Guns and butter: a no cost defense against predation for *Chrysomela confluens*

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Summary. *Chrysomela confluens* produces a salicylal-dehyde-based defensive secretion which is very effective against generalist predators and apparently produced at no cost. If no cost defenses are common, then one of the basic assumptions in the plant-herbivore literature, i.e. tradeoffs among defense, reproduction, and growth, must be reconsidered. We examined the effectiveness of this defense by exposing defended larvae and larvae whose secretion had been removed to a generalist predator. Larvae which had their secretions intact were attacked by only 7% of the ants which encountered them, and none of these larvae suffered serious damage. In contrast, those which had been "milked" of their secretions immediately prior to exposure were attacked in 48% of such encounters, and two-thirds of the larvae were killed. Larvae which had been milked 24 or 72 h before exposure, then allowed to regenerate their defenses, were attacked at rates indistinguishable from larvae that had not been milked. Thus regenerated defenses are just as effective as original defenses. We also tested the hypothesis that the cost of defense production and maintainence would be reflected in reductions in developmental rates and final adult mass and increases in leaf consumption rate. We found that larvae which were milked daily of their secretions manifested no measurable cost of recharging reservoirs. Milked larvae grew and fed at the same rates as their control sibs, and became adults of equal or slightly larger size. The liberation of glucose from salicin, a precursor present in leaves of salicaceous hosts, during the production of salicylaldehyde apparently provides enough of an energetic benefit to offset the cost of maintaining an effective defense. Consistent with this hypothesis, we did not find that milked larvae compensated for increased nutritional or salicin demands by increasing their feeding rates. Although this pattern is familiar to chemical ecologists it is generally unappreciated in the plant-herbivore literature. It is likely that many arthropod herbivore defensive systems come at little or no cost, given the intimacy of association between herbivores and their food plants. Sequestration of host plant defensive chemicals which eliminates the cost of synthesis is common in arthropods. The *de novo* synthesis of chemical defenses may be less costly than expected if it is integrated into other parts of an insects metabolism. Calculations based on the bond energies or molecular constitution of the compounds will not yield a complete perception of cost. Tests over the life of the herbivore, coupled with an understanding of the herbivore's metabolism, are necessary.

Key words: Herbivory – Chemical defense – Sequestration – Coleoptera – Chrysomelidae

Chemical defense is a widespread phenomenon among arthropods. The work of these "chemists *par excellence*" (Blum 1978) is practiced by members of a diverse group, from millipedes to wasps (Roth and Eisner 1962; Eisner and Meinwald 1966; Pasteels and Gregoire 1983). The compounds produced are diverse, as are their sources, modes of action and glandular systems (Blum 1981; Pasteels and Gregoire 1983; Dettner 1987).

Whether explicit or implied, most ecological analyses of defensive behavior have approached the production of chemical defense from a "guns *or* butter" perspective. Traditional economic theory states that a government can allocate its funds to either defense spending (to "guns") or to domestic programs (to "butter"), but not both. Similarly, in the analysis of the energetics of chemical defense of insects it has often been assumed that allocation to defense comes at the expense of energy, nutrition, or opportunity.

Although they are often considered the exception rather than the rule, many insects derive chemical defenses at little or no metabolic costs (i.e. larvae can have both guns *and* butter). For example, seqestration of host plant toxins is common among herbivores (Blum 1978, 1981; Rosenthal and Janzen 1979), in which case, the costs of synthesis is eliminated. *De novo* synthesis of

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defensive compounds by other herbivores may be an intermediate step in metabolic pathways whose primary function is non-defensive. While this pattern is known in the chemical ecology literature, it is generally not appreciated by most plant-herbivore ecologists.

An example in which a chemical defense was originally thought to have a cost based on indirect evidence, but later was found to have no cost based in insect performance, is illustrated by the case of the monarch butterfly, *Danaus plexippus*. As larvae, monarchs sequester potent cardiac glycosides from their milkweed hosts (Reichstein et al. 1968). This adaptation was reasoned to come at some metabolic cost due to three observations made about the phenomenon. First, the compounds are extremely toxic, and the physiological handling of such compounds could be energetically expensive. Second, males, whose lifetime fitness is affected less by predation between the times of mating and egg laying, have lower levels of, and less emetic, cardiac glycosides. Finally, individuals whose migrating success was greatest had the lowest levels of cardiac glycosides sequestered (Brower et al. 1972; Brower and Glazier 1975). However, results from experimental feeding trials show no such effects of metabolizing more toxic cardenolides (Erickson 1973), and a further examination of metabolic pathways in monarch butterfly larvae shows some unique enzymatic adaptations to handling the toxins at little or no energetic cost (Vaughan and Jungreis 1977). Furthermore, basing estimates of cost on lower levels of cardiac glycosides in male monarchs and those which migrate further ignores the possibility that the defensive compounds may be readily metabolized by the insect for nutrition (i.e. they beat their guns *into* butter). Also, documenting costs by using decreased recharge rates of defensive glands over time (Hill and Tschinkel 1985; Baldwin et al. 1990) without measuring the frequency of their use in the field may yield an unreasonably high estimate of costs.

This example illustrates the importance of measuring cost in ecologically important ways. Analyses which rely on indirect measures of cost may yield artificially high estimates. For example, calculating concentrations of defensive chemicals or their bond energies (Bengtsson 1982; Hetz 1988) to measure "costs" ignore the possibilities that a) the insect may be using physiological by-products or metabolic intermediates as defenses, and b) the fact that enzymatic adaptations and specialized structures can make metabolic costs ecologically negligible (Vaughan and Jungreis 1977; Duffey et al. 1978; Rowell-Rahier and Pasteels 1982; Pasteels et al. 1990).

Host-based defenses in Chrysomeline beetles

The chemical defenses of leaf beetles of the subfamily Chrysomelinae (Coleoptera: Chrysomelidae) have been studied extensively. All stages, from egg to adult, can be protected by some form of secretion (Pasteels et al. 1979, 1982, 1984, 1989, 1990). Often, the identity of these compounds differs in larvae and adults (Pasteels et al. 1982) For Chrysomelines which produce host plant based salicylaldehyde, larvae derive both guns *and* butter
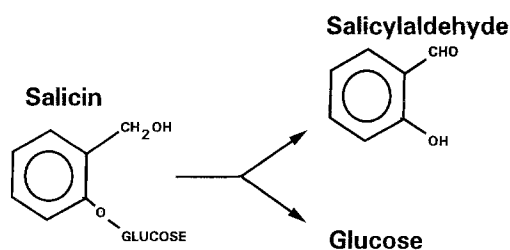

Fig. 1. Metabolism of salicin in dorsal glands of *Chrysomela confluens* larvae; The glucose molecule liberated in this reaction is available to the larvae for nutrition. (After Pasteels et al. 1990)

from their host plant (Pasteels et al. 1983, 1990; Rowell-Rahier and Pasteels 1986). Salicin, a common and abundant phenol glycoside in the Salicaceae (Palo 1984; Matsuda and Matsuo 1985), is consumed in the leaf tissue and is transported to paired dorsal glands. In the glands, it is metabolized to produce salicylaldehyde and glucose (Fig. 1; Pasteels et al. 1983, 1990). Enough glucose is liberated in this hydrolysis that *Phratora vitellinae* larvae which are forced to recharge their glands daily derive an estimated one-third of their daily caloric needs (Rowell-Rahier and Pasteels 1986). Comparisons of *P. vitellinae* adults which had been milked daily of their secretions as larvae showed no reduction in final mass relative to control adults (Rowell-Rahier and Pasteels 1986). In that study however, other ecologically important components of fitness, such as the potential for compensation by delayed pupation and/or increased leaf consumption were not addressed.

Using the leaf feeding beetle *Chrysomela confluens*, we examine the "guns *or* butter" and the "guns *and* butter" hypotheses by addressing three questions. First, is the salicylaldehyde-based defense in *C. confluens* effective against predators likely to be encountered on their host plants? Second, are regenerated secretions, produced 24–72 h after glands are milked dry, as effective against these predators as those built up over longer periods? If larvae produce "defenses" at no apparent cost, it may because the secretions have no defensive function. And third, does the defense come at a cost measurable in one or more of three ecologically important ways: a) final adult mass, b) developmental rate, and c) leaf consumption rates? Final adult size is a measure of potential fecundity as measured by Rowell-Rahier and Pasteels (1986). Developmental rate and leaf consumption rate are potentially important because they represent increased exposure to predation (Price 1987; Price et al. 1988). Because our experiments support the "guns *and* butter" (no cost defenses) hypothesis, we then review the literature to determine its potential generality.

Study organism

Chrysomela confluens is a member of the *scripta* species group which feeds on salicaceous hosts (Brown 1956). Larvae in the group are protected by defensive secretions contained in paired, dorsal glands on the thorax and abdomen (Brown 1956). These glands are everted when

the larva is threatened, exposing potential predators to a mixture of salicylaldehyde, a potent deterrent, and other compounds (Blum 1981; Pasteels et al. 1984; Smiley et al. 1985). When the threat stimulus is removed, the glands are retracted, along with most of the secretions (Pasteels et al. 1982; Rowell-Rahier and Pasteels 1982), presumably for energetic reasons.

In the study areas, populations of *Chrysomela confluens* feed exclusively on juvenile cottonwood trees (*Populus angustifolia, P. fremontii* and their hybrids and backcrosses; Kearsley and Whitham 1989). Adults emerge from the leaf litter in late April to feed on developing leaves, and mate. Females produce several clutches of 10–40 eggs which hatch within a week. Nearly all larval development is completed by mid-July at which point the new, sexually immature, adults feed briefly before dropping into the litter and going dormant.

Methods

All field work was carried out in sites along the Weber River near the mouth of Weber Canyon, 15 km. south of Ogden, Weber County, Utah. Beetle larvae for rearing experiments were collected as first instars from clutches of eggs which had been tagged and caged during a three-day census of one of the sites. The trees they were reared on were 2–6 years old. The leaf consumption experiments were carried out on trees in a naturally occurring clone adjacent to one of the planting sites. All other rearing experiments were done on rooted cuttings which had been maintained in common gardens for 3–5 years. Larvae used to test the effectiveness of their defenses were field collected as third instars and caged on common garden trees until needed.

Our tests of both the costs and the benefits of *C. confluens'* defense were based on comparisons of the performance of larvae that had their defenses removed relative to that of controls. Removal larvae were "milked" of their secretions by holding a piece of filter paper against the larva and patting until no more secretion was visible. Because such handling of larvae could cause changes in their behavior, control larvae were stimulated for an equivalent amount of time by poking them with a fine (0000) camel hair brush. This caused them to evert their glands, but when the stimulation stopped, the glands were retracted with no loss of secretions.

We tested the effectiveness of the protection provided by the secretions from the dorsal glands in two ways. In both tests, we exposed third instar larvae to attack by ants, the most common generalist predator in our study area. These ants attack other insects, especially when they are tending colonies of a free-feeding aphid, *Chaetophorus sp.*, which can be locally abundant on juvenile cottonwood trees. In the first experiment, 6 pairs of control and removal larvae were exposed individually to ants on branches heavily infested with *Chaetophorus*. Removal larvae were milked immediately prior to exposure and control larvae were stimulated with a brush. The number of ant encounters was recorded along with the number of encounters followed by an ant attack. An encounter was considered an attack only if the ant used its mandibles to grasp the larva. The percentages of ants attacking control and removal larvae were compared using Wilcoxon' s sign rank test.

For a chemical defense to have a measurable cost it must be regenerated after it is expelled and the regenerated substance must be effective. To test this, we performed a second experiment in which we quantified the deterrent effects of regenerated secretions by exposing individual larvae from four groups to the same species of ants at the nest entrance, rather than on branches. Two groups, control and removal, were treated in the same manner as in the in the previous test. The other two groups were milked 24 or 72 h prior to exposure. All larvae which were not to be milked on a given day

(including the day of the test) were poked with a brush. On the day of the test, We placed larvae in the center of an open 11 cm petri dish on top of the nest entrance and stimulated the ants by tapping the dish and/or the entrance. During a two-min test period, we again recorded the number of attacks and the total number of encounters. The percentage of ant attacks was arcsine transformed and tested with a one way analysis of variance. We tested for differences among group means for percent attacks and total number of encounters with a Tukey' s test.

The energetic costs of producing the defensive secretion were assessed in two rearing experiments comparing removal larvae, which were milked daily of their secretions, to their control sibs. In the first experiment, 98 individuals from 10 clutches of larvae were split between control and removal cages on adjacent branches of young trees. Each day during milking, the number and instar of larvae remaining in the cage was recorded, and adults were collected as they emerged. Cages were moved to different shoots every second day to prevent larvae from consuming all the leaf tissue in the cage and to avoid potential effects on leaf chemistry due to caging. The average difference in days to pupation between control and removal sibling groups was compared with a Wilcoxon's T statistic. Adults from 8 of these clutches were brought back to the lab, dried and weighed. The difference in dry mass between control and removal sibs was compared with a Wilcoxon's T. In both tests, clutch means were averaged within the six host genotypes, as strong host genetic effects on herbivores exist in this system (Whitham 1989). Although this reduced the degrees of freedom in the test statistic, by considering groups of 10–20 larvae per host we felt that the tests were sufficiently powerful.

We also tested the hypothesis that larvae could compensate for increased energetic and salicin demands by consuming more leaf tissue per unit time. We examined this possibility in a second rearing experiment in which sibling pairs of second and third instar larvae were caged individually on adjacent leaves of rapidly growing shoots. As with the growth rate and adult size experiment, one member of each pair was milked daily and the other was merely stimulated with a brush. Because larvae would be reared on intact leaves, we needed a nondestructive method for estimating initial leaf mass, which we derived from the product of leaf length and width, an very accurate predictor of leaf blade dry mass ($n = 58$, $r = 0.99$, $p < 0.001$). We therefore measured initial leaf mass by measuring blade length and width before the larva was transferred, and collected the leaves when larvae were moved to a new leaf. Leaves were dried and weighed in the lab to determine final leaf mass. The difference between pair members' consumption was compared with a Wilcoxon sign rank test.

Results

An effective defense for Chrysomela confluens

Control larvae whose defensive secretions were intact were defended far better than their sibs whose secretions had been removed (Fig. 2; $T = 0$, $n = 6$, $p < 0.05$). In the first experiment, the 6 control larvae averaged roughly 16 ant encounters per trial at a rate of 2.5 encounters per min of exposure. In 93% of these encounters, ants which came in contact with the salicylaldehyde would immediately withdraw and alternate between a vigorous grooming of mouthparts or antennae and moving in an agitated manner around the leaf and shoot. In three cases, the control runs had to be stopped after 10 min because all ants on the branch had fallen to the ground and were continuing their agitated grooming there. No control larvae were seriously damaged in attacks. Larvae whose secretions had been removed averaged a similar number
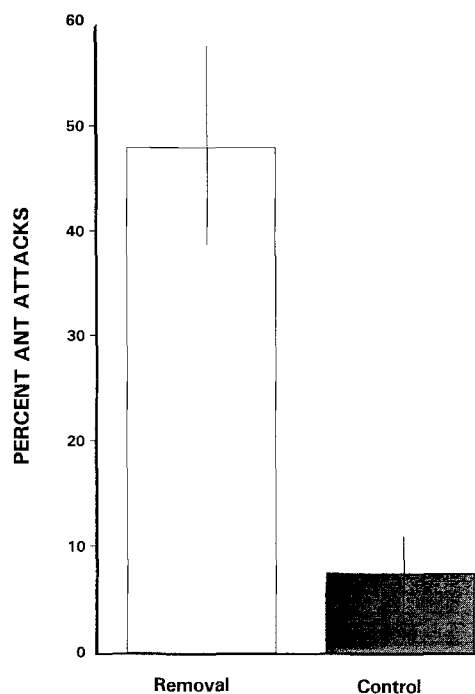
Fig. 2. Effects of the removal of secretions from *Chrysomela confluens* larvae on the behavior of ants; larvae with their defenses removed are attacked in nearly 7 times as many of their encounters with ants as their control siblings. Vertical bars represent ±1 SD
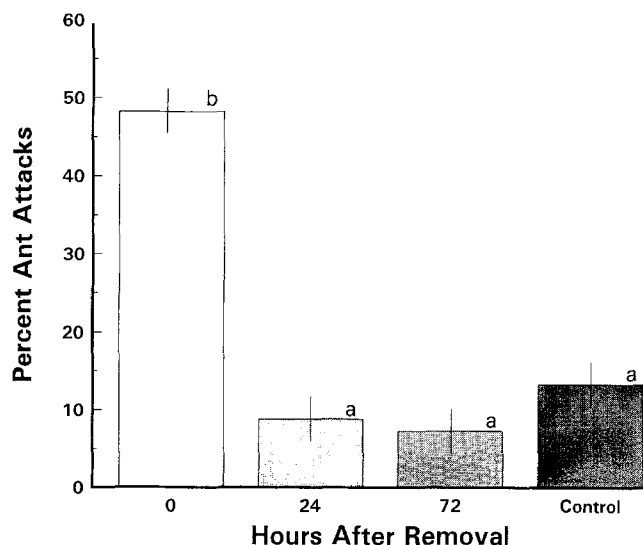

Fig. 3. Defensive secretions from larvae which have recharged their glands over the previous 24 or 72 h are as effective against generalist predators as secretions from larvae which have not been milked ($F_{3,39} = 24.429$, $p < 0.001$). Lower case letters denote groups not significantly different at $p = 0.01$. Vertical bars represent ±1 SE (pooled)

of ant encounters over the course of the trials (20 per trial), but at a much higher rate, averaging 4.9 per min. Overall, 48% of the ant encounters with removal larvae resulted in attacks, and 4 of 6 larvae were pulled off their leaf and onto the ground by the ants within 5 min and eventually dragged into a nest entrance at the base of the tree. Thus, the effectiveness of *C. confluens'* defense was confirmed.

Furthermore, the defense was rapidly regenerated. In 24 h, larvae were capable of replenishing their defenses to where they were indistinguishable from larvae milked 72 h earlier or not milked at all. However, ants encountering members of these three groups attacked at a rate far lower than that of larvae whose defenses had been removed just prior to the encounter (Fig. 3; $F_{3,39} = 24.429$, $p < 0.001$). Although the number of ant encounters per two min test did not differ among groups ($F_{3,39} = 1.503$, n.s.) attack rates did differ. Larvae that had just been milked were attacked in approximately 49% of their encounters with ants, whereas the other groups were attacked by only 7–13% of their encounters with ants.

A no-cost defense for C. confluens

The prediction that the energetic requirements of daily salycylaldehyde production would be reflected in reduced performance measures was not supported. The developmental rates of 79 larvae showed that groups of removal larvae developed no slower than their paired control sibs (Fig. 4a; $T = 9$ $n = 6$ host genotypes, $p > 0.10$). These developmental rates were generated from the performance of 79 surviving larvae from 14 clutches which had been reared on 6 different host genotypes.

Nor did the daily milking affect adult fecundity, measured as adult dry mass. Comparisons of 42 adults collected from 8 clutches reared on 6 host genotypes showed no difference between control and removal groups (Fig. 4b; $T = 6$, $n = 6$ host genotypes, $p > 0.10$).

The increased consumption hypothesis was not supported either. Because removal larvae were losing and regenerating their secretions rather than exposing them, and because we were measuring leaf consumption in the ultimate and penultimate instars when most larval mass accumulation takes place, we expected removal larvae to show much higher feeding rates. However, comparing 22 larvae in sibling pairs, removal larvae consumed no more leaf area than their paired controls (Fig. 4c; $T = 23$, $n = 11$ sibling pairs, $p > 0.10$).

Discussion

Guns and butter for Chrysomela confluens

The results presented here demonstrate that *C. confuens* derives both "guns and butter" from the production of salicylaldehyde. None of our measures of potential costs showed any differences between control and removal groups. This strongly supports the hypothesis that insects can have both guns and butter, because the sequestered defense also results in the production of an energy source (Fig. 1). Thus there appears to be no cost to chemical defense in these beetles. The lack of effect of milking on final adult mass has been demonstrated elsewhere (Rowell-Rahier and Pasteels 1986), but neither the effectiveness of the recharged defenses nor the potential for
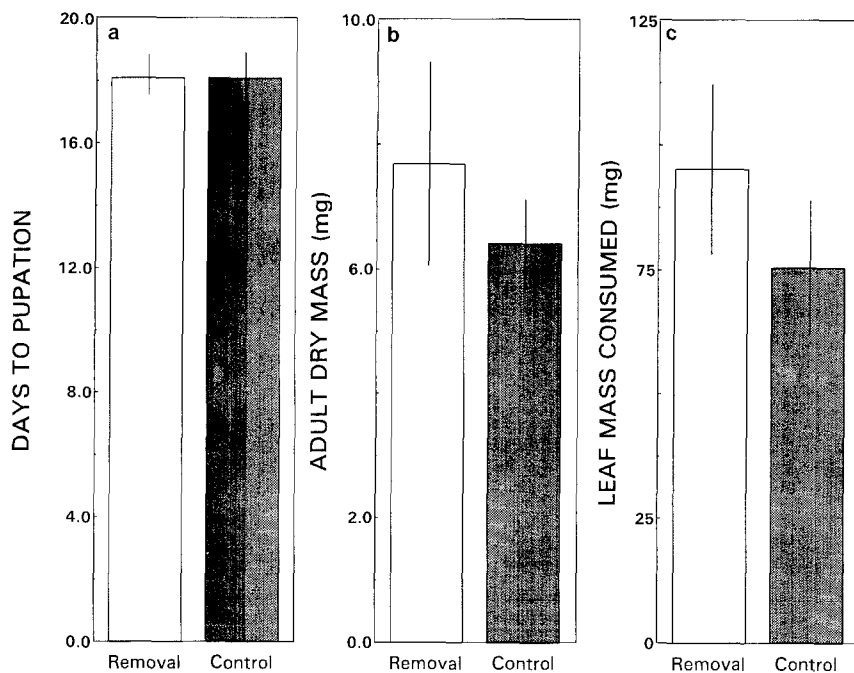
Fig. 4a–c. Effects of the removal of secretions from *Chrysomela confluens* larvae on growth performance measures; **a** larvae with their defenses removed grow at the same rate as their paired control siblings; **b** adults from larvae which had their defenses removed are of the same size as adults from their paired control siblings. **c** larvae which have their secretions removed daily do not compensate by consuming more leaf tissue during the penultimate and ultimate instars. Vertical bars represent ± 1 SE

compensation by extended developmental time and/or increased consumption have been addressed previously.

A cheap, effective defense would be especially important to *Chrysomela confluens* which feeds in open habitats on juvenile trees (Kearsley and Whitham 1989) exposed to many predators. This increases the probability of their encounters with generalist predators. The likelihood of discovery and the high frequency of expected encounters would increase the value of large amounts of metabolically cheap defenses. For example, at the observed 4.9 encounters per min on juvenile tree branches larvae could expect to experience as many as 300 ant encounters per hour.

The data presented here do not address all potential measures of cost. First, there must be a cost to producing defensive glands and associated musculature, but assessing their costs is beyond the scope of this study. Second, survivorship of control and removal larvae in a noncaged setting or of post diapause adults from the two groups in the year following may differ. However, by examining growth performance measures of larvae we feel that this study represents a major step towards realistic assessments of the costs of chemical defenses in herbivorous insects.

Generality of no-cost defenses

Although conversion of salicin to salicylaldehyde may be limited to chrysomelids (Pasteels et al. 1984, 1989, 1990), the use of plant toxins for insect defenses in a "guns and butter" manner is likely more common than is generally acknowledged. However, such situations will go undetected unless costs are measured directly via their effects on fitness components. Indirect measures can miss physical and physiological adaptations which minimize or eliminate the cost of such defenses. For example, milk-

weed bugs have an emulsion-based system for concentrating cardiac glycosides from the hemolymph with no expense of energy (Duffey et al. 1978).

The strategy of using deactivated or ineffective toxins in the hemolymph as a low- or nocost chemical defense is widespread in invertebrates which feed on toxic plants (Blum 1981; Hay and Fenical 1988). Six of 25 documented cases of insect defensive chemicals listed by Luckner (1984) come from sequestered host plant toxins. Approximately 10% of lepidopteran genera feeding on plants with flavonoid pigments convert them to their own use (Harborne 1979). It is interesting to note that a similarly large proportion of insects' sex pheromones are derived directly from host plant compounds as well with little or no processing (Luckner 1984; Blum 1987).

Insects from diverse orders feeding on hosts with similar allelochemicals have converged on this strategy. Aphids and butterflies feeding on plants containing iridoid glucosides sequester them for defense (Stermitz et al. 1986, 1988; Franke et al. 1987; Bowers and Puttick 1989; Nishida and Fukami 1989). Hemipterans, grasshoppers, aphids, butterflies and beetles are known to sequester cardiac glycosides from their host plants (Brower and Brower 1964; Vaughan and Jungreis 1977; Duffey et al. 1978; Blum 1981; Aldrich 1988). Host plants are also the source of defensive alkaloids for grasshoppers, beetles, and moths (Blum 1981), and glucosinolates for zygaenids, pierids, and pentatomids (Brattsten 1979; Blum 1981; Aldrich 1988).

Nor is this phenomenon limited to terrestrial herbivores. Opisthobranch and nudibranch molluscs acquire toxins from the sponges and algae they feed on (Schulte et al. 1980; Thompson et al. 1982; Jensen 1984) and sequester them on their dorsal surfaces where predators are most likely to encounter them. Parasitic flies reared from chemically defended larvae can appropriate the defenses of their hosts (Reichstein et al. 1968).

Guns and Butter for all?

We do not assume that all chemically defended herbivores acquire their defenses directly from their host plants. There are numerous cases in which the biosynthetic pathways used to produce defensive compounds do not involve host toxins (Rosenthal and Janzen 1979; Blum 1987). Nor do we believe that all chemical defenses produce energetic or nutritive benefits to the herbivore. The de novo synthesis of glues, cyanogenics, sterols, cardiac glycosides, histamines and other defensive compounds is likely to come at some cost (Meinwald et al. 1977; Pasteels and Daloze 1977; Fescemyer and Mumma 1983; Nahrstedt and Davis 1983; Prestwich 1983; Dettner and Schwinger 1987; Jonsson et al. 1988).

However, we do feel that analyses of the energetic and chemical components of defensive compounds (Bengtsson 1982; Hetz 1988), or equating toxicity of the compounds with energetic costs (Brower and Brower 1964; Brower and Glazier 1975) does not give the whole picture of the cost of defense. Cases in which ATP, glucose, or amino acids are shown to be by-products of the synthetic process (Blum 1981, 1987; Luckner 1984; Rowell-Rahier and Pasteels 1986) or relate changes in the pattern of defense production to the physiological needs of the individual (Baldwin et al. 1990) provide a good starting point for a complete analysis, but such studies will be incomplete without field or laboratory tests over the lifetime of the herbivore (Erickson 1973; Brower and Glazier 1975; Vaughan and Jungreis 1977).

In the same way that the presence of detectable levels of toxins in plants merely indicates that they are not being degraded as fast as they are created (Mothes 1964, cited in Robinson 1974), the presence of defensive chemicals in herbivores should not be construed as having come at a cost. In the analysis of plant defenses, there has been a shift towards viewing chemical defenses through an understanding of their role in the overall metabolism of the plant (Robinson 1974; Seigler and Price 1976; reviews in Rosenthal and Janzen 1979), the physiological condition of the tissues in question (Adams and Hagerman 1976; Kearsley and Whitham 1989) and the plant's interaction with the environment (Kingsbury 1964; Bryant et al. 1983; Coley et al. 1985; Larsson et al. 1986; Bryant 1987). We feel that a similar view should be taken towards the economics of defense in herbivorous arthropods.

Even though the biochemical pathways for detoxification of host defensive compounds are rarely examined in an ecological context, in several cases it has been shown that insects derive energy or nutrition from the production of defensive compounds (Blum 1981, 1987; Luckner 1984; Rowell-Rahier and Pasteels 1986; Pasteels et al. 1990). These cases are distributed across 4 orders, suggesting that it may be more widespread than is generally believed. Research into optimal allocation of energy among the competing interests of growth, reproduction, and defense in herbivores should be carried out with this in mind.

References

Adams RP, Hagerman A (1976) A comparison of the volatile oils of mature versus young leaves of *Juniperus scopulorum:* Chemosystematic significance. Biochem Syst Ecol 4:75–79

Aldrich TR (1988) Chemical ecology of Heteroptera. Annu Rev Ecol Syst 33:211–238

Baldwin IT, Dusenbery DB, Eisner T (1990) Squirting and refilling: dynamics of *p*-benzoquinone production in defensive glands of *Diploptera punctata.* J Chem Ecol 16:2823–2834

Bengtsson G (1982) Energetic costs of amino acids exudation in the interaction between the predator *Gammarus pulex* L. and the prey *Asellus aquaticus* L. J Chem Ecol 8:1271–1281

Blum MS (1978) Biochemical defenses of insects. In: Rockstein M (ed) Biochemistry of insects. Academic Press, New York, p. xiv+649

Blum MS (1981) Chemical defenses of arthropods. Academic press, New York

Blum MS (1987) Biosynthesis of arthropod exocrine compounds. Annu Rev Ecol Syst 32: 381–413

Bowers MD, Puttick GM (1989) Iridoid glucosides and insect feeding preferences: Gypsy moths (*Lymantria dispar*, Lymantridae) and buckeyes (*Junonia coenia*, Nymphalidae). Ecol Ent 14:247–256

Brattsten LB (1979) Biochemical defense mechanisms in herbivores against plant allelochemicals. In: Rosenthal GA, Janzen DH (eds) Herbivores: their interactions with secondary plant metabolites. Academic Press, Orlando, FL, pp 199–270

Brower LP, Brower JVZ (1964) Birds, butterflies and plant poisons: a study in ecological chemistry. Zoologica 49:137–159

Brower LP, Glazier SC (1975) Localization of heart poisons in the monarch butterfly. Science 188:19–25

Brower LP, McEvoy PB, Williamson KL, Flannery MA (1972) Variation in cardiac glycoside content of monarch butterflies from natural populations in eastern North America. Science 177:426–429

Brown WJ (1956) The new world species of *Chrysomela* L. (Coleoptera: Chrysomelidae). Can Ent 88 [Suppl III]: 5–54

Bryant JP (1987) Feltleaf willow – snowshoe hare interactions: Plant carbon/nutrient balance and floodplain succession. Ecology 68:1319–1327

Bryant JP, Chapin S, Klein DR (1983) Carbon/nutrient balance in boreal plants in relation to vertebrate herbivory. Oikos 40:357–368

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Dettner K (1987) Chemosystematics and evolution of beetle chemical defenses. Annu Rev Ecol Syst 32:17–48

Dettner K, Schwinger G (1987) Chemical defense in the larvae of the leaf beetle *Gonioctena viminalis* (Coleoptera: Chrysomelidae). Experentia 43:458–462

Duffey SS, Blum MS, Isman MB, Scudder GGE (1978) Cardiac glycosides: a physical system for their sequestration by the milkweed bug. J Insect Physiol 24:639–645

Eisner T, Meinwald J (1966) Defensive secretions of arthropods. Science 153:1341–1348

Eisner T, Johnessee JS, Carrel J, Hendry LB, Meinwald J (1974) Defensive use by an insect of a plant resin. Science 184:996–999

Erickson JM (1973) The utilization of various *Aesclepias* species by larvae of the monarch butterfly, *Danaus plexippus*. Psyche 80:230–244

Ferguson JE, Metcalf RL (1985) Cucurbitacins. Plant derived defense compounds for Diabroticites (Coleoptera: Chrysomelidae). J Chem Ecol 11:311–318

Fescemyer HW, Mumma RO (1983) Regeneration and biosynthesis of Dytiscid defensive scents (Coleoptera: Dytiscidae). J Chem Ecol 9:1449–1464

Franke A, Rimpler H, Schneider D (1987) Iridoid glycosides in the butterfly *Euphydrias cynthia* (Lepidoptera: Nymphalidae). Phytochemistry 26:103–106

Harborne JB (1979) Flavanoid pigments. In: Rosenthal GA, Janzen DB (eds) Herbivores: their interactions with secondary plant metabolites. Academic Press, Orlando, FL, pp 619–655

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Annu Rev Ecol Syst 19:111–145

Hetz M (1988) Costs and benefits of mimicry. Ph.D. Dissertation. Northern Arizona University, Flagstaff, Arizona. vii + 66 pages

Hill CS, Tschinkel WR (1985) Defensive secretion production in the tenebrionid beetle *Zophobas attratus*: effects of age, sex, and milking frequency. J Chem Ecol 11:1083–1092

Jensen KR (1984) Defensive behavior and toxicity of Ascoglossan opisthobranch *Mourgona germaineae*. J Chem Ecol 10:475–486

Jones CG, Hess TA, Whitman DW, Silk PJ, Blum MS (1987) Effects of diet breadth on autogenous chemical defense of a generalist grasshopper. J Chem Ecol 13:283–297

Jonsson S, Bergstrom G, Lanne BS, Stensdotter U (1988) Defensive odor emission from larvae of two sawfly species, *Pristiphora erichsoni* and *P. wesmaeli*. J Chem Ecol 14: 713–721

Kearsley MJC, Whitham TG (1989) Developmental changes in resistance to herbivory: implications for individuals and populations. Ecology 70:422–434

Kingsbury JM (1964) Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, NJ

Larsson S, Wiren A, Lundgren L, Ericsson T (1986) Effects of light and nutrient stress on leaf phenolic chemistry in *Salix dasyclados* and susceptibility, to *Balerucella lineola* (Coleoptera). Oikos 47:205–210

Lindroth RL, Scriber JM, Hsia MTS (1988) Chemical ecology of the tiger swallowtail: mediation of host use by phenolic glucosides. Ecology 69:814–822

Luckner M (1984) Secondary metabolism in microorganisms, plants, and animals. Second ed. Springer-Verlag, New York

Matsuda K, Matsuo H (1985) A flavonoid, Luteolin-7-glucoside, as well as salicin and populin, stimulating the feeding of leaf beetles attacking salicaceous plants. Appl Ent Zool 20:305–313

Meinwald J, Jones TH, Eisner T, Hicks K (1977) New methylcyclopentanoid terpenes from the larval defensive secretion of a chrysomelid beetle *(Plugiodera versicolora)*. Proc Nat Acad Sci, USA 74:2189–2193

Morrow PA, Bellas TE, Eisner T (1976) *Eucalyptus* oils in the defensive oral discharge of Australian sawfly larvae (Hymenoptera: Pergidae). Oceologia 24:193–206

Nahrstedt A, Davis RH (1983) Occurrence, variation, and biosynthesis of the cyanogenic glucosides Linamarin and lotaustralin in species of the Heliconiini (Insecta: Lepidoptera). Comp Biochem Physiol 75B: 65–73

Nishida R, Fukami H (1989) Host plant iridoid-based chemical defense of an aphid, *Acyrthosiphon nipponicus*, against ladybird beetles. J Chem Ecol 15:1837–1845

Palo RT (1984) Distribution of birch *(Betula* spp.), willow *(Salix* spp.), and poplar *(Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. J Chem Ecol 10:499–520

Pasteels JM, Daloze D (1977) Cardiac glycosides in the defensive secretion of Chrysomelid beetles: evidence for their production by the insects. Science 197:70–72

Pasteels JM, Gregoire JC (1983) The chemical ecology of defense in arthropods. Annu Rev Entomol 28:263–289

Pasteels JM, Daloze D, Dorsser W van, Roba J (1979) Cardiac glycosides in the defensive secretion of *Chrysolina herbacea* (Coleoptera: Chrysomelidae). Identification, biological role and pharmacological activity. Comp Biochem Physiol 63C: 117–121

Pasteels JM, Braekman JC, Daloze D, Ottinger R (1982) Chemical defense in Chrysomelid larvae and adults. Tetrahedron 38:1891–1897

Pasteels JM, Rowell-Rahier M, Braekman JC, Dupont A (1983) Salicin from host plant as precursor of salicylaldehyde in defensive secretion of Chrysomeline larvae. Physiol Ent 8:307–314

Pasteels JM, Rowell-Rahier M, Brakeman J-C, Daloze D (1984) Chemical defenses in leaf beetles and their larvae: the ecological, evolutionary and taxonomic significance. Biochem Syst Ecol 12:395–406

Pasteels JM, Rowell-Rahier M, Braekman JC, Daloze D, Duffey S (1989) Evolution of exocrine chemical defense in leaf beetles (Coleoptera: Chrysomelidae). Experentia 45: 295–300

Pasteels JM, Duffey S, Rowell-Rahier M (1990) Toxins in Chrysomelid beetles. Possible evolutionary sequence from de novo synthesis to derivation from food-plant chemicals. J Chem Ecol 16:211–222

Prestwich GD (1983) The chemical defenses of termites. Sci Amer 249:78–87

Price PW (1987) The role of natural enemies is insect populations. In: Barbosa P, Schultz JC (eds) Insect Outbreaks. Academic Press, New York, pp 287–312

Price PW, Westoby M, Rice B (1988) Parasite-mediated competition: some predictions and tests. Am Nat 131:544–555

Reichstein T, Euw J von, Parsons JA, Rothschild M (1968) Heart poisons in the monarch butterfly. Science 161:861–866

Robinson T (1974) Metabolism and function of alkaloids in plants. Science 184:430–435

Rosenthal GA, Janzen DH (1979) Herbivores: their interaction with secondary plant metabolites. Academic press, Orlando, FL

Roth LM, Eisner T (1962) Chemical defenses in arthropods. Annu Rev Entomol 7:107–136

Rowell-Rahier M, Pasteels JM (1982) The significance of salicin for a *Salix*-feeder, *Phratora (Phyllodecta)* vitellinae. In: Visser JH, Minks AK (eds) Proceedings of the 5th International Symposium on Insect-Plant Relationships. Pudoc, Wageningen, pp. 73–79

Rowell-Rahier M, Pasteels JM (1986) Economics of chemical defense in Chrysomelinae. J Chem Ecol 12:1189–1203

Schulte G, Scheuer PJ, McConnell OJ (1980) Two furanosesquiterpene marine metabolites with antifedant properties. Helv Chim Act 63:2159–2167

Seigler D, Price PW (1976) Secondary compounds in plants: primary functions. Am Nat 110:101–105

Smiley JT, Horn JM, Rank NE (1985) Ecological effects of salicin at three trophic levels: new problems from old adaptations. Science 229:649–651

Stermitz FR, Gardner DR, Odendaal FJ, Erlich PR (1986) *Euphydryas anicia* (Lepidoptera: Nymphalidae) utilization of iridoid glycosides from *Castilleja* and *Besseya* (Scrophulariaceae) host plants. J Chem Ecol 12:1459–1468

Stermitz FR, Gardner DR, McFarland N (1988) Iridoid glycoside sequestration by two aposematic *Penstemmon*-feeding Geometrid larvae. J Chem Ecol 14:435–441

Thompson JE, Walker RP, Wratten SJ, Faulkner DJ (1982) A chemical defense mechanism for the nudibranch *Cadlina luteomarginata*. Tetrahedron 38:1865–1873

Vaughan GL, Jungreis AM (1977) Insensitivity of Lepidopteran tissues to Ouabain: physiological mechanisms for protection from cardiac glycosides. J Insect Physiol 23: 585–593

Whitham TG (1989) Plant hybrid zones as sinks for pests. Science 244:1490–1493

Witz BW, Mushinsky HR (1989) Pygidial secretions of *Pasimachis subsculatus* (Coleoptera: Carabidae) deter predation by *Eumeces inexpectatus* (Squamata; Sinaidae). J Chem Ecol 15:1033–1044