Feeding II: Physiological Adaptations

I. Introduction.

A. Today's lecture concerns the physiological aspects of feeding. We begin with a general classification of insect feeding habits. We then explore the physiological mechanisms of food selection and food processing.

B. General classification of feeding habits.

1. **Plant feeders**. Food of herbivores is highly variable in quality. Feeding problems faced by herbivores are locating food, extracting nutrients, and disposing of toxins.

2. **Predators**. Food of predators usually of uniformly high quality. Feeding problems faced by predators are detecting, capturing and subduing prey.

3. **Scavengers**. Food of scavengers is rapidly changing in quality. Feeding problems faced by scavengers are the rapid temporal change in food quality and its rapid consumption by microorganisms or large vertebrates.

4. **Parasites**.

a. **Ectoparasites** live on the outside of their host. Food is uniformly high in quality. Feeding problems of ectoparasites are locating a suitable host and avoiding behavioral defenses of its host.

b. **Endoparasites** live inside their host. Food is uniformly high in quality. Feeding problems faced by endoparasites are locating a suitable host, avoiding the physiological defenses of its host, and avoiding competition from other ectoparasites (**superparasitism, multiparasitism**).

II. Food selection.

A. Extent of diet specificity.

1. Classification of diet specificity.

a. **Monophagy**. Diet restricted to single species. Many scale insects and sawflies feed on a single species of host plant. Some of these insects are so host-specific that they are specialized on local populations of host plants. Some parasitoids are also extremely host specific. Most of the 100 or so species of phorid parasitoids in the genus *Apocephalus* seem to be restricted to one species of ant host.

b. **Oligophagy**. Diet restricted to a few species. The sulfur butterfly *Pieris rapae* feeds on plants in the family Cruciferae and other species that contain mustard oil glycosides.

c. **Polyphagy**. Diet includes many species of plants or animals. Most predators are polyphagous. Grass- feeding orthropterans such as the locust *Schistocerca* are also polyphagous. The painted lady butterfly (*Vanessa*) is polyphagous, but prefers a restricted set of plants in several families.

2. The range of food items taken by an insect is first restricted by evolved limitations of its structural and physiological features. For example, a phytophagous insect that requires the detection of mustard oils glycosides to identify a host plant will not feed on a plant without these compounds, regardless of its nutritional quality. Herbivores that do not have the physiological machinery to neutralize secondary plant compounds such as mustard oil glycosides cannot consume a plant that contain them, regardless of it nutritional quality. Predatory species obviously cannot consume prey items that are too large to subdue. The diet may be limited further by other, more ecological considerations, including the relative abundance or spatial distribution of food items.

B. Kinds of stimuli used in food selection.

Phagostimulants are nutritionally important substances that promote feeding activity by insects. Sugars are important phagostimulants for many scavengers and herbivores. Detection of sugars by tarsal chemoreceptors is sufficient to cause proboscis extension in butterflies, houseflies and blowflies. Curiously, nutritionally important amino acids by themselves do not stimulate or only weakly stimulate feeding in insects.

2. **Token stimuli** are nutritionally **unimportant** substances that promote feeding activity. Mustard oil glycosides are not nutritionally important to sulfur butterflies in the genus *Pieris*, but the presence these compounds nonetheless are required to elicit feeding behavior. These butterflies feed on plants in the family Cruciferae (mustard family) that contain mustard oil glycosides.

3. **Feeding deterrents** are nutritionally unimportant substances that deter feeding activity. Many secondary plant compounds are feeding deterrants for insect herbivores. For example, feeding behavior of the polyphagous aphid *Myzus persicae* is deterred by the presence of mustard oils. The presence of spines or sequestered toxins on potential prey items deter feeding behavior in predators.

C. **Synergistic effects**. These various kinds of stimuli may interact synergistically to promote or deter feeding behavior in insects. For example, weak concentrations of sugar and the amino acid L-proline individually only weakly stimulate feeding behavior in the spruce budworm (*Choristoneura fumiferana*), but together they are highly stimulating.

D. **Hierarchy of cues**. Most insects use a hierarchy of cues to increasingly narrow the selection of appropriate food items. The beewolf wasp, *Philanthus*, is a specialized predator of bees. When hunting a female orients to a variety of insects of the appropriate size. On approach the wasp will attempt to capture an insect only if it smells like a bee. Wasps will capture insects that have been given the odor of bees experimentally. After capture the wasp uses tactile cues to determine if the insect actually is a bee. If so, the wasp stings the bee and carries it to the nest; if not, the wasp releases it and continues hunting.

E. **Motivation**. The sensitivity of a insect to the various stimuli that promote or deter feeding behavior depends on its physiological state. For example, the phagostimulant sugar will not elicit proboscis extension in a blowfly with a full gut, because this reflex action is inhibited by excitation of stretch receptors in the gut. Likewise, feeding deterrents are less effective against a hungry insects than their are against a full one. Within limits the diet range of an insect vary depending on its motivational state.

III Food processing

A. Problem substances in food processing.

Secondary plant compounds.

a. **Toxins** are low molecular weight compounds that act as metabolic or neurological poisons. Examples: alkaloids (cocaine, codeine, caffeine, quinine in tonic water, novocain, nicotine), cyanogenic compounds, peptides (α-amanitin), glycosides, and phototoxins.

b. **Digestibility reducers** are compounds of high molecular weight that bind with plant or animal tissue to reduce its digestibility to insects. Tannins in oaks and tea and other plants are an example.

c. **Insect hormone analogues** of ecdysone (molting hormone) and juvenile hormone.

2. Food of low quality or low digestibility. Foods of low quality include wood, cartilage, chitin, hair and wool.

3. **Insecticides** are natural or human produced chemical substances used to kill or debilitate insect pests. Examples: chlorinated hydrocarbons (DDT, heptachlor, aldrin, chlordane), organophosphates (parathion, malathion), carbamates (sevin, furaden).

B. Insect solutions to problem substances (xenobiotics).

get rid of

1 **Excretion**. Many insects adapted to feed on plants with specific xenobiotics do not metabolize these compounds, but instead excrete them directly. The tabacco specialist *Manduca sexta* can eliminate 93% of a dose of nicotine in 2 hr, whereas the omnivorous housefly (*Musca domestica*) takes 18 hr to eliminate only 10% of an equivalent dose.

store

2. **Sequestration** of metabolized or unmetabolized ingested toxicants is very common among specialist feeders. These toxicants are stored in tissues or specialized structures where it cannot interfere with the intended target site. For example, some DDT-resistent insects store this insecticide in fat tissue where it cannot have its intended effect on the nervous system. In some instances specialized feeders actually appropriate the toxicant directly or in a modified form for their own defense against predators. Monarch butterflies, for example, active sequester caridac glycoside from their milkweed host plants and use it as a defense insect-eating birds.

tolerate

3. **Tolerance** of specialized feeders to specific toxicants may be enhanced by modifications in ~~the~~ membrane permeability or ~~the~~ permeability of the integument.

degrade

4. **Degradation**. Many insects have evolved metabolic machinery to degrade or otherwise detoxify xenobiotic compounds through oxidation, hydrolysis, hydroxylation, methylation, sulfation or conjugation with amino acids. **Mixed-functional oxidases**, for example, are common in many generalist feeders. These enzymes can oxidize a wide variety of xenobiotics.

C. Insect solutions to low quality food.

1 Enhancement of food quality through external manipulation. Examples: food storage in seed-harvesting ants, leaf-rolling by pyralid and ctenuchid caterpillars.

2 Evolution of specialized enzyme systems. Examples: presence of cellulase in cerambycid beetles, presence of collagenase in blowfly larvae, presence of chitinase in the intestinal juices of *Periplaneta* cockroaches.

3. Symbiosis with other organisms. Examples: microorganisms in the gut of termites and *Cyptocercus* cockroaches, fungus-growing ants and termites.