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The Effect of Plant Chemistry on the Acceptability of Caterpillar Prey to the Argentine Ant *Iridomyrmex humilils* (Hymenoptera: Formicidae)

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Experiments were performed to test the acceptability of two palatable, cryptic caterpillars, the tobacco hornworm, Manduca sexta, *and the cabbage looper,* Trichoplusia ni, *reared on different diets, to the Argentine ant,* Iridomyrmex humilis. *Ants preferred larvae reared on artificial diet, groundcherry, or cowpea to tobacco-reared larvae. Ants also preferred larvae reared on artificial diet without nicotine to larvae reared on diet containing nicotine (5% dry wt). Experiments were also performed to test the response of ants to larval extracts and chemicals applied to the surface of palatable prey. Ants did not respond differently to larvae of the potato tuber moth,* Phthorimaea operculella, *treated with larval extracts or regurgitate from tobacco-reared larvae compared to artificial-diet-reared larvae, but ants were deterred by* P. operculella *larvae treated with nicotine compared to untreated larvae. The results of this study indicate that caterpillars can derive at least some degree of chemical protection from their food plant without sequestering and storing plant compounds and without the development of elaborate aposematic characteristics.*

KEY WORDS: *Iridomyrmex humilis*; predation; chemical defense; nicotine; Lepidoptera; plant/insect interactions; herbivore.

INTRODUCTION

Herbivorous insects often utilize plant allelochemicals as defenses against predators (Blum, 1981). Best-known examples of host-plant-derived chemical

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defenses against predators involve conspicuous, brightly colored insects that are relatively host specific and have developed specialized physiological mechanisms for sequestering host-plant compounds and storing them in the hemolymph, cuticle, or specialized organs (Reichstein *et al.*, 1968; Rothschild, 1972; Bowers, 1990). Research on the importance of host-plant-derived chemical defenses in phytophagous insects has focused on these species. But unpalatable, aposematic larvae that actively sequester and store plant compounds comprise only a small percentage of lepidopteran species that feed on plants with toxic compounds and may represent only the most obvious cases where host-plant chemicals affect the defensive strategies of lepidopteran larvae. There are a variety of ways in which insects deal with toxic plant compounds, including elimination, metabolism, and sequestration (Bowers, 1990). Herbivorous insects that deal with toxic plant compounds primarily by metabolizing or eliminating them may still contain quantities of toxins in their hemolymph or cuticle that could potentially influence their acceptability to predators. In addition, the gut when full may be more than half of the body weight and the plant food therein may be unacceptable to potential predators.

This study examines how host-plant chemicals affect the acceptability of two palatable, cryptic caterpillars, the tobacco hornworm, *Manduca sexta*, and the cabbage looper, *Trichoplusia ni*, to a predatory ant, *Iridomyrmex humilis*. The tobacco hornworm is restricted to plants in the family Solanaceae, while the cabbage looper is polyphagous. Both are able to feed on plants containing alkaloids such as nicotine by eliminating the toxin through extrarapid excretion rather than by sequestering or metabolizing it (Self *et al.*, 1964b).

MATERIALS AND METHODS

Insect Cultures

The caterpillar prey used in this study were the tobacco hornworm *Manduca sexta* (Lepidoptera: Sphingidae) and the cabbage looper *Trichoplusia ni* (Lepidoptera: Noctuidae). *M. sexta* is an oligophagous herbivore which feeds on a number of species in the family Solanaceae in nature. The cabbage looper is a polyphagous species that feeds on species from several plant families. The solanaceous plant species used in these experiments were tomato, *Lycopersicon esculentum*; tobacco, *Nicotiana tabacum*; potato, *Solanum tuberosum*; and groundcherry, *Physalis ixocarpa*. Cowpea, *Vigna sinensis* (Fabaceae), a nonhost plant on which *M. sexta* larvae have been succesfully reared in the laboratory, was also used in some experiments. Tobacco hornworm eggs were obtained from a laboratory culture at the Division of Biological Control in Albany, CA. Cabbage looper eggs were obtained from a laboratory culture at the Department of Entomology, University of California, Berkeley. Larvae were either kept on artificial diet or transferred to a plant during the first instar or second instar. The artificial diet contained wheat germ, casein, sucrose, Wesson's salt mix, Torula yeast, cholesterol, sorbic acid, methyl paraben, ascorbic acid, vitamin mix, agar, antibiotics, and formalin (Yamamoto, 1969).

The predator used in this study was the Argentine ant, *Iridomyrmex humilis* Mayr (Hymenoptera: Formicidae). It lives in very large colonies and has very generalized feeding habits. It frequently forages on plants for honeydew (Bartlett, 1961; Washburn, 1984) and extrafloral nectar (Koptur, 1979). It is an opportunistic predator that will attack a wide range of small insects and soft-bodied larvae. Ants are important predators of lepidopteran larvae (Laine and Niemela, 1980; Skinner and Whittaker, 1981; Risch and Carroll, 1982; Jones, 1987; Weseloh, 1988) and in some cases ants may act as biological control agents against agricultural and forest pests (Carroll and Risch, 1990; Perfecto, 1990).

Several studies have found that insects can use chemical defenses to deter ants (Honda, 1983; Peterson *et al.*, 1987; Bowers and Larin, 1989). In previous studies, we found that several species of chemically defended aposematic larvae were unpalatable to Argentine ants (Bernays and Cornelius, 1989). An interesting feature of the biology of this ant is the opportunistic foraging activity. Workers foraging for honeydew readily switch to attacking small caterpillars if these are stumbled upon. A small acceptable caterpillar placed on a plant being used as a sugar source by Argentine ants is invariably and rapidly attacked within minutes. Group transport of caterpillars is usual, but if ants lose contact with the prey they may rejoin a trail to a sugar source. This aggressive foraging behavior enabled us to always have a source of workers that would quickly attack caterpillar prey.

Experimental Design

General Methodology

These experiments were conducted in a greenhouse of approximately 150 m^2 at the Division of Biological Control, University of California, Berkeley, located in Albany, CA. There were large colonies of Argentine ants living in and around the experimental greenhouse. They habitually collected honeydew from homopteran colonies infesting greenhouse plants, and probably preyed upon various small insects on the plants and soil. Removal of large numbers had no apparent impact on foraging activity. Experiments were carried out under a small potted citrus bush where large numbers of ants were foraging for homopteran honeydew.

Experiments were performed to test the response of ants to larvae reared on different diets by presenting ants with a choice of two caterpillars of the same size and species reared on different diets on a 9-cm-diameter filter paper placed next to an ant trail. All trials were videotaped using a Canon VC-20A video camera and Sony SL-2500 recorder. After each replication, the filter paper, remaining caterpillars, and ants were placed in a bucket lined with fluon to prevent ants from escaping, and later disposed of. In this way the majority of experienced ants were excluded from future trials, so that we could be confident that for each trial and each experiment we used ''naive'' workers.

Experiments were performed using both freshly killed and living caterpillars. In experiments using freshly killed caterpillars, the positions of the treatment and control caterpillars were alternated between each replicate to avoid any positional bias. There were between 10 and 22 trials for each experiment. When ants encountered freshly killed larvae, they would antennate and/or bite them. The relative acceptability of caterpillars was probably based primarily upon superficial contact with the larval cuticle. In some instances, the ants probably bit through the cuticle and contacted hemolymph. In the experiments using live larvae, ants would attack and bite larvae. The larvae usually responded by rearing up on their prolegs and striking out or regurgitating fluids at the ants. In some cases, caterpillars also released an anal discharge.

Accumulation of ants at each larva during a trial was probably a combination of random encounter, the length of time that ants remained in contact with the larva, and short-range recruitment. Apart from the increasing numbers coming to acceptable prey, the likelihood of arrestment at contact, how tenacious the hold, and whether or not a worker returns after losing hold, mean that there are rapid comings and goings.

The net effect of all the factors causing accumulation can be measured by the numbers of ants counted at larvae over a given time. It will vary with the numbers of ants in the vicinity, but at any trial, differences give a measure of relative vulnerability. The length of time that an ant remains in contact with a larva is probably most important as an indication of acceptability. If prey is unpalatable, the ants will briefly antennate it and then move away. If it is palatable, they will generally remain in contact for much longer and may begin feeding on it. Also, Argentine ants indicate the presence of a food source by applying trail pheromones as they leave. New individuals wandering onto the filter paper are probably following trail pheromones left by other ants, so the differences in the numbers of ants contacting each larva may involve short-range recruitment.

Argentine ants will readily prey upon early-instar larvae of *T. ni* and *M. sexta* when they are encountered. However, Argentine ants rely upon rapid recruitment of large numbers of individuals to overcome larval defenses. If larvae are only attacked by a few ants, they will escape. Even small larvae can fend off attacking Argentine ants and they often kill many ants before they are finally overwhelmed. Because larvae are much more likely to escape predation when they are being attacked by fewer ants, differences in the number of ants attacking each larva in a pair indicate relative risk of predation. Previous work has demonstrated in more detail that a larger number of ants at a caterpillar in such experiments is a good predictor of greater mortality (Bernays and Cornelius, 1989). Ant preference was therefore measured by counting the number of ants in contact with each larva at 10-s intervals for a maximum of 5 min or until one of the caterpillars was dragged away. The total number of ants at each larva was summed over the length of the trial. These totals were compared using a Wilcoxon signed rank test for matched pairs.

Tests were carried out with freshly killed larvae fed on different diets, or on live larvae fed on different diets, or on an unrelated species treated with different plant chemicals or extracts.

Preference Tests with Freshly Killed Larvae

Experiments were performed to compare the palatability of larvae reared on artificial diet with plant-fed larvae. The comparisons were as follows:

Diet-reared *M. sexta* vs tobacco-reared *M. sexta*
Diet-reared *M. sexta* vs tobacco-reared *M. sexta*
Diet-reared *M. sexta* vs potato-reared *M. sexta*
Diet-reared *M. sexta* vs groundcherry-reared *M. sexta*
Diet-reared *M. sexta* vs tobacco-reared *M. sexta* that had been transferred to diet 24 h before the test
Diet-reared *T. ni* vs tobacco-reared *T. ni*
Diet-reared *T. ni* vs tomato-reared *T. ni*

The two caterpillars for each replicate were killed by placing them on dry ice just prior to a test and allowing them to thaw for no more than 5 min. Also, because ants preferred larvae reared on artificial diet to larvae reared on tobacco, tests were performed to determine if the influence of diet on ant preference depended on the effect of long-term feeding or if it could be influenced by the caterpillar's most recent feeding. One group of tobacco-reared *Manduca sexta* larvae was transferred to artificial diet 24 h before running the experiment, whereas the other group of larvae was reared entirely on artificial diet.

Preference Tests with Live *Manduca sexta* Larvae

Experiments were performed to compare the palatability of *M. sexta* larvae reared on different plants, or reared on artificial diet vs larvae fed on plants, or on diet with or without nicotine. The comparisons were as follows:

Tobacco-reared vs diet-reared
Tomato-reared vs diet-reared
Nicotine-diet-reared vs plain diet-reared
Diet-reared and transferred to tobacco for 5 h vs tobacco-reared
Tomato-reared vs tobacco-reared

Groundcherry-reared vs tobacco-reared
Cowpea-reared vs tobacco-reared

All plants except cowpea are host plants of this species. The effect of nicotine in the diet was tested by adding nicotine (hydrogen tartrate salt form) to the diet just before it hardened. Nicotine was tested at 2.5% and 5% dry wt. Most tobacco varieties contain 2–5% nicotine on a cured-leaf basis (Parr and Thurston, 1972). Ants were presented with a choice between caterpillars reared on regular diet or diet containing nicotine.

Tests were conducted to determine how long a caterpillar needed to feed on tobacco plants in order for the tobacco effect to be seen. One group of *M. sexta* larvae was reared on tobacco plants, while the other group was reared on artificial diet. Then, the diet-fed larvae were placed on tobacco plants 5 h prior to testing. Only larvae that had actually taken a meal on tobacco were used in these experiments. Ants were then presented with a choice between tobacco-reared larvae and diet-reared larvae that had only been feeding on tobacco for 5 h.

Tests with Chemically Treated *Phthorimaea operculella*

Experiments were performed to test the response of Argentine ants to chemicals on the surface of their prey. In a previous study Montllor *et al.* (1991) found that ants were almost as deterred by a cuticular extract of the unpalatable *Uresiphita reversalis* larva as by the caterpillar itself and that ants were also deterred by two alkaloids found in the host plant of *U. reversalis.* As in this previous study, potato tuber moth larvae, *Phthorimaea operculella* Zell. (Lepidoptera: Gelechiidae), were used as palatable prey upon which chemicals could be placed. Comparisons of chemicals placed on the palatable larvae were as follows:

Nicotine vs solvent only
Surface extract of *M. sexta* reared on tobacco vs surface-extract of *M. sexta* reared on diet
Surface extract of tobacco leaves vs solvent only
Regurgitate of tobacco-fed *M. sexta* vs untreated

The larvae were reared on potatoes in an insectary to final instar, killed by placing them in hot water for several minutes, and then treated with extracts or chemical solutions in order to determine if chemicals affected their palatability to ants.

Nicotine

P. operculella larvae were treated with nicotine. Tests were performed at two levels: 100 μg/insect and 150 μg/insect. These concentrations were used because it was found in previous experiments that ants and paper wasps were deterred by extracts of the alkaloids sparteine and cystine at a concentration of 100 μg/insect. The nicotine was dissolved in methanol and 5 μl of solution was applied to each treated larva, while 5 μl of solvent was applied to each control. Ants were then presented with a choice between nicotine-treated and solvent-treated larvae placed in pairs approximately 2 cm apart on a filter paper.

Larval Cuticular Extract

Because Espelie and Bernays (1989) found that the surface chemistry varied substantially between tobacco-reared and diet-reared *M. sexta* larvae, an experiment was done to determine if ants responded differently to *P. operculella* larvae treated with the tobacco-fed or diet-fed larval extract. *P. operculella* larvae were treated with a surface extract of the larval cuticle of *M. sexta* larvae reared on tobacco plants or on artificial diet. The extract was made from 100 third- to fourth- instar *M. sexta* larvae, swirled around in chloroform for 1 min. The dried extract was redissolved in 400 μl of chloroform and applied to potato tuberworms, 5 μl per larva.

Tobacco Leaf Extract

Tobacco leaves have glandular trichomes which can seriously inhibit the movement of insect predators such as chrysopids (Elsey, 1974) and coccinellids (Belcher and Thurston, 1982). Argentine ants often become trapped by the sticky globules (M. Cornelius, personal observation). Espelie and Bernays (1989) found that almost half of the cuticular extract of tobacco-reared larvae was comprised of duvatrienediols, the major component of tobacco trichomes. Hence, it is possible that ants are deterred by contact with chemicals on the tobacco leaf surface and that ants avoid larvae fed on tobacco because of the presence of material from the glandular trichomes on the larval surface. Ant response to tobacco leaf extract was tested in order to determine if ants were deterred by contact with tobacco leaf surface compounds. Twenty-five tobacco leaves were dipped in chloroform for 10–20 s each. The dried extract was dissolved in 400 μl of chloroform. *P. opercuella* larvae were treated with either the tobacco leaf extract or the solvent, 5 μl per larva.

Regurgitate

Peterson *et al.* (1987) found that ants were deterred by regurgitate of *Malacosoma americanum* and that the effectiveness of the regurgitate in repelling ants depended upon the diet of the caterpillar. Tobacco hornworms regurgitate gut fluids when they are disturbed. Regurgitate was collected by holding the head of a caterpillar and pinching it until the larva produced a droplet of liquid on its mandibles. The liquid was collected in a small plastic pertri dish. Regurgitate was collected from approximately 20 tobacco-reared third- to fourth-instar larvae. Regurgitate was applied to *P. operculella* larvae, 10 μl per insect. The regurgitate was collected and applied to larvae immediately before starting the experiment. Ants were presented with pairs of treated and untreated larvae.

RESULTS

Preference Tests with Freshly Killed Larvae

Ants responded similarly in tests with *T. ni* and *M. sexta* larvae. Ants strongly preferred diet-fed larvae to tobacco-fed larvae ($P < 0.01$) (Fig. 1). Also, ants preferred diet-fed larvae of *M. sexta* to potato-fed larvae ($P < 0.01$). There were larger numbers of ants contacting diet-fed larvae compared to other plant species as well, but these differences were not significant (Fig. 1). There

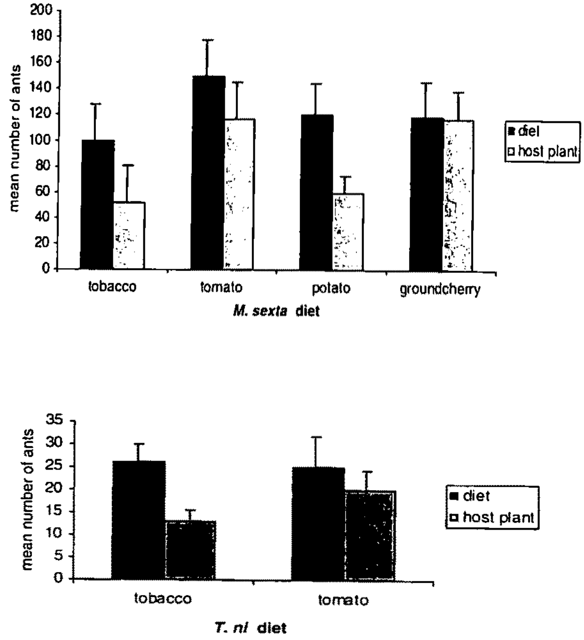

Fig. 1. Mean total number of ants contacting freshly killed diet-fed and plant-fed larvae of *M. sexta* (above) and *T. ni* (below) in paired choice tests. Vertical lines represent standard errors. Ant preference was compared using a Wilcoxon signed rank test for matched pairs. For *M. sexta* there were 10, 22, 10, and 22 trials for the four experiments. For *T. ni* there were 15 trials in each experiment.

was no difference in the response of ants to tobacco-reared caterpillars that had fed on artificial diet for 24 h prior to the test and diet-reared caterpillars ($P < 0.05$) (data not shown).

Preference Tests with Live *Manduca sexta* Larvae

As in the previous experiments, ants significantly preferred diet-fed larvae over tobacco-fed larvae ($p = 0.008$), but not tomato-fed larvae ($p = 0.60$) (Fig. 2). Ants preferred caterpillars reared on diet without nicotine to those reared on diet containing nicotine, but the difference was only statistically significant when nicotine made up 5% dry wt of the diet. Ants did not respond differently to larvae that had been on tobacco for only 5 h prior to testing compared to larvae that had been feeding on tobacco for 5 d. Also, in direct comparisons between *M. sexta* larvae feeding on different plant species, ants preferred larvae reared on groundcherry and cowpea to larvae reared on tobacco (Fig. 3). Ants also tended to attack larvae reared on tomato more than larvae reared on tobacco, but the difference was not statistically significant.

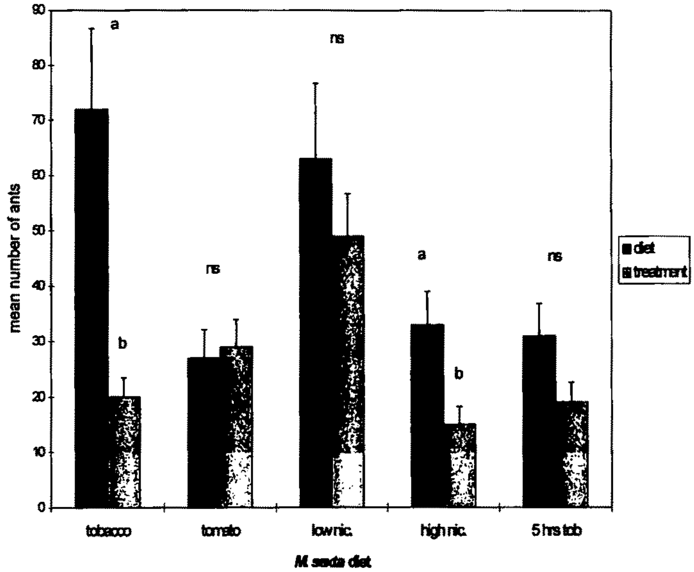

Fig. 2. Mean total number of ants contacting live *M. sexta* larvae in paired choice tests. Experiments compare diet-fed larvae with larvae fed on different foods: tobacco, tobacco-fed larvae; tomato, tomato-fed larvae; low nic, nicotine added to diet (2.5% dry wt); high nic, nicotine added to diet (5% dry wt); 5 hrs tob, diet-reared larvae fed on tobacco for 5 h prior to test. Vertical lines represent standard errors. Ant preference was compared using a Wilcoxon signed rank test for matched pairs. For the experiments shown from left to right, respectively, the number of trials was 11, 11, 21, 17, and 21.

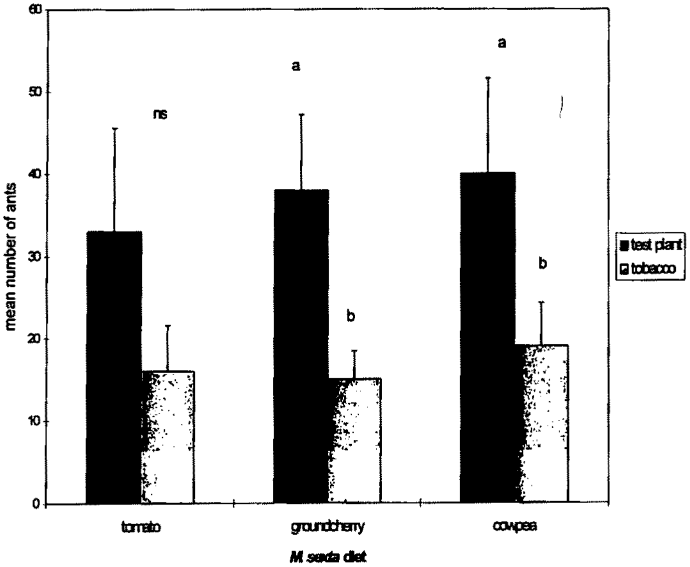

Fig. 3. Mean total number of ants contacting live *M. sexta* larvae in paired choice tests. Experiments compare tobacco-fed larvae with larvae reared on different plant species. Vertical lines represent standard errors. Ant preference was compared using a Wilcoxon signed rank test for matched pairs. The number of trials was 12, 20, and 9 for tomato, groundcherry, and cowpea, respectively.

Tests with Chemically Treated *P. operculella* Larvae

The response of ants to the presence of nicotine on the surface of *P. operculella* larvae was dosage dependent. Ants were deterred by nicotine on the surface of turberworms at 150 μg/larva, but not 100 μg/larva (Fig. 4). There was no significant difference in ant behavioral response to cuticular extracts of tobacco-fed and diet-fed *M. sexta* larvae when added to *P. operculella* larvae, although there were larger numbers of ants contacting *P. operculella* larvae treated with diet-fed larval extracts in both experiments. Ants did not distinguish between *P. operculella* larvae treated with tobacco leaf extract versus a solvent control or between *P. operculella* larvae treated with regurgitate from tobacco-reared *M. sexta* larvae and untreated *P. operculella* larvae (Fig. 4). However, in both cases there were larger numbers of ants in contact with controls compared to treated larvae.

DISCUSSION

In this study, ants responded to differences in the diets of two relatively palatable caterpillars, indicating that host-plant chemistry influences the degree

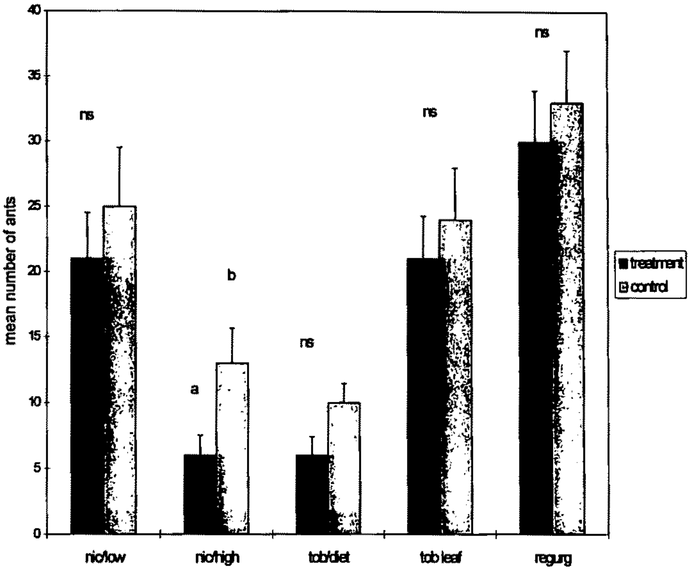

Fig. 4. Mean number of ants contacting treated and control *P. operculella* larvae in paired choice tests. Extracts or chemicals added to dead larvae: nic/low, 100 μg nicotine vs solvent control; nic/high, 150 μg nicotine vs solvent control; diet/tob, surface extract of diet-reared *M. sexta* vs surface extract of tobacco-reared *M. sexta*; tob leaf, surface extract of tobacco leaves vs solvent control; regurg, 5 μl of regurgitate collected from tobacco-reared larvae vs untreated control. Sample sizes, nic/low 20, nic/high 13, diet/tob 23, tob leaf 15, regurg 24. Vertical lines represent standard errors. Ant preference was compared using a Wilcoxon signed rank test for matched pairs.

of palatability of herbivorous insects to predators even among species that do not actively sequester plant compounds.

Most of the work focusing on how the natural enemies of nonaposematic lepidopterans are affected by the chemical attributes of their prey has been done with parasitoids. Many studies have demonstrated that plant alkaloids such as nicotine and tomatine can adversely affect the development and survival of parasitoids (Thruston and Fox, 1972; Campbell and Duffey, 1979; Barbosa *et al.*, 1986; Thorpe and Barbosa, 1986; El-Heneidy *et al.*, 1988; Barbosa *et al.*, 1991).

Much less work has been done on the influence of caterpillar diet on the acceptability of nonaposematic lepidopterans to predators, but there are some studies that suggest plant chemistry could potentially be important. For example, Isenhour *et al.* (1989) found that fall armyworm larvae fed on a resistant corn genotype were more susceptible to predation by *Orius insidiosus* than larvae fed on a susceptible genotype and that corn earworm larvae fed on artificial diet containing corn silks from a resistant genotype suffered higher predation rates than larvae fed on a diet without silks.

Many unpalatable lepidopteran larvae sequester compounds used for defense from their host plants. However, different species of chemically defended insects and different individuals of the same species vary in their ability to sequester plant allelochemicals and thus in their palatability to predators (Blum, 1981; Brower *et al.*, 1975). In some cases, only some of the host-plant species included in an herbivore's host range may actually provide chemical protection (Denno *et al.*, 1990). Peterson *et al.* (1987) found that eastern tent caterpillars use plant-derived cyanogenic compounds as a defense against ants when they feed on cyanogenic plants. Mealworms treated with regurgitate from caterpillars fed on young black cherry leaves were less palatable to ants than mealworms treated with regurgitate from caterpillars fed on less cyanogenic mature cherry or acyanogenic crabapple leaves.

Specialist lepidopterans were found in surveys to be less acceptable than generalists to vespid wasps (Bernays, 1988) and Argentine ants (Bernays and Cornelius, 1989), even when they are not aposematic. For instance, the cryptic specialist species such as *Manduca sexta* and *Phryganidia californica* were less palatable to wasps and ants than generalist feeders such as *Heliothis zea* and *Trichopulsia ni.* Wasps that attacked *P. californica* often left part of the caterpillar's remains behind. Maclean *et al.* (1989) also found that lepidopteran diet breadth was an important indicator of prey acceptability to birds.

In the present study ant preferences were similar in tests using freshly killed and living caterpillars. In tests using freshly killed larvae, ants were primarily contacting larval cuticle, but may have been biting through the cuticle to contact hemolymph. In tests using living larvae, ants also contacted gut fluids from both regurgitate and anal discharge. Ants did not distinguish between *P. operculella* larvae treated with regurgitate and untreated larvae, but they were deterred by the presence of certain concentrations of nicotine on the cuticle of a palatable larva. This perhaps suggests that the surface chemicals are important. Surface chemicals from the aposematic larvae of *Uresiphita reversalis* were found to be deterrent to these ants (Montllor *et al.*, 1991). It is possible that ants respond to the combined influence of hemolymph, cuticle, caterpillar gut fluids, and possibly odor. Ants did not distinguish between diet-reared larvae that had been placed on tobacco plants for only 5 h before the test and tobacco-reared larvae, or between tobacco-reared larvae that had been placed on diet for 24 h before the test and diet-reared larvae. Hence, it seems that the difference in response to diet-fed and tobacco-fed larvae depends upon the effects of recent, rather than long-term, feeding by the caterpillar, indicating that recently acquired chemicals are responsible for the deterrent effect.

Since nicotine is clearly deterrent to ants when applied to *P. operculella* larvae, and the tobacco-reared *T. ni* or *M. sexta* larvae will contain a certain amount of nicotine, it is possible that this is one of the factors affecting palatability of tobacco-reared caterpillars. The surface-wax- and the leaf-surface-derived compounds are apparently not involved, but the unambiguous demonstration that nicotine is the key factor awaits a study of the precise quantities present and its location in the larvae.

Although *Manduca sexta* does not actively sequester and store plant alkaloids, it does have mechanisms to deal with them. First, it can tolerate and absorb a certain amount of nicotine in its diet. It also uses rapid excretion to get rid of alkaloids from the hemolymph (Self *et al.*, 1964a), perhaps using an alkaloid-specific transport mechanism located in the Malpighian tubules (Maddrell and Gardiner, 1976). *M. sexta* also has the ability to detoxify nicotine (Morris, 1983, 1984; Snyder *et al.*, 1994). These mechanisms apparently allow the tobacco hornworm to ingest higher levels of nicotine than some of its natural enemies can tolerate.

The present study indicates that caterpillars can derive at least some degrees of chemical protection from their food plant without specifically sequestering plant compounds, and without the development of elaborate aposematic characteristics.

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