

## Herbivory in holometabolous and hemimetabolous insects: contrasts between Orthoptera and Lepidoptera

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**Summary.** Adaptation to a phytophagous diet involves physiological compromises that may be influenced by developmental constraints. In this review, we compare patterns of hostplant utilization with respect to nutrition and allelochemistry in representative holometabolous (lepidopteran) and hemimetabolous (orthopteran) species in order to identify those potential constraints. Overall, in Lepidoptera greater molting efficiency and gut permeability, which enhance nutritional efficiency, result in higher exposure to allelochemicals and are associated with greater activity and inducibility of cytochrome P 450 monooxygenase detoxication enzymes. In contrast, in Orthoptera, relative impermeability to allelochemicals due to the peritrophic membrane and cuticular sclerotization is associated with reduced nutritional efficiency and lower detoxication enzyme activity.

**Key words.** Lepidoptera; Orthoptera; digestive efficiency; allelochemistry; cytochrome P 450; nutrition.

Almost 88% of all living insect species are holometabolous; the separation of larval feeding stages from reproductive adult stages by a pupal stage has greatly influenced patterns of life cycle dynamics and ecological interactions with other organisms. Among the holometabolous orders, the Lepidoptera is almost exclusively phytophagous. Like the Lepidoptera, the Orthoptera, a hemimetabolous order, is dominated by phytophagous species. However, fundamental differences exist in the ways in which members of these orders locate, assess, and utilize plant material. These differences may well result from constraints imposed by their different developmental patterns. In this paper, differences in host finding and utilization are examined for the Lepidoptera and the orthopteroid orders<sup>22</sup> within the context of development in order to gain insights into evolutionary advantages or disadvantages relative to a phytophagous lifestyle.

### *Life history contrasts*

Without doubt, one of the greatest differences between holometabolous and hemimetabolous insects involves ontogenetic changes in feeding habits. Whereas phytophagous orthopterans tend to feed in the same manner at all life stages, lepidopterans show a universal disparity between adult and larval feeding habits. The majority of adult lepidopterans are nectarivorous or nonfeeding altogether, while the majority of adult orthopterans feed on the same tissues consumed by immatures. One possible explanation for this separation of feeding and reproductive stages in Lepidoptera is that greater feeding efficiency in the larval stages (see below) obviates the need to continue acquiring nutrients for egg production in the adult stages. Another clear difference between orthopteran and lepidopteran plant-feeders is in the manner of feeding. Most if not all orthopterans are foliage feeders, specifically, leaf chewers; in contrast, larval lepidopterans include in their ranks not only leaf chewers but leaf miners, gall formers, and stem borers as well. These more specialized feeding habits may result from holo-

metabolous development in that the pupal stage allows for either a partial or complete reorganization of larval tissues such that specialized trophic apparatus suited for different life stages can arise. Specialized feeding habits extend not only to plant parts consumed and manner of feeding but to host preference as well. Oligophagy among orthopterans is largely restricted to those species associated with several genera of Gramineae (Poaceae)<sup>13</sup>, or with low-diversity plant assemblages<sup>65</sup>. In fact, several studies<sup>62,77</sup> have demonstrated that mixed diets are nutritionally superior to single plant diets for polyphagous acridids; a mixed diet offered to the red-legged grasshopper, *Melanoplus femurrubrum*, resulted in greater fecundity than any of four single-plant diets<sup>3</sup>. In contrast, among holometabolous herbivores, oligophagy may well be the rule rather than the exception. For example, over 80% of North American butterflies for which host data are available feed on only a single-plant family and fewer than 1% are reported to feed on more than four families<sup>43</sup>.

### *Nutrition*

Patterns of growth and development differ between holometabolous and hemimetabolous species. In particular, holometabolous species show considerably higher growth ratios, i.e. proportional increases in size over successive molts<sup>38</sup>. An examination of growth ratio data for 105 species of insects revealed that growth ratios for holometabolous species average 1.52 whereas ratios for hemimetabolous species average 1.27<sup>38</sup>. The data summarized in this study for Lepidoptera and Orthoptera are consistent with the overall trend; percentage increase in size of body part from one molt to the next averaged 18.6 for Orthoptera (sensu lato) and 45.2 for Lepidoptera (calculated from table 1<sup>38</sup>). Enders<sup>44</sup> attributed small growth ratios to high mobility of immature stages which expend energy while foraging widely to find adequate food. Although this explanation may generally hold for Lepidoptera and Orthoptera, which overall represent ex-

tremes in a continuum from sedentary to highly mobile immature stages, it falls short on explaining individual cases; for example, among the lowest growth ratios exhibited for Lepidoptera is that of *Dichomeris marginella*, a gelechiid leafroller that rarely moves during the entire course of larval development. Its percentage increase in body part size between successive molts, 27, is virtually identical to that of the more mobile acridid *Dendrotettix quercus*.

A far more plausible explanation for differences in growth ratios between holometabolous and hemimetabolous insects is that the two groups of insects differ fundamentally in the efficiency with which they utilize their food. In a discussion of the nutritional ecology of graminivorous insects, Bernays and Barbahenn<sup>13</sup> compiled a table presenting approximate digestibilities and efficiencies of conversion of digested food to body substance for both orthopterans and lepidopterans. Even on the same hostplant, foliage-feeding orthopterans tend to be less efficient than foliage-feeding lepidopterans; for example, on seedling wheat, approximate digestibilities for six orthopteran species ranged from 34 to 42% (mean 38.8) and for four lepidopterans ranged from 32 to 59% (mean 50.8). Similarly, efficiencies of conversion of digested food into body mass for orthopterans ranged from 7 to 39% (mean 30.5) and for lepidopterans ranged from 39 to 73% (mean 49.5). In a subsequent study, Bernays<sup>12</sup> directly compared growth and performance of a holometabolous and a hemimetabolous species on the same foodplant (seedling wheat) under identical rearing conditions. She found that the lepidopteran, the armyworm *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), had growth rates 2 to 3.5 times higher than the migratory grasshopper *Melanoplus sanguinipes* (Orthoptera: Acrididae), both at stages during which the two insects were of similar mass and over the entire developmental period. Efficiency of conversion of digested food to body mass was 50% higher and consumption rate 100% higher in the lepidopteran.

Bernays<sup>12</sup> suggested that the major factor causing differences in digestive efficiencies is that the grasshopper produces a cuticle mass relative to body weight about ten times greater than the caterpillar; whereas only 4.2% of dry body weight of the armyworm is cuticle, 49% of the dry body weight of *M. sanguinipes* is cuticle. A survey of the literature by Bernays<sup>12</sup> revealed that this enormous difference in cuticle content is consistent throughout the two orders; cuticle as a percent of dry weight of orthopterans ranges from 40 to 56% and of lepidopterans ranges from 1.3 to 8%. Plants with low amounts of phenylalanine and other aromatic amino acids used in cuticle synthesis may be adequate to support growth of lepidopterans but inadequate to support growth of orthopterans<sup>20</sup>; iceberg lettuce (*Lactuca sativa*), for example, supported growth and development of the cabbage looper, *Trichoplusia ni* (Lepidoptera: Noctuidae), through pupation but failed to support *M. sanguinipes*

through the third instar (MB, personal observation). Bernays<sup>11</sup> observed a 30% increase in dry matter weight gain in desert locust, *Schistocerca gregaria*, nymphs on lettuce when it was supplemented with phenylalanine. The major effects of phenylalanine supplementation occurred in the first four days of the instar, presumably when cuticle production and stabilization are taking place.

Once stabilized, cuticular proteins may not be available or reclaimable at the next molt. While no studies have been carried out on the efficiency of recovery of cuticular components as a result of molting fluid action, there are data that show that lepidopteran cuticle may contain more accessible proteins. While Cox and Willis<sup>40</sup> found that almost two thirds of caterpillar dorsal abdominal cuticle protein could be solubilized with denaturing agents such as NaOH, Andersen<sup>2</sup>, albeit using different methods, found that 5 days after ecdysis to the fifth instar only 32–50% of cuticular protein was extractible from *Schistocerca gregaria*. The caloric content of shed cuticle of *Encyrtolophus sordidus* (Orthoptera) represents 18.9% of total energy accumulated during immature stages; comparable measures for lepidopterans range from 2.6 to 10.2%<sup>71</sup>. Not only is less cuticle lost to ecdysis, but many caterpillars consume shed skins and possibly reclaim even more nutrients.

The substantial loss of both protein and carbohydrate (chitin) in orthopteran cuticle at each molt may well account for the lower growth ratios and efficiencies of plant-feeding orthopterans in comparison with plant-feeding lepidopterans. Moreover, in contrast with Lepidoptera, the peritrophic membrane in the Orthoptera forms an intact sheath around fecal pellets and is continually excreted along with the feces<sup>34</sup>, representing an additional loss of cuticular material. Finally, intra-stadial growth of holometabolous insects, in which epidermal DNA replication and mitotic division take place between molts, may allow holometabolous insects to reach adulthood with fewer molts. In general, holometabolous species reach maturity in fewer molts than do hemimetabolous species, even taking the pupal molt into account<sup>80</sup>. Given that the molting process itself is energetically expensive and involves metabolism of both lipid and carbohydrate reserves<sup>71</sup>, reduction in the number of molts may increase overall growth efficiencies.

#### Responses to allelochemistry

Utilization of plant nutrients is only one component of phytophagy; coping with plant allelochemistry is perhaps equally important in determining patterns of host-plant use. Orthopterans and lepidopterans display many conspicuous differences in the ways in which plant allelochemicals are processed.

#### Orientation to hostplants

The vast majority of acridoid orthopterans (the major group of plant feeders in the Orthoptera) oviposit not on

the hostplant itself but rather in soil. In contrast, the majority of Lepidoptera oviposit on or near their hosts (conspicuous exceptions being grass-feeding Satyridae among others). Olfactory orientation responses by ovipositing lepidopterans are well documented<sup>45</sup>. Demonstrations of orientation responses to plant volatiles by ovipositing females are virtually nonexistent for Orthoptera. In fact, Norris<sup>64</sup> provided evidence that ovipositing *Schistocerca* females avoid laying eggs close to plants and that some plant extracts are actually repellent. Rather more important in regulation of oviposition behavior by orthopterans are properties of soil such as moisture, chemistry, and texture<sup>78</sup>.

Since hatching nymphs must find food on their own, one would expect some degree of response to hostplant volatiles. In point of fact, there is little evidence to indicate any olfactory orientation to hosts among acridoid orthopterans at any life stage<sup>78</sup>. Although anecdotal observation of olfactory orientation abounds<sup>66, 78</sup>, experimental evidence is far from definitive<sup>48</sup>. According to Uvarov<sup>78</sup>, 'if an attraction to the smell of a foodplant exists, there is still very little evidence of its effective range and on this depends its influence on food selection in the field.' It may be coincidental that acridoid orthopterans do not rely heavily upon olfaction for mate finding either; acoustical signals predominate throughout the suborder<sup>78</sup>.

Gustation, however, is a different story. Contact chemoreception is highly developed in both Orthoptera and Lepidoptera. Different mechanisms may underlie behavioral responses to chemosensory stimuli. Grasshoppers, with over 15,000 neurons associated with the mouthparts, are capable of detecting and distinguishing among literally hundreds of plant chemicals and complex mixtures thereof<sup>82</sup>. Chapman and Thomas<sup>36</sup> documented a correlation between the numbers of receptors on the mouthparts of grasshoppers and host breadth. Oligophagous species have fewer sensilla than polyphagous species, whereas monophagous species have the fewest of all. Thus the evolution of dietary specialization in grasshoppers appears to have been accompanied by a reduction in numbers of sensilla, towards the numbers found in highly monophagous lepidopterans. Some caterpillars and other holometabolous larvae are believed to possess specialized receptors for particular chemicals; at the level of central processing, a 'labelled line' mechanism exists, with its attendant specific receptor cells with a narrow sensitivity spectrum<sup>72</sup>. Tarsal chemoreceptors of this sort have been identified in caterpillars<sup>72, 79</sup>. In Lepidoptera, differentiation can be made at the central nervous system level between stimulatory and deterrent signals based on receptor cell inputs<sup>18</sup>. Less definitive evidence of such receptors has been found in Orthoptera. Instead, neurophysiological responses to chemical stimuli in Orthoptera generally consist of activity in at least two receptor cells in any sensillum regardless of the behavioral effects of the chemical on the whole

insect<sup>21</sup>; that is, no set pattern of neurophysiological response is associated with either acceptance or rejection<sup>81</sup>. However, Chapman<sup>34</sup> suggests that labelled line systems do exist for nordihydroguaiaretic acid in *Boottettix*, a creosote bush grasshopper, and for azadirachtin in *Schistocerca*.

The inability to perceive specific chemical cues via specialized receptors may be linked to the relative lack of feeding specialization among phytophagous orthopterans (but see Rowell<sup>67</sup>). For polyphagous species, the greater mobility of immature stages of orthopterans would make avoidance of those plants triggering neurophysiological deterrence considerably more adaptive than it would be for the relatively immobile immature stages of most lepidopterans (particularly miners, borers, or other concealed feeders). Thus, orthopterans display sensitivity to the presence of allelochemical deterrents in the diet<sup>17</sup> and a relative lack of sensitivity to nonnutritive 'token stimuli' (although sugars and other nutritive substances are phagostimulatory)<sup>35</sup>. In general, ovipositing female lepidopterans are responsible for much of the process of host selection for their offspring, while orthopteran nymphs are on their own as much as adults are in terms of hostplant selection. It is surprising, therefore, that a quantitative comparison of feeding inhibition (table 1) shows no conspicuously greater ability on the part of orthopterans to detect plant chemicals and cease feeding. For almost every class of plant chemical tested, orthopterans displayed equivalent or less sensitivity to antifeedants than do lepidopterans. This relatively greater insensitivity to allelochemicals may be associated with a relatively greater tolerance for allelochemicals after ingestion (see below).

#### *Metabolism of allelochemicals*

Cytochrome P450 monooxygenases are generally regarded as the primary system for metabolism of xenobiotics, including plant secondary compounds, in insects<sup>24, 25</sup>. Despite the fact that acridoid orthopterans are almost exclusively phytophagous, their P450 system has been only infrequently investigated; most work focuses on synthetic substrates, such as insecticides, rather than plant-derived chemicals, and on nonphytophagous representatives of the order, such as cockroaches. Nonetheless, comparisons of the few available data are informative. As is the case for all animals and plants, orthopteran and lepidopteran systems require NADPH and oxygen<sup>4</sup>; both groups also display inhibition by carbon monoxide and synergism by methylenedioxyphenyl derivatives such as piperonyl butoxide<sup>5</sup>. As is the case for most other insect groups, substrate specificity is broad and considerable age and sex variation exists<sup>6</sup>.

Despite the similarities, differences do exist between orthopteran and lepidopteran P450 systems. Crankshaw et al.<sup>41</sup> prepared rabbit antibodies against NADPH cytochrome C reductase from the southern armyworm *Spodoptera eridania* (Noctuidae) and examined their

Table 1. Deterrency of plant chemicals to Orthoptera (O) and Lepidoptera (L)

Chemical	Insect	Inhibitory concentration (ppm/% of normal feeding response)	Reference
Glycosides			
Aucubin	<i>Locusta migratoria</i> (O)	1000/50%	17
Catalposide	<i>Lymantria dispar</i> (L)	1000/54%	56
Alkaloids			
Quinine	<i>Locusta migratoria</i> (O)	100/50%	17
	<i>Pieris brassicae</i> (L)	5/50%	47
Tomatine	<i>Locusta migratoria</i> (O)	1500/50%	17
	<i>Pieris brassicae</i> (L)	40/0%	47
Senecionine	<i>Locusta migratoria</i> (O)	10/50%	17
Senkirkine	<i>Choristoneura fumiferana</i> (L)	180/11%	47
Phenylpropanoids			
Chlorogenic acid	<i>Locusta migratoria</i> (O)	2 × 10 <sup>4</sup> /50%	17
	<i>Pieris brassicae</i> (L)	570/60%	47
Umbelliferone	<i>Locusta migratoria</i> (O)	1 × 10 <sup>4</sup> /50%	39
	<i>Schistocerca gregaria</i> (O)	1 × 10 <sup>5</sup> /50%	39
	<i>Mythimna unipuncta</i> (L)	2000/96%	61
Sesquiterpenes			
Warburganal	<i>Locusta migratoria</i> (O)	100/50%	63
	<i>Spodoptera exempta</i> (L)	0.1/5%	63
Diterpenes			
Ajugarin I	<i>Schistocerca vaga</i> (O)	1000/≤20%	57
	<i>Schistocerca gregaria</i> (O)	0.06/≤20%	57
	<i>Spodoptera exempta</i> (L)	100/≤20%	57
	<i>Spodoptera littoralis</i> (L)	300/≤20%	57
Triterpenes			
Azadirachtin	<i>Schistocerca gregaria</i> (O)	0.04/0%	56
	<i>Spodoptera frugiperda</i> (L)	0.01/0%	47
	<i>Melanoplus sanguinipes</i> (O)	500/100%	30
	<i>Peridroma saucia</i> (L)	0.3/50%	30
Miscellaneous			
Aristolochic acid	<i>Locusta migratoria</i> (O)	0.01/50%	17
	<i>Papilio glaucus</i> (L)	5000/71%	60

Table 2. Inhibition of NADPH-cytochrome c reductase of different species by anti-armyworm reductase IgG<sup>41</sup>

Order	Family	Species	NADPH-cytochrome c reductase activity (nmoles/min/mg protein)	Inhibition (%) (IgG/protein, 4:1)	
Lepidoptera	Noctuidae	<i>Spodoptera eridania</i>	63.4	84.0	
	Lasiocampidae	<i>Malacosoma americanum</i>	58.3	72.0	
	Noctuidae	<i>Xestia smithii</i>	29.0	62.5	
	Oecophoridae	<i>Depressaria pastinacella</i>	40.3	59.6	
	Arctiidae	<i>Euchaetius egle</i>	64.0	52.4	
	Papilionidae	<i>Battus philenor</i>	56.7	48.7	
	Papilionidae	<i>Papilio polyxenes</i>	159.3	48.2	
	Pieridae	<i>Pieris rapae</i>	77.1	47.2	
	Noctuidae	<i>Trichoplusia ni</i>	38.0	45.0	
	Danaidae	<i>Danaus plexippus</i>	40.3	40.0	
	Tortricidae	<i>Choristoneura fumiferana</i>	103.0	36.0	
	Sphingidae	<i>Hyles lineata</i>	84.0	22.6	
	Orthoptera	Acrididae	<i>Melanoplus femurrubrum</i>	32.2	35.8
		Blaberidae	<i>Gromphadorhina portentosa</i>	62.6	30.5
Blattidae		<i>Periplaneta americana</i>	69.7	10.2	

cross-reactivity (via % inhibition) with 22 other insect species. While overall cross-reactivity was high for other Lepidoptera (over 40% generally and over 60% for con-familial noctuids), percent inhibition was invariably less than 40% and as low as 10% for orthopterans (table 2). Curiously, immunological cross-reactivity, though present at high levels in Diptera, was nonetheless lacking in

the holometabolous Coleoptera and Hymenoptera examined. It is difficult to determine whether cross-reactivity results from phylogenetic relationship, convergence, or nonimmunochemical factors; however, between-order differences appear to be greater than within-order differences for Lepidoptera and Orthoptera (table 2).

### Localization

In general, highest activity levels of cytochrome P450 enzymes in Lepidoptera are found in larval midguts<sup>24-26</sup>. In contrast, other organs often show high activity in Orthoptera. Oxidizing activity in fat body and gastric caeca was four and two times higher respectively than in midgut of *Schistocerca gregaria*<sup>28</sup>. Feyereisen and Durst<sup>46</sup> found that the fatbody of fifth instar *Locusta* nymphs had cytochrome P450 content equivalent to or greater than that found in the larval midgut of several species of noctuids<sup>1</sup>, while locust midgut had approximately 7 times less P450 than the fatbody. Yu<sup>83</sup> and Benke and Wilkinson<sup>4</sup> found very high activity in the Malpighian tubules, both on a per-insect and per-mg protein basis, in several species of crickets. As the main excretory organs, Malpighian tubules may be exposed to considerable quantities of unmetabolized allelochemicals which for one reason or another were not processed in the gut. Grasshopper Malpighian tubules are known to actively transport toxins such as phlorizin and ouabain<sup>23</sup>. Uvarov<sup>77</sup> makes the observation that five of the most injurious genera of Orthoptera, all of which are broadly polyphagous and could be expected to encounter a wide range of allelochemicals, have relatively high numbers of tubules.

### Inducibility

Ample evidence exists for the inducibility of P450 enzymes in a variety of insect and noninsect taxa<sup>49, 74, 75, 83</sup>; at least for Lepidoptera, evidence exists that naturally occurring allelochemicals in hostplants can serve as P450 inducers<sup>27</sup>. Virtually all demonstrations of inducibility irrespective of the nature of the inducer involve holometabolous species. In one investigation of *Schistocerca gregaria*, Chakraborty and Smith<sup>29</sup> failed to observe enhanced oxidation by 'phenobarbitone' or 3,4 benzopyrene, although enhancement was observed in rats following pretreatment with these chemicals. Khan and Matsumura<sup>55</sup> provide the only evidence of inducibility of orthopteran P450 enzymes; they demonstrated induction in insecticide-resistant strains of both German and American cockroaches. The importance of induction in hostplant relations<sup>27</sup> is as yet undetermined for orthopterans.

### Activity

Activity levels are extremely difficult to compare; published data from different investigators likely reflect within-study variation due to biological factors such as diet and age and between-study variation due to differences in pH, temperature, and tissue preparation procedures. Comparisons are made here from one study in which many species were surveyed simultaneously<sup>58</sup> and from studies conducted at different times but by one investigator or laboratory group<sup>82, 83</sup>.

Table 3. Cytochrome P-450 and mono-oxygenase activity in microsomal preparations of different insect species. (Modified from Kulkarni<sup>58</sup>)

Species	O-Demethylation (nmol pNP mg <sup>-1</sup> protein)	NADPH cytochrome c reductase (O.D. 5 min mg <sup>-1</sup> protein)
<i>Heliothis virescens</i> (L)	30.00	2.22
<i>Manduca sexta</i> (L)	21.33	3.685
<i>Prodenia eridania</i> (L)	18.00	3.36
<i>Galleria mellonella</i> (L)	4.65	1.510
<i>Gromphadorhina</i> <i>portentosa</i> (O)	2.75	1.195
<i>Blaberus craniifer</i>	1.0	0.870
<i>Periplaneta brunnea</i> (O)	0.23	0.15
<i>Periplaneta fuliginosa</i> (O)	0.06	0.887
<i>Blattella germanica</i> (O)	0.0	0.088
<i>Periplaneta americana</i> (O)	0.0	0.00

What appears clear from the data of Kulkarni et al. (table 3), is that orthopterans in general have considerably lower levels of P450 enzyme activity. Unfortunately, Kulkarni et al.<sup>58</sup> did not examine acridoid orthopterans; cockroaches, which are generally omnivorous, may differ fundamentally from phytophagous orthopterans in the manner in which they process plant allelochemicals. Yu's studies<sup>82, 83</sup> reveal comparable aldrin epoxidase activity in caterpillars and crickets. A direct comparison of enzyme activity relative to naturally occurring plant-derived substrates would be most instructive but is not yet available. There is evidence of orthopteran metabolism of host allelochemicals consistent with P450 activity. The grasshoppers *Melanoplus differentialis* and *M. femurrubrum* are capable of rapidly metabolizing nicotine to non-toxic products<sup>69</sup>, and *M. sanguinipes* metabolizes the chromenes enecalinal and precocene II<sup>7, 51</sup> and the pyrrolizidine alkaloid senecionine-N-oxide<sup>42</sup>. The precise mechanisms of metabolism and role of P450 in these cases, however, are not yet known.

### Discussion

Relatively substantial cuticle production characterizing immature stages of orthopteran insects may serve an important role in protecting the insect from injury by or penetration of xenobiotics. Due to this enhanced protection from both topical and oral toxicants, the need for a powerful microsomal P450 system for processing allelochemicals may never have arisen. Isman<sup>50</sup> demonstrated that toxicity of sesquiterpene lactones to the migratory grasshopper, *Melanoplus sanguinipes*, is greatly enhanced when they are injected directly into the hemocoel, rather than applied topically or orally, suggesting that the integument and the alimentary canal provide effective barriers limiting the bioavailability of these compounds to the sensitive target sites in the hemocoel. For example, the sesquiterpene lactone, parthenin, is toxic to *M. sanguinipes* when injected into the hemocoel, with an LD<sub>50</sub> of 0.55 μmol per insect. However, this grasshopper

can tolerate oral doses of 1.0  $\mu\text{mol}$  with no apparent signs of distress<sup>50</sup>. Similarly, another sesquiterpene lactone, tetraeurin-A, has an  $\text{LD}_{50}$  by injection of 0.68  $\mu\text{mol}$  per insect, but the grasshopper can tolerate oral doses of 4.0  $\mu\text{mol}$  without ensuing toxicity. Cottee et al.<sup>39</sup> reported that, among five different allelochemicals toxic by injection to both *Locusta* and *Schistocerca*, only two of the chemicals had significant oral toxicity to *Locusta*, and none had significant oral toxicity to *Schistocerca*. The two chemicals which were toxic by both injection and oral administration to *Locusta*, allylisothiocyanate and nicotine hydrogen tartrate, were 17 and 7 times less toxic via the oral route, respectively. In at least one case, involving *Melanoplus sanguinipes*, the 3.5-fold reduction in toxicity of an ingested (vs injected) compound (azadirachtin) is associated with P450 action (D. Champagne, pers. comm.). Scudder and Meredith<sup>68</sup> found no evidence for the presence of either polar (ouabain) or nonpolar (digitoxin) cardenolides in the hemolymph of *Schistocerca gregaria* adults following oral administration of radiolabeled cardenolides. When radiolabeled forms of the phototoxins xanthotoxin (a furanocoumarin) or  $\alpha$ -terthienyl (a thiophene) were fed to adult *Melanoplus sanguinipes*, virtually 100% of the unchanged label was found in the feces (Champagne and Isman, unpublished data).

In contrast, both xanthotoxin and  $\alpha$ -terthienyl have been shown to cross the gut wall and enter the bloodstream in lepidopterans to a large extent<sup>52, 53</sup>. Similarly, while only 21 and 25% of radiolabeled malathion and carbaryl respectively enter the serosal fluid of *Blabrus discoidalis* (a cockroach) through the midgut, 56% and 67% of the corresponding radiolabeled compounds transit the gut of the tobacco hornworm, *Manduca sexta*<sup>76</sup>.

Thus, in Lepidoptera, where cuticle comprises less than 4% of total immature body dry weight (compared to more than 40% for orthopterans), physiological exposure to ingested toxins is likely and P450 metabolism of xenobiotics is highly inducible. The midgut of orthopterans, although not cuticular on the inner surface, is nonetheless lined with a cuticular peritrophic membrane renewed constantly by delamination (formation of a template by microvilli) from the gut epithelium<sup>33</sup>. This cuticular lining in *Schistocerca gregaria* is impermeable to most lipophilic compounds<sup>59</sup>. Moreover, the peritrophic membrane and other gut tissues of some orthopterans are capable of adsorbing plant allelochemicals<sup>8-10</sup>. Bernays and Chamberlain<sup>14</sup> demonstrated in vitro that peritrophic membrane of *S. gregaria* can adsorb up to five times its own weight in tannic acid and in vivo adsorbs minimally its own weight. When radiolabeled gallic acid was fed to the tree locust *Anacridium melanorhodon*, more than half of the label recovered from the insects resided in the gut tissues<sup>19</sup>. Similarly, when the chromene enecalinal was fed to *M. sanguinipes* only 20–25% of the administered dose could be recovered in the feces (parent and metabolites combined) (Isman, unpublished

data). However, no enecalinal (or metabolites) could be found in the hemolymph, suggesting that enecalinal is adsorbed onto, but not through, the gut. Whereas in Orthoptera peritrophic membrane is composed of a regular fibrillar network with overlapping fibrils, in Lepidoptera peritrophic membrane consists of irregularly oriented fibrils in an amorphous matrix<sup>31</sup>. Such a system may not be as effective in preventing penetration by allelochemicals<sup>15, 16, 73</sup>.

Gut impermeability to allelochemicals for orthopterans has a potential price, however, in terms of decreased permeability to nutrients and greater metabolic expense. Peritrophic membranes are substantially impermeable to polysaccharides and proteins<sup>33</sup> and a peritrophic membrane that excludes allelochemicals may also exclude nutrients and reduce overall growth efficiency. The cuticular investment of orthopterans may also exact metabolic costs at the same time that it reduces exposure to environmental toxicants. The great advantage of lepidopteran cuticle is not only that it is more extensible and can accommodate growth but also that it conserves material – cuticle carbohydrates and proteins can be digested and reabsorbed at each molt. The relatively high investment in cuticular carbohydrate by orthopterans, with less metabolic return, may account for the feeding behavior observed by Simpson et al.<sup>70</sup>. An oligophagous acridid, *Locusta migratoria*, and a polyphagous lepidopteran, *Spodoptera littoralis*, were permitted to select among several nutritionally incomplete artificial diets. The orthopteran displayed a marked preference for carbohydrate-rich diets relative to the lepidopteran, which selected a mixture representing 20% carbohydrate: 80% protein. In another study Cohen et al.<sup>37</sup> demonstrated a similar (even more marked) preference for carbohydrates in the cockroach *Supella longipalpa*. This tendency by orthopterans to consume preferentially greater quantities of carbohydrates than their lepidopteran counterparts may reflect a lesser ability to extract the nutrients in the first place (due to a relatively less permeable peritrophic membrane) and a lesser ability to conserve ingested carbohydrate (due to the continuing necessity of renewing cuticle).

### Conclusion

If this review serves no other purpose, it will serve to highlight areas of research in dire need of attention. In order to draw any robust conclusions about the existence of an adaptive compromise between nutritional efficiency and exposure to plant allelochemistry, additional data are needed. It is, for example, necessary to determine precisely relative recoverability of nutrients in cuticle shed at ecdysis and their importance in overall nutrition and growth; the activity and inducibility of cytochrome P450 enzymes (and indeed other enzymatic detoxication systems) relative to substrates naturally found in host plants; the quantitative association between antifeedant

responses and toxicological sensitivity; and the metabolic disposition of ingested allelochemicals within the digestive system for a wide variety of both hemimetabolous and holometabolous phytophagous species. Until such data become available, patterns remain tantalizingly suggestive rather than convincingly documented.

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## Are host plants important in pheromone-mediated mating systems of Lepidoptera?

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**Summary.** The role of host plants in the synthesis and release of lepidopteran sex pheromones is examined. Females synthesise pheromones de novo and pheromone quality is not markedly influenced by larval food sources. However, host plants may have a significant effect on different physiological and behavioural parameters associated with pheromone production. Males in some species of Nymphalidae and Arctiidae use secondary plant compounds, such as pyrrolizidine alkaloids, as a pheromone precursor. In such cases these plant compounds serve an additional role, such as protection against predation, and may reflect potential male reproductive investment. In the one instance where the effect of larval host plants on the de novo synthesis of a male sex pheromone was examined, larval nutrition did not alter either the quality or quantity of the hairpencil contents.

**Key words.** Lepidoptera; semiochemicals; sex pheromones; host plants; secondary plant compounds; calling behaviour; mate choice; *Homoeosoma electellum*; *Pseudaletia unipuncta*.