. Detailed experimental studies analysing the effects of robbery on male function in this dichogamous plant are clearly needed.

Our results indicate that nectar robbing in *S. gesneriflora* caused a significant decrease in nectar availability. Indeed, previous results of standing crop nectar production (*i.e.* repeated nectar measure in the same flowers) in this plant species suggest that their flowers produce similar nectar volumes 12 h after nectar is removed (Alcalá 2010), so nectar robbers seems to have an important energetic cost to the plants (Pike 1991). Therefore, a selective pressure against floral traits related to attracting nectar robbers is expected. Since primary nectar robber and legitimate pollinator belong to the same functional group (*i.e.* bird), they should share similar flower sensing abilities, so floral traits related to advertising the former are expected to attract the latter, resulting in opposing selection on these floral traits. In addition, given the inability of legitimate visitors to discriminate between robbed and unrobbed flowers, and the large temporal and spatial variation in robbing levels, it is expected less consistent selection pressure against floral traits related to attracting primary nectar robbers. Alternatively, a selection pressure favouring floral traits related to robber avoidance (*e.g.* calyx morphology) could be expected.

Finally, if nectar robbers were stronger competitors than legitimate floral visitors, then hummingbirds could select the floral phenotypes that are not attractive to the flower piercing bird. For instance, Castro *et al.* (2009) found that bigger flowers were more prone to be visited by bumblebee nectar robbers, whereas legitimate floral visitors (another species of bumblebee) seem to prefer smaller flowers. Further comparative studies among populations that vary in the presence of nectar robbers are needed to corroborate this hypothesis.

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