from intact B photoreceptors after training. The increase in input resistance and the persistent tonic depolarization of the B photoreceptor could be explained by a decreased potassium conductance.

Specific ionic conductances invoked during a light stimulus (step) have been recently examined (*12–15*). The initial depolarizing transient arises mainly from an inward Na^+ current. The hyperpolarizing phase of the light response arises from an outward K^+ current. A sustained depolarizing light response during stimulation arises from an inward voltage-dependent Ca^{2+} current (*15*). After a light step, the slowly decreasing depolarization, long-lasting depolarization (LLD), arises from a slowly decreasing inward Ca^{2+} current and probably a decrease of resting K^+ current (*15*).

The amplitudes of the hyperpolarizing phase (measured with respect to the peak amplitude of the initial depolarizing transient ($U = 5$, $P = .024$) and the depolarizing tail (LLD) of the light response ($U = 7$, $P = .053$) were significantly increased in cut nerve preparations from trained animals as compared with random controls. These differences in generator potential waveforms are consistent with the other cellular changes, indicating that training results in a persistent depolarization of type B photoreceptors. Namely, for a more depolarized cell the amplitude of the initial depolarizing transient would decrease as the cell membrane potential is moved closer to the sodium equilibrium potential (E_{Na}), and the hyperpolarizing phase would increase as the membrane potential is further from the potassium equilibrium potential (E_K). The LLD after the light step would increase in the more depolarized cells of trained animals because of the voltage-dependence of the light-induced Ca^{2+} current.

All of the results can be explained by a persistent decrease of a voltage-dependent K^+ conductance across the type B photoreceptor membranes. Such a decrease of K^+ conductance in darkness would produce an increase in input resistance. It would also cause the observed changes in the light-induced voltage responses. These findings, in turn, may be a consequence of long-term changes of intracellular Ca^{2+} to which dark K^+ conductances are sensitive (*15*).

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Chemical Feeding Deterrent Mobilized in Response to Insect Herbivory and Counteradaptation by *Epilachna tredecimnotata*

Abstract. *Experimentally damaged leaves of* Cucurbita moschata *mobilize substances to the damaged region within 40 minutes. These substances stimulate feeding by* Acalymma vittata *(Coleoptera: Chrysomelidae) and inhibit feeding by* Epilacha tredecimnotata *(Coleoptera: Coccinelidae). Under natural conditions,* Epilachna *cuts a circular trench in the leaf before feeding on the encircled leaf material, thus preventing mobilization of the deterrent substances to the feeding area.*

Levin (*1*) has divided chemical defenses of plants into two broad classes: those present before herbivore attack and those that change in response to herbivore attack. The latter class of defense, termed induced resistance, is commonly used by higher plants in response to infections by microorganisms but is considered to be less commonly used to counterattack insects.

Most examples of insect-induced resistance are characterized by long response times. Wallner and Walton (*2*) demonstrated that gypsy moth female larvae that fed on oak leaves from previously defoliated trees weighed less than moths reared on leaves from trees with no history of defoliation. Röttger and Klingauf (*3*) found that physiological changes in beets that had been attacked by the beetfly *Pegomya betae* caused a 29 percent increase in beetfly mortality. Developmental time increased in the geometrid larva *Oporinia autumnata* when fed on undamaged leaves of branches from which a single leaf had been torn 2 days earlier (*4*). In general, the time response for an insect-related, induced resistance appears long, relative to the feeding times of individual insects. Rhoades (*5*) lists plant response times that range from 12 hours to several years.

We now present experimental evidence for rapid, induced resistance and a behavioral counterresponse by *Epilachna tredecimnotata* (Coleoptera: Coccinelidae) when feeding on leaves of squash, *Cucurbita moschata* (Cucurbitaceae), in southeastern Mexico (*6*). *Epilachna tredecimnotata* and perhaps other cucurbit-feeding species in this genus (for example, *E. borealis*) engage in characteristic solitary feeding. Enlarged apical mandibular teeth are used to cut a circular trench in a squash leaf. The leaf tissue is almost completely cut through; only a few veins and bits of lower epidermal tissue hold the encircled leaf section in place. The beetle then feeds on the encircled material. Trenching behavior takes approximately 10 minutes while complete feeding on the leaf disk takes between 1 and 2 hours. After a morning feeding period the beetle crawls away from the damaged leaf and does not feed until the following morning. We propose that this trenching behavior is an adapt-

Table 1. Feeding rates on leaf squares of *Cucurbita moschata*. *Acalymma* feeding is recorded as the number of discrete feeding scars. *Epilachna* feeding is recorded as percent classes of eaten leaf area. The columns represent squares cut from leaves that had been damaged 20 minutes previously or squares that were cut immediately from undamaged leaves (Wilcoxon's signed ranks test). N.S., not significant.

Acalymma		*Epilachna*	
20 minutes	Immediate	20 minutes	Immediate
0	0	0	0
0	0	0	1 to 10
0	0	1 to 10	1 to 10
0	0	1 to 10	40 to 50
0	0	40 to 50	40 to 50
0	0	40 to 50	60 to 70
1	0	40 to 50	70 to 80
2	0	70 to 80	70 to 80
4	2	80 to 90	70 to 80
4	5	80 to 90	80 to 90
Mid-class averages			
Mean 1.1	0.7	39.0	47.5
N.S.		N.S.	

ive response to rapid mobilization of chemical deterrents to the site of insect feeding.

Cucurbitacins act as feeding stimulants for various chrysomelid beetles that feed on cucurbits, such as *Diabrotica balteata* and *Acalymma vittata* (7). For some herbivores, high levels of cucurbitacins inhibit feeding (8). We used *A. vittata* (Coleoptera: Chrysomelidae) as a bioassay organism for ascertaining cucurbitacins in leaves of *C. moschata* that were damaged and fed to adult freshly captured beetles after three different time periods. Similarly, damaged leaves were fed to freshly captured adult *E. tredecimnotata*.

Leaves were damaged by making two parallel cuts 4 cm long and 2 cm apart into the edge of each leaf. Leaves were damaged while on the vine only once, and the distance between damaged leaves was at least 3 m. Damaged sections were either immediately cut from the leaf ($N = 40$), left for 20 minutes ($N = 20$), or left for 40 minutes ($N = 20$) before they were detached completely. This allowed three damage-response times while the sections were attached to the otherwise intact leaves. Detached sections were cut into two equal-sized squares (2 by 2 cm). One leaf square was placed in a petri dish with a single freshly caught adult *Acalymma* and the other was put into a petri dish with a single freshly caught adult *Epilachna*. The dishes were lined with moistened filter paper to keep the leaf squares turgid, and the edge of each leaf square was trimmed to present fresh edges to the beetles. Leaves were damaged at night to minimize wilting and at staggered time intervals so that all sections could be simultaneously detached from the leaves.

Feeding comparisons within petri dishes were always made between a leaf square cut immediately from an intact leaf and leaf squares that had remained attached to the leaf for 20 or 40 minutes before the final cut was made severing the section from the leaf. Thus, a petri dish contained one-half of a leaf section that was removed immediately from the leaf, one-half of a leaf section that had remained partly attached to a leaf for either 20 or 40 minutes, and an adult *Acalymma* or *Epilachna*. Each original leaf section was therefore divided equally between *Acalymma* and *Epilachna* to reduce variance between leaves. After 12 hours, the amount of leaf area eaten was recorded.

Both beetles regarded leaf squares removed from the leaf after 20 minutes as essentially the same as leaf squares that were immediately cut from the leaves. *Acalymma* refused to feed on either group, and *Epilachna* fed extensively on both groups (Table 1).

Acalymma fed extensively on the leaf squares partly attached to the leaves for 40 minutes and rejected leaf squares that had been cut immediately from the leaves. *Epilachna* had the reverse response. The leaf squares attached for 40 minutes were rejected while the squares that had been cut immediately were extensively eaten (Table 2).

We interpret our results to mean that a substance which is a feeding inhibitor for *Epilachna* and a feeding stimulant for *Acalymma* is rapidly mobilized to damaged leaf tissue of *C. moschata*. We believe that the circular trenching behavior of *Epilachna* prior to feeding is an effective adaptation to counter the mobilization of the feeding inhibitor for the following reasons.

Table 2. Feeding rates on leaf squares of *Cucurbita moschata*. *Acalymma* feeding is recorded as the number of discrete feeding scars. *Epilachna* feeding is recorded as percent classes of eaten leaf area. Columns represent squares cut from leaves that had been damaged 40 minutes previously or squares that were cut immediately from undamaged leaves (Wilcoxon's signed ranks test).

Acalymma		*Epilachna*	
40 minutes	Immediate	40 minutes	Immediate
0	0	0	0
1	0	0	0
2	0	0	1 to 10
4	0	0	40 to 50
5	0	0	40 to 50
7	0	0	70 to 80
8	0	1 to 10	70 to 80
10	1	1 to 10	70 to 80
10	1	1 to 10	70 to 80
11	6	10 to 20	90 to 100
Mid-class averages			
Mean 5.8	0.8	3.0	49.0
$P < .01$		$P < .01$	

Table 3. Distance between successive recaptures of adult *Epilachna*.

Days between recapture	Distance moved (m)
1	1
1	5
1	5
1	14
2	3
2	13
3	3
4	2
7	12
	Mean = 6.4

In our feeding experiments, no inhibitor for *Epilachna* was present in leaf tissues damaged 20 minutes prior to feeding. Thus the trenching behavior occurs before the mobilization of the inhibitor. However, complete feeding time is more than the 40 minutes required in the laboratory experiments to produce a strong feeding inhibition in *Epilachna*. Thus, the circular trenching behavior is most likely an adaptive mechanism to prevent effective mobilization of the feeding inhibitor.

Acalymma has a positive feeding response to leaf tissue damaged 40 minutes prior to feeding. Since *Acalymma* has a specific positive response to high levels of cucurbitacins (7, 9), the most likely substances to be mobilized and have these opposing effects are cucurbitacins. It is difficult to imagine what other substances in leaves of *Cucurbita* could have such opposite effects on *Epilachna* and *Acalymma*. Further evidence of cucurbitacins is the bitter taste detectable in the damaged tissue after 40 minutes but nearly absent in newly damaged tissue. Sharma and Hall (10) and others have correlated bitter taste in cucurbits with high levels of cucurbitacins.

Finally, it is highly unlikely that the inhibitor or stimulant levels are increased in situ in the damaged tissue. The absence of a response by the beetles to any continued change in inhibitor or stimulant levels during the 12-hour experiment following the detachment of the turgid leaf squares is evidence for mobilization rather than local biosynthesis.

In no case was more than a single beetle, whether adult or larva, observed feeding on a leaf in the field. Solitary feeding behavior is not universal for the genus since the larvae of the related legume-feeding *E. varivestis* frequently feed in groups. Although a leaf may have several old feeding scars, no leaves with multiple fresh scars were seen. When a leaf is damaged, the wound-induced substance may increase in the entire leaf. We have no direct evidence that this happens but extensive responses to damage are known. Green and Ryan (*11*) found an increase in proteinase inhibitors in damaged tomato leaves. After several hours, levels of proteinase inhibitors increased in much of the undamaged parts of the plant as well. Ryan and others (*12*) have subsequently described the widespread occurrence of mobilized proteinase inhibitors in many plants.

We found long-distance movements after single morning feeding periods (Table 3). Between two successive feeding periods (two morning periods) the beetles traveled an average of 6 m (*13*), but the much less mobile larvae move as well. Larvae were never feeding any closer than 2 m from fresh feeding scars. It is difficult to understand why behavior for such frequent movements should be favored unless such behavior results in avoiding areas where levels of chemical feeding deterrents are increasing. It is unlikely that parasitoid or predator avoidance is involved since these reflexively bleeding, brightly colored, conspicuous insects are not likely to counter predation by moving.

The phenomenon described for *E. tredecimnotata* may be common. For example, the larvae of monarch butterflies occasionally cut into the leaf petiole before feeding on the leaf (*14*). Adult milkweed cerambycids often chew into the stem tissue above their egg deposition site (*14*). *Heterocampa* larvae often cut into the petioles of sugar maple leaves before feeding on the leaf (*14*). This curious behavior may perhaps be explained as an adaptive response to rapidly mobilized plant defenses. More generally, the frequent observation that herbivores often move before the food supply is exhausted may be a common method to avoid a local accumulation of chemical defenses. Thus, wasteful feeding may be adaptive. Of agricultural significance is the possibility that such frequent movements to avoid local increases in chemical deterrents may increase the spread of pathogens that are carried by herbivore vectors.

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13. Beetles and the leaf on which they were observed feeding were marked. Each of 36 beetles was marked with a small dot of Testors nontoxic paint on the right elytra, and a number was written on the dot. Marked beetles were captured in the morning near the end of the feeding period. After being marked, the beetles were left individually in gauze bags for the paint to dry. After approximately 30 minutes, the bags were opened beneath the leaf on which they had been feeding. Invariably, the beetles crawled onto the lower surface of the leaf and showed no alarm behavior. Over 20 days, beetles were recaptured and their new feeding site was marked. Distances between successive feeding sites were measured. The average distance between nearest-neighbor squash leaves was approximately 0.25 m. Of the 36 marked beetles, only 9 were recaptured (Table 3).
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Tumor Anorexia: A Learned Food Aversion?

Abstract. *Anorexia can occur when a specific diet is associated with a developing illness. The studies reported here show that the decline in food intake which accompanies tumor growth is accompanied by the development of aversions to the specific diet consumed during tumor growth. An immediate elevation in food consumption occurred when a novel diet was introduced. Therefore, the development of learned aversions to the specific diet eaten during tumor growth may be a causal factor in the development of tumor anorexia.*

Reduced appetite and subsequent weight loss are often seen in patients with neoplastic disease (*1*). Although a number of possible mechanisms for this anorexia have been suggested, agreement about the actual causes of tumor-produced loss of appetite and weight has not been reached (*2*). One possible explanation for anorexia in patients receiving treatments with severe and unpleasant side effects [such as chemotherapy and radiotherapy (*3*)] is the acquisition of learned food aversions. Pediatric cancer patients form significant aversions to specific foods consumed before a drug treatment that induces nausea and vomiting (*4*). Thus appetite loss in these patients may be due not only to the direct effects of these treatments but to aversions learned as a consequence of the association of foods with these side effects.

Learned food aversions may be of more general significance if learned aversions develop in response to the association of a diet with aversive physiological effects of the tumor itself. Thus, tumor-induced appetite loss, like drug-induced appetite loss, may be based indirectly on learned aversions, with the unconditioned stimulus being some chronic unpleasant symptoms of tumor growth rather than the acute effects of a drug injection. In our studies, we examined the food intake and diet preference of rats bearing transplantable tumors and found that when a novel diet was introduced to anorexic, tumor-bearing animals, (i) the new food was strongly preferred to the food eaten during tumor growth and (ii) food consumption was immediately elevated. These results suggest that the development of learned aversions to the specific diet eaten during tumor growth contributes to tumor anorexia.

In our experiments, we subcutaneously implanted the flanks of male syngeneic Wistar-Furth (W/Fu) rats (M.A. Bioproducts) with 40- to 60-mg pieces of polyoma virus-induced sarcoma [PW-739 (*5*)]. Control animals received an incision and suture but no tumors were implanted. (The PW-739 tumor grows progressively and is lethal to animals within 8 to 12 weeks. In addition, we have found (*6*) that the growth of this tumor is associated with anorexia and cachexia; a marked decline of food intake and body weight typically begins approximately 5 to 6 weeks after the tumor is implanted.) In all three studies, animals were housed