

HERBIVORE OFFENSE

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■ **Abstract** Herbivore offense describes traits that allow herbivores to increase their feeding and other uses of host plants when these uses benefit the herbivores. We argue that ecological interactions and coevolution between plants and herbivores cannot be understood without an offense-defense framework. Thus far, plant defense theory and data have far outpaced knowledge of herbivore offense. Offensive tactics include feeding and oviposition choices, enzymatic metabolism of plant compounds, sequestration, morphological adaptations, symbionts, induction of plant galls, and induced plant susceptibility, trenching, and gregarious feeding. We propose that offensive tactics can be categorized usefully depending upon when they are effective and whether they are plastic or fixed traits. The advantages of offensive traits have not been adequately described in terms of herbivore fitness. Similarly, a more complete understanding of the costs and limitations of offensive traits will help put the herbivore back in plant-herbivore interactions and coevolution.

INTRODUCTION

The past 30 years have seen incredible advances in our understanding of plant defenses, the mechanisms that plants use to protect themselves from being eaten by their herbivores. By comparison, biologists have paid much less attention to herbivore offense, the mechanisms that herbivores use to exploit their host plants. Offensive traits are those that currently allow herbivores to increase their feeding and use of a host when this use benefits the herbivores. These offensive traits increase herbivore performance or fitness. Offensive traits are determined from the herbivore's point of view; they do not necessarily cause more damage to plants or reduce plant fitness.

We have devised a dichotomous key to define offensive traits and to help organize our thinking and research about them (Table 1). We start by asking whether the herbivore's traits appear to match the challenges that its host plant presents. For

TABLE 1 A dichotomous key for offensive traits

	No	Yes
1. Do herbivores have traits that correspond to host traits?	The trait is unlikely to be involved in herbivore offense	Possible offensive trait (proceed to 2)
2. Does the trait produce a measurable increase in the rate or efficiency of the herbivore's feeding or other uses (e.g., oviposition) of the host?	The trait is not involved in herbivore offense	Probable offensive trait (proceed to 3)
3. Does the trait increase herbivore performance (fitness)?	The trait is not beneficial	The trait is currently offensive (proceed to 4)
4. Did the trait evolve as an adaptation to herbivory?	The trait is currently beneficial but was shaped or maintained by other selective pressures	The trait is currently beneficial and has been shaped or maintained by herbivory (adapted offensive trait)

example, do its mouthparts or ovipositor correspond to features of its host? This effort often takes the form of examining variation in herbivore traits when the herbivore feeds on different species. We compare the traits observed with alternative traits that are observed in other herbivores.

Our next step should be to examine whether the herbivore trait increases the rate or efficiency of feeding or other host use. The comparison is with herbivores that exhibit alternative traits. The fitness consequences of possibly offensive herbivore traits have rarely been quantified, although a connection between herbivore efficiency and fitness is often assumed. Ideally, fitness should be measured over the entire lifetime of the herbivore, as traits may increase performance during one stage but decrease performance during other stages (e.g., Scheirs et al. 2000). The relationship between traits that appear offensive (correspond to the host and increase herbivore efficiency) and herbivore fitness deserves much further study.

Offensive traits can include plastic traits that change over ecological time as well as fixed traits that change over evolutionary time. Our definition does not require an offensive trait to have evolved in response to host plant traits (adaptation sensu; Reeve & Sherman 2001). Demonstrating that a trait has been shaped by a particular selective factor is a very difficult task that requires information about the selective environment and how the trait performs, its genetic variability and heritability, and a comparison among related species (Endler 1986, Reznick & Travis 1996). We presently have an incomplete understanding of the selective pressures that shaped any of the adaptations that we observe in nature. Many traits that now appear offensive may have evolved for other reasons.

Expanding on the scheme proposed by Rhoades (1985), we envision three strategies that have been employed by herbivores to exploit hosts (Table 2). The first and

TABLE 2 Herbivore offensive strategies and their consequences^a

	Strategy	Tactic	Employed by	Resulting population dynamics
Least aggressive	Choice	Avoidance, attraction	Opportunistic herbivores	Variable populations
	Change herbivore morphology, physiology	Metabolize, detoxify		
Most aggressive	Manipulate the host	Change host nutrition & defense	Stealthy herbivores	Low, invariant populations

^aModified from Rhoades 1985.

least aggressive of these is choice. Herbivores do not randomly eat the green world but can make sophisticated choices, avoiding many potential foods and selectively seeking others. We consider choice to be offensive when it increases herbivore efficiency and performance. The second strategy is altering the herbivore's morphology and physiology over ecological and evolutionary time to better exploit existing hosts and to begin to exploit novel ones. The third and most aggressive strategy is active manipulation of the host. Herbivore offense may occur prior to ingestion, for instance, by suppressing the host's ability to respond defensively or by inducing the host to create a highly nutritious gall. It may also occur after ingestion by metabolizing the plant's secondary chemicals (those that are not part of the plant's primary metabolism and presumed to be defensive) or by sequestering them to protect the herbivore against its own predators. Many specific tactics that exemplify each of these strategies will be elaborated below although in only a few cases have the tactics been linked to herbivore fitness.

BEHAVIORAL MECHANISMS—LEAST AGGRESSIVE

Feeding Choices

Herbivores are faced with a food supply that is not very nutritious. The tissues of all animals contain one to several orders of magnitude more nitrogen than their plant foods (Mattson 1980). Other nutrients and water are also commonly limiting to herbivores. In addition, plants contain many physical and chemical traits that reduce their digestibility or are directly toxic to most herbivores. Natural selection has favored herbivores that are selective about the foods they ingest. For several well-studied species of insect herbivores, individuals that were allowed to select their own diets grew faster than individuals that were fed different ratios of the same nutrients or diets that lacked a self-selected nutrient (Waldbauer & Friedman 1991). Self-selection of food is likely to be more important for herbivores that are more mobile and can gain access to varied diets. Of course, not all foraging

decisions by herbivores are optimal. When herbivores fail to make appropriate decisions, these "mistakes" tend to be conservative, such that herbivores reject foods that are actually nutritious to them (Waldbauer & Fraenkel 1961).

Plant quality can vary greatly in time and space. In response, many herbivores compensate for suboptimal foods. For example, when faced with a diluted diet, herbivores may eat more, increasing meal size, eating meals more frequently, or altering their diets (Simpson & Simpson 1990, Slansky 1993). It appears that compensatory feeding among insect herbivores occurs as the result of nutritional feedback; herbivores respond to the osmolality and amino acid content of their hemolymph. Herbivores may also assess the bulk of digested food and its rate of passage through their guts and adjust their decisions about intake accordingly.

Insect herbivores can supplement their diets with food that is not living vegetation but is high in protein and other essential micronutrients. These supplemental foods include pollen, their own cast skins, and even other living animals. Cannibalism is very common among herbivorous insects, in fact more common than among predators (Fox 1975). Cannibalism and predation on other herbivores is associated with nutritional benefits and is more likely when plant foods are scarce or less nutritious (Fox 1975, Via 1999). For example, when omnivorous western flower thrips feed on plants with high levels of defense, they shift their diet to include more small arthropods (Agrawal et al. 1999). Similarly, adult Lepidoptera of many families feed from the margins of moist ground, as well as on carrion and excreta (Arms et al. 1974, Beck et al. 1999). Cafeteria choice experiments revealed that this "puddling" behavior in some butterfly species was associated with sources of sodium, whereas other butterflies were more interested in protein.

Generalist herbivores (e.g., caterpillars and grasshoppers) have been found to perform best when offered a variety of food plants rather than a single plant. This result has been explained by mixed diets balancing nutrient intake (Pulliam 1975) or by facilitating avoidance of high levels of any single secondary compound (Freeland & Janzen 1974). It has been suggested that these two different mechanisms will produce different signatures that can be used to distinguish the mechanisms causing the pattern (Pennings et al. 1993, Bernays et al. 1994). If the mechanism involves critical complementary nutrients, then an herbivore will grow more on a mixed diet without necessarily ingesting more. However, if a mixed diet allows ingestion of low doses of several different toxins, then an herbivore will eat more of a mixed diet and will perform better as a result of eating more food. However, as is often the case, inferring process from pattern in ecology is very tricky. To separate these mechanisms we must assume that no single diet will satisfy the nutritional requirements as well as a mixed diet and that nutrients and toxins are distinct categories (Hagele & Rowell-Rahier 1999). Not only are these assumptions questionable, but alternative selective pressures can also make it very difficult to see a correspondence between the outcome of selection (pattern) and the selective force (process). For example, an herbivore's choice of diet will affect many other aspects of its life such as risk of predation and disease, likelihood of mating, thermal balance, and so on.

Innate preferences are probably responsible for much of food selection by herbivores, although there is growing evidence that most insects are capable of learning (Papaj & Prokopy 1989). Prior experience alters the ability of many herbivores to acquire food. Some authors (e.g., Bernays 1993) argue that learning is responsible for the ability of herbivores to self-select their diets, although no specific data are offered to support this argument. It is well substantiated that grasshoppers can avoid nutritionally inadequate foods and foods associated with adverse physical responses (Bernays & Lee 1988, Bernays 1993). Grasshoppers can also learn to associate plant odors with limiting nutrients, and they actively seek these odors (Simpson & White 1990). Such associative learning allows grasshoppers to grow more rapidly when compared with individuals that are prevented from learning (Dukas & Bernays 2000).

Even without learning, herbivores can choose to avoid patchy plant defenses. Small insects with mouthparts that are smaller than the distance between defensive structures in their host plants can eat around those structures. Young caterpillars of several species “window feed” on maple leaves, removing discrete pieces of mesophyll and epidermis and avoiding sclerenchymous bundle sheaths (Hagan & Chabot 1986). *Trichoplusia ni* caterpillars feed between the veins of wild parsnip leaves and in so doing reduce their intake of furanocoumarins (Zangerl & Bazzaz 1992). Similarly, larvae of the cotton leaf perforator skeletonize the leaves of their wild cotton host plant, eating everything except the epidermis and the pigment glands, which contain defensive terpenoid aldehydes (R. Karban & A.A. Agrawal, personal observations).

Many of these examples of individual feeding choices should be classified as possible offensive traits (sensu Table 1). In the cases of window feeding and cannibalism, the observations are primarily behavioral and no benefit to the herbivores, as required for our definition of offense, has been demonstrated. Compensatory feeding increases consumption (probable offense), but lack of true comparisons with noncompensatory feeding individuals makes benefits and offense ambiguous in these cases. Increases in herbivore performance associated with self selection and diet mixing lack mechanistic detail but do demonstrate herbivore offense.

Oviposition Choices

Many herbivorous insects cannot move much during the course of their development. According to the prevailing paradigm, mobile ovipositing females assess different host plant species and place their eggs or offspring on those hosts that result in the highest performance. A review of the recent literature found that just slightly more than half of the studies supported this positive correlation between adult oviposition and offspring performance (Mayhew 1997). This conclusion echoes previous findings that the relationship between oviposition preference and offspring performance is weaker than expected (Thompson 1988). Many explanations have been proposed for the bad fit between oviposition preference and offspring performance (Thompson 1988, Mayhew 2001). The empirical studies

reviewed by these authors consider the correlation between mean oviposition preference and survival and growth of larvae averaged across many females in an herbivore population. The relevant question from the perspective of natural selection is whether individuals select the best hosts for their own offspring (Thompson & Pellmyr 1991). Singer et al. (1988) considered this relationship at the individual level and found a strong correlation between the host species preferences of adult *Euphydryas editha* butterflies and the growth rates of their offspring. However, two studies that have looked for similar correlations among individuals have failed to find them for fruit flies and bruchid beetles (Jaenike 1989, Fox 1993). More studies of individual preferences and performance are required to resolve this issue.

Herbivores may select host plants that provide poor growth but good protection from their own natural enemies (Price et al. 1980, Bernays & Graham 1988). For example, a marine amphipod specializes on a seaweed that minimizes its risk of predation by fish (Hay et al. 1990). If host choice affects risk of predation then correlations between choice and growth in the laboratory may be much poorer than correlations between choice and fitness in the field.

Most investigators have looked for correlations between adult choices and performance of offspring. One recent study that considered the correlation between adult oviposition decisions and adult performance of the parents in leaf-mining flies found a very strong correlation between these two (Scheirs et al. 2000). Adult herbivores may be maximizing their own lifetime fitness, and this may come at the expense of some of the individual offspring. Future field studies of the preference-performance correlation should consider adult performance as distinct from offspring performance.

In general, female herbivores seem more adept at making appropriate intraspecific choices among host plants than they do at choosing among host species. This greater discrimination between plants within a species seems counterintuitive, although here too there are examples of less than optimal choices. *Pemphigus* aphids provide a good example of intraspecific preference that correlates very well with offspring success. *Pemphigus* colonists make appropriate choices about leaf size and location on a leaf. Large leaves are much preferred by colonists and these large leaves increase the weight of stem mothers and their progeny, the number of progeny, their development rate, and their fecundity (Whitham 1978). Colonists at the base of leaves were more likely to survive and produced more progeny than those at other leaf positions and this corresponded to choices of colonists and to their willingness to engage in aggressive territorial behaviors (Whitham 1980).

Preference for appropriate host plants is a possible offensive trait sensu Table 1. In most cases, when differences in performance have been observed (step 3, "herbivore offense" in Table 1) the causal mechanisms (step 2) have not been examined or were not well documented. Knowledge of mechanism is not essential for determining if a trait is offensive. However, failure to grasp the mechanisms limits our understanding of the conditions under which the trait will be effective and how it may have evolved.

PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS OF HERBIVORES—SOMETIMES AGGRESSIVE

Enzymes

Herbivores possess various physiological and morphological traits that enable them to exploit their host plants. For example, all herbivores must deal with chemicals that are potentially damaging to their cellular processes; these come from various sources including secondary chemicals of plants that can be toxic or antinutritive to them (Duffey & Stout 1996). One class of traits that allows them to deal with such threats is enzymes that reduce the detrimental effects of these plant compounds. Mixed function oxidases are widespread enzymes that are thought to function in detoxification by catalyzing oxidative reactions (Brattsten 1988, Feyereisen 1999). In particular, cytochrome P-450 enzymes have been causally linked to detoxification of plant secondary metabolites. Production of these enzymes is induced facultatively by exposure to plant metabolites and such induction is also correlated with diet choice. For example, *Manduca sexta* caterpillars only increase consumption of food containing nicotine after increasing activity of P-450 enzymes in their midguts (Snyder & Glendinning 1996). Conversely, consumption of inhibitors of P-450 enzymes caused caterpillars to reduce consumption of foods with nicotine. Spider mites also use P-450 enzymes (Mullin & Croft 1983). Spider mites with inducible enzyme systems have higher fecundity when feeding on toxic host plants compared with mites with their detoxification systems blocked (Agrawal et al. 2002). This advantage was not apparent on nontoxic hosts, providing evidence that inducible P-450 systems are offensive.

Plants also contain antinutritive compounds that make essential constituents unavailable for digestion by herbivores. Proteinase inhibitors in plants have received considerable attention as antinutritive agents that inhibit the action of digestive protease enzymes in herbivores and thus make protein unavailable (Ryan 1990). However, careful work has revealed that although proteinase inhibitors effectively reduced the function of particular proteases in the guts of six lepidopteran species, corresponding reductions in caterpillar growth were minimal (Broadway 1995, 1997). After feeding on diets with proteinase inhibitors, these caterpillars responded by producing other proteases that were relatively insensitive to the inhibitors in their diets. Similar induction of insensitive proteases has been reported for proteinase inhibitors expressed in high levels in transgenic plants (Jongsma et al. 1995, Cloutier et al. 2000) and for proteinase inhibitors induced by methyl jasmonate (Bolter & Jongsma 1995). Both P-450 mediated detoxification and production of alternative proteases increase feeding and growth by reducing effects of plant defenses that are induced following ingestion.

Herbivores also produce salivary enzymes constitutively, prior to ingestion, that minimize the effectiveness of plant defenses. Such enzymes are applied to leaf wounds as the herbivores chew and these may reduce the activation of induced defenses in plants. Glucose oxidase is a major constituent of caterpillar

saliva that appears to suppress early signaling events in plant defense (Felton & Eichenseer 1999). Glucose oxidase inhibits lipoxygenase activity, a critical step in the biosynthesis of the induction signal, and thereby reduces induced resistance in plants. Caterpillars that were inhibited from producing glucose oxidase fed less and grew less, indicating that offense had been blocked (Musser et al. 2002).

Like caterpillars, other herbivores may also secrete saliva that interferes with plant defenses. Aphid saliva gels into a sheath at the interface between the aphid's stylet and the plant's cells. This sheath may prevent signals from diffusing from the site of penetration, reducing the plant's induced response (Felton & Eichenseer 1999). The evidence for this interaction and its possible mechanism are less well established for aphids compared with similar processes in caterpillars. It has also been suggested that constituents of the aphid sheath may oxidize defenses produced by the plant and reduce their spread (Miles 1990). Salivary constituents from grasshoppers have been implicated in enhanced growth of plants (Detling & Dyer 1981, Dyer et al. 1995, Dyer 2000). In this case, the offensive strategy may be to stimulate plant growth. However, a benefit to the individual herbivore has not been demonstrated in this example.

Herbivores that specialize on particular host plants often have very specific enzymatic systems that allow them to metabolize the secondary chemicals of those hosts. For example, some tropical legume seeds contain nonprotein amino acids that are potent defenses against most herbivores (Rosenthal et al. 1978, 1982). Specialized bruchid beetles are able to metabolize these compounds, synthesizing their own amino acids in the process. Similarly, specialized *Heliconius* caterpillars employ a novel enzymatic system that allows them to convert cyanogenic glycosides into thiols (Engler et al. 2000). This process prevents the plant from releasing cyanide and allows the caterpillars to use the normally toxic compounds as a source of nitrogen. These tactics result in increased feeding ability and may be offensive; however their effects on herbivore performance have not been widely measured.

Sequestering Host Chemicals

Many herbivorous insects incorporate or sequester the biologically active chemicals of their host plants into their own tissues or glands, and thereby gain protection from their predators and parasites (Duffey 1980). Sequestration as an offensive strategy involves several components (Dobler 2001). First, the herbivore must be willing to ingest the host's secondary chemicals. Second, the herbivore must be relatively tolerant of the chemicals. Third, the herbivore must ingest the chemicals without metabolizing them into biologically inactive products. Fourth, the herbivore must deposit the secondary chemicals in particular tissues, or otherwise store them. Some herbivores such as decorator crabs sequester protective chemicals behaviorally by attaching noxious plants to the outsides of their bodies and thereby reduce their risk of predation (Stachowicz & Hay 1999). Sequestration may be relatively expensive as an offensive strategy. Although the strategy allows herbivores to save the costs associated with synthesis of defensive chemicals, it

often requires specialized structures to separate, selectively uptake, and/or modify plant compounds (Bowers 1992). Common sense suggests that sequestration may require a very specialized diet. Indeed, in a survey of 70 lepidopteran species from Costa Rica, narrow diet breadth was correlated with defense against predators that was acquired by consumption of plant-derived chemicals (Dyer 1995), although generalists are also known to sequester (Blum et al. 1990, Pennings & Paul 1993).

Morphological Adaptations

Morphological traits of herbivores affect their abilities to exploit particular host plants. A comparative approach revealed striking correspondence between feeding morphologies and the type of food ingested, indicating possible offense (Bernays 1991, Labandeira 1997). Within insect families and feeding guilds, particular mouthparts are associated with particular strategies of consumption. For example, within the Sphingidae, some species have typical incisors for tearing and chewing relatively softer leaves whereas other species have toothless snipping mandibles for cutting larger, tougher grasses or mature leaves of trees (Bernays & Janzen 1988).

Morphological traits of herbivores track their particular diets over evolutionary time as the result of natural selection and over short periods of time as the result of phenotypic plasticity. An example of rapid evolution to novel hosts is provided by soapberry bugs that have mouthparts of precisely the right length to reach the seeds of their native sapindaceous host plant (Carroll & Boyd 1992). In the past century, three new sapindaceous plants have been introduced to North America; soapberry bugs that feed on each of these three new hosts have evolved mouthparts of the appropriate length to feed on seeds of each new plant. These feeding adaptations give the bugs enhanced fitness on their new hosts and concomitant reductions in performance on the ancestral host, demonstrating offense (Carroll et al. 1997, 1998).

Within the lifetime of an individual herbivore, diet can determine its feeding morphology. For example, caterpillars and grasshoppers fed on hard diets developed larger heads with correspondingly greater mandibular power than individuals fed on soft diets (Bernays 1986, Thompson 1992). This morphological plasticity was associated with enhanced feeding abilities for each of the morphs. Mandibular power and wear can potentially limit herbivore fitness (Raupp 1985). Genetic variation in the ability to respond to variability supports the notion that this plasticity in head shape is subject to natural selection (Thompson 1999).

Many other herbivore traits besides mouthparts can be important and offensive. For bruchid seed beetles, for example, females adjust egg size and probably other traits in response to particular host plants. On hosts with hard seeds, fitness is maximized by laying large eggs whereas on hosts with softer seeds, fitness is higher when females lay more, but smaller, eggs (Fox et al. 1997).

Symbionts

Herbivores harbor and vector microbial symbionts that allow them to exploit their host plants more effectively. Symbionts allow herbivores to use foods that the

herbivores cannot themselves digest, exploit foods that would otherwise be toxic to herbivores, and weaken the host plant's defenses to the point of submission.

No herbivores can digest cellulose, although several groups of herbivores house bacteria, fungi, and protozoa that carry out this task for them (Heath 1988, Leschine 1995). Some herbivores feed on xylem and phloem sap, diets that lack sufficient amino acids for insect survival (Buchner 1965, Douglas 1998). Phloem-feeding aphids harbor bacteria in their guts that produce the missing nutrients and individuals that have been "cured" of their symbionts perform very poorly, if at all. Leafhoppers, scales, and aphids that have shifted away from phloem diets over evolutionary time no longer have symbiotic bacteria (Douglas 1998).

Symbionts may also be responsible for some of the advantages that accrue to herbivores that eat mixed diets. Turtles that supplemented their duckweed diet with insect larvae became more efficient, especially at digesting the duckweed (Bjorndal 1991). Nutritional analyses suggested that much of this effect resulted from insect larvae in the diet enhancing the numbers or diversity of cellulolytic microbes.

Herbivores must overcome the defenses of the plants that they exploit. As mentioned above, enzymatic detoxification systems are widespread among herbivores and some of these services are provided by microbial symbionts (Jones 1984, Dowd 1991). For example, fungal symbionts in the guts of cigarette beetles use a variety of plant allelochemicals as a carbon source and produce detoxification enzymes (esterases) in response to other potential toxins. Thus, symbionts may increase feeding and exploitation of plants by herbivores by providing nutrients, digestion, and detoxification.

More aggressive strategies involve inoculating hosts with microbes that mobilize nutrients or diminish plant defenses. Herbivores that vector plant diseases (thrips, beetles, mites, homopterans) may manipulate plants to their own benefits through infection. Aphids that vector plant viruses have shorter developmental times, higher fecundity, and a greater intrinsic rate of increase on virus-infected hosts compared with uninfected hosts (Ferreles et al. 1989, Blua et al. 1994). In these systems, changes in sugar, total protein, and specific amino acid concentrations following infection may partly explain the benefit to aphids (Blua et al. 1994). Other insects may benefit by inoculating plants with pathogens that diminish the plant's ability to defend against herbivores; recent evidence leads to the speculation that defenses against pathogens may inhibit defenses against herbivores (Felton et al. 1999, Preston et al. 1999, Thaler et al. 1999).

Some herbivores are far more successful on damaged and weakened host plants, and symbionts may facilitate these herbivore attacks. For example, many species of bark beetles would be killed by defensive reactions of their host trees. However, invading beetles introduce blue stain fungi that cause necrotic lesions and reduce the tree's ability to respond defensively (Whitney 1982, Nebeker et al. 1993). Although the causal mechanisms have not yet been elucidated, it is clear that the fungus causes many physiological changes in an attacked tree and these greatly facilitate beetle colonization (Klepzig et al. 1996).

HERBIVORES MANIPULATE THEIR HOSTS—AGGRESSIVE

The examples discussed above mostly involve traits of herbivores that enable them to make efficient use of their host plants. In some cases (e.g., salivary enzymes, symbionts), herbivores manipulate the traits of their hosts rather than their own morphology, physiology, and behavior. The ability to manipulate the host's defensive reactions falls into this more aggressive category, as do other tactics discussed below.

Galls and Induced Plant Susceptibility

Galls are plant structures that are inhabited and fed upon by small herbivores (or by fungi or microorganisms). These structures are made of plant tissue, although gall morphology is controlled by the herbivores (Price et al. 1987). Variation in the morphology of the gall depends upon the phylogeny of the gall-making insect and is independent of the host phylogeny (Crespi & Worobey 1998, Nyman et al. 2000). Gall form is determined by substances secreted by the ovipositing female or by the spatial pattern of larval or adult feeding. In most cases, the interior of the gall where the herbivore feeds is made up of highly nutritious tissue. For example, observations using labeled ^{14}C in galled cottonwood leaves showed that aphid galls are strong physiological sinks that drew resources from surrounding plant tissues (Larson & Whitham 1991). In general, aphids that feed in galls are more efficient than free-feeding aphids (Llewellyn 1982). This evidence implicates the induction of galls as probable offensive traits. Data on the nutritional quality of the specific tissues fed on by gall makers rather than the entire gall would strengthen this case (Nyman & Julkunen-Tiitto 2000). Better comparisons of herbivore performance on galled and ungalled tissue would provide a more definitive test of offense. Galls provide the gall maker with a specific microhabitat that may include relative safety from pathogens, predators, and parasites, as well as a source of high quality nutrition (Cornell 1983, Weis & Kapelinski 1994).

Herbivores also modify the microhabitat that their host plants provide when they tie, fold, or glue foliage around themselves. These herbivore tactics can greatly reduce the effectiveness of photoactive plant defenses (Berenbaum 1987). Leaf rolling reduces light inside the roll and this behavior was associated with a reduction in leaf toughness and tannin concentration (Sagers 1992). Many herbivores that feed on plants containing photoactive hypericin reduce its activity by tying leaves and feeding in the dark (Sandberg & Berenbaum 1989). This tactic increases rates of development and decreases mortality of larvae and qualifies as offensive.

Damage by many herbivores causes their plants to become better hosts, a phenomenon we term induced plant susceptibility (Karban & Baldwin 1997, Table 4.2). Induced susceptibility is often caused by herbivores manipulating the ontogeny of their host plant to that stage that is most favorable for the herbivores. For example, feeding by green spruce aphids accelerated senescence of spruce

needles (Fisher 1987). Senescent needles were superior hosts for aphids compared with unmanipulated needles that remained in the less mature green stage, making this an example of herbivore offense (sensu Table 1).

Trenching, Mowing, Haying, and Gardening

Herbivores exhibit a great diversity of behaviors associated with feeding that deactivate the defenses of their host plants. Plants can immobilize herbivore mouthparts and reduce feeding by releasing secretions from pressurized canals such as laticifers when herbivores bite. In response, many insects cut veins across the leaf blade prior to feeding. The herbivores then feed beyond the cuts, free from the plant exudates that would normally deter herbivory (Dussourd & Denno 1994, Dussourd 1999). This herbivore behavior precisely matches the architecture of secretory canals in each host plant (Dussourd & Denno 1991). For example, vein clipping is found on plants with arborescent canals, whereas continuous trenching is found on plants with net-like canals. Caterpillars that exhibited these offensive behaviors fed more efficiently and survived much more frequently than those lacking the behaviors on plants in many families that contained pressurized exudates (Dussourd 1993).

Herbivores manipulate plants in many other ways reminiscent of human agriculture. Many insect herbivores reduce the harmful effects of trichomes (plant hairs) by mowing them before they start to feed (e.g., Hulley 1988). Some caterpillars avoid the trichomes by laying down a silk covering or scaffolding over them (e.g., Rathcke & Poole 1975). Certain mammalian herbivores clip vegetation and cache it before consuming it, a behavior known as haying (Vander Wall 1990). For example, pikas cache food in summer that they consume in winter (Dearing 1997). Plants cached in "hay piles" facilitated food storage and also allowed toxins to degrade so that cached food became much more palatable after storage (probable offense).

Herbivores occasionally maintain elaborate gardens. For example, leaf-cutting attine ants gather pieces of fresh leaves and flowers, which they use to culture fungi, their ultimate source of nutrition (Holldobler & Wilson 1990). The ants prepare the pieces of vegetation, chewing, licking, and trimming the fragments before inoculating them with mycelia. The ants maintain a monoculture of their preferred fungus by carrying another mutualist, a filamentous bacterium that produces antibiotics that are particularly effective against parasites of their fungus garden (Currie et al. 1999). Phylogenetic evidence suggests that farming fungi on leaves arose from ants that collected fungi from insects and other substrates (Holldobler & Wilson 1990). More work on the phylogeny of this and other offensive traits could suggest important insights into how the traits evolved and if they have been responsible for diversification of herbivores.

Gregarious Feeding

Group feeding appears to enhance the ability of herbivores to exploit their host plants. There are other advantages to feeding in groups, such as enhanced host

finding and reduced predation risk (Wilson 1975, Breton & Addicott 1992). Homopterans that suck phloem sap from plants create sinks that are preferentially supplied with nutrients (Way & Cammell 1970, Larson & Whitham 1991). The more aphids there are over a wide range of densities, the stronger the sink is. As a result, *Brevicoryne brassicae* showed increased per capita population growth in larger groups (Lopez et al. 1989). Benefits of gregarious feeding have also been reported for chewing insects. Gregarious caterpillars grew twice as fast in large groups (30 individuals) compared with smaller groups (1–10 individuals) (Denno & Benrey 1997). This effect was completely ameliorated when groups of these sizes were grown on excised foliage. Thus large groups either caused nutrient sinks or prevented induced defenses in intact plants compared with smaller groups of herbivores. Gregarious *Battus philenor* caterpillars showed a growth benefit that was positive and linearly associated with group size (J. Fordyce, unpublished manuscript). This effect was caused by a density-dependent induced plant response, perhaps through creation of a nutrient sink. Intraspecific competition and density dependent parasitism may be costs of herbivore aggregations. In most of the cases studied so far, evidence for a benefit to the herbivore preceded a mechanistic understanding of host manipulation.

SYNTHESIS

Models of Herbivore Offense

Herbivore offense has not received much consideration by theoreticians beyond general foraging theory and theories of optimal oviposition in different environments including host plants. These theories are not considered in this review. The small amount of specific herbivore offense theory that exists posits that different strategies will be used by different herbivores and that the strategies will be associated with particular suites of herbivore life-history traits and population dynamics (Rhoades 1985; Price 1990, 1992).

Rhoades described a dichotomy between opportunistic herbivores that avoid plants that are well defended and stealthy herbivores that metabolize plant defenses and manipulate their hosts (summarized in Table 2). Opportunistic herbivores are attracted to plants that provide abundant nutrients and repelled by secondary chemicals and other “deterrents.” Feeding by opportunists often involuntarily causes induced resistance (not present prior to feeding), making their host plants more resistant to subsequent feeding. In contrast, stealthy herbivores metabolize or detoxify the secondary chemicals of their hosts. They manipulate their hosts, inducing them to provide more nutritious tissue for the herbivore to exploit. Stealthy herbivores co-opt the defenses of their hosts and use them for their own benefit, as feeding stimulants, mating rewards, or defenses against their own enemies. They also can inhibit the plant’s induced responses by suppressing the recognition, deployment, or effect of induced resistance.

Offensive strategies may be associated with suites of herbivore life-history traits. For example, stealthy herbivores are posited to be solitary, territorial, and

TABLE 3 Price's (1990) model of herbivore offensive strategies and their consequences

Syndrome	Resources consumed	Choice?	Life history traits	Population dynamics
Latent herbivore	High quality	Ovipositing females choosy	High host specificity, emigration from high density	Relatively low Number, low variation
Eruptive herbivore	Lower quality	Females cannot assess quality or choose	Low host specificity, low dispersal	Can reach high numbers, high variation

have overdispersed damage, whereas opportunists are more likely to be gregarious, colonial, and clumped in space. These life-history traits produce very different patterns of population dynamics for opportunist and stealthy herbivores. Opportunists have a greater intrinsic growth rate and exhibit much more variable population dynamics. Rhoades argues that most outbreaking herbivores are opportunists although there are clearly exceptions.

Price (1990, 1992) also described a dichotomy in herbivore strategies but suggested very different relationships. Price was more explicit in assigning causality: the quality of the resource eaten by different herbivores determines how choosy ovipositing females are, which determines other life-history traits and ultimately population dynamics (Table 3). For "latent" species (whose populations do not outbreak), high-quality resources are scarce. This scarcity causes ovipositing females to be choosy, resulting in a suite of life-history traits including high specificity of host use, emigration from high density sites, and ultimately latent population dynamics. In contrast, eruptive species feed on lower quality resources and females lack the ability to assess or choose host quality. Low-quality resources and lack of choosiness result in the opposite set of life-history traits compared with those associated with latent herbivore species. These life-history traits allow populations to sometimes become very large. The key distinction according to this model is whether females assess and respond to resource quality.

The models of both Rhoades and Price consider host plant choice to be an important determinant of life histories and population dynamics, although they reach rather different conclusions and predictions. Rhoades is much more detailed about specific strategies and tactics. However, his conclusions about the consequences of those strategies are based on intuition rather than a thorough review of the literature. Price does not develop the distinction between the strategies, although his conclusions about their consequences are a first attempt to synthesize the existing literature, which is roughly supportive of his ideas (Price 1992). In a more recent treatment of this model, he and coworkers cite examples of latent herbivores that exhibit strong correlations between oviposition preference and larval performance (Pires et al. 2000). Similarly, eruptive species failed to exhibit choice or to demonstrate a positive correlation between preference for a host and performance

on that host. These patterns from the literature support Price's conceptual model, although the review is clearly selective, as some herbivores with eruptive dynamics have been found to make appropriate choices (e.g., willow beetles; Rank et al. 1998) and some with latent dynamics fail to make appropriate choices (e.g., the pearly marbled butterfly; Karban & Courtney 1987). However, these exceptions do not falsify the generality and a more complete meta-analysis of the many reported preference-performance studies would be a useful contribution.

The Importance of Choice

The theories of herbivore offense developed by Rhoades and especially by Price emphasized the importance of choice. We wish to underscore that observation and to note that many plant defenses will be effective only if herbivores make appropriate and rather sophisticated choices. A plant that poisons its herbivores will not necessarily have higher fitness than one that does not, unless poisoned herbivores reduce plant fitness less than herbivores that have not been poisoned. All else being equal, plant defenses that cause herbivores to avoid feeding on the plant will be most effective from the plant's perspective. Defenses that act prior to significant damage to the plant will be more effective than those that act after ingestion. Defended plants will probably benefit most from pre-ingestive herbivore strategies because herbivores will be deterred. In contrast to plants, herbivores can accrue benefits from both pre- and post-ingestive strategies.

Selection may favor plants that respond to their risk of herbivory as well as herbivores that assess plant quality and choose accordingly (Karbon et al. 1997, 1999). Traits that allow herbivores to accurately assess plant quality may benefit herbivores as well as plants. Hamilton & Brown (2001) suggest that plants may provide reliable information to their herbivores indicating their level of defense. They interpret autumn coloration of tree leaves as a signal to colonizing herbivores that the brightly colored leaves are not very good hosts. There is some empirical support for this contention. For example, maple aphids were more likely to place overwintering offspring on maple leaves that were yellow or orange and less likely to oviposit in trees with red foliage (Furuta 1986). Those aphids that colonized the reddest trees experienced reduced fitness (Furuta 1990, in Hamilton & Brown 2001).

Herbivore Offense and Adaptive Plasticity

The models of Rhoades and Price were useful as broad generalizations, although their ability to offer a predictive framework was limited. As an alternative, we suggest that herbivore offense can be categorized along two axes: when they work and whether they are plastic or fixed (Table 4A). Offensive traits may work before the herbivore ingests the plant or after ingestion. The herbivore may alter its offensive traits depending upon the host and other conditions or the traits may be fixed. In theory, phenotypic plasticity can maximize fitness in variable environments (Levins 1968, Agrawal 2001). We consider two different ways for an herbivore to exhibit plasticity: (a) by choosing which resources to exploit or

TABLE 4 Herbivore offense categorized by plasticity and time of action

	Pre-ingestion	Post-ingestion
A Examples of offensive tactics		
When does the trait work?		
Plastic	Behavioral choice Trenching, haying of selected hosts	Diet mixing, learning Inducible enzymes, morphology
Not Plastic	No behavioral discrimination Galling and leaf rolling Salivary enzymes	Fixed physiology, morphology Sequestration Internal digestive symbionts
B Predictions		
When does the trait work?		
Plastic	Generalist Unpredictable resource Can be aggressive	Generalist Unpredictable resource Less aggressive
Not Plastic	More specialized Predictable resource Most aggressive	More specialized Most predictable resource Less aggressive

(*b*) by altering its morphology and physiology rather than its choice. There are examples of herbivores that are plastic in both ways (e.g., inducible enzymes of generalists), not plastic in either (e.g., many specialists), or plastic in one category but not the other.

Arranging offensive tactics along these two axes of when they work and whether they are plastic leads to several predictions (Table 4B). First, plastic offensive traits are often employed by generalist herbivores that feed on many plant species and adjust their traits accordingly. Conversely, more specialized herbivores are more likely to have offensive traits that are not plastic. Some offensive traits of generalists are nonplastic, such as the salivary enzymes or filter chambers of xylem-feeding homopterans. However, these traits have widespread utility against chemical and physical obstacles that are highly conserved across plant species. Similarly, xylem feeders are faced with a food source that is much more homogeneous across plant species than are other plant tissues. Second, offensive traits that are not plastic are most often associated with plant resources that are highly predictable to the herbivore. This seems particularly true for post-ingestive traits; once a food has entered an herbivore's gut, if the morphology and physiology of the gut are not plastic, the food had better be predictably palatable and nutritious. It is interesting to note that many of the offensive traits of specialist herbivores that are plastic involve unpredictable resources. For example, specialized monarch caterpillars do not cut veins consistently in their milkweed hosts. Vein cutting only occurs when latex volume and pressure in the milkweed host are high (A.A. Agrawal, personal

observation). Third, most of the examples of aggressive offensive traits work prior to ingestion, especially for nonplastic traits. An herbivore has less opportunity to manipulate its host once it has ingested it. Rapidly growing, young, intact plants are generally the most inducible and most subject to manipulation by the herbivore (Karban & Baldwin 1997). In summary, the early attempts to categorize herbivore offense by Rhoades and Price have served as useful starting places for development of a theory for this field. However, we found their categories less than satisfying and have proposed that consideration of when a trait works and whether it is plastic may lead to more robust predictions. These categories are simplifications of a continuum and can never capture the full richness of species interactions. Although the categories have heuristic value, a systematic and objective analysis of many herbivore species is required to assess whether this framework adds clarity or just more arm waving.

Costs and Limitations to Herbivore Offense

A consideration of the costs and benefits has been very instructive in structuring our thinking about the ecology and evolution of plant defenses. Much of this review has been a compilation of the potential and realized benefits of traits that herbivores use to exploit their host plants. Generally, we have found only a limited number of studies demonstrating that these traits increase herbivore fitness. Similarly, there have been few tests of the notion that offensive traits are costly for herbivores.

Potentially, costs and limitations of offensive strategies can take many forms. One of the greatest costs of choosiness is that many suitable host plants will be rejected as unacceptable (Waldbauer & Fraenkel 1961). In such cases, herbivores are passing up good opportunities in order to minimize the likelihood of adversity. There are also likely to be limits to the processing abilities of herbivores; the ability to recognize some foods may come at the expense of recognition of other foods or potentially important stimuli (Bernays 2001). Similarly, enzyme systems that respond to food constituents carry potential allocation costs. In other words, resources that are allocated to enzyme systems cannot then be used by the herbivore for other purposes (growth, reproduction, etc.). Several workers have looked for allocation costs of enzyme systems that metabolize plant secondary chemicals and have failed to observe reductions in food utilization or growth parameters associated with the induction of enzymes (Neal 1987, Appel & Martin 1994). A few studies have found circumstantial evidence for measurable costs of enzymatic metabolism, although other costs such as autotoxicity or hormonal imbalances may be larger but unexamined (Berenbaum & Zangerl 1994, Agrawal et al. 2002).

Essentially, all the tactics considered in this review may be costly to the herbivores, although these costs have not been well documented. Symbionts may also be expensive for herbivores to maintain. Bacterial endosymbionts of aphids greatly increase aphid fecundity while reducing other aspects of aphid fitness on some hosts (Chen et al. 2000; T. Leonardo, unpublished manuscript). Clipping plant veins makes herbivores conspicuous to their predators and exposes them

to physical challenges of sticky exudates. Mortality associated with this behavior is relatively high (Zalucki et al. 2002). Gregarious feeding increases levels of intraspecific competition, attracts predators, and may increase the likelihood of induced plant responses (e.g., Dyer & Gentry 1999, Williams & Whitham 1985). Sequestration of plant chemicals can come at the expense of growth. For example, specialist buckeye caterpillars, fed on diets high in iridoid glycosides, sequestered the glycosides but became less efficient at digesting their food (Camara 1997). Better measures of the costs and benefits of offensive tactics in terms of herbivore performance and especially fitness will sharpen our ability to predict the outcome of ecological interactions and coevolution.

CONCLUSIONS

We have outlined a list of criteria (questions) for herbivore offense. Do herbivore traits match their host plants? Have those traits been found to increase feeding and other uses? Do they increase herbivore performance? What is the evidence that herbivore traits have evolved to increase fitness on those hosts? For each of these questions, are alternative explanations possible? Answering these questions should allow us to be much more explicit about the nature and strength of the evidence for herbivore offense and allow more rapid progress in this subdiscipline. In the future, the theory and evidence for herbivore offense should match that accumulated for plant defense.

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