



E-ISSN: 2320-7078

P-ISSN: 2349-6800

JEZS 2019; 7(3): 574-579

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Received: 25-03-2019

Accepted: 29-04-2019

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A brief review on food recognition by insects: Use of sensory and behavioural mechanisms

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Abstract

Insects feed on almost every kind of organic matter irrespective of living or dead. Moreover, most insects are specific to their food selections and restrict themselves within some particular kind of food. Obviously, insect-plant interactions are also of crucial importance in selection, finding and recognition of host. Recognition of host plants, prey and cell sap by different herbivores or natural enemies or blood sucking insects respectively is important for gathering energy to complete their life cycle. Recognition of food by insects involves behavioural responses to food, sensory mechanisms and perception of odours released by host. Visual, olfactory and gustatory cues act as a sensory system; and experience-learning and orientation mechanism acts as a behavioral mechanism for an insect to recognize their source of food. Moreover, semiochemicals also plays a vital role in food location and recognition by insects in the form of kairomones. On the other hand, thermal stimuli, CO₂ and odours are acts as cues for recognition by blood sucking insects.

Keywords: Food recognition, herbivores, olfactory, gustatory, sensory system

1. Introduction

Insects are most diversified group of hexapod invertebrates under phylum Arthropoda. Insects are found in all types of habitat, they feed on almost every form of food materials ranging from living to non living materials and majority of insects are more specific, being restricted to a particular category of food (either plant or animal). So, location and recognition of food sources is an important part in their life. Most of the insects are species specific for host recognition. Insects foods are incredibly heterogeneous, so that it is essential to classify insects based on food habit, herbivores they used to feed on plant and its products; carnivores feed on vertebrates and other insects; omnivores require both plants and animals and lastly Detritivores insects feeds on dead and decaying matters. In case of herbivorous insects food preferences is most diversified some are feeds on only one plant species and some are feeds on a wide range of plants in many different families. The commonly recognized categories of herbivores are: monophagous, oligophagous and polyphagous. Alternative terms occasionally found in the literature are stenophagous, refers to insects with a restricted host-plant range, and euryphagous, for insects with abroad host-plant range ^[1].

A particular type of stimulus or configuration of stimuli initiating from the external world matches a model in the neural world and that upon the occurrence of congruency a specific relevant behavior usually ensues, which can be termed as recognition ^[2]. According to Visser ^[3] Recognition refers to the insect's decision to feed and/or oviposit on host plants and to leave on the host plants. Recognizing a host plant is essential for a phytophagous insect to fulfil its nutritional requirements and to find suitable oviposition sites. The recognition of a host plant by the insects will be occur by using either species specific compounds or specific ratios of ubiquitous compounds. Recognition of host plants, prey and vertebrates for phytophagous insects, predators and parasites and blood sucking insects respectively is important for their survival. For better understanding of recognition process adopted by the insect species knowledge of host selection process and insect plant interaction is essential. In present study mainly focussing on how herbivore insects can recognize their host plants and mechanisms involved in that process and shortly on entomophagous insects.

2.1 Insect - plant interaction

Nearly half of all existing insect species on earth feed on living plants. Thus, more than 400,00 herbivory insect species live on about 300,000 vascular plant species ^[4].

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Therefore, it is essential to know insect-plant interaction for clear understanding of host plant recognition by phytophagous insects. The host plant of a herbivorous insect is the universe in which it finds nourishments and shelter [5]. The evolution of plants in the Devonian period and the subsequent development of flowering plants in the Cretaceous period have provided valuable resource for the herbivore community. Herbivores cannot exist without green plants, which serves as a source of energy rich compounds for them. Some insects are flower pollinators and some are herbivores [6]. The distinct colour and scents of flowers make them easily recognizable by the pollinators like bees, wasps and lepidopteran insects. To understand the equilibrium existing between insects and their host plants, the role of orientational, feeding and oviposition factors, allomonal factors and plants nutrients must be understood.

Herbivorous insects mostly live in an environment where plant chemicals are abundant. Phytochemicals present in plant tissues act upon the insects when they start feeding on the plant. Therefore, plant volatiles are one of the main source in which an insect can recognize their host plants by using their sensory systems and some time by behavioural mechanisms. The visit of herbivorous insect on plants not only to find hosts, but it is important for mate, feed and oviposition on plants. Hence, both the organisms are intimately associated with each other, because insects have some beneficial activities like pollination, whereas plants provides shelter, oviposition sites and food to herbivores [6]. A large number of volatile plant compounds released by the plant enter in the surroundings, air or soil, away from their source of production. Olfactory receptors systems have evolved in phytophagous insects enabling them to perceive some of the volatiles, which can be used as source of recognition of host plants [3]. During the evolution of insect-plant interactions, insects also evolved some amounts of behavioral changes, for selection and reorganization of their food source to survive. The adaption of insects to the host plants involves behavioural and metabolic changes which enable insects to cope with the physical and chemical defence systems of plants. Scriber [7] has suggested that discrimination between such factors and insect adaptation involving feeding specialization tend to influence post-ingestive growth performance.

2.2 Host-plant selection by insects

Host plant selection by herbivorous insects can be considered as “choice behavior” [8, 9, 10]. The host-plant selection by the insect consists essentially of a series of ‘take it or leave it’ situations in which the insect either accepts or rejects the plants at hand in response to food preferences for itself or its offspring [11]. The host selection process is a chain of events (plant stimuli-insect response) in which each link facilitates the unfolding of the next one [12]. The process of the stimulus-response patterns involved in the selection of plants by herbivores, insect hosts and prey by parasites and predators, and vertebrates hosts by blood feeders are somewhat different. Generally, five phases are defined in this process [6, 13]. Host habitat finding, host finding, host recognition, host acceptance and lastly host suitability.

2.3 How phytophagous insects recognize their host plants

When a particular kind of stimulus or configuration of stimuli initiating in the external world matches a model in the neural world and that upon the event of agreement or harmony with a specific relevant behavior usually termed as recognition [14].

Finding a host plant is critical for a herbivorous insect to satisfy its nutritional requirements and to discover suitable egg laying sites. Moreover, the process of host-recognition is governed by different plant volatiles. Phytophagous insects are highly specific, which may be monophagous, oligophagous or polyphagous [15]. A sophisticated recognition mechanism is very much essential for evaluating the existence and location of suitable host plant. The host selection procedure can be seen as a continuum between two extremes, insects ‘choosing’ their host from a distance by employing olfactory as well as visual cues, on the other hand, insects ‘selecting’ their host only after the use of gustatory cues [16]. This process is mediated by integration of different factors, inside the insect central nervous system (CNS), of numerous sensory inputs, including olfactory or gustatory cues. In addition to this, physical information such as plant color, shape and texture also plays a vital role to complete the process. Afterward the plant can be recognised for feeding or oviposition by using those sensory inputs by an insect. With the correct combination of sensory inputs, a plant is recognized as a host. Conversely, when the wrong cues are perceived, a plant is recognized as a non-host, eliciting an avoidance response by the insect. Generally, the insect can recognize their food or host by visual cues, chemical cues (Chemoreception) – it includes both olfactory and gustatory and tactile cues. In addition to these cues some insects use mechanical stimuli; thermo reception, CO₂ and radiant heat by blood sucking insects. Recognition of food by insects involves behavioural responses to food and sensory mechanisms and perception of odours released by hosts. Where olfaction is an effective means of long distance communication among insects, most available evidence indicates that it functions most commonly over only short distances in host selection [17].

2.3.1 Visual cues

The response of phytophagous insects to the colour of vegetation seems to play an important part in food location but not in the discrimination of host species. As Thornsteinson [11] suggested, the narrow spectrum of the light reflected from green plants would probably prohibit the decisive recognition of food plants by colour. Attraction to a food plant from a distance can occur visually or by olfaction, probably varying very much with the species and the situation. *Schistocerca* (Orthoptera), is attracted by the sight of any solid object of an appropriate size and especially by a pattern of vertical stripes [17]. Colour may also play a part in recognition. A number of phytophagous insects including aphids, leafhoppers, and white fly are strongly attracted to yellow and yellow-green and it seems likely that these pests can recognise crops by the colour contrast between them and the surrounding native vegetation [18, 19]. The colour of flowers also attracts bees from a distance, although selection may be made at close range on the basis of fragrance; finally, visual cues provided by the nectar guides may lead the bee to the location of the nectar [14].

2.3.2 Chemical cues

Fraenkel [20] found that the insects are influenced not only by plant morphology or primary nutrient substances but also by their chemistry. He proposed that insects choose and recognize their host plants exclusively by responding selectively to plant secondary compounds such as alkaloids, glycosides, and aromatic oils.

2.3.3 Olfactory stimuli

Generally, an insect is surrounded by olfactory cues of diverse semiochemicals. Therefore, insects may use a variety of senses, such as the sense of smell (olfaction), taste, vision, and touch to select the appropriate host. Though the all kinds of senses are important, but olfaction often plays a most important in selection of mates and hosts ^[15, 21]. In addition to visual cues, insects are famously sensitive to olfactory cues, including those of food. Plants emit a variety of volatiles, these volatiles are often similar or identical to chemicals that can serve as feeding deterrents ^[22]. Because of the general lack of visual factors in insects, olfaction must usually play an important part in arriving and recognizing the food. Thorsteinson ^[11] suggests that the initial effect of odors is to inhibit locomotion so that once a plant is found, presumably largely as a result of random searching, there is little tendency for the insect to move away again. Odors means several chemicals produced from plants either primary or secondary compounds. For many herbivorous insects, plant secondary compounds are critical in stimulating or deterring feeding ^[15]. For many herbivores, plant secondary compounds serve as “token stimuli” for feeding or oviposition ^[22]. The ability to respond via taste or olfaction to these compounds is conferred by odor and taste receptors.

2.3.4 Gustatory stimuli

- Gustatory action can be defined by the response of an insect to relatively high concentrations of non volatile stimulatory components which generally come into contact with the receptors in aqueous solution. So, the gustatory sensilla are also known as contact chemoreceptors and due to which insect may avoid unpalatable food or reject endoparasitic larvae for egg laying. These sensilla are commonly situated on the tarsi, the maxillary and labial palps and sometime on the antennae. Generally, taste receptors come into contact with the stimulus in a solid or liquid form via a single terminal pore in the receptor. For example, two cells of cabbage butterfly, *Pieris brassicae*, respond to glucosinolates present on cruciferous vegetable ^[22].
- Contact chemoreceptors commonly occur on the tarsi, and stimulation of tarsi of blowflies and butterflies with sugar leads to extension of the proboscis.
- In nectar-sucking insects such as bee, the strength of these responses increases with the concentration of sugars.
- Host selection in aphids occurs mainly after alighting when the insect probes the plant with its proboscis ^[17].

2.3.5 Tactile stimuli

Tactile stimuli, in addition to contact reception, also plays a role in host location finding and recognition. The surface characteristics of bark and foliage influence the choice of both feeding and oviposition sites. Bark beetle often displays a preference for rough bark over smooth bark areas. The cereal leaf beetle prefers smooth-leaved wheat over varieties that are pubescent ^[23].

2.3.6 Thermoreception

In addition to general sense of temperature, some insects use heat detection for specific purposes, such as the location of hosts. Many parasites of warm-blooded animals' apparently orient to their hosts by following the temperature gradient surrounding the hosts' body.

2.4 Mechanism of host recognition (sensory coding, odor perception)

Host plant recognition and preference involve the integration of a complex of neural and metabolic events *viz.*, the sensing and encoding characteristics of the sense organs, decoding mechanisms in the central nervous system, assessment of across-fiber patterns and deterrent/stimulant ratios, pre-and post-ingestion factors such as level of satiety, nutritional balance, and experiential factors such as induction and aversion-learning ^[14]. However, recognition of the host plant by a herbivore not only depends on the nature of the characteristics (e.g., form, color, texture, water content, and hundreds of chemical compounds), but also on the characteristics of the herbivore's sensory system, its detecting and coding capacities, and on the central neural system. Therefore, recognition of host plants deals with a herbivore's perceptual system, where perception can best be defined as how an animal "sees" the entire world ^[14].

2.4.1 Behavioral mechanism of food recognition

There is a long held widely accepted view that insects use a sequence of behavioral responses in host selection. This was first recognized in parasitoids and later in phytophagous insects ^[24]. The suggestion of Daniel ^[25] that the behavior of phytophagous insects consists of three component phases, seems equally applicable to blood feeders, parasites, and others. These phases are; Orientation to food (kinesis and taxes, transverse orientation), Initial biting response and continued response.

The host selection behavior of entomophagous insects has been divided into phases defined as host habitat finding, host finding, host acceptance, and host suitability ^[26]. Each of the phases defined by Dethier ^[14] is in turn made up of sequence of responses, often to stimuli of various kinds (visual, chemical, tactile). Stimuli obviously interact, as when the convection currents generated by a warm-blooded organism carry olfactory cues perceived by biting flies.

2.4.2 Orientation mechanisms

According to Fraenkel ^[20], oriented behavior has divided into three basic kinds like; Kinesis, Taxes and Transverse orientations. These three mechanisms are exceedingly important in directing the movement of insects from inhospitable to hospitable environments, and to the requisites for life (food, mates, shelter, etc).

2.4.3 Role of experience and learning in food recognition by insects

The insect behavior especially learning, memory and forgetting – are important behavioral experience for the host selection process. It may be short-lived or prolonged depending on insect species and exposure time of the stimuli. Learning is the manipulation of insect behavior due to the effect of prior experience. Learning can be defined as a “Individual's behavior changes in a repeatable way as a consequence of experience”. Hence, learning may occur very quickly and it implies some beneficial adaptive change in behavior ^[27].

2.4.4 Role of learning in food recognition and food location

Any herbivore or saprophagous insect acquires food by a series of process involving different phases like finding the habitat, finding a plant within the habitat, examining a plant,

and using a plant for food or oviposition, respectively [28]. Gravid female of cabbage butterfly can approach to particular cultivars of cabbage for oviposition [28]. Similarly, gravid *Rhagoletis* fruit flies also learn to accept particular cultivars of apples for egg laying [27, 29]. Interestingly, gravid female of *Battus* butterflies can best host with good size, suitable phenological age and the presence of a leaf bud.

2.4.5 Role of learning in phytophagous insects

There are some herbivores, such as grasshoppers and locusts (Acrididae, Orthoptera), that are mobile generalists for which we might expect associative learning to be advantageous because of the large amount of environmental variation they encounter. Lepidopterans are generally herbivorous as larvae and pollinating flower visitors as adults. There is substantial research on associative learning of flower colors and odors in adult lepidopteran flower visitors [30]. Learning of floral colors has been demonstrated in multiple species of Papilionid pierid and nymphalid butterflies and the diurnal moth *Macroglossum stellatarum* learns flower colors and sizes. The majority of research on learning in pollinators has been conducted with bees, but wasps, adult Lepidoptera, beetles, and flies are also important pollinators for many plant species. The range of floral traits learned by bees is extraordinary. Honey bees, *Apis mellifera*, and bumblebees, *Bombus* spp., can learn to associate flower colors, odors, shapes, patterns, electric fields, textures, and locations with nectar rewards [31].

2.4.6 Role of semiochemicals in insect food recognition

Semiochemicals are involved in behavioral or physiological interactions between organisms. Intraspecific semiochemicals are termed as pheromones, and interspecific one are allomones, this includes kairomones, allomones. Among these kairomones are plays a very important role in the food recognition and finding

Kairomones means, these are chemical signals that benefit the receiver. Here, we will concentrate on host-produced volatile chemical cues (kairomones) because they play an important role in enabling the insect to recognize host plants at a distance [15, 16].

Table 1: Kairomones used by some Phytophagous Insects

Species	Compound name
<i>Amrasca devastans</i>	Camphene, a-Pinene [32].
<i>Popillia japonica</i>	Phenethyl propanoate, Eugenol [33].
<i>Delia antiqua</i>	Propanethiol, Dipropyl disulfide [34].
<i>Drosophila melanogaster</i>	Ethanol, I-Propanol, Ethyl acetate, Ethyl propanoate, Acetic acid [35].
<i>Ostrinia nubilalis</i>	Phenyl acetaldehyde [36].
<i>Rhagoletis pomonella</i>	Hexyl acetate, Hexyl propanoate [37].

3. Host recognition by entomophagous insects

The cues which are used by entomophagous insects for recognition of food is totally differs from those that of phytophagous insect. In case of predators mainly they use visual cues than that of gustatory and tactile stimuli.

3.1 Food finding and recognition by Predators

Predators catch their prey by sitting and waiting for it to come their way or by actively pursuing it. Mantis for example sits and waits for its prey and as it has a mobile head, the movements of the prey can be followed without the whole mantis moving [38]. In case of dragonfly larvae wait for their prey, laying concealed in the mud at the bottom of a pool and

seizing the prey with the labial mask. A few insects make traps in which they catch their prey. Tiger beetle hunt on the ground and have long legs, which increase their speed and prognathous mouthparts with large mandibles. In predaceous larval forms with poorly developed eyes and often with subterranean habitat such as tabanid larvae, the finding of prey must be largely olfactory.

Mechanical stimulation is sometimes important in finding the prey and some dragonfly larvae depend on mechanoreceptors on the antennae or tarsi for this. Mechanical stimuli may also be important in recognition of food, as in case of water striders, for example, locate prey trapped in the surface film by orienting to the ripples that radiate outward as the prey struggles to free itself.

In some cases, sense of touch maybe very important, in cases of damselfly larvae, when the prey is in contact with both antennae, the range and position are ideal, and the antennae spring back out of the way, allowing the labium to spring forward and capture the prey.

3.2 How aquatic insect predator recognise their prey.

Visual, mechanical and chemical cues are available to predators to detect prey. From the limited data that have been reported we can see that some aquatic insect predators use tactile or mechanical cues to detect or recognize their prey (some odonata, plecoptera, trichoptera and dipteral) and some use visual cues (some odonata, hemiptera and coleopteran) [39] and many predators probably use a combination of cues (hemiptera).

3.3 Host recognition by parasitoids

How carnivorous insects select herbivorous host insects has been mainly studied in insect parasitoids, because host selection behaviour directly determines the developmental success of these species. In case of parasitoids, the host selection process typically involves the following sequence of behaviour [40, 41]: searching for the appropriate host habitat (often, the plant), usually by oriented flight; searching on the plant for the host by an exploration by antennal examinations of leaf area and faeces of the host; examination of the host; and finally, egg-laying [42, 43].

3.4 Food finding and recognition by Internal Parasites

In case of internal parasites the parent insect oviposits inside a suitable host. Smell and possibly also contact chemoreception, are involved in the host finding and recognition. In some cases the parent does not seek out the larval host, but oviposits or larviposits in the places frequented by the host so that the larvae make their own way on to the host when the occasion presents itself. The human warble fly *Cordylobia anthropophaga* lay its eggs in sand fouled with urine. The larvae hatch in a day or two and then remain inactive until the stimulated by the vibrations and rise in temperature associated with the visit to the host and bore in through the skin [43].

3.5 Food finding and recognition by blood-sucking insects

The blood sucking process can be schematically divided into four successive steps; attraction to the host and settling (orientation) probing and tasting (initiation of feeding) sucking or gorging (continuation of feeding) and withdrawal of mouthparts (termination of feeding).

The orientation through active movement toward the warm blooded host, guided by visual and thermal stimuli and a

complex of airborne chemical stimuli emanating from the host includes CO₂, water vapour, fatty acids and their derivatives, ammonia and amines. Thermal stimuli have been shown to be important in attracting ticks, bugs, lice, mosquitoes and tsetse flies to their hosts. The importance of upward current of air for host finding has been demonstrated for ticks, black flies, fleas and mosquitoes [44]. However in the case of *Rhodnius*, *Triatoma* and bedbug *Cimex* the thermal response is probably to a temperature gradient.

3.6 How mosquito can recognize their host

Concerning host finding by mosquitoes, Hocking [44] states that “every imaginable part of the human body and its products must by now have been fractionated in every possible way in search for a specific chemical attractant”.

Although many compounds including amino acids, sex pheromones found to be attractive to mosquitoes. Brown [45] found that moisture to be the most powerful single attractant to mosquitoes with warmth next in importance. CO₂ seemed to be an importance activator.

3.7 How nocturnal insect can recognize their food

Nocturnal insects like Elephant Hawk moth, *Deilephila elpenor* use scotopic colour vision or achromatic vision to discriminate flowers during night time [46]. They have superposition compound eyes with a large superposition aperture and tracheal tapeta and are therefore well adapted to nocturnal vision [47]. Flowers that are typically pollinated by nocturnal hawk moths, in contrast, tend to be white, cream-colored or bright yellow [48], thus offering a strong intensity (or achromatic) contrast to the green vegetation or the dark night sky.

4. Conclusion and future prospects

Generally insects employ both sensory and behavioral mechanisms to recognize their food or host. Insect uses Visual, olfactory, gustatory and tactile cues as a sensory mechanisms and experience – learning as a behavioral mechanisms. The mechanism of recognition is same for all type of insects but cues used by them is different. In some cases genetic base of recognition will be occur. Host plant choice is a complex task for herbivores insects comprising the integration of intrinsic (innate preferences, behavioral plasticity, larval mobility) and extrinsic factors (plant suitability, natural enemies, competitors). However, phytophagous insects generally recognize host odor by using ratios of common plant volatiles, and recognition is thus not restricted to species-specific compounds, it would appear that the central processing of peripheral signals is extremely host preferences can have similar peripheral receptor systems for plant volatiles but show different behavioral response. In addition, learning behavior involving central processing can occur when a particular blend of volatiles become associated with a more abundant or more rewarding host. Understanding of host recognition by parasitoids is much more complex as compare to herbivore insects, these mainly use chemical cues as a source for their host recognition it may be species specific or ratio specific. In case of predators they mainly use visual cues as a main source for prey recognition however, the mechanism of recognition will be same for all type of insects. We have to give more concentration on recognition by herbivore as well as by parasitoids. by understanding the recognition mechanisms and their sources it is easy to develop resistance against particular pest by adopting host plant

resistance mechanism and by understanding the recognition of host by parasitoids it is easy to evolve them as efficient biocontrol agents. In future, genetic basis of host recognition by insects is to carried out

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