1998

The effects of nectar robbing on *Arctostaphylos silvicola* fruit output

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THE EFFECTS OF NECTAR ROBBING ON
ARCTOSTAPHYLOS SILVICOLA
FRUIT OUTPUT

A Thesis

Presented to

The Faculty of the Department of Biology
San Jose State University

In Partial Fulfillment

Of the Requirements for the Degree
Master of Science

By

Diane Elizabeth Romo

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ABSTRACT

THE EFFECTS OF NECTAR ROBBING ON *ARCTOSTAPHYLOS SILVICOLA* FRUIT OUTPUT

By Diane Elizabeth Romo

This thesis addresses the topic of nectar robbing effects on fruit production of the silverleaf manzanita (*Arctostaphylos silvicola*), an endemic to the sandhills of the Santa Cruz Mountains in California. It examines, over a two-year period, the number of fruits produced from flowers that have been either robbed or unrobbed. In addition, the amounts of nectar were compared among flowers on different shrubs.

Sample flowers were monitored at the research site, Bonny Doon Ecological Reserve, throughout their blooming period for indications of robbery. Fruits produced from both robbed and unrobbed flowers were counted per inflorescence. Nectar amounts were found to vary from flower to flower in accordance with other bee pollinated flowers. Nectar robbing was found to have no correlation with fruit production during the first field season. Yet, during the second field season, with a slightly different collecting technique, robbery did have a negative effect on fruit production of the silverleaf manzanita.

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INTRODUCTION

Plants many times offer food as a reward for a pollinator, and this reward may come in the form of nectar. An insect species may take the nectar but not pick up pollen from or deposit pollen on the flower by avoiding contact with the flower's anthers and stigma. When this occurs, the "thief" is known as a nectar robber (Inouye 1979). The nectar robbing taking place in the silverleaf, or Bonny Doon, manzanita occurs when the insect punctures or chews a hole at the base of the corolla tube and takes the nectar but touches neither the anthers nor the stigma. The insect, therefore, does not work (by pollinating the flower) for its nectar reward, yet it may damage reproductive tissues important for flower pollination and fruit growth and also cause reduced attractiveness to pollinators (Roubik 1982). The robber may also cause enough damage to the flower to shorten the life span of that flower, thereby decreasing the amount of time pollen is available and pollen receptiveness. The silverleaf manzanita has no evident adaptations in its flower (thicker tissues of the corolla tube surrounding the nectaries) to prevent or reduce the robbing behavior.

It has been suggested that the lower nectar volumes per flower attributable to nectar robbing cause pollinators to visit more flowers in order to collect required amounts of nectar, thus increasing the pollination rate and, thus, the reproductive fitness of the plant (Zimmerman, Cook 1985). The nectar volumes and concentrations, as well as how they are displayed can not only determine the type of visitor (pollinator, robber), but also the type of visit (Guitian et al. 1994).

Figure 1. *Arctostaphylos silvicola* at Bonny Doon.

The silverleaf manzanita is one of the largest manzanitas measuring one to six meters in height (fig 1). This evergreen shrub is endemic to the marine sandstones of Santa Cruz County (Barbour, Major 1995) on the central coast of California and is listed by The California Native Plant Society as “rare, threatened, or endangered in California” because it is limited to fewer than 20 occurrences (Skinner 1994). It has bell-shaped flowers, clustered together in a raceme, which have openings that are constricted, thus, preventing insect entry to nectar sources without specially adapted proboscis lengths.

The soils to which the silverleaf manzanitas are restricted consist of the coarse, well-drained, and erodible Zayante soil series composed of 80 to 85 percent sand, 7 to 8 percent silt, and 4 percent clay (USDA 1980). Zayante soils were formed from the weathering of the Santa Margarita Formation that contains several sandstone beds

derived from fossils and Miocene marine sand deposits (Harvey, Stanley 1983). The surface layer is dark grayish brown with medium to strong acidity down to 30 inches, while the underlying material is light grayish brown and less acidic down an additional 30 inches. The bedrock is greater than 60 inches deep. Permeability is very rapid and roots must reach more than 60 inches deep for effect. The low to very low available water capacity is 2.5 to 5.0 inches (USDA 1980). Because the soil is so coarse and porous it dries quickly, lowering the humidity and causing higher temperatures than in adjacent forested soils.

The area is exposed to the warm, dry summers and mild, wet winters consistent with the Mediterranean climate, yet the microclimates in the sandhills are harsh during the summer months compared with the adjacent forested habitats (Morangio 1985). The mean annual air temperature is 55 degrees Fahrenheit with 220 to 245 frost-free days, and the mean annual precipitation is 48 inches (USDA 1980).

In 1978 Davilla termed the vegetation type studied here in the sandhills as “Silverleaf Manzanita Mixed Chaparral” which is characterized by woody shrubs in dense stands. This plant community is dominated by the silverleaf manzanita and is common in the Santa Cruz sandhills (Morangio, Morgan 1987). Associated species in the community include *Ceanothus cuneatus*, *C. ramulosus*, *Salvia mellifera*, *Eriodictyon californicum*, and *Mimulus aurantiacus*. Because the soils are so sandy, the vegetation is limited to those species that are adapted to drought. *Pinus ponderosa*, *P. attenuata*, and *Quercus agrifolia* make up the overstory in minimal amounts. It has been suggested that silverleaf manzanitas develop into pure stands replacing *P. ponderosa* as a fire type

replacement (McMinn 1939), and also that the knobcone pine is increasing in dominance because of frequent fires in previous times (Griffin 1964).

The heavily forested mixed evergreen and redwood forest communities that surround the sandhill community are much more common in the Santa Cruz mountains. The dominant species found in these surrounding areas are the redwood, Douglas-fir, madrone, laurel, and tanbark oak. Many of the plant species found in the sandhills are restricted to the sandy soils and are drought tolerant. They are most likely restricted because of being out competed in adjacent soils by the mixed evergreen species.

Because of the conflicting reports on the impact of nectar robbers on reproductive fitness, the impact of robbing insects on the fruit output of the silverleaf manzanita (*Arctostaphylos silvicola*, all nomenclature from Hickman 1993) was tested. This was accomplished by monitoring flower-to-fruit productions of robbed and unrobbed flowers. Fruit production was expected to decrease when flowers had been subjected to nectar robbers. Nectar amounts were also measured to determine if there was a preferential attraction by pollinators and nectar robbers towards flowers with high nectar amounts. Pleasants and Zimmerman found the expected nectar standing crop is that for which the average volume is approximately equal to the standard deviation of the distribution, so this proportion of variation was expected in the silverleaf manzanita (1983).

LITERATURE REVIEW

The silverleaf manzanita (*Arctostaphylos silvicola*) has bell-shaped tubular flowers that restrict the entry to their nectaries by non-adapted insects. Because of this entry restriction, some insects need to find other means of getting to the nectar other than the flower opening. Nectar robbing insects, insects that cut a hole in the corolla tube and steal nectar without coming in contact with the anthers and stigma, can impact the amount of fruit produced by a plant. The attractiveness or amount of nectar reward can impact flower visits by pollinators, as well as fruit production.

Arizmendi (1996) studied the relationship between the nectar robber *Diglossa baritula* and two flowering plant species, the hermaphroditic *Salvia mexicana*, and the androdioecious *Fuchsia microphylla*. He also compared the pollination efficiency of the nectar robber with those of five hummingbird species that visit the same plant species. The study was conducted at the Laboratorio Natural Joyas field station in the Mexican States of Jalisco and Colima in the Sierra de Manantlan. In patches of both plant species, direct observations were made of the species of flower visitor and the number of flowers probed by those visitors. The frequency of damage to flowers by nectar robbers was measured, as well as occurrence of damage to ovaries and stamens. Fruit set was monitored for both plant species in the two categories of robbed and unrobbed flowers. The effect of experimentally induced nectar robbery on nectar secretion and seed set was also determined. Pollination manipulation was carried out to determine its effect on seed set. *S. mexicana* incurred no damage to the ovaries, styles, or stamens. The robbed and intact *S. mexicana* flowers did not differ in fruit set under field conditions. The amount

of nectar did not differ between robbed and unrobbed flowers, but the unrobbed flowers produced more concentrated nectar. Seed production among *S. mexicana* flowers did not differ, but there were differences among pollination treatments. Damage to the ovaries and stamens of *F. microphylla* was also not detected. The robbed and intact *F. microphylla* flowers did not differ in fruit set under field conditions, nor did nectar robbing affect either nectar quantity or concentration. Like *S. mexicana*, *F. microphylla* did not show differences of seed production per flower among plants but did show differences among pollination treatments. The results from these two plant species show that the nectar robbing did not have an effect on fruit production due to visits to the undamaged flowers by pollinators other than the robbers.

David W. Roubik (1982) examined the impact of the nectar robbing bee, *Trigona ferricauda*, and the pollinating hummingbird, *Phaethornis superciliosus*, on the tropical forest edge shrub, *Pavonia dasypetala*. The study was conducted on a transect of tropical moist forest within Parque Nacional Soberania in Panama. Both pollinator and robbing flower visitors were observed. The amount of nectar consumed by nectar robbing bees was determined by squeezing the abdomen of the bee and collecting the nectar from the mouthparts in a capillary tube. Flowers were counted based on panicle number, and nectar crop was determined by inserting capillary tubes directly into the nectary at the base of the corolla tube. Seed production was determined by harvesting capsules. Roubik found that robbing bees chased the hummingbird pollinators away from plants, but the hummingbirds would not abandon the patch and usually were able to extract nectar from a flower before being driven away. Furthermore, robbing bees did not

deplete nectar amounts. Seed set was not different in heavily robbed patches between robbed and unrobbed flowers, but all patches combined showed that robbed flowers produced fewer seeds than unrobbed flowers. This result shows that lower seed production of robbed flowers in all patches was not caused by damage to the flowers, but rather by the prevention of hummingbird visitation in the patch.

The effect of the nectar-robbing bumblebees (*Bombus mixtus* and *B. frigidus*) on bluebells (*Mertensia paniculata*) was examined by William F. Morris (1996). The corolla of unopened bluebell flowers is pink and contains little nectar; as the flower matures, the stigma protrudes out of the corolla tube. The anthers dehisce as the corolla changes from pink to blue as it opens. Pink and blue flowers are present on each inflorescence at the same time. The study was conducted at three sites near Kennicott, Alaska. Marked female flowers were examined daily, and collars were placed over control flowers' corolla tubes to prevent nectar robbing. Fruits were collected and nutlets counted and weighed prior to abscission from the plant. Nectar robbing did not cause a reduction of female success in the bluebells. There were no differences in the percent of flowers initiating fruits, the number of nutlets, or the mass of seeds produced by robbed and unrobbed flowers. Male bluebell reproductive success was measured by pollen removal rates. The amount of pollen in robbed flowers was less than that in unrobbed flowers one day after anthesis, but equal by the second and third days after anthesis. Bees paid legitimate visits to unopened pink flowers, thus, picking up pollen, but these were found to rob nectar from the open blue flowers. Most flowers were previously pollinated when pink before they were ever robbed when blue. The artificial removal of

mature blue flowers by the researcher lowered the visitation rate to the pink flowers. The flowers appeared to take advantage of the bumblebees' frequent switching between nectar robbing and pollen collection by providing both types of flowers at the same time. In this case, nectar robbers may be an important factor in the success of bluebells.

Differing nectar concentrations in the flower *Petrocoptis grandiflora* were studied for their effects on pollinator behavior, as well as the effects of nectar robbing on fruit set by J. Guitian (1994). The study took place in the El Bierzo region of the Province of Leon. Nectar amounts were extracted from the nectaries with capillary micropipets. The numbers of robbed and unrobbed flowers were recorded, as were the number of flowers that produced fruit. A paintbrush was used for a supplemental pollination study. Limited quantities and volumes of sugars were produced by *P. grandiflora*, and the volumes of nectar did not vary according to time of day. Nectar robbing was frequent by the bee *Xylocopa violacea*, and was found to affect the probability of a flower setting fruit when the effect of source population was also taken into account. Artificially pollinated flowers did not show differences in fruit set rates compared with controls indicating that pollinator activity was not the limiting factor.

Zimmerman and Pyke examined the population ecology of Christmas bells (*Blandfordia nobilis*), a perennial herb, with a particular focus on standing crop of nectar patterns (1988). Micropipets were used to extract nectar from flowers so that the volume and concentration of the nectar could be measured. The number of unopened flowers, flower buds, spent flowers and the height of each plant was measured. Also measured were the width of the flower opening and the length of the floral tube of some of the

flowers that had nectar samples taken from them. Most of the samples showed that flowers producing large volumes of nectar had lower sugar concentrations than flowers producing smaller amounts of nectar. There were no differences between samples taken in the morning or afternoon. Sugar concentrations were different for the two field seasons in which they were sampled (95% and 25%). Neither plant height nor number of flowers per plant had an effect on the volume or the concentration of nectar. The width of the floral tube was positively correlated with the volume on one of the sampling dates, but not with the concentration of nectar. The length of the floral tube was not correlated with either the volume or the concentration of nectar on any of the sampling dates. Positive correlations were found between both the volumes and concentrations of nectar within flowers on the same plants but were found only half of the time between flowers on different plants. Pollinator-excluded flowers were not different from open flowers in either nectar volumes or concentrations. Because of this, Zimmerman concluded that the nectar was not being used extensively during the study by pollinators. He also concluded that since plant size (height, number of flowers, floral size) had no correlation with nectar volumes or concentrations, pollinators could not use plant cues to visit high reward plants selectively. Moreover, Zimmerman cautions that since the rate of nectar production can change during a single season, multiple samples need to be taken during the season in order to characterize the population's production and standing crop of nectar.

These four nectar robbing studies showed varying effects on fruit or seed production. *Fuchsia microphylla* and *Salvia mexicana* did not incur any effects on seed production due to nectar robber activity. *Pavonia dasypetala* showed lower seed

production of robbed flowers on all patches caused by nectar robbing bees chasing away the pollinating hummingbirds. The bluebells were affected in quite a different manner. Open older blue bluebell flowers were robbed, but the robbers also pollinated the younger pink flowers at the same time. Fruit production in bluebells was lowered when blue, robbable flowers were excluded. The flower *Petrocoptis grandiflora* was only affected by robber behavior when the effect of source population was also taken into account. Artificially pollinated flowers did not show differences in fruit set rates compared with controls. When examining the nectar volumes and concentrations of Christmas bells, Zimmerman found that multiple sampling dates during a single season needed to be taken because of varying rates of nectar production.

METHODS

Study Area

The sampling site location is in the Bonny Doon Ecological Reserve (fig 2). The site size is 83 km². The reserve, managed by California State Fish and Game, is found in the central coast of California in the Santa Cruz Mountains near the town of Bonny Doon. The Bonny Doon site is one of less than twenty sandhill locations in the Santa Cruz Mountains to which the silverleaf manzanita, *Arctostaphylos silvicola*, is endemic. The plant community type is the Silverleaf Manzanita Mixed Chaparral.

Plant Selection / Nectar Robbing

Fifteen silverleaf manzanita plants were selected using random points along a transect line on January 16 and 17, 1997 (fig 3). The transect line was the hiking trail traversing the reserve beginning where the trail bisects Martin Road on the east side. The transect line had two branches. The main line plus the two branches were considered terminated when the vegetation type changed to redwood forest, and the presence of silverleaf manzanitas disappeared. The main transect line followed an easterly direction for 504.91 m with the first branch breaking off at 101.25 m following the southerly direction of Martin Road for 65.84 m. The second branch departed from the main transect line at 180.5 m with a south easterly direction for 467.93 m. Whether the sampled silverleaf manzanita fell on the left or right side of the transect line was randomly selected. Each individual plant was selected based on its proximity to the random point on the transect line. Each shrub was then visually sectioned into sixteen parts, eight on the upper one half of the shrub, and the remaining eight on the lower one

Figure 2. USGS topographic map of Bonny Doon Ecological Reserve from Davenport quadrangle 7.5 minute series.

Figure 3. Transect line used for *A. silvicola* sampling with random shrubs selected.

half. Each section faced one of the following eight directions: north, northeast, east, southeast, south, southwest, west, northwest. One inflorescence (fig 4) was randomly chosen from each of the 16 sections. During the 1997 season all flowers and buds of the chosen inflorescence were counted on January 16 and 17 and noted as either robbed or not robbed. A robbed individual had an incision or hole at the base of the corolla tube (fig 5). Inflorescences were checked weekly for additional flower production and robbery. After flowers were spent, netting was placed around each inflorescence to prevent herbivory of newly developing fruit (fig 6). When fruit production became

Figure 4. *A. silvicola* inflorescence.

Figure 5. *A. silvicola* flower damaged at base of corolla tube by nectar robber.

Figure 6. *A. silvicola* inflorescence bagged to prevent herbivory of fruit.

Figure 7. *A. silvicola* fruit.

apparent about one month later (fig 7), the number of fruits per inflorescence was recorded.

On January 8, 20, and 21, 1998, twelve new inflorescences were selected from each of the same 15 plants. Six of the inflorescences were designated robbed and six were designated unrobbed. In “robbed” inflorescences, any unrobbed flowers were removed by snipping the flower off at the pedicel with scissors. In “unrobbed” inflorescences, any robbed flowers were similarly removed in order to track flower to fruit. Both robbed and unrobbed inflorescences were checked weekly for additional newly formed flower buds, which were removed. Flowers designated “unrobbed” that were found robbed on subsequent visits were removed. The number of fruits per inflorescence was then recorded approximately one month later.

Nectar Concentration

To determine whether nectar amount varies between flowers, 27 silverleaf manzanita shrubs (including 15 from the above study) were chosen at random from the same transect line used for the above robbery study. Flowers were sampled on November 20, 1997 between 12 PM and 2 PM (a period of greatest insect activity during the day, personal observation). One flower from each shrub was sampled for nectar amount by placing a 3 μ l capillary tube into the corolla tube while contacting the nectaries. The amount of nectar was measured by length of the tube that was filled with nectar. The mean and standard deviation among shrubs were calculated.

Phenology

The 27 individuals sampled in the above nectar concentration study were used to determine the phenology of the silverleaf manzanita at this location. One branch, representing the current year's growth, was chosen randomly from one of the 16 sections of each plant. Inflorescences were monitored on the branch weekly between January 18, 1997 and January 08, 1998 to determine the percent flowers in bud, anthesis, and fruiting. A new vegetative bud was selected from each branch on April 10, 1997 and was measured weekly for length of growth through August 4, 1997.

Associated Species

Associated species were determined within a ten-meter radius placed around each of the 15 shrubs chosen for the nectar robbing study. Species were identified based on Hickman (1993), and their presence was recorded. Presence of shading by species in the overhead canopy was also recorded for each shrub. Shading was defined as one-half or more of the shrub being shaded between the hours of 10:00AM and 3:00PM during the flowering months between October 1997 and March 1998. Shrubs were then recorded as either shaded or not shaded. The percent of the shrub shaded by adjacent plants was also recorded, and was defined as the percent of the shrub's perimeter that was touching adjacent shrubs.

RESULTS

Nectar Robbing

In order to test whether the location of the inflorescence on the plant had an effect on the production of fruit or the number of robberies, two-way ANOVAs were performed on the data (table 1) collected during the 1997 field season. The 1997 data were converted to two ratios: number of fruits divided by number of flowers in that inflorescence (percent fruit) and the number of flowers robbed divided by the number of flowers in that inflorescence (percent robbed). A two-way ANOVA showed that the height of the inflorescence on the plant ($p = 0.992$), the direction the inflorescence was facing ($p = 0.606$), and the interaction of height and direction ($p = 0.760$) did not affect

Table 1. 1997 raw data of number of flowers, number of flowers robbed, and number of fruit produced on different locations of *A. silvicola*.

	Total flowers	Flowers robbed	Fruit produced
Upper 1/2	1228	201	93
Lower 1/2	822	126	58
North	248	45	8
Northeast	302	51	18
East	267	36	16
Southeast	270	47	19
South	300	46	32
Southwest	195	35	19
West	213	24	23
Northwest	225	43	16
Total	2020	327	151

mean # of flowers per inflorescence 10.919, std dev 4.523

Table 2. Two-way ANOVA of robberies among inflorescences in different locations on *A. silvicola* ($n = 185$).

Source of Variation	df	ss	ms	F	P
Height	1	0	0	0	0.992
Direction	7	0.176	0.025	0.779	0.606
Heights * Direction	7	0.134	0.019	0.594	0.760
Error	169	5.456	0.032		

Table 3. Two-way ANOVA of fruit productions among inflorescences in different locations on *A. silvicola* ($n = 185$).

Source of Variation	df	ss	ms	F	P
Height	1	0.005	0.005	0.267	0.606
Direction	7	0.127	0.018	1.040	0.405
Heights * Direction	7	0.059	0.008	0.485	0.844
Error	169	2.943	0.017		

the percent robberies that took place during the 1997 field season (table 2). A two-way ANOVA also showed that the height of the inflorescence on the plant ($p = 0.606$), the direction the inflorescence was facing ($p = 0.405$), and the interaction of height and direction ($p = 0.844$) did not affect the percent of fruit produced (table 3).

Spearman Correlation was used to calculate correlation between percent fruit and total flower number in an inflorescence ($r = -0.029$, $p = 0.694$) and between percent robbed and total number of flowers in an inflorescence ($r = 0.042$, $p = 0.570$) per inflorescence because the samples did not come from a normal distribution (table 4). Neither of these correlations was large. To determine if robbery was related to fruit output per inflorescence, Spearman Correlation coefficient was calculated on percent fruit verses percent robbed and was also found to be weak ($r = -0.227$, $p = 0.002$, fig 8). Because there were so many inflorescences with either zero (111/185) fruit produced or

zero (58/185) robberies, a G-test for independence also assessed whether robbery (yes, no) and fruit production (yes, no) were related (table 5). The G-test verified the Spearman Analyses, indicating that fruit production was independent of robbing ($G(1) = 3.487$, $p = 0.062$).

The 1998 field season's data (table 6) were collected in order to track the outcome of each individual flower. Randomized block ANOVA (table 7) was performed on the 1998 field season data in order to test the effect of robbing on the percent of fruit produced (percent fruit = number of fruit per inflorescence divided by number of flowers per inflorescence). Flower robbery lowered the fruit output, ($p < 0.001$) and the different shrubs (blocks) sampled had different fruit outputs ($p < 0.001$). The mean percent fruit produced from robbed flowers was 0.0204, stdev = 0.122 while the mean percent fruit produced from unrobbed flowers was 0.0922, stdev = 0.171 (fig 9). The G-test verified the randomized block ANOVA indicating that fruit production was dependent on robbing (table 8).

Table 4. Spearman Correlation Coefficients for 1997 *A. silvicola* data (n = 185).

	r	P
% Fruit vs flwr #	-0.029	0.694
% Robbed vs flwr #	0.042	0.570
%Fruit vs % Robbed	-0.227	0.002

Table 5. Test of independence between robbery and fruit production in 1997 *A. silvicola* data.

	Robbery	
Fruit	yes	no
yes	45	29
no	82	29

$G(1) = 3.487$, $p = 0.062$

Figure 8. In *A. silvicola* correlation between percent robbed flowers in an inflorescence and percent fruit in an inflorescence ($r = -0.227$).

Table 6. 1998 raw data of number of flowers robbed / unrobbed and number of fruit produced in *A. silvicola*.

	Flower number	Fruit produced
Robbed	206	3
Unrobbed	647	65

Table 7. Block ANOVA of fruit produced on *A. silvicola* from robbed or unrobbed flowers.

Source of Variation	df	ss	ms	F	P
Robbing (yes, no)	1	0.227	0.227	12.848	<0.001
Shrub (block)	14	1.013	0.072	4.093	<0.001
Error	163	2.883	0.018		

Figure 9. Mean + standard deviation of percent fruit of robbed and unrobbed flowers (1998 data, n = 179).

Table 8. Test of independence between robbery and fruit production in 1998 *A. silvicola* data.

Fruit	Robbery	
	yes	no
yes	3	65
no	203	582

$G(1) = 21.10, p < 0.001$

Nectar Concentration

To determine whether there were differences among the flowers with respect to the amount of nectar each flower contained, the samples were summed and the mean and standard deviation among flowers were calculated ($\bar{X} = 16.832$ mm, $s = 19.252$). The results indicate a very large variability in nectar amounts among flowers (fig10).

Phenology

Phenology data were collected from January 18, 1997 to January 08, 1998.

Figure 11 indicates the time periods in which the sample plants were budding, flowering, or fruiting. Day one (October 30, 1997) represents the beginning of the blooming period when data collection began, while day 172 (April 18, 1997) represents the end of the

Figure10. Nectar amounts of twenty seven randomly selected *A. silvicola* plants taken on November 20, 1997

Figure 11. Phenology of *A. silvicola*. Day 0 = October 13; Day 172 = April 18.

fruiting period. Because the immature buds remained unopened much longer than mature flowers were open, the percent bud was higher than percent flowers until February 11, 1997 (day 106). Fruit production followed slowly behind flower maturation until January 08, 1998 (day 71) when it began to increase rapidly while percent bud went down drastically. By February 04, 1997 (day 99) the majority of the flowers had matured and senesced (10% remained as either bud or flower and 89% were fruiting). New shoots (vegetative growth) began to grow by the end of March 1997 (fig 12). The average growth was about five centimeters by the middle of June 1997. During the summer months, the tips of the vegetative stems (peduncle) began to curve where the future inflorescences would grow.

Figure 12. Mean vegetative growth rate of *A. silvicola* in 1997.

Associated Species

The majority of the 15 sampled silverleaf manzanita shrubs had the same species of associated plants within a ten-meter radius. Table 9 lists the plants that are within the ten-meter radius of each of the 15 sampled shrubs. The most common and abundant associated species were *Eriodictyon californicum*, *Quercus agrifolia*, *Ericameria ericoides*, *Mimulus aurantiacus*, *Pinus ponderosa*, and *Lotus scoparius*. More than one-half of the 27 shrubs sampled for shading were found to fit in that category (table 10). The most prevalent species causing the shading were the ponderosa and knobcone pines. Silverleaf manzanitas that were touching adjacent shrubs were in the majority. They ranged from having between 0 % to 90 % of the shrub's perimeter touching adjacent

shrubs. An average of 58 % of the perimeter was exposed (not touching adjacent shrubs).

The average height of all the sampled shrubs was 7.2 feet.

Table 9. Associated species within a 10m radius around each sampled *A. silvicola*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Achillea millefolium</i>															X
<i>Adenostoma fasciculatum</i>	X			X	X										
<i>Anaphalis margaritacea</i>				X											
<i>Arbutus menziesii</i>			X												
<i>Dendromecon rigida</i>		X													
<i>Ericameria ericoides</i>	X	X		X	X	X	X	X	X	X	X	X	X	X	X
<i>Eriodictyon californicum</i>															
<i>Eriogonum nudum</i>															X
<i>Erysimum teretifolium</i>				X											
<i>Lithocarpus densiflorus</i>			X							X					
<i>Lotus scoparius</i>		X					X		X				X		
<i>Lupinus albifrons</i>				X								X			X
<i>Mimulus aurantiacus</i>	X			X								X		X	X
mushroom													X		
<i>Pinus ponderosa</i>			X											X	X
<i>Pseudotsuga menziesii</i>			X												
<i>Pteridium</i> spp	X			X			X			X	X	X		X	
<i>Quercus agrifolia</i>	X		X	X	X		X	X	X	X	X	X	X	X	X
various grasses					X							X	X		X

Table 10. Shading of individual *A. silvicola*. Shading is based on one half the shrub shaded between the hours of 10am and 3pm; exposure is % of plant perimeter not touching adjacent plants.

Height (ft)	Shade	Exposed (%)	Height	Shade	Exposed (%)
11	yes	80	8	yes	100
5	no	90	4.5	yes	20
6	yes	100	15	yes	40
12	no	85	6	yes	10
12	no	25	4.5	yes	50
5	no	65	7	no	90
5	no	55	6	yes	10
4	yes	75	5.5	yes	20
6	no	50	6	yes	45
8	no	25	6.5	yes	90
6	yes	90	4	yes	80
12	no	50	6	yes	55
10	no	35	6	yes	50
7.5	yes	75			
average			7.20		57.78
std dev			2.90		28.36

DISCUSSION

Although I expected lower fruit production when flowers of the silverleaf manzanita were robbed, I found no evidence to support this view from the 1997 field study. The flowers that had been robbed apparently had no damage to the reproductive organs that would reduce the fruit output. Any decrease in flower attractiveness to pollinators caused by nectar robbers should also be detrimental to the plant's reproductive fitness, yet the results do not support this idea since fruit production did not depend on whether or not the inflorescence had been robbed.

Contrary to the 1997 season study, the 1998 results showed significant effects of robbery on fruit production. When a robbery occurred to a flower, the likelihood of the flower producing fruit was decreased. The differences between the two field season results may be due to the different sampling techniques used. The 1997 study was nonmanipulative; it could, therefore, not be determined which flowers in each inflorescence produce the fruit (robbed / unrobbed). Thus, inflorescences with robbed flowers may have produced fruit, but those fruit may have come from unrobbed flowers on the same inflorescence. During 1998, the inflorescences had either only robbed or unrobbed flowers on them making it possible to track individual flowers.

Because the silverleaf is not self-fertile (Jacobson 1994), it is obligated to be pollinated from an outside source. The flower will not produce fruit unless pollen has been brought from a different flower by a pollinator for fertilization. This shrub is also an obligate seeder, which means it is dependent on pollinators for species survival (Marangio 1985).

The amount of seed set was not analyzed in this study but may play an important role in determining the reproductive effects of the nectar robbing. Individual fruits were counted, yet the viability of the seeds within each fruit was not determined. In self-fertile runner beans (*Phaseolus coccineus*), there is a slightly higher seed set in robbed flowers than in control flowers (Kendall, Smith 1976). Contrary to this, Roubik found in *Pavonia dasypetala* that seed production was dependent on the proportion of robbed flowers and that robbed flowers produced fewer seeds than unrobbed flowers (1982). These conflicting reports make individual species' analysis important because the results from one plant species may not be extrapolated to another species.

In my experiments, the fruit numbers were very low (151) with respect to the number of flowers present (2020), with a ratio of one fruit produced for every 13.4 flowers. Of these 2020 flowers, 327 were robbed. There may be an internal factor determining the amount of fruit produced whether or not robbery has occurred. A forced pollination study would be beneficial in determining if all pollinated flowers produce fruit or if the shrub has a predetermined number of fruit it will produce regardless of excess flowers being pollinated due to energy requirements. The large number of flowers produced may be a guarantee that one in every 13.4 will be pollinated since the peak flowering time is during the cold months of fall and winter when pollinators are few. The blooming period of the silverleaf manzanita, extending over a six-month period, also would help ensure some pollination by guaranteeing a broad range of pollinators. During this period the only other associated plant in the Bonny Doon sandhills blooming or competing for pollinators was *Ericameria*.

I found that the location of the silverleaf manzanita's inflorescence did not affect the amount of robbing. Both upper and lower portions of the plant were examined, as well as the direction in which the particular inflorescence was facing and were found to have no effect on insect robbery or fruit production. Robbers appear to be choosing flowers on a random basis. It would be beneficial to examine the nectar concentrations of the flowers that have been robbed compared with those unrobbed. Perhaps individuals are robbing only flowers with larger amounts of nectar; therefore, legitimate pollinators still have ample quantities of nectar themselves.

As expected, I found high variability in nectar amount among the flowers. When assuming random foraging by pollinators and constant nectar production, the expected distribution of nectar standing crop is that for which the average volume is approximately equal to the standard deviation of the distribution (Pleasants, Zimmerman 1983). If a pollinator encounters a flower with a low amount of nectar it will more likely need to visit additional flowers to fulfill its nectar requirements, thus pollinating a greater number of flowers. Yet if the insect encounters a flower on the other end of the nectar scale with a high nectar amount, it will not need to visit as many flowers provided it can stay at this flower long enough undisturbed to extract the nectar needed. The variations in nectar amounts reward the pollinator enough to keep it interested in the shrub.

The sandhill community at the Bonny Doon Ecological Reserve is a unique blend of xeric forms of vegetation surrounded by heavily forested Redwood communities. Live oak saplings have been found taking shelter under many of the sampled silverleaf manzanitas perhaps indicative of a successional species. McMinin suggested that

silverleaf manzanitas “develop into nearly pure stands of chaparral as a fire type replacement of *Pinus ponderosa*” (1939). The chaparral coverage has expanded with the burning and cutting of the original forest (Griffin 1964). But contrary to this behavior, in more recent years, fire suppression has been established to prevent damage to man-made structures in the area. The fire suppression has allowed the encroachment of mixed evergreen forest species that are not tolerant to frequent fires (Marangio, Morgan 1987).

Not many of the sampled silverleaf manzanitas were in such close proximity with other species as to inhibit flower growth at the perimeter of the silverleaf shrub. The major reason for non-interspecies competition for sunlight was because most of the plants associated with the silverleaf manzanita were smaller shrubs. The most prevalent associated species was *Ericameria*, which on average was about two feet in height, thus not preventing much sunlight from reaching the much taller silverleaf manzanita at an average height of 7.2. Although *Quercus agrifolia* was frequently found with the sampled plants, the majority of the oaks were less than one foot tall and underneath the silverleaf manzanita. Ponderosa and knobcone pines caused the majority of the overstory shading. These two shading species were generally in their mature forms and were up to 30 m away, still producing shade on the shrubs. Although no counts were made, shading from these taller individuals appeared to make no difference in flower or fruit production. The majority of the shrubs with low percentages of their perimeters exposed were in dense silverleaf manzanita stands, meaning that they were being shaded on their sides by other silverleaf manzanitas. Many adjacent silverleaf manzanitas were so close that determination of individuality was difficult. In these cases there were no flowers on the

portions of the shrubs that were so closely intertwined that the adjacent perimeters were completely shaded by the neighboring silverleaf manzanitas. In the very densely populated silverleaf areas only the shrubs on the perimeter produced flowers on the sides of the shrub, the remaining individuals produced their flowers on the top of the shrub or on portions that were higher up in the canopy than adjacent shrubs. When pollinator numbers are low the shrubs with more accessible flowers will more likely be pollinated.

Very little is known about the silverleaf manzanita, and it would be interesting for a much more in-depth study to be carried out on the nectar quantities, concentrations, and volumes and how these factors influence pollinators and nectar robbers. It would also be informative to look in more detail at the nectar robbers themselves to determine if they are exclusively robbers, or if they are also legitimate pollinators. A supplemental pollination study would be beneficial to determine if pollinators limit the silverleaf manzanita's fruit production, or if there is some other limiting resource.

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IMAGE EVALUATION TEST TARGET (QA-3)

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