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Patterns of nectar robbing on two manzanita species

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ABSTRACT

Pollinators provide ecosystem services and facilitate plant reproduction. Plant-pollinator interactions often benefit both partners and are considered mutualisms. However, cheating can occur in these interactions when floral visitors take resources from plants without providing any benefit (Smithson 2013). One example of this kind of cheating is nectar robbing, which occurs when a pollinator collects nectar from a hole in the flower's corolla and bypasses pollination. We compared the variation of floral nectar robbing between two species of manzanita, *Arctostaphylos viscida* (whiteleaf manzanita) and *A. manzanita* (common manzanita). We examined both buds and blooms to explore the relationship between age on the robbing behavior of floral visitors. We found no difference in the percent of nectar robbing between whiteleaf and common manzanita. There was no notable difference of nectar robbing between blooms and buds in common manzanita, however, there was nearly three times more nectar robbing on blooms than buds in whiteleaf manzanita. Studying nectar robbing behavior, as well as its impact on flowering plants, can help monitor successful and unsuccessful pollination.

Keywords: mutualism, nectar robbing, common manzanita, whiteleaf manzanita, phenophase

INTRODUCTION

Pollination aids in the sexual reproduction of plants and the evolution of floral morphology, which influences pollinator preference (Kevan et. al 1990). Pollinator preferences can impact visitation rates to certain plant species and affect their reproductive output. For example, certain species of bees prefer magenta-colored flowers to white flowers, causing white flowers to set fewer fruits (Urbanowicz et. al 2020). These selection pressures influence changes in floral character, which leads to the coevolution of pollinators and plants (Chittka et. al 2006).

One aspect of coevolution between plants and pollinators is mutualism, which is an interaction that benefits both species (Richardson and Bronstein 2012). An example of mutualism is between the Nile crocodile and the Egyptian plover, where the bird eats decaying meat from the crocodile's mouth, who in turn avoids oral infection. Another mutualism is between plants and pollinators. A plant's flower gets pollinated, which increases its fitness, and in return pollinators are rewarded with nectar.

However, temporary changes in pollinator behavior can give rise to exploitation, where they benefit themselves more than their mutualist partner. An example of this exploitation is nectar robbing, which occurs when a floral visitor collects nectar from a flower, through a hole made in the corolla, and therefore neither acquires nor distributes pollen in the process (Richardson and Bronstein 2012). Nectar robbing impacts both the flower, through a reduction of pollen donation, and other pollinators, by influencing their choices of flowers to visit.

In this study, we examined *Arctostaphylos viscida* (whiteleaf manzanita) and *A. manzanita* (common manzanita), which are targets of exploitation from pollinators through nectar robbing. Whiteleaf manzanita is endemic to serpentine soil and is an obligate seeder, depending on a seed bank for regeneration after a fire (Duren and Muir 2010). Conversely, common manzanita does not tolerate serpentine soil and is a facultative seeder, able to resprout and germinate post-fire (O'dell et. al 2006). On whiteleaf and common manzanita, we focused on two phenophases or stages in a plant's annual life cycle. We defined these phenophases as buds (unopened flowers) and blooms (opened flowers).

Since whiteleaf manzanita is an obligate seeder, it presumably invests more energy in nectar production to attract pollinators, so we hypothesized that it would experience more robbing (Manetas 2000). We also hypothesized that buds in whiteleaf and common manzanita would have more nectar robbing holes because they would be more appealing to pollinators, as seen in *Bombus spp.* (bumblebee) who was found to favor young flowers (Willmer et. al 1994). We also hypothesized that a higher number of flowering neighbors would decrease the amount of nectar robbing seen on the sampled tree, as the pollinators have more options to choose from.

METHODS

2.1 Study System and Natural History

The study was conducted at the McLaughlin Natural Reserve and adjacent property owned by the Bureau of Land Management in Lake County California from February 24–27 2021. A complex geological history of tectonic plate movement, and volcanic and hydrothermal activity, formed a mosaic of serpentine and sedimentary soils. These features support diverse plant communities including oak woodland, chaparral, and grassland. Whiteleaf and common manzanita are associated with the chaparral community, but isolated by soil type. Whiteleaf manzanita is endemic to serpentine soil, while common manzanita is found on non-serpentine soils (O'dell et al. 2006; Grace et al. 2007). Both species of manzanita are evergreen, grow to a height of nearly 6 m, and share similar phenological flowering periods (Richardson and Bronstein 2012). In late winter, trees bloom with white to pink, urn-shaped flowers arranged in clusters (Eliyahu et al. 2015). Manzanitas attract a wide variety of floral visitors including hummingbirds, butterflies, bees, wasps, moths, and flies (Richardson and Bronstein 2012).

2.2 Flower Inspection for Evidence of Nectar Robbing

Whiteleaf and common manzanita were identified flowering at four locations across the study area. Two sites, Devilhead and Southbound, hosted whiteleaf manzanita on serpentine soil. Common manzanita was present at the Campground and Northbound sites on non-serpentine soil. At each site, five trees of a given species were sampled with a minimum distance of 50 m between individuals, to ensure independence. On each manzanita tree, we haphazardly collected 60 flowers of each phenophase, bud, characterized by closed petals, and bloom, characterized by open petals. Each flower was inspected for nectar robbing. Unrobbed flowers were defined by the absence of holes, whereas robbed flowers were categorized as having 1, 2, or 3 holes. If flowers were eaten through such that there were no distinct holes, they were categorized as 3+. The number of flowering manzanita within a 10 m radius of the sample tree was also recorded.

2.3 Insect Collection and Species Richness

On February 24, we collected insects present on common manzanita using a sweep net method. Individuals were captured and dispatched with acetone in a sealed jar. The specimens were later classified to the most detailed taxonomic rank as possible using iNaturalist (v3.1). The collection was preserved for future reference and study at McLaughlin Natural Reserve. Due to inclement weather, we were unable to adequately survey the species richness of insects on whiteleaf manzanita.

2.4 Statistical Analysis

Statistical analysis was conducted using JMP statistical software v14.1. We ran a two-way mixed model ANOVA to determine the effects of manzanita species and floral phenophase, as well as their interaction, on the percent of nectar robbed flowers. In this model, site was considered a random effect.

RESULTS

We collected a total of 1,200 buds and 1,200 blooms from whiteleaf and common manzanita. We found that nectar robbing did not differ between manzanita species (N = 2400, F = 1.47, p = 0.349; Fig. 1). There was no pronounced difference in nectar robbing between blooms and buds of common manzanita, however, there was nearly three times more nectar robbing on blooms than buds of whiteleaf manzanita (N=2400, F=19.02; Fig. 1). Notably, blooms from whiteleaf manzanita represented almost half of all nectar robbed flowers. Furthermore, we found a significant interaction of flower phenophase and manzanita species on nectar robbing, such that nectar robbing differs with flower phenophase, but only in whiteleaf manzanita (N = 2400, F = 15.78, p = 0.0004; Fig. 1).

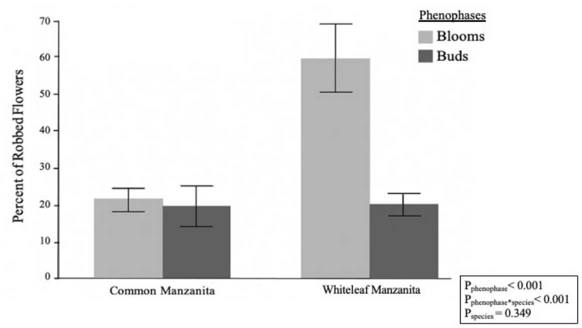

Figure 1. Percent of nectar robbed flowers on common vs. white-leaf manzanita trees. Buds (N = 600) and blooms (N = 600) were sampled from 10 common and 10 whiteleaf manzanita trees. Buds were identified as closed flowers and blooms as opened flowers. Nectar robbing is defined as one or more holes in the corolla, which was calculated as a percentage for each manzanita species. On common manzanita the percent of robbed blooms was similar to buds. However, on whiteleaf manzanita, a higher percent of blooms was robbed than buds. Error bars represent ±1 S.E.

The Southbound Road site accounted for 54.2% of all robbed flowers, which included buds and blooms (Fig. 2). In contrast, the percent of nectar robbed flowers at the other three sites, including whiteleaf and common manzanita, only ranged from 18.3% to 20% (Fig. 2). According to our results, 51.7% of the variance in nectar robbing was explained by site.

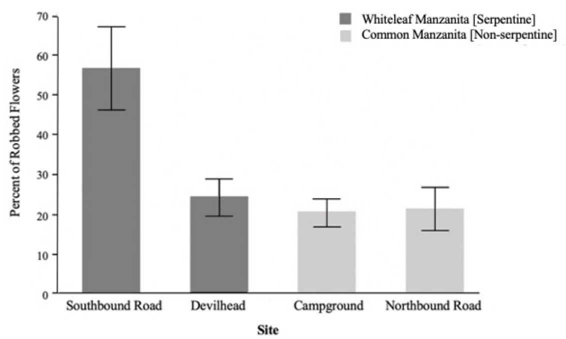

Figure 2. Percent of nectar robbed flowers on two manzanita species across four sites. Manzanita flowers, including buds and blooms, were inspected for nectar robbing at four sites. Nectar robbing is defined as one or more holes in the corolla, which was calculated as a percentage for each site. At Southbound Road and Devilhead sites, flowers from 5 common manzanita (N = 600) were sampled. At Campground and Northbound Road sites, flowers from 5 whiteleaf manzanita (N = 600) were sampled. Whiteleaf manzanita is endemic to serpentine soil, whereas common manzanita does not tolerate serpentine. Nearly three times more flowers were robbed at the Southbound Road site than at the other three sites and 51.7% of the variance in nectar robbing was explained by site. Error bars represent ±1 S.E.

The percent of nectar robbed flowers on a manzanita did not depend on the density of flowering manzanitas within a 10 m radius.

DISCUSSION

We predicted that whiteleaf manzanita would experience more nectar robbing than common manzanita, because whiteleaf manzanita are obligate seeders that presumably invest more resources into nectar production. Therefore, the flowers of whiteleaf manzanita may be more attractive to nectar robbers than those of common manzanita which are facultative seeders. Whiteleaf manzanita at the Southbound Road site had the highest percentage of nectar robbing. However, there was no difference in nectar robbing when comparing whiteleaf manzanita from the Devilhead site and common manzanita flowers from the Northbound Road and Campground sites. This could be explained by the overlapping flowering periods and close geographic proximity of common manzanita and whiteleaf manzanita.

Additionally, we hypothesized that there would be more nectar robbing in buds than blooms because certain pollinators have a preference for younger flowers (Willmer et. al 1994). However, our results did not support this hypothesis as we observed that common manzanita buds and blooms were robbed nearly equally. Furthermore, whiteleaf manzanita blooms were robbed more than buds. Potentially, the nectar robbers visiting whiteleaf manzanita are different species from those visiting common manzanita, and that these two groups target flowers of different phenophases (Irwin & Maloof 2002). Since a nectar robbing hole remains permanently visible, it is difficult to distinguish during which phenophase the flower was robbed. It may be that buds are the primary targets of nectar robbing in common manzanita as opposed to blooms. This would explain the subtle difference in the number of robbed buds and blooms. Conversely, the large difference in nectar robbing between buds and blooms in whiteleaf manzanita, suggests that flowers in both phenophases are being robbed.

Our final hypothesis stated that a manzanita surrounded by a high density of flowering neighbors would have a lower percent of nectar robbing. We suspected that fewer flowering neighbors would limit resources and increase competition among pollinators, and drive some pollinators to become generalists (Sowig 1989). This hypothesis was supported by previous research which found that pollinators tended to visit fewer flowers on large patches and more flowers on smaller patches (Ohashi and Yahara 1999). However, in contrast to the findings of Sowing (19889) and Ohashi and Yahara (1999), our results showed that the percentage of nectar robbed flowers did not depend on the number of flowering neighbors in the area. This may be due to the many small insects we observed on whiteleaf manzanita flowers that may not travel long distances and depend on one specific tree.

The Southbound Road site accounted for 54.2% of all flowers that were nectar robbed and 51.7% of the variance in nectar robbing was due to site. Although whiteleaf and common manzanita have similar flowering periods, spanning from February to March, there is variation between species and among individuals (Minore et al 1988). So, it is possible that the blooms from the white leaf manzanita at the Southbound Road site developed earlier than those at the Devilhead site. Since this study took place in late winter, when many pollinators are still overwintering, it is possible that the existing blooms were at their peak attractiveness when many pollinators made their first foraging trips, therefore being susceptible to high levels of nectar robbing. Furthermore, there is scientific literature that reports variation in nectar robbing across species and locations (Irwin & Maloof 2002).

To accurately compare the percent of nectar robbing of both species, further studies could highlight the difference of nectar robbing rates between the two species by marking individual clusters and observing them as they bloom. This would allow a more accurate comparison of nectar robbing rates between flowers of the same phenophase. It has also been seen that flower visitors can exhibit mixed behavior at the species and individual level, acting as both pollinators or nectar robbers (Richardson & Bronstein 2012). A collection of floral visitors and examination of the difference in their foraging behavior on different manzanita species would clarify how these visitors act as pollinators or nectar robbers. Improving our understanding of nectar robbing and the effects of cheating in a mutualism, can help explain the dynamics of selection pressures and coevolution of plants and pollinators.

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