THE FUNCTION OF EXTRAFLORAL NECTARIES IN OPUNTIA ACANTHOCARPA (CACTACEAE)[1]

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ABSTRACT

Opuntia acanthocarpa (Cactaceae) possesses extrafloral nectaries embedded in the areoles of new reproductive and vegetative growth. The nectar secreted by these glands attracts ants and is a nutritional food source. Members of one attracted ant species, Crematogaster opuntiae (Myrmicinae), are aggressive and efficient defenders of the plants against cactus-feeding insects. The results of our study are consistent with the ant-guard hypothesis for the role of extrafloral nectaries in O. acanthocarpa. Additionally, individuals of O. acanthocarpa are well protected in comparison with those of O. phaeacantha. The latter generally possess ephemeral extrafloral nectaries and consistently maintain fewer ants.

EXTRAFLORAL NECTARIES are glands which secrete nectar from leaves, petioles, sepals, petals or fruits, or, as in Campsis radicans (Elias and Gelband, 1975), from several of these structures in a single species. They are not known to function in pollination, though they are, with few exceptions, confined to angiosperms. Extrafloral nectaries range in structure from simple glandular surfaces, where the nectar is exuded through stomata, to modified spines and specialized vascularized glands which conduct the nectar through phloem (Buxbaum, 1950; Elias, 1972; Elias and Gelband, 1976; Elias, Rozich, and Newcombe, 1975; Esau, 1965; Luttge, 1977; Wergin et al., 1975). Extrafloral nectar usually contains sugars, most commonly glucose, fructose and sucrose, and occasionally amino acids or other organic compounds (Bentley, 1977a).

The role of extrafloral nectaries in attracting and maintaining protective ants has been implicated for more than a century, based largely on correlative data (Bentley, 1977a). Recently, protection by ants has been demonstrated experimentally in members of Acacia (Janzen, 1966, 1967), Barteria (Janzen, 1972), Phaseolus (Bentley, 1976), and Bixa (Bentley, 1977b). The extra-

floral nectaries of Opuntia species attract copious numbers of ants (Lloyd, 1908), yet the ecological role of these glands has not been elucidated. In this paper we present evidence that the extrafloral nectaries of Opuntia acanthocarpa Engelm. & Bigelow var. major (Engelm. & Bigelow) Benson function in attracting and maintaining protective ants.

MATERIALS AND METHODS—Opuntia acanthocarpa var. major (hereafter referred to as O. acanthocarpa) is a succulent, diffuse shrub to 1.7 m tall which is common in gravelly flats and washes of southern Arizona and northern Sonora, Mexico from 300 to 900 m in elevation (Benson, 1969). The population studied is located 72 km northeast of Phoenix, Arizona, in the Arizona Upland Zone of the Sonoran Desert as delimited by Shreve and Wiggins (1964). The study site is undisturbed except for occasional grazing cattle. We chose O. acanthocarpa because it is locally abundant.

Scanning electron micrographs were made of fresh material, the specimens being glued to stubs with silver paint. The specimen in Fig. 1C was quick-frozen in liquid nitrogen before mounting. Charging was evident immediately and increased rapidly so the micrographs were taken within as short a time as possible. All SEM was performed on an AMR 1000A scanning electron microscope.

Six plant segments of Opuntia acanthocarpa were potted and maintained in the greenhouse for observing the distribution and activity of extrafloral nectaries during the spring of 1977. The volume of nectar produced per gland was measured by banding field plants with tanglefoot (The Tanglefoot Co., Grand Rapids, MI) to prevent access by ants and periodically collecting
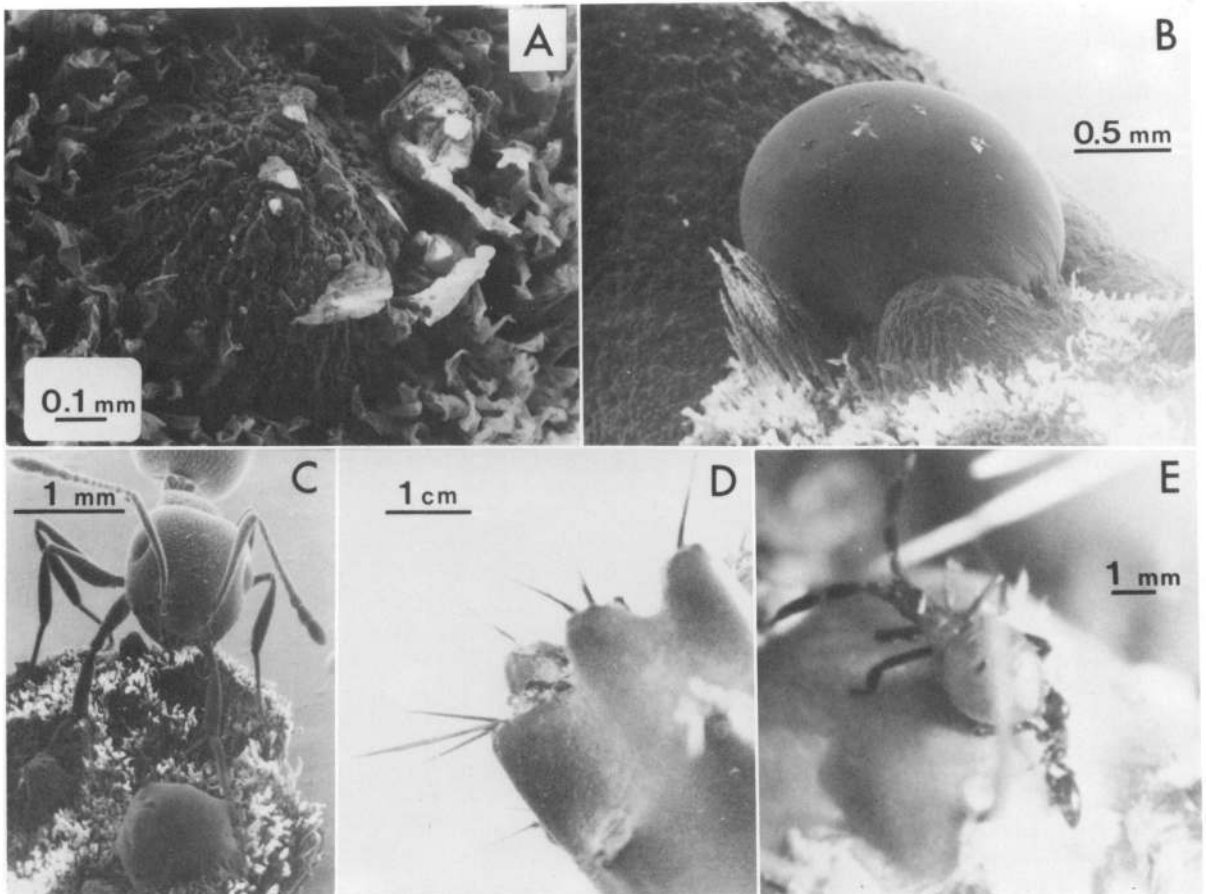
Fig. 1, A–E.   **A.** SEM of a floral cup nectary of *Opuntia acanthocarpa*. **B.** SEM of a nectary that has secreted a nectar droplet. **C.** SEM of *Crematogaster opuntiae* foraging on an areole with active nectaries. **D.** *C. opuntiae* on a floral cup areole. **E.** *C. opuntiae* attacking nymph of *C. vittiger* on a floral cup.

the secretions in microliter pipets over 24 hr, once in early May 1978 and again two weeks later; the same glands were measured at each time interval. Nectar was also collected in micropipets during the spring of 1977 and 1978 for chemical analysis from plants banded in the field and brought into the laboratory. Sugar composition was determined by paper co-chromatography with standards in n-propanol, ethyl acetate and water (7:1:2, v/v), followed by detection with standard spray reagents (Harborne, 1973). Relative sugar concentrations were determined from the color depth of the spots. The absolute concentration of total carbohydrates was determined by the anthrone test (Ashwell, 1957). The qualitative and quantitative analyses of the amino acids of one nectar sample were performed on a Beckman Amino Acid Analyzer. The "histidine scale" method of determining total amino acid concentration (Baker and Baker, 1973) was used for population samples since it is more rapid.

Floral nectar was partially analyzed for comparison with extrafloral nectar.

The diurnal activity of *Crematogaster opuntiae* Buren, the most common ant species associated with *O. acanthocarpa*, is implied from the number of individuals recorded on stem apices or floral cups (*sensu* Benson, 1969) every 3 hr throughout each of 3 different 24-hr periods in the summer of 1977. Seasonal activity was recorded during the peak activity hours of one day of each month except November and December of the year beginning May 1977. Each sample consisted of counting ants on 1–3 branches on each of 7–10 plants. The same plants were observed throughout the sampling for both diurnal and seasonal ant activity. Additionally, peak diurnal ant activity was correlated with nectar production. The density of ants on 1 stem apex on each of 10 plants was recorded during the peak activity period. The ants were then removed and the branches were banded to prevent

access by ants to the apices. The nectar quantity produced by each apex was measured 18 hr after banding.

The coreid insect, *Chelinidea vittiger* Hamlin, is one of the most common pests of *Opuntia* in the southwestern United States (Mann, 1969) and is the most common pest of *O. acanthocarpa* at our study site. It is a species of sucking insects which causes necrotic circular spots around punctures due to chloroplast extraction and toxogenic reactions (Alcorn, pers. commun.). Additionally, the gregarious behavior of larval individuals makes *C. vittiger* one of the most destructive of the cactus-feeders in the southwestern U.S. (Hunter, Pratt, and Mitchell, 1912; Mann, 1969). The effect of ants against these insects is implied by the length of time artificially placed insects spent on ant-occupied *O. acanthocarpa* fruits. Similarly placed insects on fruits without ants were used as controls. Two separate experiments were conducted, one with adults and one with nymphs of *C. vittiger*, between 2:00 AM and 4:00 AM on plants with relatively high ant activity. A different branch was used for each trial.

The number of fruit set per branch was correlated with ant activity on each floral cup on plants in a north-south transect through the study site. The first 100 plants along the transect were tagged and from these, 14 sample plants were picked using a random number generator on a Texas Instruments Model SR-51A calculator. Data were taken between 6:00 and 8:00 PM in June 1978.

The vulnerability of the buds of *O. acanthocarpa* to *C. vittiger* was demonstrated experimentally. Thirty-eight branches, each from a different plant, with developing buds were individually potted and covered with a fiberglass cloth screen. Three individuals of *C. vittiger* were placed on each of 19 branches and the remaining 19 branches were maintained as controls, without insects. The number of buds that flowered by the end of 4 weeks was recorded. Additionally, the preferred feeding location of *C. vittiger* was determined. Ten individuals were placed with each of 12 branches which had been used as controls in the previous experiment. The location of each insect on the plants was recorded at the end of 24 hr.

For comparative purposes field surveys of phytophagous insects, ants, and fruits damaged on *O. acanthocarpa* and *O. phaeacantha* Engelm. var. *discata* Benson & Walkington were conducted. *Opuntia phaeacantha* is also common at our study site, and during the first stages of our study we noted that this species produces highly ephemeral extrafloral nectaries and maintains fewer ants. These nectaries are glochid-like glands rather than modified spines as in *O. acanthocarpa* (personal observation). Every individual of *O. acanthocarpa* and *O. phaeacantha* 3 m on either side of a north-south transect through the study site was sampled for the presence of ants and phytophagous insects until an adequate sample size was obtained according to a running means test. Data were taken once in June 1978, between 7:00 and 10:00 AM. Even though ants and cactus-feeding insects are generally nocturnal, we believed that night observations of the insects would be difficult and unreliable since they tend to be camouflaged by the plants. We also surveyed populations of *O. acanthocarpa* and *O. phaeacantha* for damage by phycitid lepidopteran larvae. These larvae are common parasites of *Opuntia* fruits and leave easily detectable burrow holes (Mann, 1969). Fifty individuals of *O. phaeacantha* and 30 of *O. acanthocarpa* were sampled within a 30 × 30 m plot at the center of the study site. We recorded the percentage of damaged fruit in each sample population.

RESULTS—Active extrafloral nectaries occur in the areoles of the developing stem tissue of new stems and of the floral cup which surrounds the ovary (Fig. 1A,B). We found an average of 4.3 ± 0.44 (n = 59) active nectaries per floral cup between April 24 and June 14, 1977, out of 12.9 ± 0.35 (n = 30) areoles per cup. Active glands on floral cups appear in March and last through August. Active stem nectaries are observable from February through March and July through October.

The nectar production per gland is difficult to measure and perhaps dependent on environmental conditions. The average volume of nectar produced per gland in 24 hr was 0.3 ± 0.06 μl (n = 15), as measured on two occasions in May 1978. Three sugars were found in the nectar: glucose and fructose in relatively equal amounts, and a slightly smaller quantity of sucrose. The average total carbohydrate concentration of 5 samples was 11 ± 1.4 M. Extrafloral nectar amino acids and their concentrations are shown in Table 1. The sum of these concentrations, 169.8 mM, is lower than the average total amino acid concentration of 279 ± 34.4 mM (n = 41) in a population of *O. acanthocarpa* as determined by the histidine scale method. The population sample revealed a high variability, ranging from 55 to 1009 mM. We found that the floral nectar of *O. acanthocarpa* contains the same sugars as does the extrafloral nectar, but differs by having a 2 ± 0.4 mM (n = 17) concentration of amino acids.

The seasonal activity of *C. opuntiae* on extrafloral nectaries generally corresponded with periods of new vegetative and reproductive growth
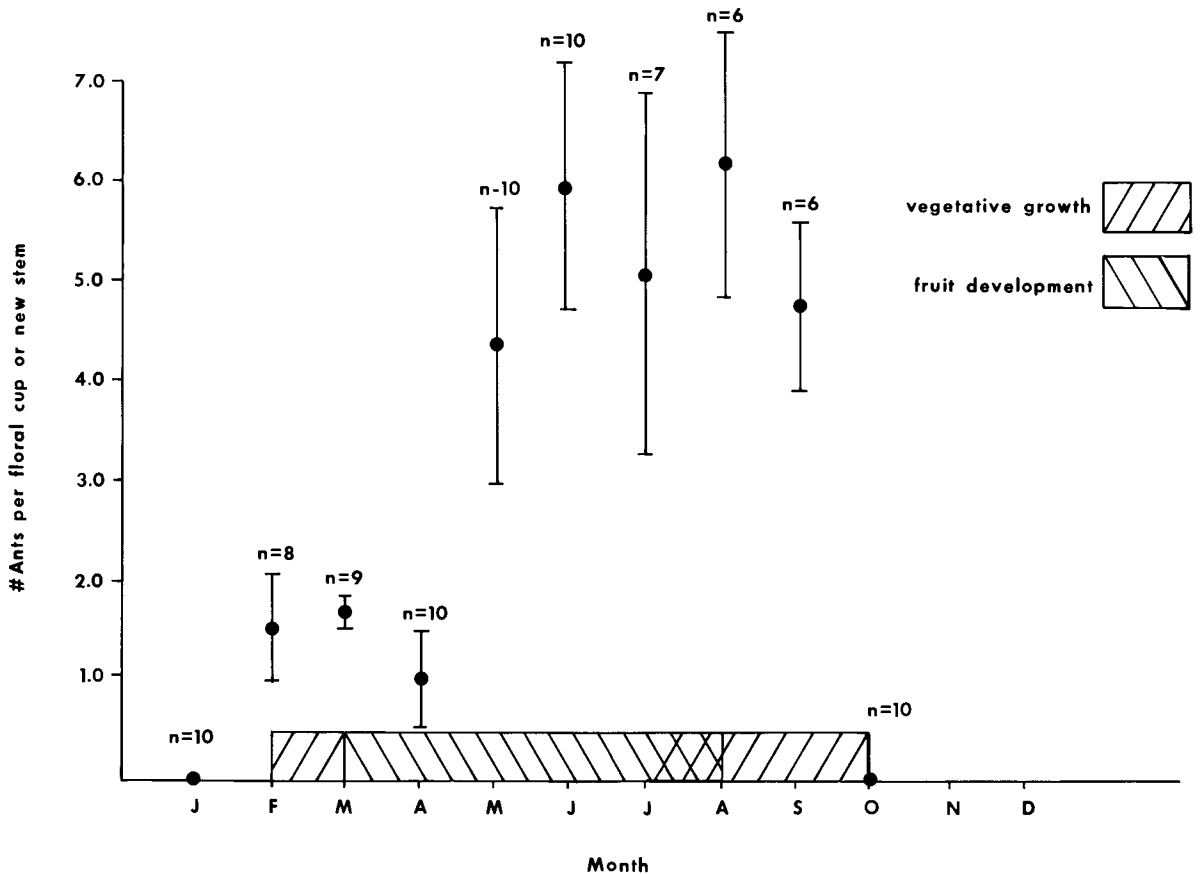
Fig. 2. Seasonal ant activity of *Crematogaster opuntiae* visiting *Opuntia acanthocarpa*, 1977–1978. Means ± one standard error is given.

of *O. acanthocarpa* (Fig. 2). During peak seasonal activity ants were most active at night (Fig. 3). Ants are typically found on the areoles of young stem apices or floral cups, feeding on nectar (Fig. 1C,D). The number of ants on each stem apex is strongly correlated with its quantity of nectar production ($r_s = 0.73$, $P < 0.02$). Thus, areas of high nectar production maintain larger numbers of ants.

In measuring the effects of *Crematogaster opuntiae* on herbivores, we found that individuals of *Chelinidea vittiger* spent less time on *O. acanthocarpa* fruits that were occupied by ants than on those without ants (Table 2). Nymphs were usually attacked by the ants before they could escape (Fig. 1E), and 6 of 10 were killed. Most of the adults fled before being attacked, and those that were attacked eventually escaped.

The number of fruit set per branch showed a positive Spearman rank correlation with the number of ants per floral cup of *Opuntia acanthocarpa*. However, this correlation was not significant ($0.2 < P(r_s = 0.4) < 0.1$).

As measured by the percent of aborted buds, the reproductive fitness of artificially maintained plants with insects was significantly reduced in comparison with plants without insects (Table 3). Also of note was the success of *Chelinidea vittiger* on *Opuntia acanthocarpa*; the 3 individuals initially placed with each plant had produced 10–15 second to third instar nymphs per plant by the end of 4 weeks. The preferred feeding location of these nymphs is on the floral cup of *O. acanthocarpa*; of the 120 nymphs artificially placed on potted plants (10 on each of 12 plants), 78% were found feeding on floral cups at the end of 24 hr.

Two coreid insects, *Chelinidea vittiger* and *Narnia inornata* Distant, commonly occurred on *O. phaeacantha* but were found less frequently on *O. acanthocarpa* (Table 4). In contrast, 2 ant species, *Iridomyrmex pruinosus* Roger and, more frequently, *Crematogaster opuntiae*, were observed on *O. acanthocarpa* but were absent entirely from *O. phaeacantha* at the time the data were recorded (Table 4). Additionally,
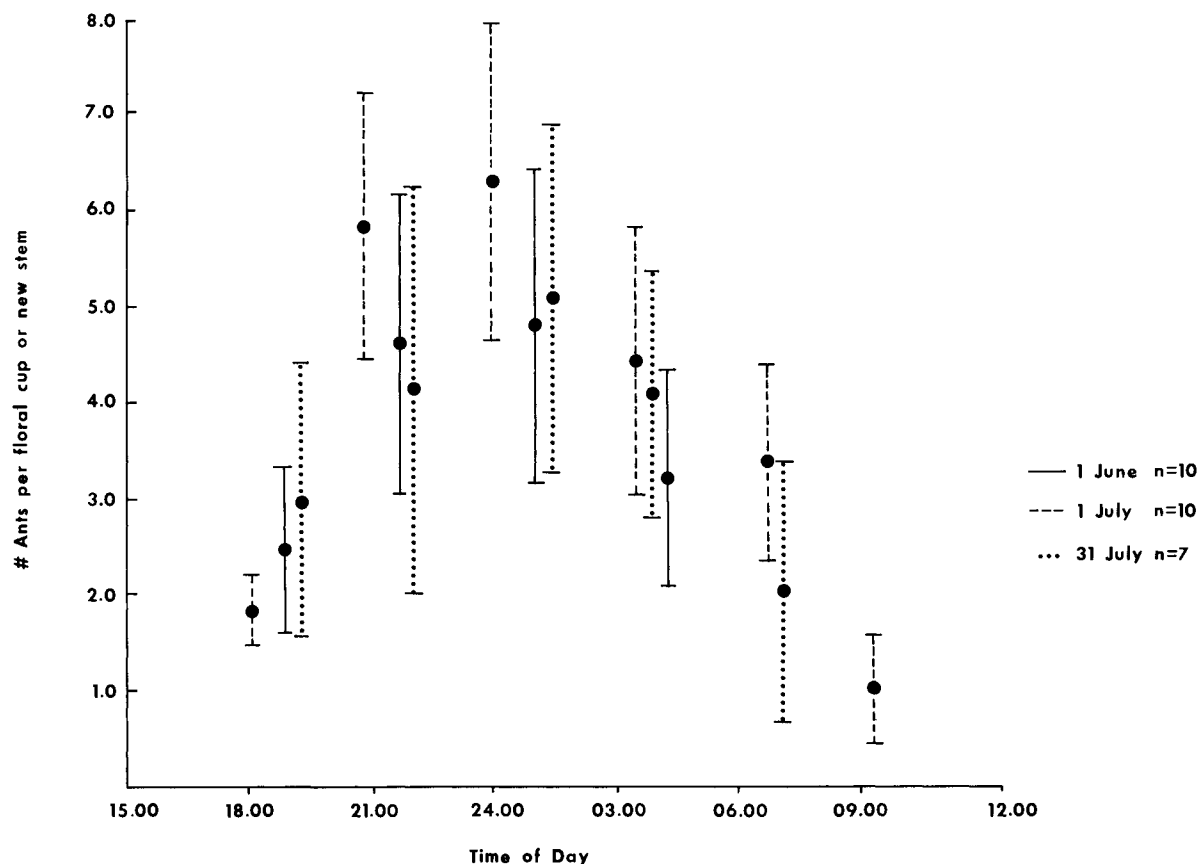
Fig. 3. Daily activity of *Crematogaster opuntiae* visiting *Opuntia acanthocarpa*. Means ± one standard error is given. Zero ant activity, during daylight hours, is not shown.

14.5% of the fruits of *O. phaeacantha* exhibited damage by phycitids, whereas 2.0% of the *O. acanthocarpa* fruits were damaged.

DISCUSSION—The sugars in the extrafloral nectar of *Opuntia acanthocarpa* (glucose, fructose, sucrose) commonly occur in the extrafloral nectar of many other plant species (Bentley, 1977a). However, this *Opuntia* nectar contains more amino acids than have been reported in floral or extrafloral nectar of other plants (Baker and Baker, 1975; Keeler, 1977), except perhaps in the extrafloral nectar of *Helianthella quinquenervis* (Inouye and Inouye, cited in Bentley, 1977a). Furthermore, the concentration of total amino acids in *O. acanthocarpa* extrafloral nectar, although quite variable, averages extremely high ($\bar{x} = 279$ mм) in comparison with that in floral nectar ($\bar{x} = 2$ mм). It is also much higher than concentrations reported by Keeler (1977) in the extrafloral nectar of *Ipomoea carnea* (petiolar, 0.0981 mм; pedicellar, 0.1368 mм) and by Baker and Baker (1973) in the most concentrated

floral secretion of any plant (ca. 15.6 mм in specialized fly flowers).

Total amino acids in flower nectar have been suggested as a nutritional food source for different pollinators at concentrations from about 0.2 mм to 12.5 mм (Baker and Baker, 1975). It has also been suggested that, for growth of individuals or a colony of insects, nectar should contain amino acids in a ratio of 1:20 or higher to the sugars (Gordon, pers. commun.), which was exceeded in some *O. acanthocarpa* samples. Two opposing points of view concerning the feeding behavior of insects are pertinent to these suggestions: 1) it is supposed that food selection is determined solely on the basis of olfactory and gustatory stimuli to which insects respond selectively, i.e., nutrition plays no role; and, 2) it is supposed that nutritional factors, in addition to olfactory and gustatory stimuli, play a significant role in initiating, promoting and sustaining normal feeding (House, 1972). The composition of *O. acanthocarpa* extrafloral nectar, which exceeds by far the nutritional amino acid level sug-

TABLE 1. *Amino acids of the extrafloral nectar of Opuntia acanthocarpa and their concentrations*

Amino acid	Concentration (mM)
asparagine/glutamine[a]	67.7
serine[b]	20.0
valine[b]	17.0
proline[b]	14.0
threonine[b]	14.0
aspartic acid	8.7
glutamic acid	5.6
phenylalanine[b]	4.2
alanine	3.3
isoleucine[b]	3.3
tyrosine	2.8
histidine[b]	2.7
methionine[b]	2.0
leucine[b]	1.3
glycine[b]	1.1
tryptophan[b]	1.0
taurine	0.8
lysine[b]	0.3
arginine[b]	trace
	Total = 169.8

[a] Co-detected and therefore could be 1 or 2 compounds.
[b] Essential or quasi-essential amino acids according to Baker and Baker (1975).

gested by Baker and Baker, but which averages somewhat less than the 1:20 amino acid to sugar ratio suggested by Gordon, is probably a nutritional food source as well as a feeding stimulus. This is supported by our field observation that the nectar is the major, and perhaps the sole, food source for *Crematogaster opuntiae*; rarely were these ants seen foraging outside of the canopy of *O. acanthocarpa*. Additionally, the nectar contains 19–20 amino acids, of which ten are essential amino acids for insect nutrition. Three others are the "quasi-essential" insect amino acids as described by Baker and Baker (1975; Table 1). Demonstration of the nutritional value, or lack of it, of *O. acanthocarpa* extrafloral nectar to *C. opuntiae* demands rigorous proof. Detailed studies along this line by insect nutritionists are needed.

TABLE 2. *Time spent by manually placed Chelinidea vittiger individuals on fruits of Opuntia acanthocarpa with and without Crematogaster opuntiae ants*

	$\bar{x}$ (s)	±2 S.E.	n
Nymphs			
with ants	24.1	4.4	10
without ants	282.0	18.0	5[a]
Adults			
with ants	75.7	13.9	10
without ants	220.0	38.7	7[a]

[a] The maximum trial time without ants was 300 s.

TABLE 3. *Reproductive vulnerability of Opuntia acanthocarpa to Chelinidea vittiger*

	No. of plants	Initial no. of buds	% Aborted buds	Mean no. of fruits per plant (±2 S.E.)
Plants with insects	19	101	62	1.6 ± 1.02[a]
Plants without insects	19	115	19	5.7 ± 0.38[a]

[a] Highly significant difference, Mann Whitney U-test ($P < 0.0005$).

The two methods employed to determine the total amino acid concentration in the extrafloral nectar gave somewhat different values: Beckman amino acid analyzer, 169.8 mM; histidine scale, 279 mM. The latter value was computed for a larger sample size, so we feel that it is more representative since it reflects intraspecific variability, which the former value does not.

The nectar flow rate in *Opuntia acanthocarpa*, 0.3 μl per gland per day, is higher than the 0.2 μl per leaf per day reported for *Ipomoea carnea* (Keeler, 1977). Our figures represent maximum rates since we tried to sample the most active glands. Any one gland can actually vary in activity, with alternating periods of complete inactivity for up to a week at a time, causing ants to move to another gland, areole or floral cup. The within and between plant pattern of variation in nectar activity and composition may depend on the cost of nectar secretion and the probability of herbivore damage to the plant, or may depend on the immediate physiological demands of the plant (Bentley, 1977a). More studies are needed to determine the exact role of the control of extrafloral nectar flow in plants.

Correlative data which support the beneficial role of extrafloral nectaries in the interaction between ants and plants include the presence of ants and their seasonal and diurnal activity patterns (Bentley, 1977a). *Crematogaster opuntiae* is commonly associated with *O. acanthocarpa* at our study site. Ants are most active nocturnally, as are cactus-feeding insects (Mann, 1969), and seasonally during periods of new, suppos-

TABLE 4. *Occurrence of ants and phytophagous insects on Opuntia species*

	% of plants with ants (n = 30)		% of plants with insects	
	Crematogaster opuntiae	Iridomyrmex pruinosus	Chelinidea vittiger	Narnia inornata
O. acanthocarpa	57	17	17	7
O. phaeacantha	0	0	73	30

edly more vulnerable (Rhoades and Cates, 1976), vegetative and reproductive growth (Fig. 2, 3). These data suggest that members of *C. opuntiae* are timely defenders of *O. acanthocarpa*. The underlying cause of these activity patterns is more likely the summer (June–August) ambient temperatures, with which ant activity is negatively correlated ($r_s = -0.58$; $P < 0.05$). Extrafloral nectar production on a plant part follows ant activity, forming a significant correlation between nectar quantity and number of ants ($r_s = 0.73$; $P < 0.02$).

The aggressive behavior of *Crematogaster opuntiae* toward *Chelinidea vittiger* is further correlative evidence of the protective role of ants on *O. acanthocarpa*. The genus *Chelinidea* has been listed as the most destructive predator of *Opuntia* species (Hunter et al., 1912). The presence of *Crematogaster opuntiae* caused individuals of *Chelinidea vittiger* to leave fruits of *O. acanthocarpa* (Table 2). Bentley (1977b) suggested that the mere presence of ants on a plant reduces the abundance of other insects. Furthermore, it is known that the aggressive behavior of ants is most pronounced near their nest and can be induced at a food source (Way, 1963). Our experiments were conducted at the food source of *C. opuntiae*, and each individual of *O. acanthocarpa* examined that maintains ants also harbors an ant nest in the ground directly under it. Thus, the behavior and nest location of *C. opuntiae* individuals effect an efficient defense for *O. acanthocarpa* against phytophagous insects.

Defense against predators by ants would be meaningless unless the plants are actually vulnerable to the predators (Bentley, 1977a). Such vulnerability should be reflected by the increased reproductive capacity of ant plants over non-ant plants in the same population. We found that, in the field, the number of fruit set per branch showed a positive correlation with the number of ants per floral cup, but the correlation is not significant. The low correlative value may be explained by our method of monitoring ants. Ants were counted at dusk, between 6:00 and 8:00 PM, which is a period of rapid change in ant activity. This may have introduced a significant amount of error into the statistical analysis, thereby decreasing our degree of confidence. However, our correlation is supported by the experimentally determined reproductive vulnerability of *O. acanthocarpa* to *C. vittiger*. The control plants, those which were maintained without insects, can be thought of as well defended ant plants. They produced a significantly greater number of fruits and had fewer aborted buds than did the experimental plants (Table 3). This experiment indicates that members of *C. vittiger* have a harmful effect on the fruits of *O.*

acanthocarpa, which is corroborated by our observation that 78% of the insect individuals placed with potted plants were feeding on floral cups within 24 hours. However, we were not able to demonstrate these reproductive effects in the field, since we couldn't maintain ant-free plants for an entire fruiting season. Ants were always able to overcome our efforts to keep them off of "control" (non-ant) plants, usually within a week of initial removal.

Although our experiments have established the reproductive vulnerability of *O. acanthocarpa* to *C. vittiger* under artificial conditions, our only indications that *C. vittiger* is an important herbivore on *O. acanthocarpa* under natural conditions are indirect: *C. vittiger* is the most frequently observed cactus feeder at our study site and, perhaps more importantly, it successfully grew and reproduced when restricted to a sole diet of *O. acanthocarpa* for 4 weeks.

In a simple comparative survey at our study site we found *C. vittiger* and *Narnia inornata,* another cactus feeder, in greater abundance on *O. phaeacantha* than on *O. acanthocarpa* (Table 4). *Opuntia phaeacantha* plants had no ants at the time of our survey, but 56% of the *O. acanthocarpa* plants maintained *Crematogaster opuntiae* and 16% were occupied by *Iridomyrmex pruinosus* (Table 4). Both ant species were found on some plants. These data are undoubtedly underestimates of peak ant and insect activity, since the data were recorded in daylight (7:00 to 10:00 AM) on a warm day in June. These ants and insects are normally nocturnal in summer months, and we have observed ants on *O. phaeacantha* on other occasions. Nevertheless, we believe our data to be representative of the comparative levels of ant and insect activity between *O. acanthocarpa* and *O. phaeacantha*. If so, according to the ant-guard hypothesis, *O. phaeacantha* should be more subject to insect damage. The predicted differential levels of insect damage are documented by our observations that 14.5% of the fruits of *O. phaeacantha* in a sample population exhibited damage by phycitid lepidopteran larvae, whereas only 2.0% of the *O. acanthocarpa* fruits were damaged. These data indicate a stronger ant-plant interaction in *O. acanthocarpa* than in *O. phaeacantha*. For this reason *O. phaeacantha* probably constitutes a larger proportion of the diet of *Chelinidea vittiger* and other herbivores than does *O. acanthocarpa*.

In conclusion, the results of this study are consistent with those of previous studies which have documented the role of extrafloral nectaries as attractors of protective ants (Bentley, 1977a). We have shown that the extrafloral nectaries of *Opuntia acanthocarpa* attract and maintain pop-

ulations of the ant species, *Crematogaster opuntiae*, which protect the plant against cactus feeding insects. This conclusion is based on several correlative and experimental data: 1) the nectar is an attractive and nutritious food source for ants; 2) the seasonal and diurnal activity patterns of ants are maximized to provide the most efficient protection; 3) ants are aggressive toward phytophagous insects; and, 4) plants are reproductively vulnerable to insect feeding. Additionally, comparative data between *O. acanthocarpa*, which produces more dependable extrafloral nectaries and consequently maintains relatively large numbers of ants, and *O. phaecantha*, which does neither, suggest that the former is relatively well guarded by ants whereas the latter relies on some other, as yet undetermined, defensive strategy.

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