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Effects of nectar robbing by *Xylocopa californica* on *Chilopsis linearis* (Bignoniaceae)

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The University of Arizona, 1989

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EFFECTS OF NECTAR ROBBING BY *XYLOCOPA CALIFORNICA* ON *CHILOPSIS LINEARIS* (BIGNONIACEAE).

by

Rachel Walker Pfister

A Thesis Submitted to the Faculty of the

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

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1989

STATEMENT BY AUTHOR

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APPROVAL BY THESIS DIRECTOR

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Richard E. Strauss — May 1, 1989

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Date

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ABSTRACT

The interaction between *Xylocopa californica* and *Chilopsis linearis* was used to test the hypothesis that nectar robbing is costly to plants. No evidence for these costs, either in terms of decreased pollination or increased energy demands, was found. In fact, the mean number of seeds per fruit and the mean individual weight of seeds per fruit was higher from fruits that developed from robbed flowers than from fruits that developed from unrobbed flowers, indicating that the presence of *Xylocopa californica* enhanced pollination. *Chilopsis linearis* pollen was isolated from the tips of the abdomens of robbing *Xylocopa californica* and it was determined that these bees could be transferring pollen from flower to flower as they position themselves to rob. This association was found to be one of mutual benefit rather than one of exploitation.

INTRODUCTION

The selective forces that plants and pollinators have on one another can often be quantified and interpreted. Flower color, configuration, and odor, for example, limit and shape the types of animal pollinators that utilize specific plants. These flower characteristics are furthur reinforced by repeated interaction with the pollinators (Heinrich and Raven 1972). Such feedback capability results in dynamic change and evolutionary responses in the species involved. This kind of coupled evolution is termed coevolution (Futuyma and Slatkin 1983). Because of this reciprocity, plant-pollinator interactions can provide us with testable biological models for understanding coevolution (Ehrlich and Raven 1964).

Plant-pollinator associations benefit the plant by ovule fertilization and benefit the animal by supplying an energy source. Generally these relationships are assumed to be reciprocal, a service rendered for a service received. Nectar robbing, one aspect of pollination biology, is an exception to this generality. It is defined as the removal of nectar from a flower, usually through a perforation, without contact with the reproductive parts of that flower (Inouye 1983). Similar behaviors have been referred to as "robbing" (Inouye 1983), "thieving" (Koeman-Kwak 1973) and "burglary" (Meeuse 1961).

The terms "robbery", "thievery" and "burglary" have been generally accepted by behaviorists as appropriate terms because the "robber" appears to cheat the flower by obtaining nectar without pollination. This assumes that the pollination service is circumvented. It is also often assumed that nectar robbing imposes costs to the plants. These costs fall into two categories. The first is decreased pollination leading to lowered seed set (Darwin 1889, Roubik 1982, Roubik et al. 1985, Soper 1952). The second catagory is increased energy expenditure such as the cost of producing additional nectar to compensate for that lost to robbers (Barrows 1976).

The concept of nectar robbing is not new. Darwin (1889) described how "humble-bees" showed much skill in foraging by biting holes on the outside of flowers as close as possible to the nectar hidden inside the corollas. He reasoned that this saved the time that would be expended climbing in and out of the corollas. He concluded that there was consequential damage to the flowers when nectar was robbed in this way. No seed would be set if ovule fertilization depended solely upon subsequent pollinators entering the flowers. Even in self-fertilized flowers, there would be no cross-fertilization following flower damage. This loss of potential viable seeds represents a mechanism by which natural selection can be effective.

Many researchers have reported insects removing nectar from flowers by incising holes or using holes incised by others (Barrows 1976 and 1980, Brian 1954, Colwell et al. 1974, Eaton et al. 1969, Hawkins 1961, Macior 1966, Roubik 1982, Roubik et al. 1985, Rust 1979, Waser 1979). If a hole made by a primary robber is used by subsequent nectivores, these foragers are termed "secondary robbers" (Inouye 1980). Several species of bees, ants, butterflies, and hummingbirds do not perforate flowers themselves; rather they act as secondary robbers. This behavior is also termed nectar "thievery" (Inouye 1980).

Pollination biology and nectar robbing studies have largely been descriptive. Many of the hypotheses developed through these descriptive methods are being reexamined through experimentation. In earlier studies it was assumed that when insects foraged on flowers with no coevolved association (eg., bees with short mouthparts foraging on flowers with long tubular corollas), an accompanying decrease in flower pollination by coevolved pollinators would result in lower overall pollination success. However, recent studies have shown that there may be little or no negative effect due to robbing (Rust 1979), and potentially some positive effects such as increased pollination (Hawkins 1961). Hawkins (1961) found a positive correlation between seed set and number of robbers (*Terrestrisbombus* spp.) that perforate red clover flowers. He stated that, on average, the exposed nectar attracted more honeybees to the flowers.

These honeybees were secondary nectar robbers but also gathered pollen from the flowers, thus increasing pollination.

In a few instances it has been suggested that, as robbing bees position themselves to rob, they inadvertantly come into contact with reproductive parts of the flowers. Thus, they obtain pollen and transport it to another flower when they land and position themselves to rob again (Macior 1966, Waser 1979).

The purpose of this research was to test the hypothesis that nectar robbing imposes costs upon the plants in which it occurs. In addition, I hypothesized that flowers subject to continual robbing respond evolutionarily by protecting themselves from theft of their nectar. For example, robbing may be correlated with thickening of the floral tissue at the base of the corolla which impedes the robbers, with development of sturdier bracts for protection of nectaries, or by promoting behavioral associations with ant species which might repel robbers (Inouye 1980).

Desert willows, *Chilopsis linearis* (Cav.) Sweet, (Bignoniaceae) and carpenter bees, *Xylocopa californica arizonensis* Cresson, (Hymenoptera: Anthophoridae) were studied because they are native species within the study sites and have had a long association in which to develop coevolutionary interactions. Carpenter bees of the genus *Xylocopa* are notorious nectar robbers.

Old and New World *Xylocopa* perforate tubular flowers in at least 36 genera in 22 plant families (Barrows 1980).

Viable seed-set was used operationally to define effects of robbing. The assumption was that costs and benefits of robbing would be reflected in the number of viable seeds produced. This study compared seed set between robbed and unrobbed flowers and between two populations of *C. linearis* at different sites. Production of flowers and fruit was compared within and between sites and years. Nectar production and pollinator census data were also collected.

MATERIALS AND METHODS

Xylocopa californica

The focal bees of this study were *Xylocopa californica arizonensis*. They are large, robust bees. Both sexes are shiny and solid black except that the male has a few white hairs on the pronotum and first abdominal segment. They range throughout the Sonoran and Chihuahuan deserts of southwestern North America and have been found from below sea level in Death Valley, California to 1500 m in the Santa Catalina Mountains (Minckley 1987).

In Arizona overwintering groups of both sexes become active in early March. At mid-March some females disperse and begin construction of new nests by tunneling in sound, dead, native softwoods including *Agave*, *Dasylirion*, *Nolina*, *Yucca*, and, occasionally, structural redwood (Krombein et al. 1979). Provisioning of the 4 to 14 brood cells, and egg laying, begin in late March. Development of the young takes about 45 days. The new generation emerges about the first of June and disperses 10-20 days later (Minkley 1987).

Adult males of *X. californica* which have overwintered also leave the nest about mid-March. They patrol and defend small areas near existing nest sites in pursuit of females. They hover and fly in small circles, sometimes for hours,

chasing other bees, other insect species, and even birds that come too close (pers obs.).

Xylocopa californica are polylectic. Krombein et al. (1979) list over 64 species of plants from which they collect pollen. A wide variety of plants are also used as nectar resources by these bees (Appendix A, Table 1).

To compare *X. californica* body size with *C. linearis* flower size, measurements were made of body length of seven female bees (from the mandibles to the tips of the abdomens). The lengths of anthers, styles and stigmas, corolla tubes and flower openings were measured on 26 flowers to look for physical correlations between the bees and the flowers.

To determine if *X. californica* were transporting *C. linearis* pollen as they moved from flower to flower, the tips of seven *X. californica* abdomens were examined for pollen. A small clump of Fuschin gel was rubbed on the bees' abdomens and then placed on a slide. The slide was heated untill the gel-containing pollen began to liquify. A coverslip was then placed on the preparation as the gel solidified. In this way the pollen was stained and permanently mounted in one step. The pollen obtained from the bees' abdomens was compared with pollen removed directly from the anthers of *C. linearis* flowers.

In a preliminary attempt to determine whether *X. californica* preferentially rob larger flowers or flowers that contain nectar with a higher sugar concentration, two pilot studies were carried out. To test for flower-size preference, a branch with 20 small flowers from Site 2 was transported from Site 2 to Site 1 (the branch was kept in water for the 45 minute trip). It was removed from the water and attached with twist-ties next to an intact branch with 20 large flowers (excess flowers were removed). The number of times that *X. californica* robbed the test flowers per 30 minute period was recorded. This trial was repeated three times in one afternoon using fresh flowers for each trial. The number of robbings was tested for independence of flower-size using a chi-square test adjusted for continuity.

To test for sugar-concentration preference, three solutions of sucrose and water (10%, 50%, and 80%) were prepared. The tests were conducted in the early afternoon when the flowers contained the least amount of nectar. Four adjacent branches were selected and the flowers in excess of 10 per branch were removed. One branch was used as a control. To each of ten flowers, 0.5 ml of 10% sucrose solution was added. The process was repeated with ten other flowers for each of the other two solutions. A tuberculin syringe was used to add the solutions to the flowers. The number of *X. californica* robbings per 30

minute trial was recorded for each group. Three 30 minute trials were conducted using fresh flowers for each trial.

Chilopsis linearis

The genus *Chilopsis* is monotypic, with two subspecies: ssp. *linearis* of the Chihuahuan Desert and ssp. *arcuata* of the Sonoran and Mojave deserts (Henrickson 1985). The trees for this study belonged to the ssp. *arcuata*. *Chilopsis linearis arcuata* is a small to moderate-sized deciduous tree, 2-9 m tall. It is a flowering perennial with narrow, mostly opposite, willow-like leaves that droop terminally. *Chilopsis linearis* is considered to be a facultative phreatophyte that typically occurs in sandy washes at elevations between 450 and 1500 m (Henrickson 1985).

The showy, sweet-scented, flowers of *C. linearis* are borne in terminal, indeterminant racemes. They are zygomorphic, sympetalous, and vary in color from white to lavender with dark purple throats. The throat floor often is light to dark yellow with deep purple lines along its long axis. This structure forms a landing platform for insects (Henrickson 1985) and the lines and colors presumably act as nectar guides to the nectaries located at the base of the corolla tubes.

The style, with its forked stigma, and the stamens lie along the dorsum of the corolla tube just inside the flower opening. The pollen grains, approximately 60 μm in diameter, are shed in tetrads and have coarsely reticulate sculpturing in raised areas on their surfaces (Henrickson 1985). The two-loculed ovary contains the nectary at its base. Radiating outward from the base of the ovary are five grooves that hold nectar. When these grooves are full, additional nectar accumulates in a pool at the base of the floral tube (Whitham 1977).

The fruits are long, narrow capsules with seeds developing in two rows in each locule. The seeds are oblong, light to dark brown, with white plumes at each end. The persistant dehiscent capsules release the seeds into the air where their plumes aid in wind dispersal.

Study Sites

Two sites in the Santa Catalina Mountain foothills near Tucson, Arizona were chosen for this study. Site 1 is located in Catalina State Park, 14 km northwest of Tucson, along the Sutherland wash at approximately 790 m elevation. It is at the base of the northwest-facing slope of the mountain range. Site 2 is 13 km southwest of Site 1, just east of North Oracle Road, 0.7 km

north of River Road, along the Pima wash. The elevation of Site 2 is approximately 700 m. It lies on the southwest side of the mountains.

Both sites are part of the Arizona Upland subdivision of the Sonoran Desertscrub region described by Shreve (1942, 1951). The vegetation type is Paloverde-Cacti-Mixed, dominated by leguminous trees. In the habitat surrounding *C. linearis*, in and along the washes at Site 1, the dominant vegetation includes *Prosopis* spp. and *Acacia greggii.* At Site 2 the habitat surrounding *C. linearis* is dominated by *Cercidium floridum* and *Cercidium microphyllum.*

Plant species associated with *C. linearis* at each site are listed in Appendix A, Table 1. This table also lists whether the plants were in bloom at the time of the study and whether *X. californica* were observed to forage on them. Rainfall records for both sites are presented in Appendix A, Figures 1 and 2.

Thirty-two trees on Site 1 and 12 trees on Site 2 were randomly chosen for the study. Voucher specimens of leaves, flowers, fruits, and seeds from these trees are on deposit in the University of Arizona Herbarium (Accession # 281895). The smaller number of trees at Site 2 is due to the construction of a private golf-course and tennis court just north of the wash, which restricted access to other trees in the area. Dates when leaves first emerged, flower buds were first seen, flowering peak was reached, and time when only a few flowers

remained were recorded (Appendix B, Table 1). Because sites were not visited daily, the dates reflect the day the event was first observed, not necessarily the actual date the event occurred.

A number of potential pollinators were observed visiting *C. linearis* flowers. A collection was made of the insects that were most frequently seen to enter the flowers and gather nectar or pollen or both (Appendix C, Table 1). The insects were collected on June 26, 1988 from Site 1. They were caught in a net as they emerged from the flowers and placed in a killing jar containing ethyl acetate. These insects were subsequently identified by Dr. Stephen Buchmann, USDA-ARS Carl Hayden Bee Research Center.

A census of potential pollinators of *C. linearis* was taken at Site 1 throughout the 1987 field season. Both sites were censused during the 1988 field season. The number of honeybees, moths, butterflies, hummingbirds, bumblebees, *X. californica* and other insects observed during a 10 minute walk through the sites at each visit was recorded at intervals during *C. linearis* flowering period. The category "others" in the figures includes such organisms as *Centris* spp., *Ericrosis* spp. and various members of the Syrphidae and Sphecidae.

Design of Study

The extent of nectar robbing at each site was determined by randomly collecting 1696 flowers from Site 1 and 396 from Site 2 from the ground and scoring them for the presence or absence of perforations at the base of the corolla tubes. The differences were analysed by a G-test of independence.

To compare seed set of flowers that had been robbed by *X. californica* with those that had not, flowers were marked and observed throughout the 1987 season until mature fruits were collected. From May 17 to July 29, 284 flowers on Site 1 and 82 flowers on Site 2 were marked with color-coded threads tied loosely around the pedicels just below the calyces. The flowers were marked with black thread if *X. californica* were observed robbing the nectar. If the flower had extra petals it was marked with a red thread. If the flower showed no evidence of robbing it was marked with white thread. The flowers were observed during development and if fruit was set it was collected when mature.

The fruits collected from the marked flowers were dried, opened, and the seeds counted and weighed on a P163 Mettler balance. The data were analysed using a one-way ANOVA. Aborted fruits and fruits that contained an herbivore were excluded from the analysis in order to reduce confounding effects on seed number.

An alternate method to compare seed set between robbed and unrobbed flowers was utilized in the 1988 field season. Instead of actual bee observation,

the presence of perforations in the corolla tubes was considered to indicate the occurrence of nectar robbing. Flowers from each of three trees at each site were marked with color-coded threads. This was done at the end of the flower-life, just before abscission, when there was no chance that nectar robbing would again occur. Records were not kept of the total number of flowers marked. Matured fruits were collected until a total of 100 fruits per tree was collected. These fruits were dried, the seeds removed, counted, and weighed. These data were analysed using a one-way ANOVA and a Student's t-test.

To determine if unrobbed flowers remained on the trees longer than robbed flowers, individual flower lifetime was recorded (Appendix D, Table 1). Flower buds were marked with numbered plastic ties hung on the pedicels just below the calyces. These flowers were examined at two hour intervals and the hours from budding and flower opening to wilting and abscission were recorded. When the flowers fell they were checked for perforations of the same type as those observed being made by *X. californica*. A test for differences in mean lifetimes of robbed vs. unrobbed flowers were done using a Student's t-test.

Sugar concentration of the nectar of 29 flowers (22 from Site 1 and 7 from Site 2) was determined using a temperature-compensated pocket refractometer. These flowers were examined for evidence of *X. californica* incised perforations. These data were used to determine if there was a

difference between the sugar-concentration of the nectar from robbed and unrobbed flowers. The results were analysed using a Student's t-test.

To determine if Site 1 and Site 2 differed in flower size, the lengths and widths of 150 flowers from each site were measured. Difference in flower size was compared between sites using a Student's t-test.

Studies were also undertaken to determine the quantity of nectar produced at intervals during the day and the mean production per flower for a 24 hour period. The data were compared between sites using a Student's t-test. At 1900 hr on the evening prior to the study, one branch, containing at least 75 flowers assumed to be depleted of daily nectar reserves, was bagged with 3 mm^2 mesh green bridal veiling to prevent robbing. At 0600 hr 25 flowers were unbagged and the nectar contained in them was collected in 10 μl micropipettes. The mean value was assumed to be the mean volume of nectar produced per flower prior to dawn. At 1200 hr another 25 flowers were unbagged and the quantity of nectar was measured. The 0600 hr mean was subtracted from the 1200 hr mean to estimate the quantity of nectar produced between dawn and noon. At 1900 hr the remaining 25 flowers were unbagged and the nectar measured. The volume at 1200 hr was subtracted from the 1900 hr volume and this was considered to be the mean production between noon and dusk. The sum total of the three daily means was an estimate of the amount of nectar

produced per flower per 24 hour period. These studies were repeated at two-week intervals three times at each site during the 1988 field season.

Site Comparisons

Site comparisons were made for floral display, fruit size, and seed production (number, size and weight). These comparisons were analysed by two-way ANOVAS. Percentages of flowers that set fruit, aborted fruit, and of fruits with evidence of herbivory were also compared using G-tests of independence.

Floral display was estimated by counting the number of flower scars on randomly selected racemes (1987 = 560 from Site 1 and 240 from Site 2; 1988 = 600 from Site 1 and 240 from Site 2). For comparisons of seed and fruit production, fruit lengths were measured, the fruits were opened, and the seeds were counted and weighed. To compare the mean lengths and widths of seeds between sites, 60 randomly collected seeds from each site were measured. To determine the percentage of flowers that set fruit, the data for number of flower scars on the racemes was used and the number of fruits on an equal number of randomly selected racemes was also counted. The mean number of fruits per raceme was divided by the number of flower scars to yield an estimate of the percentage of flowers that set fruit.

The number of aborted fruits (persistent brown and shriveled fruits without seeds) was also recorded. The fruits were examined for evidence of

herbivory and any seed predators present were collected and preserved for identification. The number of fruits that contained predators or showed evidence of invasion by an herbivore was determined for each site.

Seed Viability

To determine whether the seeds collected were viable, a tetrazolium test for seed viability was conducted on a subset of the collected seeds. The seeds were collected in September of 1987 and 1988 and were tested in February, 1989. Twenty seeds from each site and each year (N = 80 seeds) were placed overnight on moist paper toweling. The next morning the seed coats were removed. The seeds were then placed in a 1% 2,3,5-triphenyl tetrazolium chloride solution for 2 hours. They were then rinsed in distilled water and examined using a dissecting microscope for the presence of a red tetrazolium stain. A red color indicated that hydrogen produced during respiration combined with absorbed tetrazolium solution (Grabe 1970). A positive reaction (red color) qualitativly indicated seed viability.

RESULTS

Behavior of Xylocopa californica

Though not physically restricted from access into the flowers (mean diameter of flower opening at Site 1 was 8.54 mm ± 1.07 [N = 26] and the mean maximum width of *X. californica* was 9.83 mm ± 1.04mm [N = 7]), in over 350 hours of observation, *X. californica* were never seen to enter *C. linearis* flowers by walking down the throat of the flower in the manner common to smaller pollinating insects. Measurements also indicated that it was physically possible for the abdomens of robbing *X. californica* to contact the reproductive parts of the *C. linearis* flowers. The mean body length of *X. californica* was 31.6 mm ± 1.9 (N = 7). The mean length of the corolla tubes, from the nectaries to the tips of the stigmas at the flower opening was 21.7 mm ± 6.3 (N = 26).

Examination of the seven bees collected from Site 1 revealed pollen of *C. linearis* present in clumps on the tips of the abdomens of all seven of the bees.

The two pilot studies for *X. californica* flower preference showed that larger flowers from Site 1 were visited 83 times by *X. californica* while the smaller flowers from Site 2 were visited 13 times in the same amount of time. The number of visits was not independent of treatment, (X^2_{adj} = 5.85, df = 1; $p < 0.05$). The order of *X. californica* preference for nectar sugar concentration

in trial 1 was 50% > 80% > 24% (control) >10%, (X^2 = 35.17, df = 3; p < 0.001). The order of preference in trial 2 was 80% > 24% (control) > 50% > 10%, (X^2 = 15.13, df = 3; p < 0 .01). Trial 3 order of preference was 80% > 50% = 24% (control) > 10%, (X^2 = 46.84, df = 3, p < 0.001).

Phenology of Chilopsis linearis

Tree phenology varied consistently between sites throughout both growing seasons. Appendix B, Table 1 presents the dates reflecting the first day an event was observed. Flowering peak, and time period when only a few flowers remained, occurred approximately two weeks earlier at Site 1 than Site 2 in both years.

Pollinator Census

At Site 1, as buds were developing and flowering-time approached, increasing numbers of *X. californica* were seen to patrol the trees. As blooming reached its peak, so did the number of patrolling *X. californica*. Toward the end of flowering, when only a few trees had very many flowers, more than forty *X. californica* were seen to simultaneously work a single tree.

At Site 1 *X. californica* outnumbered *Bombus sonorus* during flowering peaks during both years. It can be seen in both figures 1 and 2 that the number of *Bombus* increased as the number of *X. californica* declined and flowering

waned. No *X. californica* were seen at the flowers on Site 2 in 1987 or 1988 (Figure 3), even though they nested in the immediate vicinity. By far the most frequent visitors and the major pollinators at Site 2 were *Apis mellifera* (Figure 3) from a commercial bee colony nearby. Carpenter bees were the most frequent visitors at Site 1 (Figures 1 and 2), followed by moths and butterflies and those insects listed in the "others" category. Bumble bees (*Bombus sonorus*), black-chinned hummingbirds (*Archilochus alexandri*), milkweed butterflies (*Danaus* spp.), and swollowtail butterflies (*Battus* spp.) approached the flowers from the front but also occasionaly acted as secondary robbers by using the perforations made by *X. californica*.

Many ants were on the buds and flowers but were not seen to enter the flower openings. There are glands on the nodes of young stems that may serve as extra-floral nectaries (Henrickson 1985) that attract these ants.

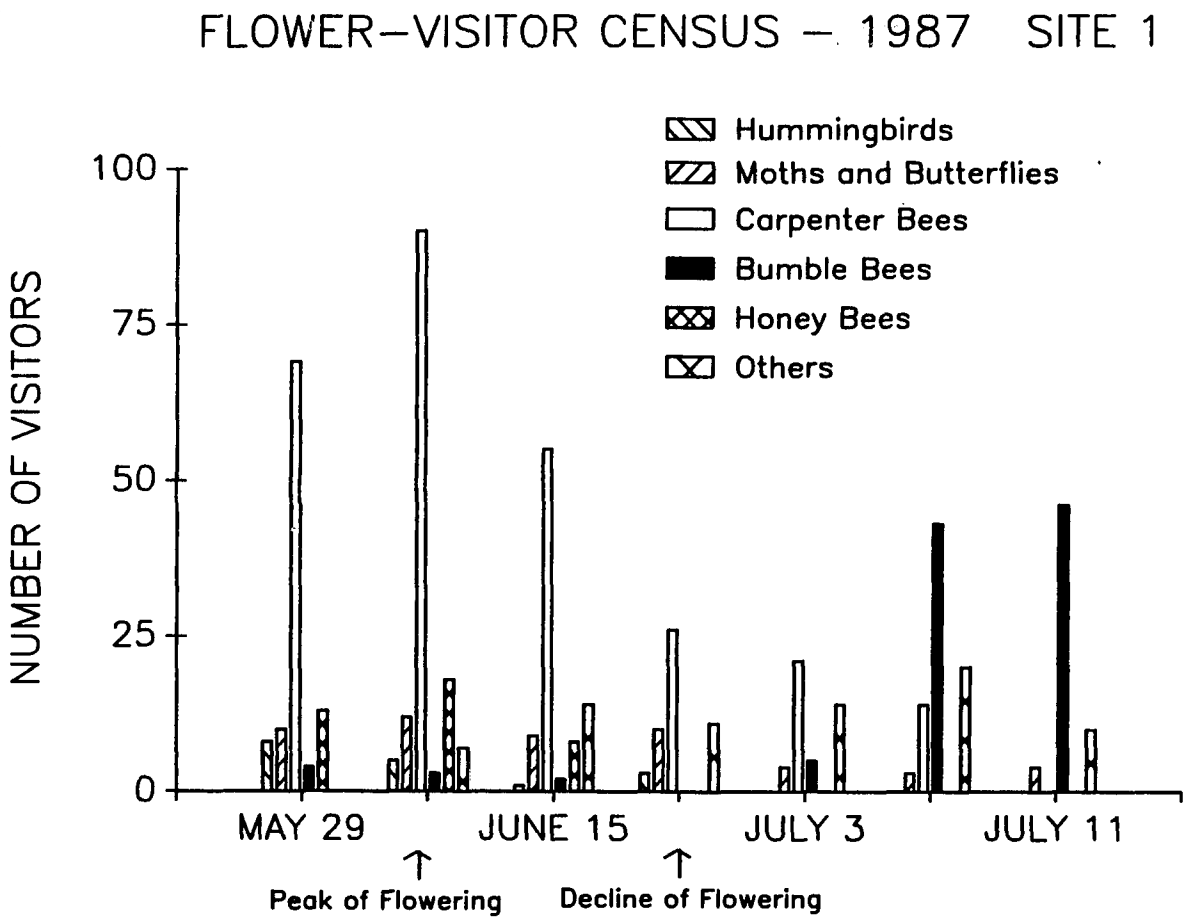

Figure 1. Census of visitors to Chilopsis linearis seen on ten minute walks throughout the flowering period at Site 1 in 1987. Others = Centris spp., Ericrosis spp., and various members of the Syrphidae and Sphecidae.

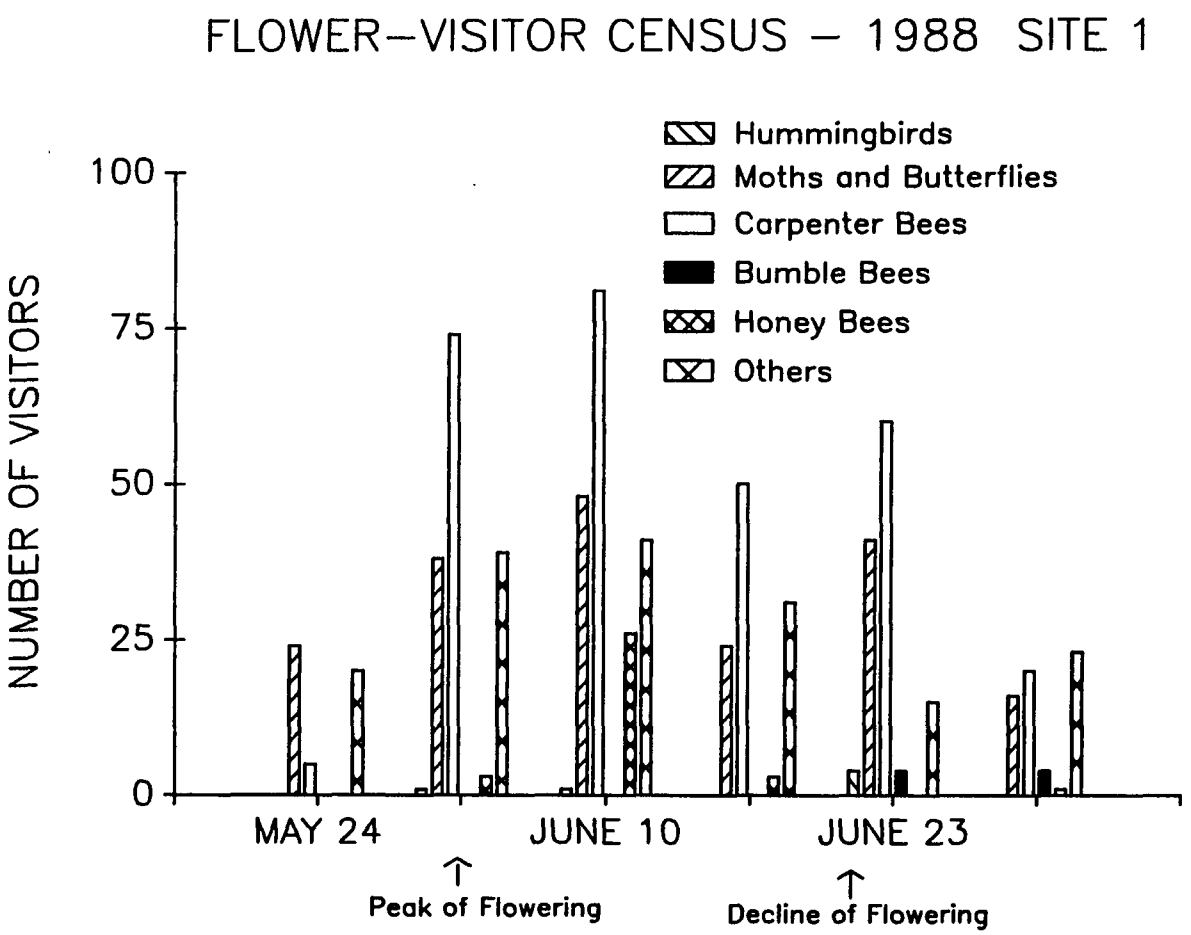

Figure 2. Census of visitors to Chilopsis linearis seen on ten minute walks throughout the flowering period at Site 1 in 1988. Others = Centris spp., Ericrosis spp., and various members of the Syrphidae and Sphecidae.

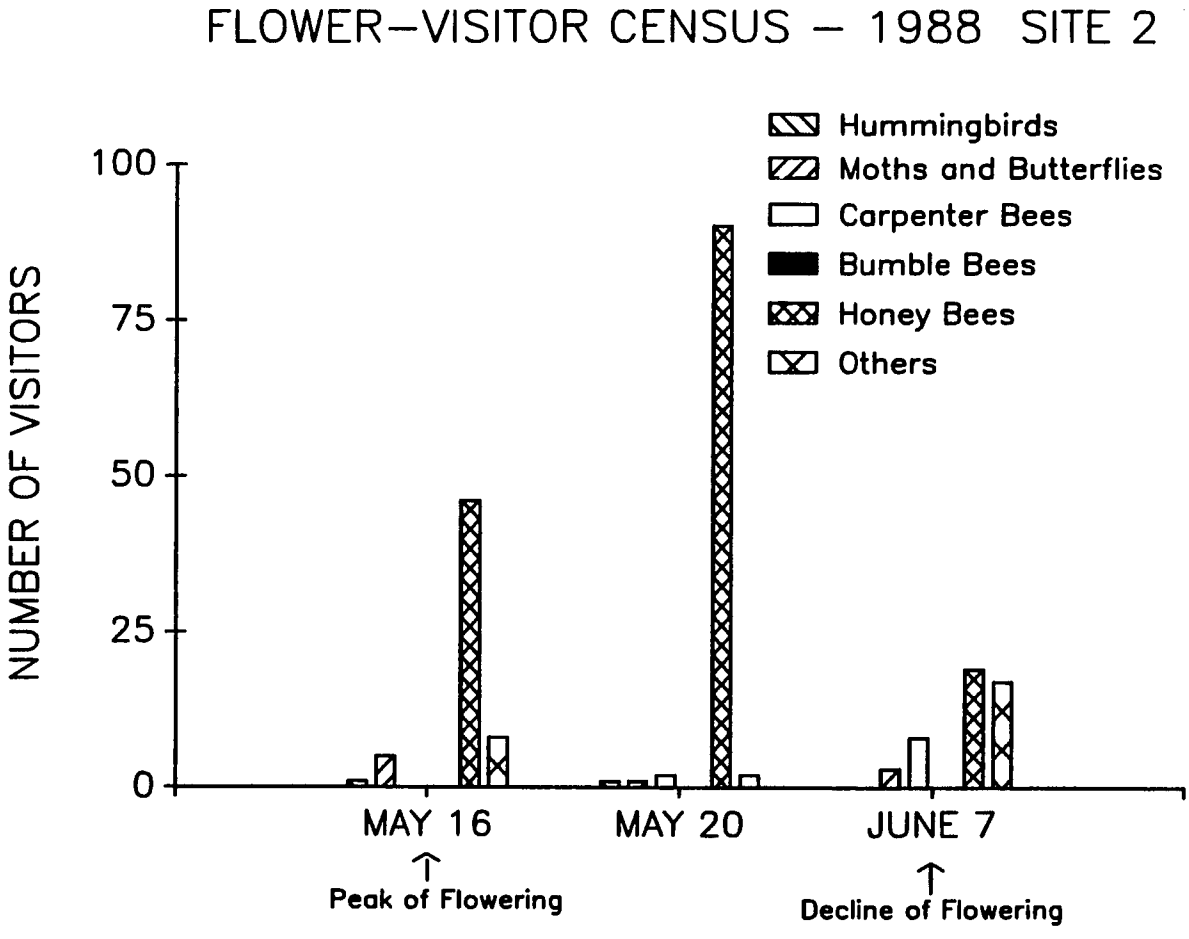

Figure 3. Census of visitors to Chilopsis linearis seen on ten minute walks throughout the flowering period at Site 2 in 1988. Others = Centris spp., Ericrosis spp., and various members of the Syrphidae and Sphecidae.

Effects of Nectar Robbing

The extent of nectar robbing was very different between sites during both years of this study (Tables 1 and 2). In 1987 85% of the flowers examined at Site 1 were robbed and in 1988 92%. This was compared to the percentages from Site 2 which were 9% in 1987 and less than 1% in 1988 ($p < 0.001$ for both years).

Seed number and seed weight differences, between flowers that were robbed and those that were not, were analysed separately for 1987 (Table 3) and 1988 (Table 4) because of the inequality of sample sizes. In 1987 the number of seeds contained in fruits from robbed flowers was significantly higher than the number of seeds from unrobbed flowers ($p < 0.05$). The mean seed weight was also significantly higher ($p < 0.001$). In 1988 the differences followed the same general pattern as the previous year. Seed number was higher in the robbed group ($p < 0.05$), as was mean seed weight ($p < 0.01$).

Chilopsis linearis flowers varied in the number of hours they remained open (Appendix D, Table 1). This may have been influenced by whether or not they were pollinated. Apparently this variation was not influenced by whether or not the flowers had been robbed because the mean number of hours that flowers with *X. californica* perforations remained open and on the tree did not differ

Table 1. Percentages of robbed flowers, flowers that set fruit, aborted fruits, and herbivory for each site in 1987.

	Site 1 Obs/total	%	Site 2 Obs/total	%	G[a]	p
Robbed	1448/1696	85.4	35/396	8.8	875.5	< 0.001
Fruit set[b]		4.4		1.9		
Fruit abortion	75/600	12.5	39/220	17.7	3.5	
Herbivory	200/600	33.3	66/220	30.0	0.8	

[a]G test of independence.
[b]method of data collection prevented statistical analysis.

Table 2. Percentages of robbed flowers, flowers that set fruit, aborted fruits, and herbivory for each site in 1988.

	Site 1 Obs/total	%	Site 2 Obs/total	%	G[a]	p
Robbed	156/170	91.8	1/157	0.64	343.9	< 0.001
Fruit set[b]		12.8		4.4		
Fruit abortion	90/581	32.7	116/240	48.3	17.5	< 0.001
Herbivory	227/580	39.1	27/240	11.3	69.7	< 0.001

[a]G test of independence.
[b]method of data collection prevented statistical analysis.

Table 3. A. 1987 - Mean number and weight of *Chilopsis linearis* seeds removed from fruits developed from robbed vs. unrobbed flowers. Aborted fruits and fruits that contained an herbivore were excluded from the analyses. B. Analyses of variance of seed number and seed weight from fruits developed from robbed vs. unrobbed flowers. Seed weight expressed in mg.

A.	FRUITS FROM ROBBED FLOWERS	FRUITS FROM UNROBBED FLOWERS
	N = 56	N = 19
SEED NUMBER	47.07 ± 14.34	37.74 ± 12.33
MEAN SEED WEIGHT	9 ± 2	6 ± 2

B. Source	df	SS	MS	F	p
Variable: SEED NUMBER					
ROBBED	1	1236.15	1236.15	6.422	0.013
ERROR	73	14051.4	192.49		
Variable: MEAN SEED WEIGHT					
ROBBED	1	157.33	157.33	38.55	< 0.001
ERROR	73	4.08			

Table 4. A. 1988 - Mean number of *Chilopsis linearis* seeds per fruit removed from fruits developed from robbed vs. unrobbed flowers. Aborted fruits and fruits that contained an herbivore were excluded from the analysis. B. Analysis of variance of seed number from fruits developed from robbed vs. unrobbed flowers. C. Results of t-test on difference between the mean seed weight of seeds per fruit. Robbed flower fruits N = 154, unrobbed flower fruits N = 170. Seed weight expressed in mg.

A.

	FRUITS FROM ROBBED FLOWERS	FRUITS FROM UNROBBED FLOWERS
SEED NUMBER	50.01 ± 11.58	47.22 ± 12.91

B.

Source	df	SS	MS	F	p
Variable: SEED NUMBER					
ROBBED	1	625.81	625.81	4.141	0.043
ERROR	322	48658.5	151.11		

C.

Variable: MEAN SEED WEIGHT

Robbed	9.0 ± 1.00
Unrobbed	4.5 ± 0.05

$t = 6.84$ $df = 4$; $p < 0.01$

significantly from the number of hours that non-perforated flowers remained open (perforated flowers = 47.6 ± 19.3 [N = 13]; non-perforated flowers = 48.0 ± 18.6 [N = 11]; t = 21.6, p = 0.96).

The sugar-concentration of nectar was higher in the flowers with perforations than in those without perforations (t = 2.7, df = 27; $p < 0.05$).

Flower Size and Nectar Quantity and Quality

The flowers were significantly longer at Site 1 ($\bar{x}_1$ = 45.23 ± 2.96 mm; N = 149) than at Site 2 ($\bar{x}_2$ = 32.31 ± 2.87 mm; N = 149) (t=38.28, df = 296; $p < 0.001$). They were also significantly wider at Site 1 ($\bar{x}_1$ = 34.28 ± 3.61 mm; N = 149) than Site 2 ($\bar{x}_2$ = 24.68 ± 2.98 mm; N = 149) (t=25.05, df=296; $p < 0.001$). The correlation between flower width and length (r = 0.86) was also significant ($p < 0.01$) (Fig. 4).

Nectar secretion in *C. linearis* at both sites was greater in the early morning than later in the afternoon (Fig. 5). This timing of secretion concurred with the findings of Brown et al. (1981) and Whitham (1977). The two sites differed significantly in total amount secreted in a 24 hour period ($p < 0.05$) (Table 5). Site 1 flowers (larger flowers) produced a mean of 1.78 µl more nectar per flower than Site 2 flowers. The mean sugar concentration of the

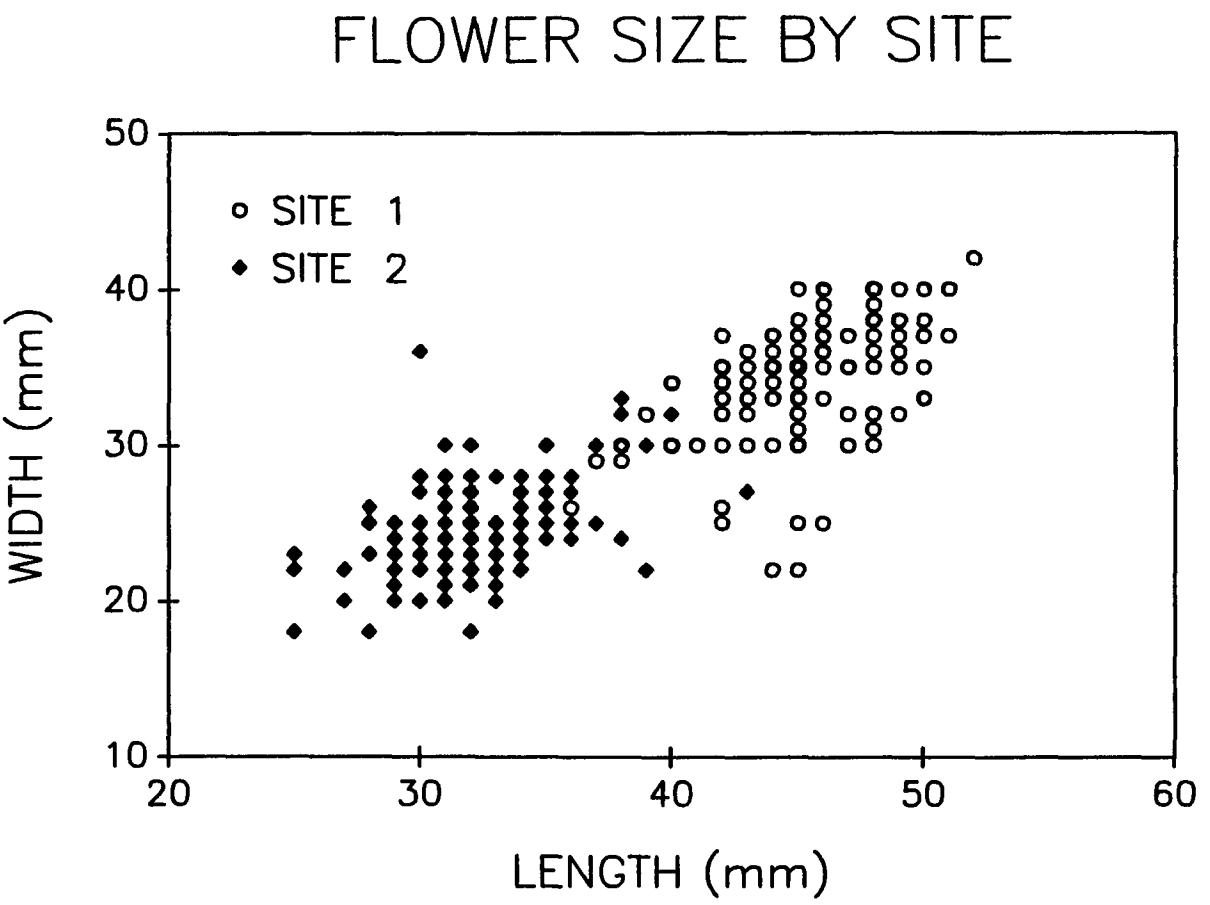

Figure 4. Correlation between Chilopsis linearis flower width and length. Open circles represent flowers from Site 1 and filled diamonds represent flowers from Site 2. r = 0.86.

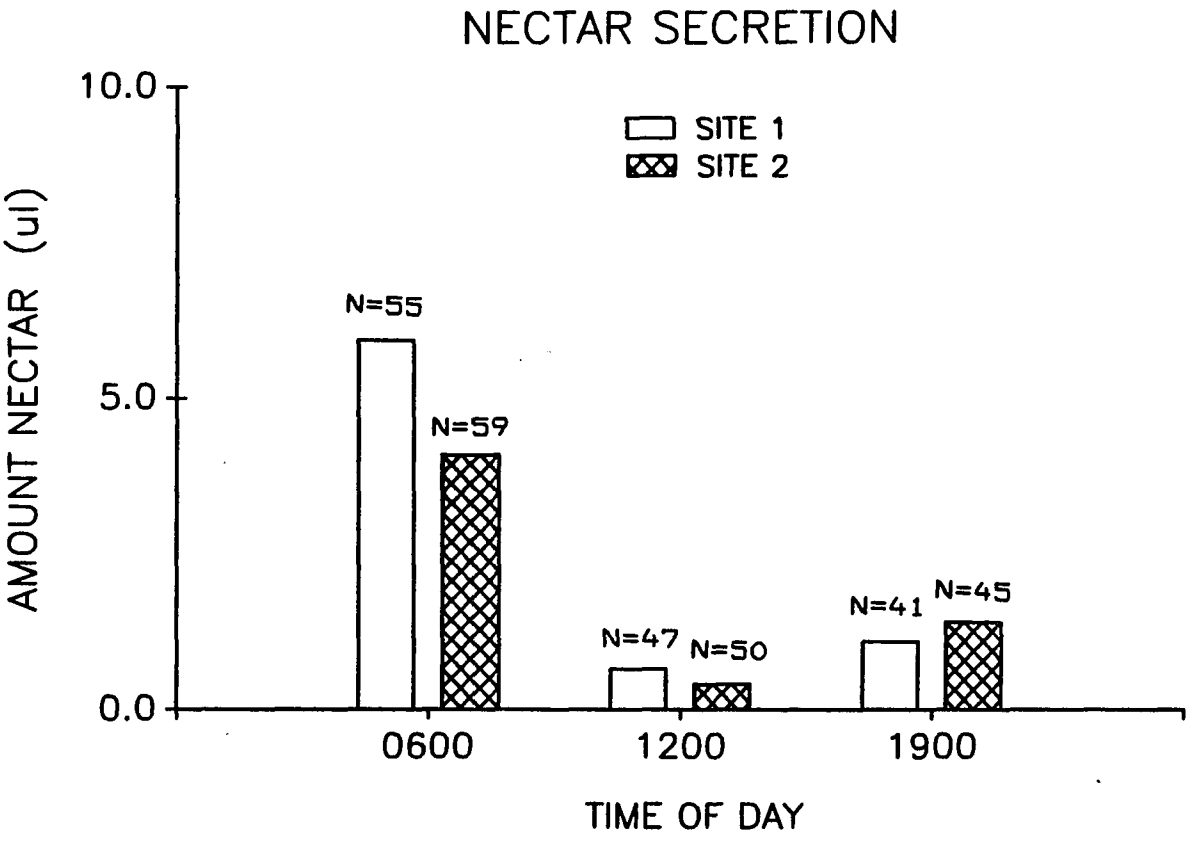

Figure 5. Mean amount of nectar per Chilopsis linearis flower at time of day indicated.

Table 5. Site comparisons of mean volume of nectar produced per flower at intervals over time, and site comparisons of mean volume produced per flower in 24 hours. Amounts in μl.

	Site 1.	Site 2.	
Time Intervals:			
1900-0600	5.93 ± 5.14 N = 55	4.09 ± 5.04 N = 59	ns
0600-1200[a]	0.66	0.41	
1200-1900[b]	1.10	1.40	
Amount per 24 Hours:			
	7.69 ± 3.47 N = 41	5.90 ± 2.94 N = 45	*

[a]based upon the mean volume of nectar per bagged flower at 1200 hr minus the mean amount of nectar produced by 0600 hr

[b]based upon the mean amount of nectar per bagged flower at 1900 hr minus the mean amounts of nectar produced by 0600 hr and 1200 hr.

ns = not significantly different.

* = $t = 2.58$ $df = 80$; $p < 0.05$

nectar in Site 1 flowers ($\bar{x}_1$ = 25.84 ± 6.16; N = 22) did not differ significantly from that of Site 2 flowers ($\bar{x}_2$ = 22.07 ± 4.55; N = 7).

Site Comparison

Floral display differed significantly between years ($p < 0.001$, Table 6). In 1988 the mean number of flowers per inflorescence at both sites was less than in 1987, but there was no significant between-site difference.

The number of seeds produced did not differ significantly between sites but there was a significant difference between years ($p < 0.01$) (Table 7). In 1988 both sites produced 35% fewer seeds. Mean individual seed weight differed significantly between sites ($p < 0.001$), seeds were consistently lighter in weight at Site 2. Seeds were significantly longer and wider at Site 1 in both years ($p < 0.001$) (Table 8).

The lengths of fruits produced varied significantly between sites and between years (Table 9). Site 1 produced larger fruits both years, but both sites produced smaller fruits in 1988 than in 1987.

The percentage of flowers that set fruit at Site 1 was higher than Site 2 for both 1987 and 1988 (Tables 1 and 2). Percentage of fruit abortion was not

Table 6. A. Floral display as measured by mean numbers of *Chilopsis linearis* flowers per inflorescence on Sites 1 and 2 in 1987 and 1988. B. An analysis of variance of *Chilopsis linearis* floral display between sites and years. Data are expressed as number of flowers per inflorescence on 20 racemes per tree.

A.	1987		1988	
	Site 1	Site 2	Site 1	Site 2
	14.08 ± 4.02	16.17 ± 2.85	8.57 ± 2.84	5.99 ±3.39
	N = 560	N = 240	N = 600	N = 240

B.	Source	df	SS	MS	F	p
	YEAR	1	681.73	681.73	59.89	< 0.001
	SITE	1	26.39	26.39	2.32	0.13
	YEAR*SITE	1	11.98	11.98	1.05	0.31
	ERROR	77	876.45	11.38		

Table 7. A. Mean seed number and mean seed weight (mg) of *Chilopsis linearis* on Sites 1 and 2 in 1987 and 1988. B. Analyses of variance of *Chilopsis linearis* seed number and weight between sites and years. Data are expressed in terms of number of seeds per 20 fruits per tree. Site 1, N = 600 fruits, Site 2, N = 240 fruits.

A.	1987		1988	
	Site 1	Site 2	Site 1	Site 2
SEEDS	650 ± 238	609 ± 171	426 ± 289	408 ± 216
SEED WT	9 ± 2	6 ± 2	9 ± 2	5 ± 2

B. Source	df	SS	MS	F	p
Variable: SEED NUMBER					
SITE	1	27187.31	27187.31	0.44	0.51
YEAR	1	641861.60	641861.60	10.44	0.002
SITE*YEAR	1	9059.94	9059.94	0.15	0.702
ERROR	77	4734897.73	61492.18		
Variable: MEAN SEED WEIGHT					
SITE	1	231.01	231.01	65.95	< 0.001
YEAR	1	7.35	7.35	2.10	0.151
SITE*YEAR	1	5.42	5.42	1.55	0.217
ERROR	76	266.21	3.50		

Table 8. A. Mean width and length of *Chilopsis linearis* seeds. B. Analyses of variance of seed width and length between sites and years. 1987 Site 1 and Site 2 N = 30. 1988 Site 1, N = 26, Site 2, N = 34. Data expressed in mm.

A.

	1987		1988	
	Site 1	Site 2	Site 1	Site 2
WIDTH	2.95 ± 0.48	2.40 ± 0.36	2.79 ± 0.35	2.38 ± 0.41
LENGTH	9.75 ± 1.01	8.42 ± 1.21	9.19 ± 1.12	7.31 ± 1.21

B.

Source	df	SS	MS	F	p
Variable: SEED WIDTH					
SITE	1	6.795	6.795	41.503	< 0.001
YEAR	1	0.239	0.239	1.458	0.230
SITE*YEAR	1	0.154	0.154	0.94	0.334
ERROR	116	18.991	0.164		
Variable: SEED LENGTH					
SITE	1	76.913	76.913	50.134	< 0.001
YEAR	1	20.618	20.618	13.440	< 0.001
SITE*YEAR	1	2.250	2.250	1.466	0.228
ERROR	116	177.962	1.534		

Table 9. A. Mean length of *Chilopsis linearis* fruit on Sites 1 and 2 in 1987 and 1988. B. An analysis of variance of *Chilopsis linearis* fruit length between sites and years. Data is expressed as mean fruit length of 20 fruits per tree. Lengths expressed in cm.

A.

1987		1988	
Site 1	Site 2	Site 1	Site 2
19.83 ± 3.97	17.12 ± 2.95	18.39 ± 2.90	12.65 ± 3.00
N = 600	N = 220	N = 580	N = 240

B.

Source	df	SS	MS	F	p
YEAR	1	276.15	276.15	41.36	< 0.001
SITE	1	129.38	129.38	19.38	< 0.001
YEAR*SITE	1	33.29	33.29	4.99	0.029
ERROR	75	500.78	6.68		

significantly different between sites in 1987 but in 1988 the percentage of aborted fruits was significantly higher at Site 2 ($p < 0.001$) (Tables 1 and 2). The percentage of fruits attacked by herbivores was not significantly different between sites in 1987 but in 1988 Site 2 had significantly less herbivory ($p < .001$) (Tables 1 and 2). The seed herbivores that were removed from the mature seed capsules were larvae of pyralid moths (Dr. Stephen Buchmann pers. comm). Leaf herbivory was not observed at Site 1 but in 1988 extensive leaf herbivory occurred on Site 2. Because it occurred after fruits were mature, leaf herbivory was not quantified.

Seed Viability

Of 80 seeds (40 from each site, randomly selected from those collected) tested for viability, 100% reacted positively to the tetrazolium test. Therefore the seeds used in the study were assumed to be viable.

DISCUSSION

The interaction between *Xylocopa californica* and *Chilopsis linearis* was used to test the hypothesis that nectar-robbing is costly to plants. This association is a typical example of the complex network of relationships that plants and animals have with one another. The assumption of negative effects of *X. californica* on *C. linearis* is influenced by the negative connotation of the anthromorphism of the words "nectar robbing" historically used to name the behavior of animals when they remove nectar from a plant in an unorthodox manner. Upon closer examination, however, this behavior in *X. californica* appeared to have a positive effect upon *C. linearis*.

No evidence for negative effects of nectar robbing on *C. linearis*, either in terms of decreased pollination or increased energy costs, was found in this study. In fact, the mean number of seeds per fruit and the mean individual weight of seeds was higher from robbed flowers than from unrobbed flowers, indicating that the presence of *X. californica* enhanced pollination. However, site differences must be taken into account when evaluating these data. Site 1, the site where much more robbing occurred, received more rain in both years, particularly in 1987, and was generally more productive.

Damage to *C. linearis* flowers, caused by multiple perforations made by robbers, did not shorten the time that flowers remained open and available for pollination. This damage exposed the nectaries to more circulating air and may be the reason that sugar concentration in the nectar of robbed flowers was higher than that of nectar in unrobbed flowers. This may have attracted more *X. californica* to the flowers since they showed preference for nectar with higher sugar concentration. If *X. californica* are pollinating, increased numbers of the bees would increase pollination.

A recent study that yielded very different results than this study is that of Roubik et al. (1985). They examined the role of nectar robbing by *Trigona fulviventris*, a social bee, in reproduction of *Quassia amara*, a tropical, hummingbird-pollinated tree. They found that the exclusion of robbers resulted in seed production 4-12 times greater than in control flowers. They concluded that increased seed set was due to increased pollen transfer because of longer, more frequent, hummingbird visits to the flowers protected from the robbing bees. The explanation for the increased rate and duration of hummingbird visitation was that protected flowers contained more nectar than those to which the robbers had access. They proposed that continued depletion of nectar by robbers may result in gradual reduction of plant reproductive success through a reduction in pollinator populations.

One explanation for the difference in the results of the two studies may be that the interactions between the animals and plants of the Roubik et al. (1985) study took place under a very different set of conditions than that of this present study. *Quasia amara* is self-compatible, whereas *C. linearis* is self-incompatible (Petersen et al. 1982), *Q. amara* is predominantly bird-pollinated whereas *C. linearis* is primarily insect pollinated, and, finally, *Trigona* were not suspected of being pollinators rather than robbers, as were *X. californica* on *C. linearis*.

In another study Waser (1979) examined the role of *Xylocopa californica* and hummingbirds in determining flowering time of ocotillo (*Fouquieria splendens*). *Xylocopa californica* rob the nectar from ocotillo flowers as they do from *C. linearis* flowers. As they rob they brush against the anthers and get pollen on the ventral surfaces of the abdomen and thorax. They transport this pollen from flower to flower. He found that flowers excluded from visitation by bees and hummingbirds set less seed than controls. Waser (1979) concluded that even though ocotillo flowers are typical hummingbird flowers, they are by no means exclusively pollinated by these birds. *Xylocopa californica* are the most frequent visitors to these flowers and he found a strong relationship between seed set and *X. californica* abundance. He concluded that these nectar robbers also pollinate the ocotillo. He stated that the exact placement and exsertion of

anthers and stigmas in flowers within his study populations may represent adaptations forcing the bees to transfer pollen.

Such pressure may also be exerted on *X. californica* by *C. linearis*. *Chilopsis linearis* pollen was found on the tips of *X. californica* abdomens collected during this research. When bees straddle the flowers their heads are oriented toward the base of the corollas and their abdomens come into contact with the anthers and stigmas just inside the flower opening. The bees grasp the flowers and incise them with their mandibles. The force exerted as the incision is made causes their bodies to curve ventrally and pollen gets deposited on the tips of their abdomens. This pollen could be transferred to the stigma of another flower as the bees repeat the robbing process. Comparison of bee body lengths with distances from the nectaries to the anthers and receptive stigmatic surfaces shows this transfer to be physically possible.

Xylocopa californica are effecting pollination in *C. linearis*. Furthur study will determine how efficient this method of transfer is. Marked pollen experiments will be useful in quantification. Closer examination of other plant-animal interactions in which animals or plants are assumed to be "cheating" the established system may reveal a similar situation.

An interesting question that arose from this study is why did *X. californica* rob flowers at Site 1 but not Site 2? This preliminary research presents some possible answers to this question.

Xylocopa californica nests found in the vicinity of both sites indicate the presence of bees in both areas. However, there are more potential nest sites, *Agave* and *Dasylirion* stalks, in the area surrounding Site 1. Thus, there may have been fewer bees at Site 2 because of limited nesting sites.

Major food sources other than *C. linearis*, such as *Acacia* and *Cercidium* spp., were flowering at both sites. However, another important food source, *Larrea tridentata*, was blooming only at Site 2. *Larrea* may be a preferred food of *X. californica*, and they may forage on it rather than on *C. linearis*. Flower species preference tests would clarify this.

Another possible explanation for the difference in robbing incidence between sites is the difference in tree phenology. Site 2 flowering peak was several weeks earlier than Site 1 flowering peak. Site 2 flowers may be blooming too early and missing the height of the *X. californica* population since only those *X. californica* that overwintered are foraging that early in the Spring.

Another explanation for why bees are not foraging at Site 2 may be that flowers there are too small to be worthwhile resources. Even though floral

display (based on number of flowers per raceme) was similar at both sites, the flowers at Site 1 were significantly larger.

The larger flowers contained more nectar, so the caloric reward might also be a basis for choice. Preference tests indicated that bees preferred the larger flowers. However, there were problems with the preference tests conducted in this study. The flowers imported from Site 2 were cut, and wilted rapidly in the 110° F heat. Therefore, the bees may have avoided the imported flowers for reasons other than size. Improved tests for *X. californica* preference, in the field and in the laboratory, will be valuable aids to understanding the behavioral mechanisms and responses of these bees.

Under the assumption that *X. californica* are pollinating rather than robbing *C. linearis*, coevolutionary responses to facilitate the process are predicted. One prediction is that greater exposure of the reproductive organs is expected for flowers in areas of continual robbing. To test this prediction comparisons of stamen and style length and distance of their protrusion from the flower opening should be made between flowers in areas where there is continual robbing pressure and areas of intermittant robbing pressure. If *C. linearis* and *X. californica* have a reciprocal relationship then it is predicted that the bees should not rob flowers before it is possible for them to contact the flowers' reproductive structures. This prediction was supported in this study

since only rarely were *X. californica* seen to land on and attempt to rob flowers before anthesis, even though these flowers already contained nectar.

Continuing research on the association between *C. linearis* and *X. californica* will reveal the extent to which plants, because of their plasticity, can adapt to, or even influence their environment. A long historical association between these flowers and *X. californica* has yet to result in the development of obvious means to protect the flowers from floral damage or loss of nectar. This is evidence that this association is not one of exploitation of the flowers by the bees, but rather one of mutual benefit.

APPENDIX A - PLANT ASSOCIATIONS

Table 1. Plant species associated with *Chilopsis linearis* at Sites 1 and 2. Plants were identified by author.

Plant Species	Site 1[a]	Site 2[a]	Flowering[b]	*Xylocopa*[c]
Dasylirion wheeleri	+	-	+	-
Agave schottii	+	-	+	-
Agave parryi	+	-	-	-
Agave palmeri	+	-	-	-
Tamarix pentandra	-	+	+	+
Sphaeralcea sp.	+	+	+	-
Larrea tridentata	-	+	+	+
Condalia lyciodes	+	-	+	-
Condalia warnockii	-	+	+	-
Celtis pallida	-	+	+	-
Celtis reticulata	+	-	+	-
Fouquieria splendens	-	+	+	+
Lycium spp.	+	+	+	-
Nicotiana trigonophylla	-	+	+	-
Solanum elaeagnifolium	+	-	+	-
Datura meteloides	+	+	+	+

Acacia greggii	+	+	+	+
Acacia constricta	+	+	+	+
Mimosa biuncifera	+	+	+	-
Prosopis juliflora	+	+	+	+
Prosopis velutina	-	+	+	+
Parkinsonia aculeata	-	+	+	+
Cercidium floridum	-	+	+	+
Cercidium microphyllum	+	+	+	+
Carnegiea giganta	+	+	+	+
Ferocactus covillei	+	+	-	-
Ferocactus wislizenii	+	+	-	-
Opuntia fulgida	+	+	+	-
Opuntia versicolor	+	+	+	-
Opuntia acanthocarpa	+	+	+	-
Opuntia bigelovii	+	+	+	-
Opuntia leptocaulis	+	+	+	-
Opuntia arbuscula	+	+	+	-
Opuntia phaeacantha	+	+	+	-
Astralagus nuttallianus	+	+	+	-
Courtsetia glandulosa	+	-	+	-
Phoradendron californicum	+	+	-	-
Sambucus mexicana	+	-	+	+

Encelia farinosa	+	+	+	-
Hymenoclea salaola	-	+	+	-
Ambrosia ambrosiodes	+	+	+	-
Ambrosia deltoidea	+	+	+	-
Psilostrophe cooperi	+	+	+	-
Dyssodia acerosa	+	+	+	-
Gutierrezia sarothrae	+	+	+	-
Haplopappus tenuisectus	+	+	-	-
Baileya multiradiata	-	+	+	-
Zinnia pumila	-	+	-	-
Aster riparius	-	+	-	-
Baccharis sarothroides	+	+	-	-
Ephedra trifurca	-	+	-	-

[a] + indicates presence of species at site.
[b] + indicates flowering during the time of the study.
[c] + indicates *X. californica* were observed gathering pollen or nectar or both from the flowers.

APPENDIX A

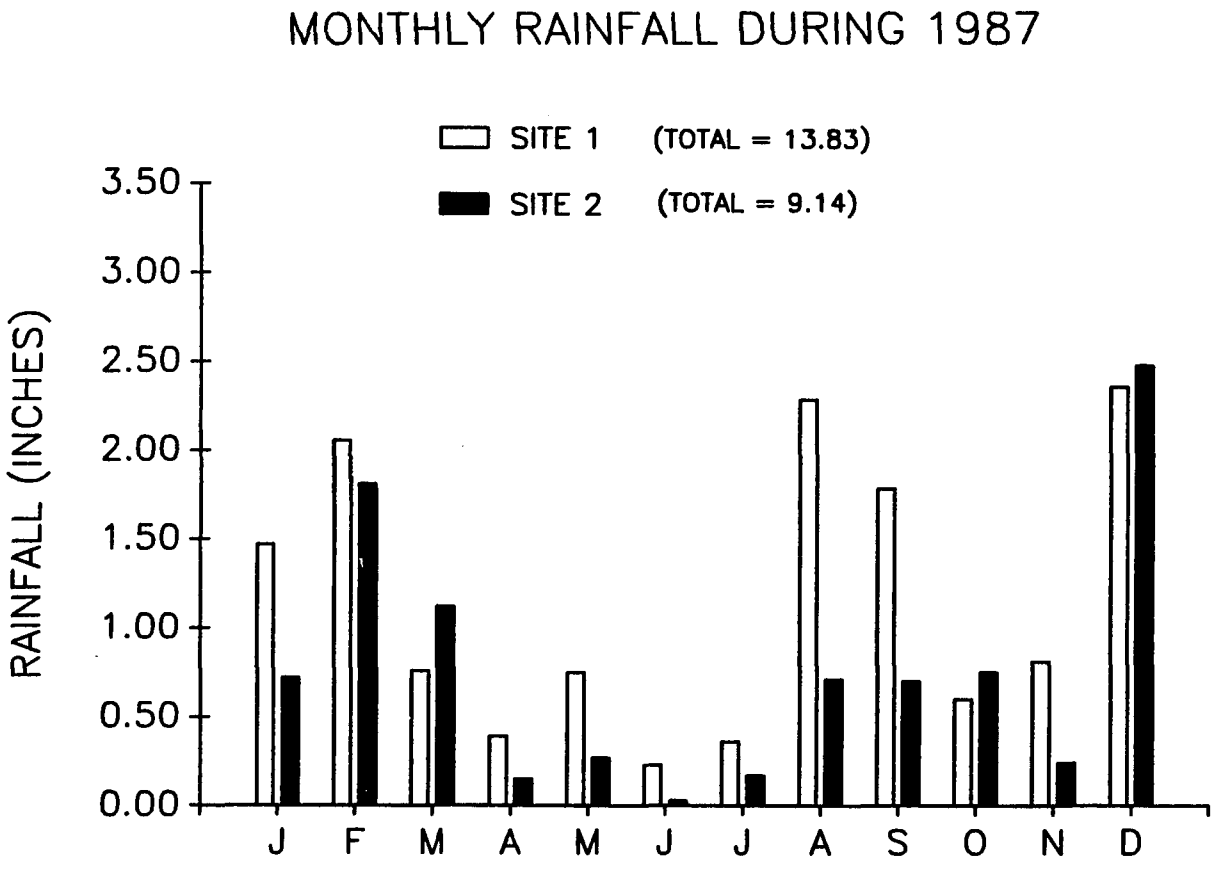

Figure 1. Rainfall received at Sites 1 and 2 in 1987.

APPENDIX A

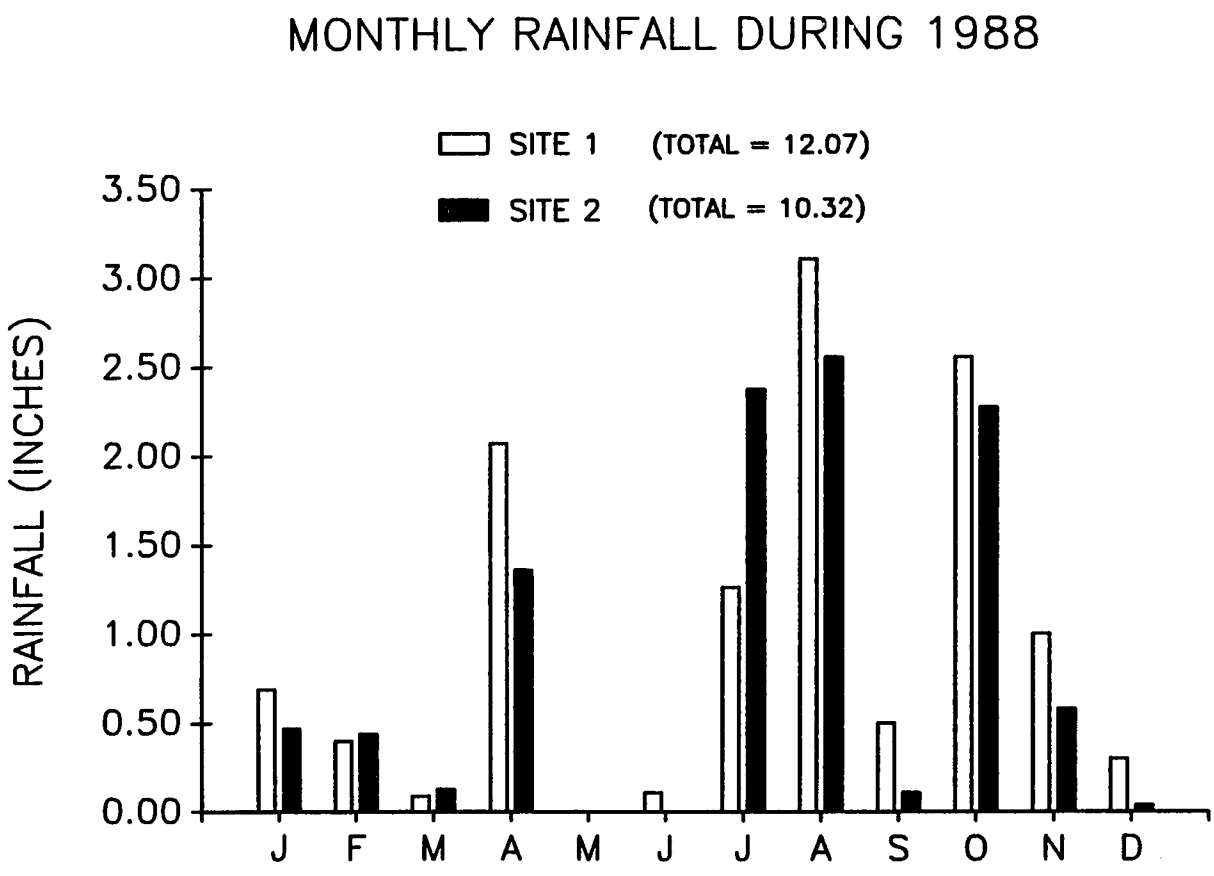

Figure 2. Rainfall received at Sites 1 and 2 in 1988.

APPENDIX B

Table 1. Phenology of *Chilopsis linearis*.

	Site 1		Site 2	
	1987	1988	1987	1988
Leaf Emergence	4/20	5/2	4/3	4/1
Flower Bud Emergence	4/26	5/5	4/18	4/13
Open Flowers	5/12	5/17	4/25	5/5
Flowering peak.	6/8	6/3	5/21	5/16
Few Remaining Flowers	6/22	6/21	6/5	6/7

APPENDIX C - INSECT COLLECTION

Table 1. Insects captured on *Chilopsis linearis* flowers.

Insects	Sex
Apis mellifera L.	Female
Xylocopa californica arizonensis	Female
Ericrosis lata Cresson[a]	Female
Syrphidae[b]	-
Bombus sonorus Say	Female
Centris caesalpiniae Cockerell	Female
Sphecidae[c]	-
Centris atripes Moscary	Female

[a]Formerly *Ericrosis arizonensis*.
[b]Flower fly. Genus undertermined.
[c]Bembicine sand wasp.

APPENDIX D

Table 1. *Chilopsis linearis* flower lifetime.

Event	Time (hrs)	N
Bud to open flower	24.9 ± 4.9	8
Open flower to wilted	48.6 ± 18.9	14
Wilted to abscissed	27.5 ± 10.6	2

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