Insect Diet

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Definition

Insect diet refers to the food usually eaten by an insect for growth, tissue maintenance, and reproduction, as well as the energy necessary to maintain these functions.

Introduction

Most insects have qualitatively similar nutritional requirements in proteins, carbohydrates, lipids, vitamins, minerals, trace elements, and water (Table 1). These chemical compounds can either be synthetized by the insects themselves, provided by beneficial symbionts or acquired in food (Chapman 2012). Insect diets, and thus the fraction of nutrients acquired in food, can considerably vary among species and developmental stages of the same species, resulting from adaptations to particular environments in which access to nutrients is restricted by the types and diversity of foods available. Herbivores, which make up the majority of insects, eat plants and are typically trophic specialists, which means that they consume only one or a few plant species. By contrast, entomophagous, carnivorous, zoophagous, detritivorous, xylophagous, graminivorous, and omnivorous insects tend to be more generalists.

While the domestication of insects started somewhere around 5000 years ago, with the cultivation of silkworms and honey bees, research on insect nutrition only developed at the beginning of the twentieth century. Key discoveries were made possible through the multiplication of attempts for designing artificial diets, whose composition can be only partly (meridic diet) or fully (holidic diet) defined. In 1908, Bogdanov was the first to rear an insect (blowflies) entirely on an artificial diet made of peptone, meat extract, starch, and minerals. Since then, famous entomologists, such as Painter, Fraenkel, Dadd, Waldbauer, Dethier, Scriber, and Slansky and Bernays and Chapman, among others, have developed methods and concepts that set a revolution for research on animal nutrition (for a brief thematic history, see (Raubenheimer et al. 2009)). These experiments demonstrate that insects actively attempt to achieve of nutritional balance by carefully regulating their intake of several nutrients simultaneously either from artificial diets or natural foods. Beyond advancing fundamental knowledge on insect nutrition, this research also provided a framework for a series of pioneering nutritional ecology studies that helped establish major concepts of biology and ecology, such as, for instance, ecological niches.

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Insect Diet, Table 1 Minimal (irreducible) nutrients shown to be useful or essential to insects. Depending on species, some of these nutrients can be nonessential or even toxic (e.g., cellulose). (Modified from (Cohen 2015))

Proteins	Lipids	Carbohydrates	Vitamins	Minerals
Polypeptides	Sterols	Hexose	Water-soluble vitamins	Calcium
Glycoprotein	Cholesterols	Glucose	Ascorbic acid	Chlorine
Lipoprotein	β-Sitosterol	Fructose	Thiamine	Copper
Essential amino acids	Stigmasterol	Disaccharides	Riboflavin	Iron
Arginine	Campesterol	Sucrose	Pyridoxine	Magnesium
Histidine	24-methyl-cholesterol	Polysaccharides	Nicotinic acid	Manganese
Isoleucine	Phospholipids	Starch	Pantothenic acid	Phosphorus
Leucine	Fatty acids	Glycogen	Biotin	Potassium
Lysine	Linoleic acid	Cellulose	Folic acid	Sodium
Methionine	Linolenic acid		Choline	Sulfur
Phenylalanine			Cyanocobalamin	Zinc
Threonine			Inositol	
Tryptophan			Lipid-soluble vitamins	
Valine			Tocopherol	
			Vitamin A	

Nutrients

Foods are complex mixtures of nutritional and non-nutritional (sometimes toxic) compounds. For insects, these compounds typically involve macronutrients (proteins, carbohydrates, and lipids), micronutrients (vitamins and minerals), and water, which all directly participate to physiological functions (Cohen 2015). Some of these nutrients are essential, which means that insects lack the ability to synthetize them on their own and must acquire them in food of from beneficial symbionts (Table 1). Others, such as food additives (stabilizers, preservatives, bulking agents) and token stimuli (plant secondary compounds) have no direct nutritional function.

Proteins

Proteins are made of amino acids (organic compounds containing an amino (-NH2), carboxyl (-COOH) groups, and a specific chain) and are the principal source of nitrogen for insects. While free amino acids can be present in foods, most often they are linked together by peptide bounds to form proteins. Once assimilated, proteins are broken down into their amino acid components and turned into different proteins that can be used for a wide range of biological functions, such as cell structure, enzymes, transport and storage, or receptor molecules. Insects require nine to ten essential amino acids (Table 1). The others, non-essential, amino acids are generally synthetized in the fat body provided that precursors are available in the food, although other tissues can also be important (e.g., proline and glutamine are synthetized in the mosquito midgut). Most proteins contain approximately half essential and half non-essential amino acids.

Lipids

Lipids consist of fatty acids, phospholipids, and sterols. Lipids are an important source of energy, essential components of cell membranes, nutrient transporters, and defensive compounds, serve as pheromones, and are involved in hormone synthesis (e.g., sterols are involved in ecdysteroid or molting hormones and fatty acids in juvenile hormone). Insects can synthesize most fatty acids and phospholipids. However, to do so, polyunsaturated fatty acids are required in the diet. Sterols can serve for energy and the production of hormones and carbohydrates. The major essential sterol, the cholesterol, is abundant in animal tissues but only present in low quantities (if not present at all) in plants and fungal food. Therefore, most phytophagous insects must synthetize cholesterol via dealkylation of plant sterols (e.g., β-sitosterol and campesterol) (Behmer and Nes 2003).

Carbohydrates

Carbohydrates include simple sugars (e.g., the monosaccharides sucrose, fructose, glucose, maltose), starch, and other polysaccharides (e.g., cellulose). They serve as respiratory fuel, provide the carbon basis in molecular synthesis, and constitute building materials for the insect cuticle (e.g., polysaccharide chitin). Insects can synthesize glucose by gluconeogenesis from lipids or amino acids (Miyamoto and Amrein 2017) in such a way that some species can live without any sugar intake at all (e.g., wax moth and screwworm). By contrast, other insects require considerable amounts of carbohydrates in their diet (e.g., honey bee or locust). Not all sugars are usable by all insects (e.g., melibiose is digested by many flies but not by honey bees), and some monosaccharides can be toxic because they compete with other essential sugars (e.g., mannose blocks glucose pathway in bees). The digestive capability for carbohydrates also varies among insect species. For instance, flour beetles can hydrolyze a broad range of polysaccharides, whereas the grasshopper *Melanoplus* only accepts simple sugars. Digestibility of carbohydrates also varies between developmental stages of the same species (e.g., mosquito larvae use starch and glycogen while adults cannot). Cellulose cannot be digested by most insects and thus has no nutritional value.

Vitamins

Vitamins are organic compounds required in trace amounts for growth. Vitamins are classified in two groups depending on their solubility in water or lipid. Water-soluble vitamins have a relatively short half-life (excreted and lost from the insect's metabolic pool), while lipid-soluble vitamins remain compartmentalized in lipid stores. The main water-soluble vitamins include vitamin C (ascorbic acid) and the B vitamins. Vitamin C serves as phagostimulant and antioxidant and promotes the synthesis of collagen and the extracellular matrix in insects. The B vitamins are involved in many metabolic pathways, including ATP production (thiamine, riboflavin, niacin), acyl group transfer (pantothenate), and growth factor (biotin and folic acids). Some insects also require small quantities of other water-soluble vitamins such as choline (for the production of cell membrane), carnitine (for lipid metabolism), cyanocobalamin, and lipoic acid. Lipid-soluble vitamins essential to insects are the vitamin A complex (β-carotene and related carotenoids relatives) and vitamin E (tocopherols). Vitamin A is required for visual pigments function and formation. Vitamin E serves as fertility factor, including spermatogenesis and egg maturation.

Minerals

Calcium, chloride, copper, iron, magnesium, manganese, phosphorus, potassium, sodium, and zinc are vital in small quantities to many insects. These compounds are involved in the synthesis of coenzymes and metalloenzymes. Potassium, chloride, calcium, and sodium are essential for the excitability of tissues (e.g., muscle cell and neurons). Potassium and magnesium are major actors of the bioenergetics activity, respectively, via the ATP and glycolysis pathway. Pollutant minerals, present in the environment and passively ingested by insects, can replace dietary minerals and act as toxins.

Water

Water is essential to all insects. It provides the medium in which all metabolic processes proceed. As such it is necessary for the absorption of macronutrients. Water often contains naturally occurring micronutrients such as mineral salts. Insects actively ingest free water, have physiological mechanisms controlling thirst, and suffer fitness consequences if water is excessive or deficient in the diet. Meal size and inter-meal duration are both influenced by free water availability.

Consequences of Diet on Behavior and Physiology

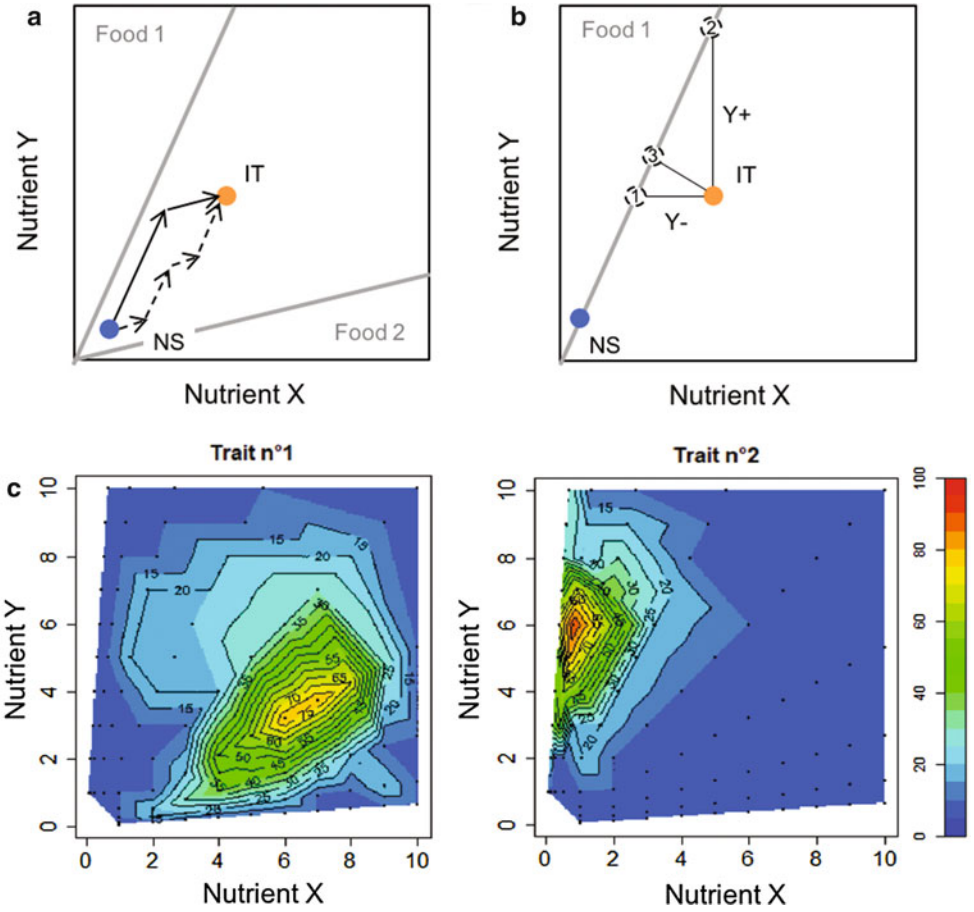
Insects have evolved behavioral and physiological strategies to acquire appropriate amounts and balances of the required nutrients from complex food mixtures. In most environments, no single food provides an optimally balanced diet for the insects. In such case, individuals must adjust their dietary choices and nutrient assimilation rates to reach and maintain a balanced diet (Simpson and Raubenheimer 2012).

Studying Nutrient Regulation: Nutritional Geometry

The study of nutrient regulation by insects took a significant step forward at the end of the twentieth century when Raubenheimer and Simpson (1993) introduced a unifying theoretical framework for nutrition studies known as “nutritional geometry.” This framework employs a state-space modeling approach taking into account the multiple interactions among mechanisms regulating the intake of different classes of nutrients. Individual insects, foods, and their interactions are represented graphically in a geometric space (a nutrient space) defined by two or more food components, typically carbohydrates and proteins (see examples Fig. 1). Foods are radials through the nutrient space at angles determined by the balance of nutrients they contain (nutritional rails). The insect’s state (nutritional state) is a point or region that changes over time. As the insect eats, its nutritional state changes along the rail for the chosen food. The functional aim for the insect is to eat foods in appropriate amounts and ratio to direct it to an optimal nutritional state (intake target). This intake target moves over time as the quantity and mix of nutrients change with activity, growth, development, reproduction, and senescence. For instance, in larval insects, early stages typically have diets richer in nitrogen than later stages. The intake target also shifts over evolutionary times as insects adapt to different diets. Insects that feed on other animals have high amino acid and fat requirements relative to carbohydrates, reflecting the relatively high protein and low carbohydrate content of animal tissues. Plant-feeding insects, however, generally require approximately equal amounts of amino acids and carbohydrates. Over the past decades, nutritional geometry has proved a powerful tool to understand how insects and other animals balance their diet across a wide diversity of taxa, feeding guilds and ecological of environments both behaviorally and physiologically (for a recent review, see (Raubenheimer and Simpson 2018)).

Behavioral Regulation

An insect can respond to a dietary imbalance in one of three ways. First, it can move from eating one food to another with a different nutrient balance. Hence, when given a choice between complementary foods (foods defining a nutrient space containing the intake target of the animal), most insects have been shown to self-compose a nutritionally balanced diet (Fig. 1a). This is possible because insects have separate appetites for different nutrients. Grasshoppers, caterpillars, aphids, flies, and cockroaches regulate their intake of protein and carbohydrates to a single intake target. Predatory ground beetles (Carabidae) have separate protein and lipid appetites. In locusts, levels of water are also regulated together with protein and carbohydrates (Clissold et al. 2014). This ability to adjust food intake to nutritional requirements implies some feedback of nutritional status on food selection and feeding behavior. In locusts, blood-borne nutrient feedback from eating a diet rich in amino acids depresses the sensitivity of peripheral contact chemoreceptors to amino acids in the diet but has no effect on the sensitivity of chemoreceptors to sucrose. Conversely, if the insect feeds on a diet with high levels of carbohydrates, the sensitivity of its receptors to sucrose is depressed. In species that heavily rely on learning and memory for foraging, such as bees, cognitive capacities are crucial for nutrient balancing by enabling insets to associate the quality of the food with feedback on their own nutrient status based on the visual, olfactory, and tactile characteristics of foods. In drosophila, protein appetite in mated females results of a sex peptide that is introduced with male’s seminal fluid during mating, which stimulates special sensory neurons in the female’s reproductive tract. An additional mechanism responding to the protein demands of egg development then controls how much yeast is eaten, involving TOR/S6 kinase and serotonin signaling pathways in the central nervous system (Vargas et al. 2010).



Insect Diet, Fig. 1 Examples of nutritional geometry models for hypothetical insects. (Modified from (Lihoreau et al. 2018)). (**a**) Nutritional rails (gray lines) represent the ratio of nutrients X and Y in foods. The blue dot is the nutritional state (NS) of the individual, and the red dot is its intake target (IT). Foods 1 and 2 are individually imbalanced but complementary (fall on opposite sides of the IT). The individual can reach its IT by combining its intake from the two foods (arrows). (**b**) The individual is restricted to a single imbalanced food and can (1) satisfy its needs for Y but suffer a shortfall of X; (2) satisfy its needs for X but over-ingest Y; and (3) suffer a moderate shortage of X and excess of Y. (**c**) Nutritional performance landscapes showing the effects of nutrients X and Y on fitness traits 1 and 2. In this example, trait 1 is maximized for a high X to Y ratio, whereas trait 2 is maximized for a low X to Y ratio

Second, insects feeding on imbalanced foods can also adjust the total amount ingested to acquire enough of the most limiting nutrients. Grasshoppers, caterpillars, cockroaches, aphids, and ants have been shown to increase the amount eaten if the entire nutrient composition of a diet is diluted with some inert non-nutritional substance. Insects can also selectively compensate for deficiencies in a class of nutrients by increasing the total amount eaten. When confined to a single, nutritionally imbalanced food (that does not allow the intake target to be reached), insects can compromise between overconsuming excess nutrients and eating too little of the nutrients in deficit. The form of this compromise in a nutrient space varies according to the nutrients involved and the ecology of species (Fig. 1b). For instance, when forced to ingest diets containing an unbalanced ratio of proteins and carbohydrates, specialist migratory locusts (*Locusta migratoria*) do not substantially overconsume the excess nutrient to decrease its deficit of the other nutrient.

In contrast, in the generalist desert locust (*Schistocerca gregaria*), individuals ingest a greater amount of either protein or carbohydrate to gain more of the more limiting nutrient. This pattern of host-plant generalists being more willing to tolerate nutrient excesses than host plant specialists is widespread across grasshoppers and caterpillars and is accompanied by a greater tendency by generalists to store excesses in body reserves (Behmer 2009).

Physiological Regulation

A third mechanism to face food nutritional imbalance is to adjust the efficiency with which the insect uses the ingested nutrients. The importance of such post-ingestive regulation has been best studied in locusts. These insects maintain a relatively constant increase in body nitrogen despite a threefold increase in the amount of nitrogen ingested. Most of the excess of protein is excreted as uric acid or some other unknown nitrogenous end product of catabolism. Other means of post-ingestive regulation include differential secretion of digestive enzymes to lower the efficiency of digestion excess carbohydrate or protein in the diet, the adjustment of the timing of gut emptying to alter the ratio of protein and carbohydrate absorbed from the gut, the increase of metabolic rate to burn off excess ingested carbohydrate, or the selection of environmental temperatures that favor the utilization of either proteins or carbohydrates.

Consequences of Diet on Fitness

Although some growth occurs on foods containing widely differing levels of nutrients, optimal performance requires the nutrient levels to be appropriately balanced. Ingesting and processing excessive quantities of food in order to obtain enough of a particular component that is present only in low concentration in the diet can prove costly in various ways. Firstly, some nutrient excess can be toxic or have deleterious effects (e.g., excess of carbohydrates can result in obesity-like syndromes in many insects). Secondly, interconversions from one compound to another can be metabolically costly and the rates at which they occur limited. These effects can affect a wide range of fitness traits such as growth, development, reproduction, immune responses, cognition, and life span. The interacting effects of nutrients on fitness traits are evident when mapping insect performances into nutrient spaces of nutritional geometry (Fig. 1c). Different traits often have different nutritional optima, which means that insects must make feeding decisions to trade-off between optimizing multiple traits simultaneously. The ability of insects to resolve these nutritional trade-offs has been first demonstrated in the fruit fly *Drosophila melanogaster* (Lee et al. 2008). When confided to 1 of 28 artificial diets varying in protein and carbohydrate content, female flies achieve a maximum life span on a diet containing a 1:16 ratio of protein to carbohydrate, while maximum egg laying rate is reached on a 1:2 protein to carbohydrate ratio. When allowed to self-select complementary foods, flies mix a diet comprising a 1:4 protein to carbohydrate ratio which maximizes lifetime egg production, a measure of global fitness. Similar trade-offs have been observed in many other insect species for life span and reproduction, immunity and reproduction, or even traits related to different stages of reproduction that cannot be attained simultaneously.

Consequences of Diet on Biotic Interactions

Upon its influence on the physiology, behavior, and fitness of individual insects, the diet can affect social behaviors and interspecific interactions (e.g., with symbionts, competitors, predators) and ultimately influence species assemblages and communities.

Social Behavior

In gregarious and social insects, diet influences collective behaviors and social structures (Lihoreau et al. 2018). At the most basic level, a deficit in key nutrients in the environment can generate mass movements. In the Mormon cricket, Anabrus the lack of proteins and mineral salts due to intense competition and food depletion during population outbreaks triggers intense cannibalistic interactions. By attempting to eat each other, crickets engage in mass migrations, whereby millions of individuals form marching bands extending over several kilometers (Simpson et al. 2006). In social caterpillars that forage in trails, differences in the nutritional states among trail members determine the identity of leaders (hungry) that guide the group and followers (well-fed) that follow behind. In more integrated insect societies, differences in early food experience can also mediate reproductive division of labor. This is the case in cooperative breeding burying beetles that feed on shared carcasses, where dominant females that access food in priority ingest more proteins and become breeders, whereas subordinate individuals that acquire relatively less proteins become sterile helpers. In eusocial insects, such as honey bees, differential nutrition of the larvae influences caste determination, so that female larvae fed a diet rich in royal jelly become reproductive queens, whereas female larvae fed lower levels of jelly become sterile workers.

Ecological Interactions

Symbionts

An estimated 10% of all insects utilize diets that are nutritionally so poor or unbalanced that they depend on beneficial symbiotic organisms for sustained growth and reproduction. These associations provide them with metabolic capabilities or additional nutrients (e.g., essential amino acids in insects feeding on plant sap, vitamins insects feeding on blood, and sterols in insects utilizing wood). In some insects, resident microorganisms degrade complex dietary components to a form that can be assimilated by the insect. This is the case of termites that rely on a rich gut microbiota community to degrade cellulose or soil matter (Bignell et al. 2010). In plant-sap feeding hemipterans that eat phloem and xylem low in essential amino acids, the microorganisms have a biosynthetic function. In *Drosophila*, where gut symbionts are acquired from the environment, variations in microbe communities can trigger different foraging strategies in the hosts that need to compensate for different nutrients (Wong et al. 2017). Other insect species have evolved ectosymbiotic associations. This is the case of fungus-farming termites and leaf-cutter ants that cultivate their own crop in well-protected gardens. In these social insects, foragers collect plant materials not digestible by the insects to feed a fungus that provides accessible key nutrients to the insects. In ants, workers regulate food intake to nourish the fungus with nutrient balances that maximize the production of edibles for the colony, at the expense of fungus reproduction (Shik et al. 2016).

Parasites and Pathogens

The diet can also affect the immunological responses of insects and their interactions with parasites and pathogens. For instance, caterpillars of the African cotton leafworm (Spodoptera littoralis) infected with either a bacterial or viral pathogen survive better as the ratio of protein to carbohydrate in the diet is increased despite the toxic effect of protein on life span. By contrast, uninfected larvae perform best on an intermediate nutrient ratio. When given a choice between multiple artificial diets, infected caterpillars tend to increase their consumption of protein, which has the consequence of enhancing the immune response, a nutritional behavior akin to self-medication (Lee et al. 2006).

Dietary Breath and Niche Partitioning

At a broader observation scale, variation in insect diet can determine the coexistence of species and shape local development of biodiversity. For instance, closely related species of generalist-feeding herbivores (grasshopper species in the genus *Melanoplus*) eat protein and carbohydrates in different absolute amounts and ratios even if they eat the same plant taxa (Behmer and Joern 2008). The existence of species-specific nutritional niches, such as this one, provides a cryptic mechanism that helps explain how generalist herbivores with broadly overlapping diets coexist.

Conclusions

There is a long history of developing artificial diets to culture insects for the food industry and academic research. This approach has showed that most insects have qualitatively similar requirements for macro- and micronutrients as other animals. Over the past decades, new concepts of nutritional ecology have moved the focus from the identification of essential and nonessential nutrients in insect diet to the study of interactions between food components and their consequences on fitness. Insects have evolved sophisticated behavioral and physiological strategies to reach and maintain nutrient balances and concentrations maximizing multiple fitness traits, and this is flexible throughout development. These consequences of diet can be observed at the individual level and beyond, across levels of biological organization. Integrative approaches of modern insect nutrition research offer a means for addressing more general problems in ecology, including the structuring of food webs, the regulation of food chain length, the flow of nutrients through ecosystems, and the dynamics of communities and ecosystems (Simpson et al. 2015).

Cross-References

- ▶ Amino Acid
- ▶ Arthropod Diet
- ▶ Digestive System
- ▶ Division of Labor
- ▶ Energy
- ▶ Feeding
- ▶ Fitness
- ▶ Food Industry
- ▶ Foraging
- ▶ Growth Diet
- ▶ Herbivore
- ▶ Hymenoptera Diet
- ▶ Lipid
- ▶ Local Resource Competition
- ▶ Nutrients
- ▶ Optimal Foraging Theory
- ▶ Protein
- ▶ Provisioning
- ▶ State Sensitive Model of Foraging

References

Behmer, S. T. (2009). Insect herbivore nutrient regulation. *Annual Review of Entomology, 54*, 165–187.

Behmer, S. T., & Joern, A. (2008). Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences of the United States of America, 105*(6), 1977–1982.

Behmer, S. T., & Nes, W. D. (2003). Insect sterol nutrition and physiology: A global overview. *Adv Insect Physiol, 31*, 1–72.

Bignell, D. E., Roisin, Y., & Lo, N. (2010). *Biology of termites: A modern synthesis*. Heidelberg: Springer.

Chapman, R. F. (2012). *The insects: Structure and function* (5th ed.. (eds: SJ Simpson and AE Douglas)). Cambridge, UK: Cambridge University Press.

Clissold, F. J., Kertesz, H., Saul, A. M., Sheehan, J. L., & Simpson, S. J. (2014). Regulation of water and macronutrients by the Australian plague locust, *Chortoicetes terminifera*. *Journal of Insect Physiology, 69*, 35–40.

Cohen, A. C. (2015). *Insect diets: Science and technology.* CRC Press.

Lee, K. P., Cory, J. S., Wilson, K., Raubenheimer, D., & Simpson, S. J. (2006). Flexible diet choice offsets protein costs of pathogen resistance in a caterpillar. *Proceedings of the Royal Society B, 273*, 823–829.

Lee, K. P., Simpson, S. J., Clissold, F. J., Brooks, R., Ballard, J. W. O., Taylor, P. W., Soran, N., & Raubenheimer, D. (2008). Lifespan and reproduction in Drosophila: New insights from nutritional geometry. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 2498–2503.

Lihoreau, M., Gomez Moracho, T., Pasquaretta, C., Costa, J. T., & Buhl, J. (2018). Social nutrition: An emerging field in insect science. *Current Opinion in Insect Science, 28*, 73–80.

Miyamoto, T., & Amrein, H. (2017). Gluconeogenesis: An ancient biochemical pathway with a new twist. *Fly, 11*, 218–223.

Raubenheimer, D., & Simpson, S. J. (2018). Nutritional ecology and foraging theory. *Current Opinion in Insect Science, 27*, 1–8.

Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: Toward an integrated framework. *Functional Ecology, 23*, 4–16.

Shik, J. Z., Gomez, E. B., Kooij, P. W., Santos, J. C., Wcislo, W. T., & Boomsma, J. J. (2016). Nutrition mediates the expression of cultivar-farmer conflict in a fungus-growing ant. *Proceedings of the National Academy of Sciences of the United States of America, 113*, 10121–10126.

Simpson, S. J., & Raubenheimer, D. (1993). A multi-level analysis of feeding behaviour: The geometry of nutritional decisions. *Philosophical Transactions of the Royal Society B, 342*, 381–402.

Simpson, S. J., & Raubenheimer, D. (2012). *The nature of nutrition: A unifying framework from animal adaptation to human obesity.* Princeton: Princeton University Press.

Simpson, S. J., Sword, G. A., Lorch, P. D., & Couzin, I. D. (2006). Cannibal crickets on a forced march for protein and salt. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 4152–4156.

Simpson, S. J., Clissold, F. J., Lihoreau, M., Ponton, F., Wilder, S. M., & Raubenheimer, D. (2015). Recent advances in the integrative nutrition of arthropods. *Annual Review of Entomology, 60*, 293–311.

Vargas, M. A., Luo, N., Yamaguchi, A., & Kapahi, P. (2010). A role for S6 kinase and serotonin in post-mating dietary switch and balance of nutrients in *D. melanogaster. Current Biology, 20*, 1006–1011.

Wong, C. A. N., Wang, Q. P., Morimoto, J., Senior, A. M., Lihoreau, M., Neely, G. G., Simpson, S. J., & Ponton, F. (2017). Gut microbiota modifies olfactory-guided microbial preferences and foraging decisions. *Current Biology, 27*, 2397–2404.