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THE EXTRAFLORAL NECTARIES OF *IPOMOEA CARNEA* (CONVOLVULACEAE)¹

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A B S T R A C T

Ipomoea carnea (Convolvulaceae) possesses two types of extrafloral nectaries, located on the petiole and on the pedicel. These secrete a complex nectar containing sugars and amino acids. The insects attracted to the extrafloral nectaries are predominantly ants and they are relatively abundant throughout the year. A number of incidents of plant defense as a result of the presence of extrafloral nectary visitors at the extrafloral nectaries of *I. carnea* were observed and are consistent with the ant-guard theory of the function of extrafloral nectaries.

RECENTLY, increased attention has been given to the question of the function of extrafloral nectaries and particularly to the hypothesis that the ecological function of these nectaries is to attract ants which protect the plant (Elias, 1972; Elias and Gelband, 1975; Elias, Rozich, and Newcombe, 1975; Bentley, 1976; 1977). In this paper the activity of the extrafloral nectaries of a tropical dry forest vine, *Ipomoea carnea* (Convolvulaceae), is described and evidence is given that supports the contention that extrafloral nectaries function to attract insects which are protective to the plant.

Extrafloral nectaries are glands which secrete an aqueous solution of sugar and other chemicals (Baker and Baker, 1973) that can be found on aboveground parts of plants outside the flower. They occur in a variety of monocotyledonous and dicotyledonous families (Zimmermann, 1932; Schnell, Cusset, and Quenum, 1963). The morphology and chemical composition of extrafloral nectaries have been analysed in a number of cases. Nevertheless, the function of extrafloral nectaries is not well established.

In the case of ant-inhabited acacias, extrafloral nectaries have been shown to provide the major source of sugar for the resident ant population (Janzen, 1966, 1967; Brown, 1960). However, where the insects which visit extrafloral nectaries do not reside on the plant, the story is less clear and has been debated for over a century (see

Elias, 1972; Carroll, 1974; Keeler, 1975b). Recent work has for the most part supported the idea that the function of extrafloral nectaries is to attract insects, especially ants, which defend the plant from herbivores. Elias' morphological work on *Pithecellobium macradenium* (Leguminosae) (1972) and *Turnera ulmifolia* (Turneraceae) (Elias et al., 1975) indicated that the extrafloral nectaries of these two plants are very complex structures with nectar production cycles correlated with the times herbivores are expected to be the most active, which would support their role in an ant-plant association.

Elias and Gelband (1975) also found that the four extrafloral nectary systems of *Campsis radicans* (Bignoniaceae) are responsible for attracting ants and that in the presence of abundant ants, there is a decrease in the frequency of flower robbing.² Bentley (1976) found that a significant amount of the variance in the percentage of buds that matured on *Bixa orellana* (Bixaceae) was explained by a linear regression of the abundance of ants at the site. She (1977) also showed that when artificial extrafloral nectaries were created on common bean seedlings (*Phaseolus vulgaris*), by placing karo syrup on the leaves, the treated plants weighed significantly more at the end of the experiment than did the control plants in the rainy season. On the other hand, Lukefahr and others (1960; 1965; 1966) have shown that strains of nectariless cotton, derived from crosses of *Gossypium tomentosum*, had significantly lower infestations of a number of important pest species, under a range of field and cage conditions, than did extrafloral nectary-bearing cotton strains.

In this paper observations and experiments on the extrafloral nectaries of *Ipomoea carnea* Jacq. (Convolvulaceae) in Costa Rica are reported

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² Van der Pijl (1954) observed the presence of ants to disturb and displace flower-robbing *Xylocopa* spp. bees in Java.



Fig. 1, 2. 1. *Camponotus brettesi* taking extrafloral nectar from petiolar nectary of *Ipomoea carnea*. $\times 1.5$. 2. Accumulation of nectar at pedicellar extrafloral nectaries of *I. carnea*. $\times 1$.

which support the work of Bentley, Elias, and their predecessors in suggesting that the extrafloral nectaries attract protective ants to the plant.

MATERIALS AND METHODS—*Ipomoea carnea* Jacq. [syn. *I. fistulosa*, (Austin, in press)] is a twining woody vine which is sufficiently robust to support itself to a height of two meters. It is found on both the Atlantic and Pacific coasts of Mexico south to Argentina (Matuda, 1964; O'Donell, 1952). The population studied was in Guanacaste Province, Costa Rica, near the Organization for Tropical Studies' Palo Verde field station. This area is in the tropical dry forest zone of Holdridge (1967), receiving 1,800 mm of rainfall a year, but having a distinct dry season between December and May.

Ipomoea carnea was chosen for study because of the abundant nectar it produced. It was thought that the function of nectaries would be more easily demonstrated in a plant which produced copious quantities of nectar. In addition, *I. carnea* was abundant near the Palo Verde field station and consequently more accessible than many other extrafloral nectar producing plants.

I. carnea has two extrafloral nectary systems. An extrafloral nectary is located on either side of the distal end of the petiole. A ring of five extrafloral nectaries occurs at the base of each flower around the pedicel. The petiolar extrafloral nectaries are most active during the rainy

season, because, as the dry season proceeds, *Ipomoea carnea* loses its leaves. Flowering is confined to the dry season, so the pedicellar extrafloral nectaries function only at that time. Consequently, there is little overlap between the period of petiolar and pedicellar extrafloral nectary activity.

The function of floral nectaries is well established to be part of the process of pollination, so the activity of the floral nectaries of *I. carnea* will not be considered here. However, it should be pointed out that although the plant is a melittophilous obligate outcrosser (Keeler, 1975a, b), the flower-visiting insects are entirely different from the insects which visit the extrafloral nectaries.

The chemical constituents of the nectars were determined by Irene Baker using spot tests and chromatography (Keeler, 1975b). The frequency and distribution of the extrafloral nectary visitors were studied in a series of surveys in which were recorded the insects visiting the nectaries of 500 or 1,000 branches. Two different branches per plant were observed whenever possible. Two such surveys were made in the rainy season (October and November, 1973) and one in the dry season (January, 1974), in the pasture study area at Palo Verde.

Insect specimens were identified as follows: pseudomyrmecine ants by D. H. Janzen, Dept. of Zoology, University of Michigan; other ants by R. R. Snelling, Los Angeles County Museum;

TABLE 1. *Free sugars in Ipomoea carnea nectars*^a

Nectar	Extrafloral		Floral
	Petiolar	Pedicellar	
Sucrose	33.8 ^b	35.8	54.8
Glucose	32.9	33.1	29.1
Fructose	24.2	29.1	16.1
Melibiose	3.9	trace	0
Raffinose	5.9	0	0

^a Determined by chromatography using solvent of Smith (1969), 316 and stain of Saini (1966).

^b Percent of total sugar.

larval lepidoptera by T. Davies, California Academy of Sciences, San Francisco; and other insects by P. A. Opler, Office of Endangered Species, U.S. Fish and Wildlife Service, Washington, D.C.

RESULTS—Extrafloral nectaries—The petiolar extrafloral nectaries are functionally mature before the lamina mature (Fig. 1). First nectar is observed when the leaf is about 4 cm long and nearly ready to unfold. The nectaries continue to produce nectar as the leaf expands to its mature size (roughly cordate, about 15 cm at its greatest length and width). The nectaries function for a few days after full size is attained and then gradually become inactive. Their total activity lasts from two to three weeks, and the rate of nectar production is about 0.2 μ l per leaf per day.

Pedicellar extrafloral nectaries develop with the flower buds (Fig. 2). They begin secreting nectar when the buds first separate from the cluster. Production continues at an average rate of about 0.2 μ l per flower per day throughout the period of development of the bud, opening of the flower, and until the capsule is dry and ready to dehisce. This process takes four to six weeks.

Nectar is produced by night as well as by day in both petiolar and pedicellar nectaries. No changes in rate were detected. However, the rate of production per nectary is low enough to make accurate measurements difficult and it is being further investigated.

Although no daily changes in extrafloral nectar production were detected, there was great seasonal variation. Plants produced much more nectar in the dry season than in the rainy season. Although the rate of nectar production on buds, flowers and fruits was found to be about the same as on the leaves (about 0.2 μ l per day), a branch which had five nectary-bearing leaves in the rainy season produced on the average four to eight clusters of flowers, each bearing ten to thirty buds. Thus, there was a ten- to fifty-fold increase in the number of extrafloral nectaries on a plant in the dry season. In addition, as indicated, the functional life of pedicellar extrafloral nectaries was

TABLE 2. *Amino acids in Ipomoea carnea nectars*^a

Amino acid	Nectar		
	Extrafloral		Floral
	Petiolar	Pedicellar	
Alanine	0.0062 ^a	0	0.076
Arginine	0.0291	0.0342	0.131
Asparagine	0.0012	0.0616	0.057
Glutamic acid	0.0029	0.0027	0.001
Glycine	0	0	0.006
Isoleucine	0.0069	0	0
Serine	0.0518	0.0383	0

^a Determined by chromatography of dansylated amino acids and fluorometry. Method of I. Baker (unpubl.). Determined by I. Baker.

^b μ m/ml.

much longer than that of petiolar extrafloral nectaries, which increased the difference in total nectar production compared to the rainy season.

The sugar and amino acid contents of *Ipomoea carnea* nectaries are given in Tables 1 and 2. The floral nectar content is included for comparison. In addition, by using spot tests of Baker and Baker (1973) floral and extrafloral nectars of *Ipomoea carnea* were found to contain antioxidants and small amounts of phenolics, aldehyde and ketones. Unsaturated lipids were absent from the extrafloral nectars but were present in small quantities in the floral nectar. No alkaloids or proteins were detected in any of the three nectars.

Variation in the nectar produced by the different types of nectaries was tested. Nectars from the petiolar nectaries on different individual plants were more like each other than like those of the pedicellar nectaries for total amino acid content. In 16 petiolar extrafloral nectaries from as many plants, the average amino acid content (ninhydrin scale of Baker and Baker, 1973) was found to be 1.9 (range, 0 to 3.0). Pedicellar extrafloral nectar from 26 nectaries averaged 2.6 (range, 1.0 to 3.5). (Because of the different times of the year that the extrafloral nectaries are active, these were not collected simultaneously.) The means were significantly different from each other ($P < 0.025$).

Nectary visitors—The extrafloral nectary visitors would be relevant to the function of extrafloral nectaries if they act as ant-guard attractants. As was stated, there was no overlap between floral nectary and extrafloral nectary visitors. A wide variety of insects was observed visiting the extrafloral nectaries of *Ipomoea carnea*.

The percent of extrafloral nectaries with a nectar-feeding insect present (but not necessarily taking nectar) when approached was found to be 4.5% in October, 3.6% in November and 0.26% in January. These figures actually represent a

much higher rate of visitation of the nectaries by insects since both flying and crawling insects tend, if undisturbed, to visit every nectary on a branch before leaving. Therefore, in the rainy season, 89.8% and 73.0% of the branches had at least one nectary-visiting insect present and in the dry season 15.5% of the flowering branches had a visitor, when encountered, suggesting considerable activity at any particular nectary.

Of the insects which visited *Ipomoea carnea* extrafloral nectaries, the majority in all surveys were ants. In October, 89.5% of the 2,761 insects were ants. In November, 63.7% of the 546 insects seen were ants. (This survey covered 503 branches, compared to 1,000 in the other surveys.) In January, ants made up 59.2% of the 191 insects seen visiting nectaries. (A fourth survey, in January, 1974 in an adjacent pasture with taller vegetation revealed that ants were 91.2% of the 522 insects observed.) In terms of both absolute and relative numbers, ants were the most abundant extrafloral nectary visitors.

Compared to other insects, ants were seen near the nectaries for sustained periods of time. In 518 min of observation of extrafloral nectaries in periods of 20 to 30 min, one or more ants were present 55.3% of the time, while flies (miscellaneous Diptera) were present only 29.9% of the time. The other visitors, largely Coleoptera and Hymenoptera, were collectively present 36.8% of the time (individuals of some additional species were present for an entire observation period but only occurred in one of the 22 observation periods; those are not included here). The variance in these estimates, which resulted from the different behaviors of the species included in each group, precludes statistical testing. A full description of extrafloral nectary visitors seen at *I. carnea* is given in Keeler (1975b).

The most important species of ants visiting *Ipomoea carnea* extrafloral nectaries were: Formicidae: *Camponotus abdominalis*, *C. substitutus*, *C. brettesi*, and *C. rectangularis*; Myrmicinae: *Crematogaster ampla*, *Monomorium ebininum*, *Solenopsis geminata*, and *S. littoralis*; Pseudomyrmecinae: *Pseudomyrmex gracilis*; and Dolichoderinae: *Iridomyrmex pruinosum*. Ant frequencies varied greatly between surveys. In all three surveys the genera *Solenopsis* and *Camponotus* were the most numerous, making up 30.7% and 24.6% of all ants observed. Of the six species in these two genera, only *Camponotus brettesi* was at all consistent in its frequency—comprising 22.6% of the ants in the first survey, 22.9% in the second, and 43.5% in the third. The other species showed great variation, including absence from the third survey (in which only 191 insects were seen in 1,000 observations).

Evidence of ant-guarding—Observations were made consistent with the theory that the activities

TABLE 3. Flower robbing in *Ipomoea carnea* at Palo Verde, Guanacaste Province, Costa Rica. Jan., 1974^a

	Flowers		Area	
	Number robbed	Percent robbed		
Experiment I				
Low-visitor area	40	69	58	M ^b
High-visitor area	36	116	31**	N ^c
Experiment II				
Low-ant plants	112	171	66	M
High-ant plants	11	36	31**	M

^a See text for details.

^b M, Midpasture area.

^c N, Area north of pasture.

**, Significantly different from control at 1% level.

of extrafloral nectary visitors resulted in reduction of damage to the plant. At the Palo Verde study site, *Xylocopa frontalis* robbed 50–70% of the *Ipomoea carnea* flowers each day. These bees are too large to enter the flower legitimately. Instead, they climb over the lamina and walk down the corolla tube on the outside toward the base of the flower. There, they pierce a hole in the corolla and take nectar without pollinating the flower. In doing so they stand close to the pedicellar extrafloral nectaries.

The results of a series of observations of the relationship of flower robbing to activity in the area of the extrafloral nectary are given in Table 3. For plants in an area of relatively high extrafloral nectary visitor density (present at 31% of the branches) 36 of 116 flowers were robbed (31%), compared to 40 of 69 flowers (59%) in an area of lower visitor frequency (15% of the branches with a visitor). This difference is statistically significant ($P \leq 0.01$). Furthermore, on plants within the low-density area that were consistently covered with ants (*Camponotus brettesi* and *Crematogaster ampla*), presumably due to proximity to nest sites, the frequency of robbing, over several days, was 31%, compared to 66% for randomly selected flowers from the same field.

Solenopsis geminata were observed to be an effective ant-guard in an unusual situation. *S. geminata* were foraging at the extrafloral nectaries of a small (1 m) *I. carnea* plant, which was growing in contact with a small (2 m) tree of *Acacia collinsii* Stafford which was occupied by *Pseudomyrmex ferruginea* ants. As described by Janzen (1966, 1967) *P. ferruginea* will defend *A. collinsii* from herbivores and will also kill parts of other plants that come in contact with it. In the Palo Verde study area, *I. carnea* usually suffered great damage from *P. ferruginea* attack when it was next to an occupied acacia. In this case, however, the presence of the *Solenopsis* workers effectively reduced the damage by

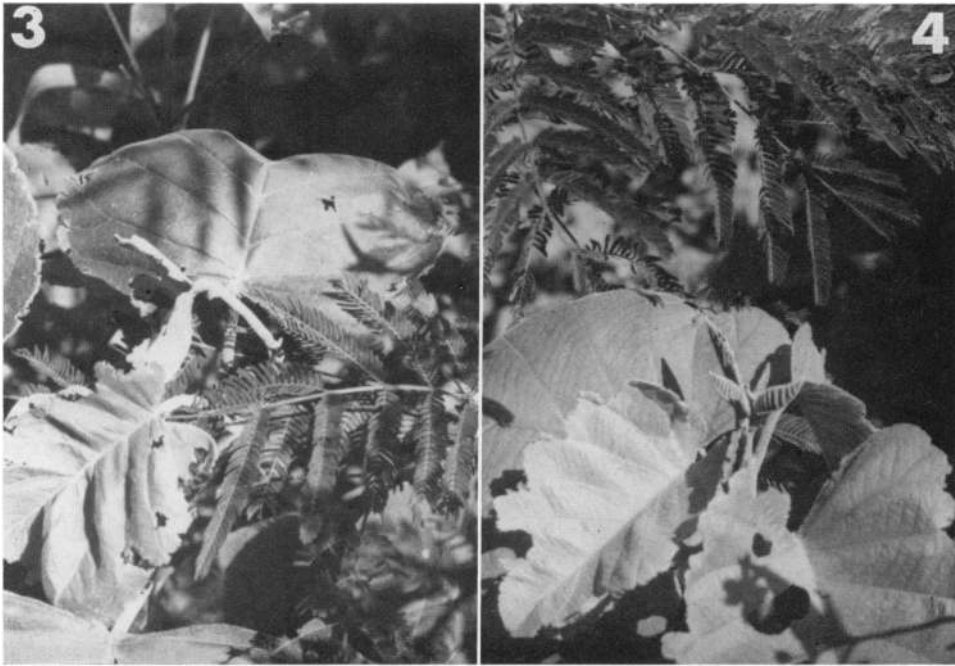


Fig. 3, 4. 3. Results of contact of *Ipomoea carnea* with *Pseudomyrmex ferruginea*-inhabited *Acacia collinsii*: shoot tip and several leaves have been chewed off by acacia-ants. $\times \frac{1}{2}$. 4. Effectiveness of foraging by *Solenopsis geminata* in reducing damage due to *P. ferruginea*. Although the *I. carnea* plant shown here was growing next to the same *A. collinsii* shown in Fig. 3, the damage was much less. Note that the shoot tip and all leaves are still intact. $\times \frac{1}{2}$.

Pseudomyrmex workers. *Pseudomyrmex* workers crossed onto *I. carnea* and attacked it fiercely at the petioles. Whenever a *Solenopsis* worker appeared, however, *Pseudomyrmex* that had been attacking the *Ipomoea* petiole would climb up onto the lamina. If it was actually encountered by a *Solenopsis*, the latter would become excited, to the point of biting the *Pseudomyrmex*. This rarely occurred, since the *Pseudomyrmex* ants almost invariably retreated as soon as a *Solenopsis* approached. The result was that the *Pseudomyrmex* ants did little damage. They chewed on the leaf surface, but much less photosynthetic surface was lost than from the usual cutting through of the petiole. Nor were they able to stay on the apical meristem long enough to sever it. In two weeks, there was little damage to the *I. carnea* visited by *Solenopsis geminata* except for pieces taken out of the leaf margins, while a similar sized *I. carnea* on the other side of the same acacia, which was not visited by *Solenopsis*, lost five leaves and the apical meristem (Fig. 3, 4). Thus ant-guarding can be effective, even against as severe an "herbivore" as *Pseudomyrmex ferruginea*.

A series of experiments aimed at excluding ants and testing the resulting levels of damage to the leaves failed because it proved impossible to exclude ants. The vine grew as much as 5 cm per internode per day amid tall vegetation and contact with the surrounding plants was continuously

reestablished in all directions. Subsequent analysis of the data did not provide any convincing evidence that some of the plants had different natural levels of ant density, and no differences in level of damage were seen between the different plants.

An example of predation on an *I. carnea* herbivore by an extrafloral nectary visitor was observed. A *Polybia occidentalis* wasp was captured on a leaf of *I. carnea* with its prey, a small larva of the Lymantriidae or Liparidae, one of the known herbivores of *I. carnea* [specimens Univ. of California survey #190376 (*P. occidentalis*) and prey 190680-692 (larva lepidoptera)]. *P. occidentalis* made up 0.3–2.0% of the nectary-visiting insects observed.

DISCUSSION—The significance of the particular combination of chemicals in the nectar is not obvious at present. In other studies of the content of extrafloral nectaries, Butler et al. (1972) found a range of proportions of fructose, sucrose and glucose in the extrafloral nectaries of cotton (*Gossypium barbadense* and *G. hirsutum*). In all cases they found sucrose to have the lowest proportion (5–24% of the nectar), with fructose and glucose about equal in amount. Bowden (1970) found the extrafloral nectar of the Nigerian grass *Andropogon gayanus* to contain 42% sucrose, 27% glucose, and 24% fructose, 1%

each of arabinose, xylose, and maltose, less than 1% raffinose and 3% of three unidentified sugars. Thus the glucose, fructose and sucrose contents of *I. carnea* extrafloral nectaries differ from those found in others species, but are similar to them.

The presence of raffinose in the petiolar extrafloral nectar (Table 1) is interesting in view of the fact that Frisch (1971) reported raffinose to be highly attractive to ants but not to honeybees. This suggests an added attractant for ants in the petiolar extrafloral nectar. Why raffinose is absent from the pedicellar extrafloral nectar requires further investigation.

Fewer amino acids are found in *I. carnea* extrafloral nectar than in cotton (*Gossypium hirsutum*) (Hanny and Elmore, 1974) but all of the ones present in *I. carnea* (Table 2) are also present in cotton. The function of amino acids in extrafloral nectar is unknown. In floral nectar they are believed to be additional attractants to pollinators because of their nutritional value (Baker and Baker, 1975).

If extrafloral nectaries function to attract ant-guards, a selective advantage must exist. Ant-guards at the nectaries must convey an advantage for the plant in terms of increased sexual or asexual reproduction. In this study the advantage has not been proven, but it is suggested by the protection afforded *I. carnea* from flower robbers and acacia-ants by activity at the plant's extrafloral nectaries.

In addition, two necessary but not sufficient conditions for ant-guarding to exist on a plant are the presence of abundant ants at the nectaries and aggressive behavior by the ants. The presence of abundant ants was demonstrated in the nectary-visitor surveys. Many of the ant species observed are highly aggressive around a food source (Wilson, 1971).

Aggressive behavior by the ants feeding at *Ipomoea carnea* extrafloral nectaries was demonstrated in the situation where *Solenopsis geminata* foragers displaced *Pseudomyrmex ferruginea* workers attacking *I. carnea*. Predation on herbivores of the plant was observed in this case for hymenoptera (*Polybia occidentalis*), but not for ants. Thus, the necessary conditions for ant-guarding exist at the extrafloral nectaries of *Ipomoea carnea* and, indeed, protection by ant-guards has been seen under some conditions.

The results of this study are consistent with those of Bentley (1976, 1977), who demonstrated ant-guarding at the extrafloral nectaries of *Bixa orellana* (Bixaceae) and at artificial "extrafloral nectaries" on *Phaseolus vulgaris* (Leguminosae). Taylor and Inouye (unpubl.) found a significant reduction in seed predation in *Helianthella quinquenervis* (Compositae) in plants with higher ant densities. Elias and Gelband (1975) observed decreased frequency of flower robbing in *Campsis radicans* with increased ant

activity on the plant. On the other hand, Lukefahr and others (1960, 1965, 1966) found greater damage by pest insects to cotton plants with extrafloral nectaries than to those without, under a range of field conditions. The cause of the differences in results for cotton has not been demonstrated, but it is likely that the explanation lies in the environment—that the agricultural conditions under which cotton is raised are sufficiently different from the natural habitats of the other studies to produce a different result. In particular, cultivation methods (plowing, tilling, application of insecticides) may reduce ant populations sufficiently to destroy their effectiveness. In any event, the results of this study support an ant-guard interpretation of the function of extrafloral nectaries in *Ipomoea carnea*.

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