# GENERAL PRINCIPLES OF INSECT NUTRITIONAL ECOLOGY

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### Böcek Beslenme Ekolojisinin Genel Prensipleri

**Özet:** Böceklerin beslenme ekolojilerinin iyi bilinmesi, onların biyoloji, davranış, doğal ecosistem ve agroekosistemlerinin anlaşılmasının ön koşulunu oluşturmaktadır. Büyüme ve üreme için gerekli olan böcek beslenme koşulları yıllardır bilinmesine rağmen sadece az sayıda böcek üzerinde beslenme koşulları ayrıntılı olarak çalışılmıştır. Bu çalışmalarda bile böceklerin beslenme koşullarındaki olağanüstü farklılıklar ortaya konulmuştur. Böceklerle yapılacak çalışmalarda, böcek beslenme koşullarının bilinmesi çok önemlidir. Beslenme ekolojisi, hem temel hemde uygulamalı olarak böcek davranışlarının ve değişik yaşam koşullarına olan adaptasyonlarının anlaşılmasında çok önemlidir. Bu derlemede, böcek beslenme ökolojisi, spesifik beslenme gereksinimleri, beslenmeyi arttırıcı ve azaltıcı faktörler sunulmuştur.

*Anahtar Kelimeler:* Böcek beslenmesi, böcek beslenme ekolojisi, beslenmeyi arttırıcı maddeler, beslenmeyi azaltıcı maddeler

**Abstract:** A comprehensive knowledge of the nutritional ecology of insects is a requirement to understand their biology, behavior, and impact in natural ecosystems and agro-ecosystems. Although, major insect nutritional requirements for growth and reproduction are known for years, only a few dozen insects have been studied to learn their nutritional requirements. Extraordinary nutritional requirements were found in a few insects from even these few studies. It is important to understand comparative nutritional requirements in order to study insects. Nutritional ecology is a useful way to synthesize research on both the basic and applied aspects of insect behavior, and it allows us to achieve a better understanding of the evolution of different lifestyles. In this review, emphasis will be placed on insect nutritional ecology, requirements for specific nutrients, phagostimulants, and feeding deterrents.

*Key Words:* Insect nutrition, insect nutritional ecology, phagostimulants, feeding deterrents

### Introduction

The principles of the major insect nutritional requirements for growth and reproduction have been established since 1940's through the studies on representatives of the major insect groups (Dadd, 1973; Davis, 1968; House, 1965; House, 1974; Nation, 2001; Simpson and Raubenheimer, 1995; Slansky and Scrieber, 1985, Genc, 2002). However, at most a few dozen insects have been studied critically to learn their nutritional requirements. Even these few studies, unusual nutritional requirements were found in a few insects. The differences in required nutrients reflect the insect's natural diets (Dadd, 1985). Nutrition describes as the chemicals required by an organism for its growth, tissue maintenance, reproduction and energy. As many of these chemicals are taken during feeding, the others are synthesized by the insects (Chapman, 1998). Even though, insects generally have the same nutritional requirements as large animals, minor variations do can occur. The balance of nutrients is very important to most studied insects (House, 1965; Dadd, 1985). Balance may be important due to small body size and the stress placed on several physiological systems by having to deal with excesses while attempting to accumulate suboptimal levels of the major nutrients (Genc, 2002). Insects may respond to imbalance diet in one of the three ways. They can alter the total amount of ingested food; they can move from one food to another with a different nutrient balance; or they can regulate the effectiveness of the nutrients. The required balance of the nutrients such as carbohydrates, proteins, lipids, vitamins and amino acids, is generally related with the natural foods of the species (Dadd, 1985). Predator insects have high amino acid requirements relative to carbohydrates, which reflect the

protein content of animal tissues (Chapman, 1998). Phytophagous insects generally require almost the equal amount of proteins, amino acids and carbohydrates such as Orthoptera, Coleoptera, and Lepidoptera. Phloem feeding insects or grain beetles has high requirements for carbohydrate. The nutritional requirements of an insect can change with time, depending on the growth, reproduction, diapauses or migration. It is usually true with the insect larvae that the nitrogen content of the early stages is greater than later stages. Lipids are important in the later larval stages for survival, reproduction, and development (Nation, 2001; Chapman, 1998).

## Nutrient Requirements for Insects

### 1. Proteins and Amino Acids

Most insects probably have need of optimum level of proteins in their diet for the best growth, but this varies largely for different species. They are used for structural purposes, as enzymes, receptors, for transport and storage (Chapman, 1998). Many insects digest proteins from their food in order to get amino acids. Haydak (1953) showed that when the dietary protein of several cockroaches is restricted, they slow down growth, but prolonged longevity. The American cockroaches grew fastest on 49 and 78% protein diet, on the other hand, survived longest on 22 to 24 % protein diet. Many adult female insects need protein to mature their ovaries and eggs. It is crucial for successfully secrete juvenile hormone (JH) that is required for ovary and egg development. Male insect usually do not require protein to mature their sperm when they become adults. In general, optimal nutritional requirements change with age, sex, and physiological stress (Nation, 2001).

Insects need a dietary source of arginine, histidine, leucine, isoleucine, lysine, methionine, phenylalanine, threonine, trythophan, and valine (all in the L-form), the same essential amino acids needed by large animals. In the absence of one of these essential amino acids, growth and development will be ended in *Pectinophora gossypiella*, *Helicoverpa zea*, *Myzuz persicae*, *Tribolium confusum* and *Apis mellifera*. Sometimes, nonessential amino acids motivate growth, because of the optimization of the nutrient balance and the good organization of the biochemical pathways concerned in the synthesis of the nonessential amino acids. For example, alanine and glycine or serine is necessary for optimal growth in *Bombyx mori* (Nation, 2001). Some amino acids are important in morphogenesis. It has been shown that tyrosine is crucial for cuticular sclerotization and tryptophan for the synthesis of visual screening pigments. Some other amino acids are known to be neurotransmitters such as γ-aminobutyric acid and glutamate. Proline is essential for development and as energy sources for *Culex spp*. and several Diptera species. Aspartic acid and glutamic acid are important for *Phormia sp*. and *B. mori* (Chapman, 1998).

### 2. Carbohydrate

Carbohydrate is a major source of energy for most insects. Although some insects are known to have an absolute requirement for a specific carbohydrate in the diet, many others do not have these requirements. For all insects, carbohydrate is a very important fuel source. They may be converted to lipids, and may contribute to the production of amino acids. Many carbohydrates, especially sugars, are powerful feeding stimulants. A functional carbohydrate sometimes may appear as non-functional if it is not ingested effectively. This may be the case of absence of some other phagostimulatory substance such as sucrose (Dadd, 1985; Nation, 2001; Genc, 2002). Carbohydrates are very important for insects but they are not essential because, they can be synthesized from lipids or amino acids (Nation, 2001). Different carbohydrate utilization depends on the ability of insects to hydrolyse polysaccharides. Some insects can utilize a very broad range of carbohydrates, most likely because they can digest the more complex structures. For example, *Tribolium sp*. can use starch, mannitol, raffinose, sucrose, maltose and cellobiose, as well as various monosaccharides (Chapman, 1998). Some stored-grain insects require carbohydrate source to reach maturity belonging in the genera of *Tenebrio*, *Ephestia*, and *Oryzaephilus*. *Tenebrio* sp. stops their development unless carbohydrate content should be at least 40% of the diet, and growth is the best with 70% carbohydrate diet (Chapman, 1998). Worker honey bees have a need for carbohydrate when they are ready to pupate (Nation, 2001). In some insects, larva and adult can use carbohydrates differently, for example, the larva of *Aedes spp*. can use starch and glycogen, but the adult can't use them (Chapman, 1998). Lepidoptera, Orthoptera, and some Homoptera use both carbohydrates and lipids to supply the energy for flight, but most insects can only utilize carbohydrate to support flight. A very few insects use carbohydrate and the amino acid, proline, to support flight. Most insects are unable to use cellulose and other plant polymers because they do not have the enzymes to digest them (Nation, 2001). In some other insect species, nevertheless, these substances are made available as a result of symbiotic microorganism activities (Nation, 2001, Chapman, 1998).

### 3. Lipids, Polyunsaturated Fatty Acids and Sterols

Lipids in biological organisms consist of free and bound fatty acids, short and long chain alcohols, steroids and theirs esters, phospholipids, and other groups of compounds. Insects are able to convert carbohydrates into lipids, and many insects can synthesize lipids and accumulate them in fat body tissue (Nation, 2001). Fatty acids, phospholipids and sterols are components of cell walls in addition to having other specific functions. Insects are capable of synthesize many fatty acids and phospholipids so they are not usually fundamental dietary requirements, but a dietary source of polyunsaturated fatty acids and sterol are essential to many insects. Lepidoptera and some other insect orders, about 50 species, have been shown require a dietary source of polyunsaturated fatty acids such as linoleic and linolenic acids (Fraenkel and Blewett, 1946; Nation, 2001 and Genc, 2002). Moths deficient in these fatty acids have defects in wing formation and their scales adhere to the pupal case on emergence (Vanderzant, 1974). Genc and Nation, 2004a identified the fatty acids in the larvae

and adults of the butterfly *Phyciodes phaon*. They found palmitic and linolenic acids predominantly both in larvae and adults. They also showed larval survival of *P. phaon* to adult stage was enhanced by addition of linseed, olive and wheat germ oil in the artificial diet.

All insects are believed to require a sterol in the diet because they can't synthesize the sterol rings, or can't synthesize enough to meet their physiological requirements. Besides being a part of all cellular membranes, a sterol is the precursor for synthesizing the 27-carbon ecdysteroid molting hormone of insects. Thus, deficiency of a sterol in the diet results in incapability of the insects to molt and they typically die in an early instar Nation, 2001; Genc, 2002). The dietary requirement of sterol was first pointed by Hobson (1935) in blowfly larvae, *Lucilia sericata*, and has been verified in many different insects. Most insects that have been studied can use cholesterol which usually satisfies the sterol requirement, the typical 27-carbon sterol of animal tissues. Phytophagous insects ingest β-sitosterol and stigmasterol as major plant sterols and normally convert the 28- and 29-carbon plant sterols into cholesterol (Nation, 2001; Feldlaufer et al. 1995; Svoboda et al. 1975), but a few species synthesize a 28- or 29-carbon ecdysteroid from a dietary sterol acquired in their feeding. Cholesterol and β-sitosterol usually satisfies the sterol requirement in many studied insects but a few insect species such as Drosophila pachea are known to require a very specific sterol in the diet, 7-stigmasten-3β-ol, uncommon sterol found in senita cactus, *Lophocereus schotti* (Nation, 2001). Even trace amounts of lipids or sterols in a diet may positively influence growth and development (Vanderzant, 1974). Lack of sterol in the diet may be manifest in any stages of an insect. Sterol deficiency in adult female houseflies results in an 80% egg hatching reduction, although the fecundity is not affected (Nation, 2001).

## 4. Vitamins

Insects usually require a good source of seven vitamins: thiamine, riboflavin, nicotinic acid, pyridoxine, pantothenic acid, folic acid, and biotin, in small amounts, because they can't synthesize the vitamins. A studied mosquito species, *Culex pipiens*, showed requirements for all seven vitamins (Dadd, 1977). Vitamins often have a role as cofactors of the enzymes catalyzing metabolic pathways. Biotin is recognized as a cofactor for several enzymatic steps in the fatty acid synthesis, and a component of the enzyme pyruvate carboxylase (Tu & Hagedorn, 1992). Folic acid is needed for nucleic acid biosynthesis. β-carotene is a very important for the normal pigmentation of leaf-eating insects. Lacking of β-carotene, they do not develop their normal yellow and green colors and melanization is also reduced (Chapman, 1998). Some other insects, notably *Musca domestica* and *Manduca sexta*, require dietary vitamin A or β-carotene for normal morphology of the compound eyes and for most sharp vision. It is known that, the eggs of *Schistocerca gregaria* normally contain adequate β-carotene to allow the growth of the larvae and also for normal body coloration (Nation, 2001). When the insects reared on a carotene free diet from eggs, their growth is delayed and molting is postponed. In addition to that, those insects are smaller and less active than usual. Carnitine, also known as BT, is essential by *Tenebrio molitor* and *Tribolium obscurus*, *T. confusum*, and *T. casteneum*. The deficiency of carnitine cause molting difficulties and fatty acids degradation of midguts and then the beetles larvae die (House, 1965). One of the crucial roles of carnitine is known as a contributor in the passage of fatty acids across mitochondrial membranes in insects. Vitamin E is required for reproduction in some insects. It is also shown that it improves the fecundity of some moths and beetles (McFarlen, 1992). Ascorbic acid is essential to maintain normal growth and development of some insects, particularly required by phytophagous insects (Nation, 2001).

## 5. Minerals

The mineral requirements of insects are inadequately known. Given the known composition of insects, it is reasonable to assume that sodium, potassium, calcium, magnesium; chloride and phosphate are essential minerals for the function of insects (Nation, 2001). Metal ions are essential as enzyme co-factors such as, molybdenum which is a part of the xanthine dehydrogenase enzyme and important in purine metabolism of insects (Nation, 2001). Insects need only trace amounts of iron and calcium. Many phytophagous insects need quite large amount of potassium and only trace amounts of sodium (Nation, 2001). Trace amounts of other minerals may be necessary, but critical studies on mineral requirements are lacking. Osborn and Mendel 1932 showed that the balance of minerals in a salt mixture used and the proportion of minerals to other groups of nutrients are also important. Wesson's salt mixture, used as mineral sources in the artificial diet, is prepared for vertebrates (Osborn and Mendel 1932), and is high in Ca, Fe, and Na. Wesson's salt mixture is not good enough to maintain European corn borer development on an artificial diet (Nation, 2001). The Ca level in Wesson's salt mixture is toxic to *Blatella germanica* (Gordon, 1959). Another salt mixture is called Beck's salt which supports development of corn borers (Beck et al., 1968) and other lepidopteran insects (Genc and Nation, 2004b).

## 6. Phagostimulants

Phagostimulants are chemical compounds having an effect on insect feeding (Nation, 2001). Phagostimulants or chemical attractants and chemical deterrents are the factors in the acceptance or rejection of potential foods by insects. Taste receptors on the mouthparts, tarsi, antennae or other body parts, allow insects to taste and identify potential foods. It is known that adult western corn rootworms express phagostimulatory responses to several L-amino acids (Kim and Mullin, 1998); to γ-amino butyric acid (GABA); and to as little as 0.1 μM cucurbitacin B (Nation, 2001). Phagostimulants may be nutritional components or nonnutritional allelochemicals. Most food chemical components stimulate feeding in one insect or another, but if a particular chemical cue that an insect needs is missing, the insect may reject an otherwise nutritionally sufficient food. Some insects feed almost continuously, while others stop feeding when

they are full, even in the presence of feeding stimuli. Hexose sugars and sucrose are main nutrients and phagostimulants for many leaf-eating insects (Chapman, 1998). Glucosides, a combination of glucose with a non-sugar moiety, have a role as phagostimulants for some insects. For example, *Pieris* larvae that feed on plants in the Brassicaceae family are stimulated to feed by mustard oil glucosides (David and Gardiner, 1966; Dethier, 1980; Renwick and Huang, 1995, Nation, 2001). Adenosine triphosphate (ATP) in the presence of sodium ions is a phagostimulant for Aedes aegypti. Lipids, phospholipids, triglycerides, sterols, sterol esters and fatty acids are usually important phagostimulants for many different insects (Nation, 2001).

In many cases, the phagostimulant is not a nutrient, and may even be a defensive chemical evolved by the plant to reduce general herbivory, such as cardenolides in milkweed plants (Brower, 1972; Brower et al. 1984), cucurbitacins in cucurbits, mulberin in mulberry leaves (Ito, 1960) and iridoid glycosides (Bowers, 1983; Bowers, 1984) in many plants.

### 7. Feeding Deterrents

Many substances have an inhibitory effect on insect feeding which are called as feeding deterrents. For example, (-)-β-Hydrastine and strychnine-HCl are great feeding deterrents for adult western corn beetles (Chyb et al. 1995). Ammonium nitrates are known to inhibit feeding of the sweet clover weevil, Sitona cylindricollis (Carrel and Eisner, 1974). Detailed information on insect feeding deterrents can be found Schoonhoven 1972 and Dethier 1980.

### Conclusions

Studies with insect nutrition have indicated that unusual nutritional requirements do can occur in insects besides the balance of required nutrients is generally related with natural foods of the species. Variations in the quantity and quality of a suitable food can have important effects on insect development. Usually, when food ingestion decreases, the duration of development is extended and the insect becomes smaller and lighter. The sufficiency of larval food is correlated in the quantity of nutrients stored for egg production; however more direct effects of nutrient levels occur in insects that feed as adults. Development of artificial diets for insects was stimulated by the need to understand comparative nutritional requirements, as well as to enable rearing in the laboratory on foods more convenient than their natural food. They are useful in mass production of insect predators and parasites for Integrated Pest Management (IPM) control programs and for producing large numbers of insects for sterile release programs (SIT). Although basic nutritional needs of insects are well understood, developing suitable diets can still be very difficult. Current challenges would be to define and develop suitable diets for specific insects and successfully mass rearing of biocontrol agents for IPM and SIT programs.

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