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The Evolutionary Ecology of Plants

EDITED BY

Jane H. Bock
and Yan B. Linhart

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CONTRIBUTORS

Barrett, S.C.H. Department of Botany, University of Toronto, Toronto, Ont. M5S 1AI, Canada

Bird, R. McK. P.O. Box 5142, Raleigh, NC 27650, U.S.A.

Bock, C.E. Department of Environmental Population and Organismic Biology, University of Colorado, Boulder, CO 80309, U.S.A.

Bock, J.H. Department of Environmental Population and Organismic Biology, University of Colorado, Boulder, CO 80309, U.S.A.

Chiang, Y.C. Department of Plant Science, University of New Hampshire, Durham, NH 03824, U.S.A.

Cook, S.A. Department of Biology, University of Oregon, Eugene, OR 97403, U.S.A.

Copsey, A.D. Department of Biology, Central College, Pella, IA 50219, U.S.A.

Cox, P.A. Department of Botany and Range Science, Brigham Young University, Provo, UT 84602, U.S.A.

Cruden, R.W. Department of Botany, University of Iowa, Iowa City, IA 52242, U.S.A.

Dickman, A.W. Department of Biology, University of Oregon, Eugene, OR 97403, U.S.A.

Dobson, H.E.M. Department of Botany, University of California, Berkeley, CA 94720, U.S.A.

Fone, A.L. Department of Botany, University of Georgia, Athens, GA 30602, U.S.A.

Frankie, G.W. Department of Entomology, University of California, Berkeley, CA 94720, U.S.A.

Fukuda, I. Division of Biology, Tokyo Woman's Christian University, Zempukuji, Suginami, Tokyo, Japan 167

Guerrant, E.O. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, U.S.A.

Hamrick, J.L. Departments of Botany and Genetics, University of Georgia, Athens, GA 30602, U.S.A.

Hendrix, S.D. Department of Biology, University of Iowa, Iowa City, IA 52242, U.S.A.

Janzen, D.H. Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, U.S.A.

Keeler, K.H. School of Biological Sciences, University of Nebraska, Lincoln, NB 68588, U.S.A.

Kiang, Y.-T. Department of Plant Science, University of New Hampshire, Durham, NH 03824, U.S.A.

Koptur, S. Department of Biological Sciences, Florida International University, Miami, FL 33199, U.S.A.

Kwankin, B. School of Biological Sciences, University of Nebraska, Lincoln, NB 68585, U.S.A.

Linhart, Y.B. Department of Environmental Population and Organismic Biology, University of Colorado, Boulder, CO 80309, U.S.A.

Loveless, M.D. Department of Biology, College of Wooster, Wooster, OH 44691, U.S.A.

Lyon, D.L. Department of Biology, Cornell College, Mt. Vernon, IA 52314, U.S.A.

Newstrom, L.E. Entomology Department, University of California, Berkeley, CA 94720, U.S.A.

Opler, P. Office of Information Transfer, U.S. Fish and Wildlife Service, 1025 Penock Place, Ft. Collins, CO 80524, U.S.A.

Pemberton, R.W. Rangeland Insect Laboratory, USDA-ARS, Montana State University, Bozeman, MT 58717, U.S.A.

Schlising, R.A. Department of Biology, California State University, Chico, CA 95929, U.S.A.

Spira, T.P. Department of Biology, Georgia Southern College, Statesboro, GA 30460, U.S.A.

Stebbins, G.L. Genetics Department, University of California, Davis, CA 95616, U.S.A.

Turner, C.E. USDA Regional Research Center, 800 Buchanan Street, Albany, CA 99710, U.S.A.

Uno, G.E. Department of Botany and Microbiology, University of Oklahoma, 770 Van Vleet Oval, Norman, OK 73019, U.S.A.

Vincent, S.B. Department of Entomology, Texas A & M University, College Station, TX 27843, U.S.A.

Wagner, L.K. Department of Biology, Georgia Southern College, Statesboro, GA 30460, U.S.A.

Whatley, J.M. Department of Plant Sciences, University of Oxford, South Parks Road, Oxford, 0X1 3RA, England

Williams, H. Department of Entomology, Texas A & M University, College Station, TX 27843, U.S.A.

IS EXTRAFLORAL NECTAR PRODUCTION AN INDUCIBLE DEFENSE?

Suzanne Koptur

INTRODUCTION

Extrafloral nectaries are plant glands located outside the flowers; they are widespread among the angiosperms, occurring in 68 of the 337 families, in 35 of 76 orders, 5 of 6 of the subclasses of dicotyledons, and 3 of the 4 subclasses of monocots (Elias, 1983). They occur on leaves, stipules, petioles, stems, bracts, sepals, and fruits (Bentley, 1977b), and their position is often related to their ecological role (see below). Nectaries are also found in some ferns, and may have similar ecological functions in ferns as in flowering plants (Koptur *et al.*, 1982; Page, 1982; Lawton and Heads, 1984).

Evidence for ants visiting extrafloral nectaries and providing protection against herbivores is abundant and ever-increasing (reviewed by Bentley, 1977b; Buckley, 1982; Beattie, 1984; Jolivet, 1986). Ants visiting nectaries on vegetative parts may protect foliage (Bentley, 1976; Janzen, 1966, 1967; Koptur, 1979, 1984; Tilman, 1978; Kelly, 1986) which in turn can translate into greater seed set and increased fitness for the plant with nectaries (Koptur, 1979; Stephenson, 1982; Barton, 1986). Nectaries on or near reproductive structures can provide ant protection of developing ovules and seeds (Elias and Gelband, 1975; Bentley, 1977a; Deuth, 1977; Inouye and Taylor, 1979; Schemske, 1980, 1982; Keeler, 1981; Horvitz and Schemske, 1984).

Extrafloral nectaries can also attract predators or parasitoids of the herbivores (Leius, 1967; Price et al., 1980; Hespenheide, 1985; Weis and Abrahamson, 1985). Parasitoids can serve as important biological control agents in agricultural systems (Crepps, 1975; DeBach, 1964; Hassell, 1980, 1982). This sort of plant protection can be extremely important in natural systems as well, especially in areas where ants are not abundant (Keeler, 1985; Koptur, 1985).

Some plants can respond to defoliation by producing more defensive chemicals when attacked (Fowler and Lawton, 1985; Greig- Smith, 1986). The response of individual plants to defoliated areas with increased levels of feeding deterrents or toxins has been demonstrated in a number of species (Rottger and

Klingauf, 1976; Dixon and Barlow, 1979; Haukioja and Niemela, 1979; Wallner and Walton, 1979; Carroll and Hoffman, 1980; Barlow and Dixon, 1980; Edwards and Wratten, 1982, 1983, 1985; Haukioja 1982; Schultz and Baldwin 1982; Rhoades, 1983; Valentine et al. ,1983; Wratten et al.,. 1984; Karban and Carey, 1984; Raupp and Denno, 1984). The possibility that communication between plants can induce defenses in an undamaged neighbor in response to defoliation of another individual has been suggested, but not yet demonstrated with certainty (Rhoades, 1983; Baldwin and Schultz, 1983; Fowler and Lawton, 1985). If plant secondary chemicals can be mobilized to attacked organs, and their production increased soon after initial herbivore damage, then it seems likely that defense involving other metabolic products (water, sugars, amino acids, and other components of extrafloral nectar) could also respond to herbivore attack.

The "sap-valve" theory of extrafloral nectar secretion, which holds that nectaries are for eliminating "excess carbohydrates" and other compounds from plants, has been discounted in various investigations (D.A. Baker et al., 1978). Nectars contain a wider variety of sugars and amino acids, and in greater concentrations, than does simple phloem sap; therefore, the production of nectar involves some sort of active selection of constituents on the part of the plant. The constituents of floral nectars have been found to vary according to what pollinators frequent the plant species in question (Baker and Baker, 1983b), and are presumably the results of reciprocating evolutionary forces between plant and pollinator for the nectar composition that is most attractive to the visitor and most economical for the plant. Some plants have been found to have nectar of different compositions at different times of day; the nectars correspond to different guilds of visitors active at different times (Baker and Baker, 1983a). Some species of plants can respond to pollinator activity by secreting more nectar in flowers from which nectar has been removed (Cruden et al., 1983; Koptur, 1983).

The constituents of extrafloral nectars are similar, but not exactly the same as floral nectars of the same species (H.G. Baker et al., 1978). Few studies have examined the significance of the sugar ratios (Koptur, 1979; Smith, Lawton and Koptur, unpub. data), or amino acid complements (Koptur, 1979; Koptur, unpub. data), to ant visitors, but it has been demonstrated that the more concentrated the sugars in nectar, the more attractive they are to ants (Taylor, 1977, 1978), and that certain amino acids are preferred by certain ant species over others (Ricks and Vinson, 1970).

My goal is to test the hypothesis that plants with extrafloral nectaries will respond to damage by secreting more extrafloral nectar. Increased amounts of extrafloral nectar could lead to greater numbers of ants or parasitoids being recruited to the plant, which could lead to increased protection against herbivores. I have looked for extrafloral nectar induction in several systems, in which biotic protection by ants and/or parasitoids has been demonstrated experimentally.

METHODS

Vicia sativa L. (Fabaceae: Papilionoideae), the common vetch, is an annual herbaceous legume native to the Old World. The plants bear stipular nectaries, and in both exotic (Koptur 1979) and native (Koptur and Lawton, 1988) habitats, ants visiting these nectaries can provide protection against insect herbivores for foliage, flowers, and developing fruit. The flowers and fruits of most *Vicia* species are borne in the axils of the leaves, and in species with stipular nectaries (such as *V. sativa* and *V. sepium*) the flowers are sessile or on very short stalks, compared with species without nectaries (such as *V. cracca* and *V. hirsuta*) which have long peduncles. Nectar secretion in *V. sativa* begins when plants initiate anthesis, and continues through fruit maturation (Koptur and Lawton, 1988); therefore, the plants become established without the aid of biotic protection, but can benefit from ants and other nectary visitors throughout their entire reproductive life.

Fifty plants growing in a greenhouse at the University of York, England, were randomly divided into five groups of ten plants each. Initial nectar production was measured, using the technique developed by Irene and Herbert Baker for measuring small quantities: micropipettes pulled out to fine points (and therefore, uncalibrated) are used to draw up the nectar and spotted onto strips of filter paper; spot diameter can be correlated with volume (Baker, 1979). Using scissors to cut a fraction off of every leaflet, the plants were all defoliated to the level designated for the group (0%, 25%, 50%, 75% and 100% damage).

Nectar production was measured each afternoon for four days following the defoliations. Because this experiment was done in a controlled environment, it was not necessary to exclude nectary visitors or to bag plants. This experiment was initially attempted in the field, with much difficulty (rainy weather and difficulty in bagging small plants).

Ipomoea carnea (Convolvulaceae) is an emergent perennial morning-glory, growing in marshland in the lowland forests of

Costa Rica. Each leaf has 2 blotch nectaries at the base of the leaf blade on the abaxial surface near the petioles; the nectaries function on young and mature leaves on the upper part of both vegetative and reproductive shoots. Although standing in water to a depth of 0.5 m, most stems were occupied by black *Crematogaster* species of ants. Field studies of this (Keeler, 1977) and other *Ipomoea* species. (Keeler, 1980) have demonstrated benefit to these plants from ants visiting the foliar nectaries.

Ipomoea plants were studied with students from The Organization for Tropical Studies (O.T.S.) at Palo Verde, Guanacaste Province. We chose vegetative shoots from separate rhizomes and randomly designated plants to three groups of 20 plants each: 1) controls (no damage); 2) 25% of each leaf on the shoot removed with scissors; and 3) 50% of each leaf removed. Early in the morning, we excluded ants by shaking the plants and then coating the stem with tanglefoot (sticky resin). We also bagged the top ten or so leaves with pollen-tector heavy paper bags to exclude flying insects. We performed defoliations prior to bagging. In the afternoon (about 4 h. later) we measured nectar, using the spots on paper method.

After insignificant results were obtained in the first experiment, Mary Ann Lee and I repeated this experiment, using a design to control for variability. We chose 50 plants, excluded ants and bagged them early one morning. That afternoon, we collected accumulated nectar, tallied the amounts and ranked the plants in order of amount of nectar produced. Every second plant was designated experimental (to be defoliated 25%), the others were designated controls (no defoliation). The next morning we defoliated the experimentals (each leaf 25%) and rebagged the shoots. Each control was unbagged and rebagged. We returned to collect nectar in the afternoon.

Inga brenesii and *I. punctata* (Fabaceae: Mimosoideae) are tropical trees with foliar nectaries which function only on young and expanding leaves (Koptur, 1984), becoming dry when the leaves are fully hardened and mature. Both ants and parasitoids visiting these nectaries provide protection against insect herbivores in different situations (Koptur, 1984, 1985). Induction experiments were performed in May 1987 on these species in the field at Monteverde, Puntarenas Province, Costa Rica.

For each species, I chose 40 branches of new leaves (distributed on 8-10 trees) and designated 20 of these experimentals (25% defoliation) and 20 controls (no defoliation). On day 1, I excluded ants and bagged the branches. On day 2, I measured initial nectar accumulation, and then performed defoliations. On day 3, I measured nectar again.

RESULTS

Vicia. Variability within groups was high (Table 1); the results are summarized (means only) in Fig. 1. The only statistically significant difference was on day 1 after defoliation: analysis of variance showed that nectar production was higher with treatment ($p < .05$) and a posteriori tests between means showed the 25% and 50% treatments to be significantly different from the control group.

The effect disappeared the next day. With greater defoliation, there was no initial increase in nectar secretion over controls.

Ipomoea. The one-day experiment gave distributions of nectar secretion shown in Fig. 2; half the plants produced no nectar at all, making parametric statistics inappropriate. Because there were no differences between the groups (Kruskal-Wallis nonsignificant), we concluded it might be necessary to measure initial nectar secretion, use only actively secreting plants, and factor out pretreatment nectar production as a covariate.

The results of the two-day experiment (Table 2) showed that the two groups were virtually identical before the treatments (mean nectar volumes equal, due to our ranking of plants on the basis of nectar secretion). Although the mean nectar volume was higher in the experimental plants after defoliation, the differences were not significant by Student's t-test ($p < .05$).

Inga. *Inga brenesii* nectar volumes (Table 3) were very close in the two groups before the experiment, and just as close after the experiment (Kruskal-Wallis H not significant). Most leaves secreted nectar, but the data were not normally distributed, so this non-parametric test was used.

Inga punctata nectar volumes (Table 4) showed greater differences between groups, and changes in the direction of an inducible response, but variability was great, and no differences were significant. For both species of *Inga*, therefore, the null hypothesis is accepted.

DISCUSSION

Unpredictable weather and the difficulties of excluding ants and bagging vetch plants in the field led to the conducting of that experiment under controlled greenhouse conditions. This was the only experiment in which any significant results were obtained. Although it was much easier to exclude ants and bag the perennial

Table 1. *Vicia* nectar volumes from plants in greenhouse experiment, volumes are in microliters, $\overline{x} \pm$ s.d.

	Treatments				
Days	Control	25% damage	50%	75%	100%
0	.67 ± .37	.70 ± .62	.60 ± 57	.73 ± .56	.78 ± .68
1 *	.39 ± .41	.96 ± .40**	.58 ± .22	.52 ± .27	.40 ± .33
2	.20 ± .15	.37 ± .19	.37 ± .25	.33 ± .27	.25 ± .18
3	.17 ± .23	.35 ± .29	.19 ± .16	.15 ± .13	.20 ± .15
4	.20 ± .17	.24 ± .16	.23 ± .17	.18 ± .13	.17 ± .19

* Indicates only day in which there was any effect of treatment on nectar volume (by analysis of variance); ** - $p < .025$, * - $p < .05$.

Table 2. *Ipomea carnea* two day experiment. Nectar volumes produced in microliters ($\overline{x}$ + s.d.).

	Before	After
Experimental	.26 + .27	.56 + .59
Control	.26 + .28	.47 + .58
t-test difference	NS	t = .53, NS
	(n = 25 each)	

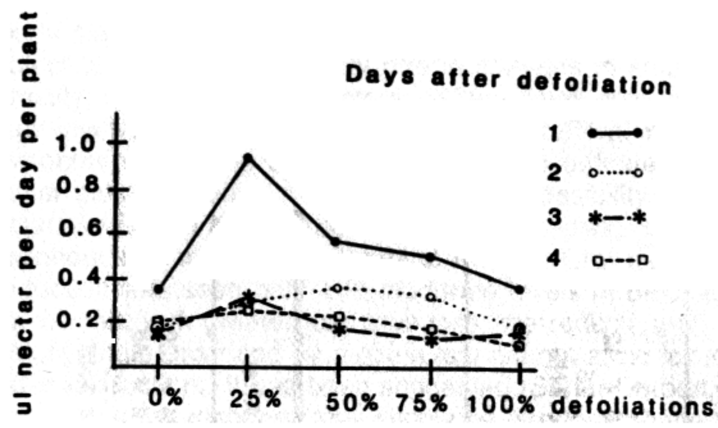

Figure 1. Nectar volumes from *Vicia* greenhouse experiment, to accompany Table 1. Only means were plotted. Note that each line depicts a day, with the treatment groups along the x-axis. The y-axis is mean nectar volume in microliters.

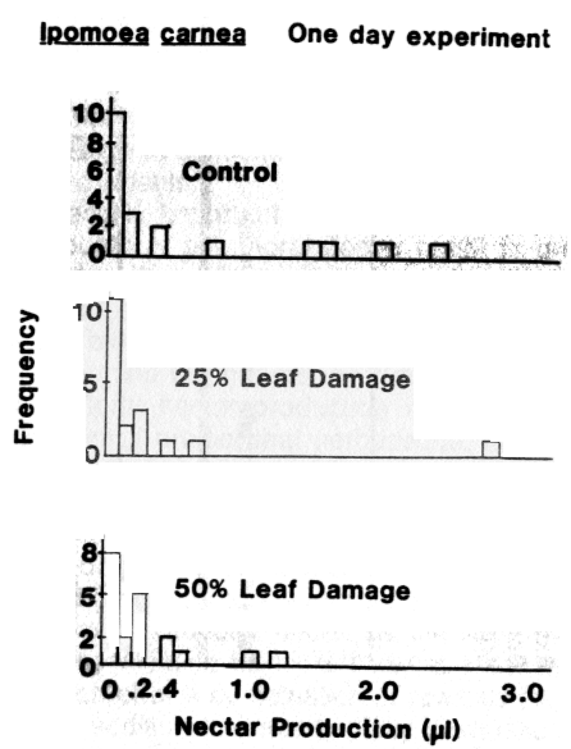

Figure 2. *Ipomoea carnea* one day experiment. Frequency distribution of nectar production for the different treatment groups.

Table 3. *Inga brenessi* nectar volumes in microliters.

	Before	After
Experimental	.16 + .09	.12 + .13
Control	.14 + .11	.10 + .12
Kruskal-Wallis H	.57	.25
probability	< .5 NS	< .7 NS

(n = 20 each)

Table 4. *Inga punctata* nectar volumes

	Before	After
Experimental	.04 + .08	.24 + .39
Control	.25 + .47	.18 + .48
Kruskal-Wallis H	.99	.30
probability	< .5 NS	< .3 NS

(n = 20 each)

woody plants in the field, any experiment conducted outside is subject to increased variability due to changes in ambient humidity, wind, and other factors. When small amounts of nectar were involved (the usual situation for extrafloral nectaries), environmental effects on variability were accentuated. This caveat must be borne in mind before the possibility of inducible nectar production is discarded for a given species. Under greenhouse conditions, an increase in extrafloral nectar production was seen only with moderate levels of defoliation. It may be that with greater leaf area loss, the reduction of photosynthate produced by a given leaf did not allow for increased nectar production. It has been suggested (Sarah Corbett, pers. comm.) that the response may simply be due to increased transpiration from cut leaf surfaces resulting in a sort of surge of liquid in the nectaries; I plan to test this by measuring floral nectar as well (since the flowers are situated in the axils of each leaf). If floral nectar increases when extrafloral nectar does, then perhaps it is only a physiological response associated with increased transpiration; if, however, floral nectar is not affected as is extrafloral nectar, the possible defensive role of this response will be supported.

I also plan to look for differences in nectar quality in response to defoliation. It is possible that, under stress, certain compounds change in concentration, and alter the attraction to biotic protective agents.

It is especially important to determine whether or not increased amounts of extrafloral nectar result in greater protection for the plant. This will be tested in field experiments in suitable systems. We will also look for this response in more systems where biotic protection has been found to be significant, in order to determine the general circumstances under which inducible extrafloral nectar production might occur.

At this point, I predict that herbaceous, annual plants will be more likely to show inducible nectar secretion than woody perennials. Annual species, which can reproduce only once, are known to expend more effort in reproduction than do perennials. They may also be able to economize on extrafloral nectar production, and produce more when herbivores are present. Plants which have extrafloral nectar as the sole reward for biotic protective agents will also be more likely to show this response than plants which offer a combination of rewards (*e.g.*, food bodies and domicile in addition to nectar). Only in situations where ants are not resident in plants can more ants be recruited to plants or to plant parts with increased nectar production. Less is known about the response of parasitoids to changes in nectar rewards, and so it is tempting to say that the inducible response will be more important in plants with ant protection than parasitoid protection resulting from extrafloral nectaries; but clearly, more information is needed.

Nectaries can play a role in agricultural systems in the biological control of crop pests (de Bach, 1964; Huffaker, 1971; Simmonds, 1971; Bentley, 1976). Ants and other insects attracted to extrafloral nectaries can reduce the effects of herbivores on crop plants (Bentley, 1977b, 1983; Risch and Carroll, 1982a, b), and although these interactions have not been exploited commercially, they may hold great potential. Recruiting natural protective agents can lessen the use of pesticides, reducing pollution and producing less-contaminated crops. A number of crop plants and their wild relatives (both temperate and tropical) have extrafloral nectaries: cotton (*Gossypium*) (Mound, 1962; Yokoyama, 1978; Adjei-maafo and Wilson, 1983), broad bean (*Vicia*) (Kupicha, 1976; Koptur, 1979), passionfruit (*Passiflora*) (Durkee, 1982; McLain, 1983; Smiley, 1986), peaches, plums, and cherries (*Prunus*) (Gregory, 1915; Dorsey and Weiss, 1920; Tilman, 1978), castor bean (*Ricinus*) (Reed, 1923; D.A. Baker et al., 1978), sweet potato (*Ipomoea*) (Beckmann and Stucky, 1981; Keeler, 1977, 1980), yam (*Dioscorea*) (Orr, 1923; Grout and Williams, 1980), rubber (*Hevea*) (Parkin, 1904, and buckwheat (*Polygonum*) (Salisbury, 1909). These traits could be utilized (or introduced from the genome of wild relatives into cultivars) for ecologically sound crop protection.

Stress on plants caused by insect herbivores has led to the evolution of many defenses, and the ability of some plants to regulate the amounts and locations of defensive substances is ecological fine-tuning that can permit adjustment of the individual to prevailing environmental conditions.

SUMMARY AND CONCLUSIONS

A number of chemical defenses of plants have been found to increase in response to presence of, or damage by herbivores, or both. Extrafloral nectaries attract ants and other beneficial insects that can provide biotic protection against a wide variety of herbivores. My goal was to test the hypothesis that plants predisposed to this type of defense (by virtue of having extrafloral nectaries) will respond to damage by secreting more extrafloral nectar. Increased amounts of nectar could serve to attract a greater number of ants or parasitoids and thereby increase biotic protection subsequent to incidents of damage.

I tested the hypothesis in three systems: 1) the annual, herbaceous legume *Vicia sativa*:; 2) the perennial woody morning glory, *Ipomoea carnea*; and 3) several *Inga* species, neotropical legume trees. Only in greenhouse experiments with *Vicia sativa* was the inducible response found: on the day following defoliation, plants defoliated to 25% and 50% levels secreted more extrafloral nectar on the average than control plants. Higher levels of defoliation (75% and 100% of the leaflets removed) did not induce any differences in nectar secretion. In field experiments with *Ipomoea* and two *Inga* species, there were no significant differences in nectar secretion between defoliated branches and controls.

More plants must be tested for this response before firm generalizations can be made. At this point, it appears that annual plants may be more likely to show inducible extrafloral nectar secretion than perennials, and herbaceous plants more than woody plants. A number of crop plants have extrafloral nectaries, and there is potential for use of this natural defense system in integrated pest management schemes. If plants are able to respond to varying levels of herbivory by adjusting their levels of extrafloral nectar secretion, this ability to economize when the defense is not needed can be an asset to increased growth and reproduction and, thereby, selective fitness.

ACKHOWLEDGMENTS

My first experiments with *Vicia sativa* were carried out as a project in Herbert Barker's Evolutionary Ecology class. Irene Baker helped with collections and measuring contents of extrafloral nectar. John Lawton encouraged me to do the first nectar induction experiments. Assistance and ideas also have been provided by Mary Ann Lee, Michael Blouin, Randy Snyder, Joe Slowinski, Kim Smart, Mary Rauchenberger (O.T.S. 85-3), and Jackie Pilliciotti. Fieldwork has been funded by the Latin American Caribbean Center of Florida International University, the Organization for Tropical Studies, and the National Science Foundation under a NATO postdoctoral fellowship awarded in 1983. Invaluable clerical support was provided by Nancy Koptur.

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