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Insects: A Potential Source of Protein and Other Nutrients for Feed and Food

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Abstract

Sustainable production of healthy food for a growing global population, in the face of the uncertainties of climate change, represents a major challenge for the coming decade. Livestock provide food with high nutritional value but are frequently fed on human-edible crops and are associated with significant production of greenhouse gases. Recent years have seen increasing interest in the farming of insects as a sustainable source of human food, or as a replacement of ingredients such as soya or fishmeal in the feeds of terrestrial livestock or fish. This review provides an overview of insect physiology and growth regulation, considers the requirements for insect farming and mass production, and summarizes the nutritional value of the 10 most commonly studied insect species, before reviewing the literature on the use of insects as feed and food. We highlight the challenges required to develop a sustainable, safe, and affordable insect farming industry.

INTRODUCTION

In the face of human population growth, increased longevity, and the uncertainties of climate change, the ability to sustainably produce sufficient food to feed the world is of increasing concern (1). Furthermore, there is an urgent need to improve the quality of diets around the world, ensuring appropriate provision of essential nutrients, while not contributing to the global epidemic of obesity and related chronic diseases, including diabetes, cardiovascular disease, and cancers of the gastrointestinal system (2, 3). The impact of diet on the health of both the population and the planet was the focus of the recent EAT–*Lancet* report (2), the major recommendation of which was to move to a primarily plant-based diet and, in many parts of the world, dramatically reduce the intake of animal products. This was based on the recognition that diets rich in such foods are often unhealthy, being both energy dense and rich in saturated fatty acids, and that animal production systems have major negative impacts on the environment. The current production systems for livestock are an unsustainable use of natural resources (2); animals are often fed on crops that are edible by humans and that require a high proportion of the planet's water resources, as well as producing a significant proportion of global greenhouse gas emissions (4). Whereas there is little doubt that much of the population of the world's wealthiest countries would benefit from reducing consumption of meat and dairy products, for the poorest societies these products represent an important source of energy, a wide range of micronutrients, and high-quality protein (5). Furthermore, livestock farming represents a major economic and societal benefit to many such populations. It thus appears that whereas consumers in richer, industrialized countries will increasingly look toward non-animal-derived, alternative sources of food, there is a need to improve the sustainability of livestock production in poorer countries with rapidly growing populations, including the identification of sources of non-human-edible feed ingredients. In recent years, insects have attracted increasing attention as both a human food and an animal feed ingredient (6–8). They are frequently considered to be a rich source of essential nutrients that can be grown on low-value feeds (9) and have a low carbon footprint (8). This review considers the potential of insects as an increasing component of both animal and human diets and considers the safety and challenges of industrial-scale production of insects.

INSECT PHYSIOLOGY

Insects are the most diverse class of the animal phylum, and one that has displayed remarkable physiological adaptations. A better understanding of the physiology of the species with the potential to be used as food or feed should help ensure that production systems maximize that potential. Commonly, insects are built on a segmental plan, with a cuticle that forms the exoskeleton and is continuous across the whole body (10). This exoskeleton is one of the main differences between insects (invertebrates) and traditional livestock species (vertebrates). Insect development and ultimately growth are divided into a series of molts, known as instars (11). Insects can be classified into three groups in terms of postembryonic development: ametabolous, hemimetabolous, and holometabolous (**Figure 1**). Ametabolous insects experience no metamorphosis; the adult is simply a larger version of the larval form. For hemimetabolous insects, the larvae hatch into a form similar to the adult, but wings form as instar proceeds. Holometabolous insects start out as larvae, followed by a pupal stage and then an adult form; they exhibit three distinct phenotypes (11).

Insect mouth physiology varies between species, which are characterized into two groups, solid feeders and liquid feeders. As the names suggests, these groups require either a solid or liquid diet, respectively (12). Intake in both types of feeders is monitored by the stretch receptors on the alimentary canal or in the body wall. The location of the stretch receptors varies in different

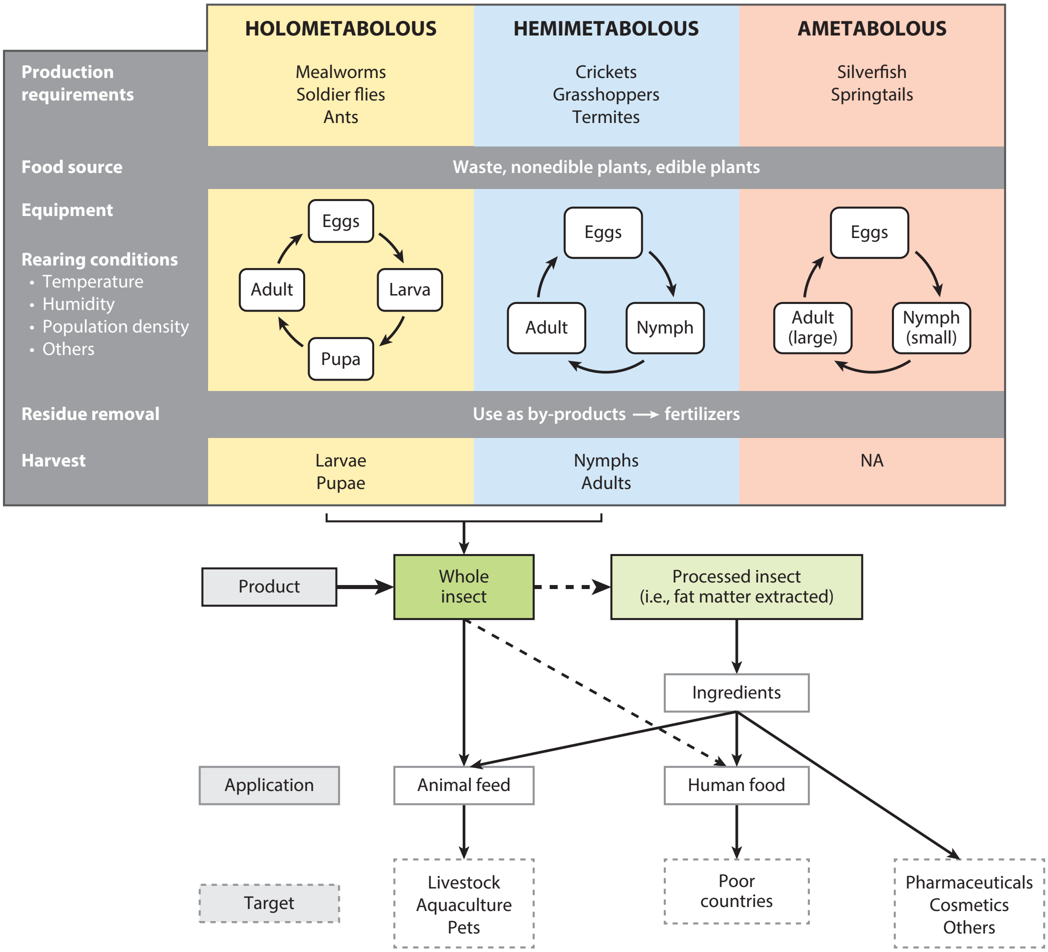

Figure 1

Overview of insect production, including classification, general life cycle, production requirement, products, and potential applications.

insect types; for example, in nectar-feeding insects, they are mainly found in the crop, whereas in grasshoppers they are at the anterior end of the gut. The insect's alimentary tract is split into three main parts: the foregut (stomodeum), midgut (mesenteron), and hindgut (proctodeum) (13). A remarkable difference between vertebrates and insects is that the lining of the insect gut is only a single cell thick, compared with its multicellular thickness in vertebrates (10). The foregut and hindgut are ectodermal; therefore, the cells secrete a cuticle, which is similar to that lining the outside of the body. Despite the fact that the midgut is not lined, it contains a peritrophic envelope, which acts as a separation layer between the epithelial cells and the food (13). The midgut is immunologically active, with the ability to produce antimicrobial peptides in response to pathogens (10). In addition, the alimentary tracts of most insects produce specific enzymes to enhance digestion of products; for example, some insects can digest cellulose, whereas most mammals cannot (14), and they can feed on plants considered nonedible by animal species (15). Moreover, owing to the microorganisms that colonize their gut, some insects can grow on waste, such as polystyrene (16), which has increased the interest in their microbiota. Insects' ability to digest ingredients that cannot be consumed by humans and other mammals, and subsequently convert them into high-quality protein, makes them attractive as an intermediate species to concentrate important nutrients, particularly essential amino acids (EAAs), polyunsaturated fatty acids (PUFAs), and possibly minerals as well.

REGULATION OF INSECT GROWTH

The regulation of insect growth has been studied in the context of body size, growth rate, nutritional value, feed conversion yield, and stress response. The main environmental factors that influence insect growth are nutrition, temperature, and population density, which modulate size, fecundity, and longevity (17). However, insects are the largest group of animals, and their growth regulation shows substantial variation across species. Indeed, size varies between insect species by up to seven orders of magnitude, a remarkable characteristic of their diverse morphology (18). The processes of development and growth in insects have been investigated for several orders, such as blattodeans, hemipterans, coleopterans, hymenopterans, lepidopterans, and dipterans, with growth rates and growth periods shown to be regulated by divergent mechanisms in dipterans, lepidopterans, and coleopterans (18).

In spite of this diversity, conserved pathways and common mechanisms have been described for the regulation of insect growth. As in mammals, insect body size is regulated through the insulin-like growth factor (IGF) and target of rapamycin (TOR) signaling pathways, which act in coordination with steroid and neuropeptide hormones (19, 20). Both body size and life span are affected by instar duration and growth cessation, which are regulated by nutrition through the insulin and TOR pathways (17). In flies, reduced TOR activity in the fat body (FB) leads to increased life span (21), and growth takes place during the different larval stages or in premetamorphic nymphs. In holometabolous insects, growth stops when the larvae surpass a critical weight to ensure a suitable size at metamorphosis. Larval growth is controlled by the insulin-signaling pathway (in peripheral tissues), which is regulated by a TOR-mediated nutrient sensor in the FB (17).

Along with the IGF and TOR pathways, the endocrine system plays a crucial regulatory role, particularly two key hormone regulators, ecdysteroids and juvenile hormone (JH) (17). The FB and prothoracic gland control ecdysone production, which regulates insect size and body growth (22). Moreover, IGF and TOR signaling also regulate the biosynthesis of these two hormones (18). Applying JH to larvae delays metamorphosis (23), maintaining the juvenile characteristics of insect larvae and determining the appropriate metamorphosis timing, which is initiated by the molting hormone 20-hydroxyecdysone (20E) (24). Therefore, these hormones control the molting process, which involves production of a new cuticle and shedding (or ecdysis) of the old cuticle (25). In adults, JH regulates reproduction by affecting vitellogenesis and oogenesis, and JH and ecdysteroids also act as pheromones, playing an important role in body size and social interactions, as reported in termites, cockroaches (26, 27), and bees (28). Currently, there are synthetic analogs of JH (juvenoids) called insect growth regulators, which block metamorphosis and are used as insecticides and research tools (29).

The FB of insects is analogous to the adipose tissue and liver of mammals, being the main tissue for nutrient storage, energy metabolism, immunity, and detoxification. Additionally, the FB has a central regulatory role, integrating nutritional and hormonal signals to control larval growth, body size, circadian clock, pupal diapause, longevity, and feeding behavior (30). In terms of nutrient storage and metabolism, the FB contains lipids (in the form of lipid storage droplets and associated proteins and lipases), carbohydrates (as glycogen), and proteins (30), with JH and 20E regulating glycolysis (24) and vitellogenin synthesis within the FB tissues (31). Unlike in mammals, trehalose is the main blood sugar in insects, and this disaccharide is important as an instant source of energy but is also involved in the regulation of stress recovery, growth, chitin synthesis, and metamorphosis (32).

A better understanding of insect growth regulation should allow improvements in both production yields and nutritional value. Several strategies can be applied, such as optimization of farming conditions, diet modifications, and genetic engineering approaches. For example, diet modifications can alter insect growth rate and body composition, as demonstrated in mealworms (33). Using RNA interference technology, Dabour et al. (19) demonstrated altered body size in crickets. Moreover, the use of genetically modified insects as a biological approach for pest control has also been developed (34). Indeed, recent insect research has focused mainly on pest control or biomedical model organisms. However, the research tools and knowledge generated by those studies can now be used to improve the efficiency of production of insects as a sustainable source of protein and other nutrients for feed or food.

REQUIREMENTS FOR INSECT FARMING

While insects have represented a significant part of the diet of many populations around the world for centuries, particularly in Africa, Asia, and South America (8), traditionally these have generally been harvested from the wild. However, more recently attention has turned to farming of insects for food and feed. Globally, a large number of producers have emerged alongside a myriad of smallholders, many of which are based in Africa and Asia. Production of insects for direct human consumption has largely centered around crickets and mealworms, with black soldier fly larvae, and to a lesser extent mealworms, being favored for animal and aqua-feed. Currently in Europe, 6,000 tonnes of insect protein are being produced, with expectations for production to meet 3 million tonnes by 2030 (35).

Insect farming is generally regarded as a sustainable way to produce high-quality protein and other nutrients. For example, direct emissions of CO_2, CH_4, N_2O, and NH_3 have been reported to be lower for a range of insect species compared to conventional livestock (36). Although energy requirements for insect production can be high, owing to the need to maintain their body temperatures, their poikilothermic nature means this is at least partly offset by their improved feed efficiency. In general, water and land requirements are considerably lower than that for conventional terrestrial livestock species (37). Ultimately, however, the sustainability of insect farming is dependent on the availability of low-cost feed materials that are unsuitable for human food, animal feed, or other uses. In a recent review of studies that have undertaken life-cycle analysis of insect production, van Huis & Oonincx (38) highlighted the reduced direct emissions and land and water use but acknowledged the need for continued development of energy-efficient facilities combined with efficient use of feed ingredients.

Equipment

Insect farming as a mass production system involves growing insects, processing, product extraction, distribution, and retail (39). There are two potential sectors: breeding and mass production, both of which involve key elements of feeding, watering, environmental control (temperature and humidity), and cleaning systems (17, 40). The breeding sector could then supply the mass production sector, which might also involve extra elements of harvesting, processing, and packaging (40). Feeding and watering could be automated through an irrigation system, similar to that used in commercial greenhouses. Both temperature and humidity must be specific for the species being reared, involving use of growth rooms, incubators, air-conditioning units, fans, and/or heaters. Insects can be reared in plastic boxes (41), with space optimization being achieved through use of shelving or a wheeled system (40). Alternatively, insects could be reared in their natural environment through semi-cultivation, with only mass production being done in captivity (8), although this would be much harder to control environmentally.

Currently, mass production of insects is expensive owing to reliance on manual labor (42), with mealworm production estimated to be 4.8 times more expensive than that for chicken feed (8). Automation would reduce both manual labor and associated high costs (42). A processing and packaging phase would follow harvesting (40), requiring robust processing methods to eliminate bacteria or microbes (43). Klunder et al. (44) suggested that a heating step could remove *Enterobacteriaceae* but not all spore-forming bacteria. Therefore, the best processing and storage methods for insects, on a mass scale, remain to be identified.

Species

Because they are invertebrates, the welfare requirements associated with insects are not as tightly constrained compared to those for traditional livestock, but this does not mean that they can be ignored. The species for mass production must be carefully selected to ensure they possess the characteristics that allow them to excel in such a system. For example, important factors for successful production include a short development cycle, high ovipositional rate and biomass productivity, and high efficiency in terms of converting substrate to product and the ability to live at high densities with good disease resistance (8).

Careful consideration of how these insect characteristics interact with the various phases of the production system is required to further optimize current production. For example, if a holometabolous insect, such as *Tenebrio molitor* (yellow mealworm), is chosen for a production system, then the timings of metamorphosis from larval to pupal stages must be controlled to avoid progression to the adult beetle, thereby ensuring mass production at the larval stage. Another factor is housing requirements in relation to controlling insect movement; for example, holometabolous insects in their larval stage are able only to crawl, whereas hemimetabolous insects (e.g., crickets) can jump and/or fly (10) and therefore require more secure housing.

Water Sources and Humidity

An advantage of producing insects over livestock is their lower water requirements (40). For mealworms, the water footprint per gram of protein is five times less than that for beef production (45). However, insects lose water through evaporation, meaning these losses must be minimized and balanced by water consumption (10). Insects have three mechanisms for absorbing water: orally from the food they eat or another water source; via uptake through the cuticle by drawing water molecules in from the air (46); and via changes in metabolism, because at low humidity insects can increase internal production of water from the oxidation of energy substrates (47).

Interestingly, insects modulate their feed intake to control water intake. For example, locusts will eat more food to obtain water from it, independent of their nutrient requirements (10). Previous work has used different methods of supplying water to insects, including using vegetables such as carrots (48), sprinkling feed with water, or using water-soaked cotton wool (49, 50). Use of vegetables adds extra cost and complexity and could introduce mold if the vegetable is not consumed completely. System humidity could be reduced if water supply methods are carefully controlled, thereby improving system sustainability.

Temperature

In tropical regions where the climate is hot and humid all year round, insects naturally tend to reproduce faster and grow bigger (40), which leads to the concept that insects must be kept at high temperatures. Many insects are ectothermic, so their body temperature reflects their environment (plus any heat produced from metabolism). Metabolic heat production is insufficient to maintain homeostasis (10), and ectoderm growth performance is directly linked to environmental temperature. However, a slight increase in temperature can be detrimental to growth performance (10). *Alphitobius diaperinus* beetles will grow optimally up to 31°C, and *T. molitor* beetle up to 23.3°C, but anything above these temperatures is detrimental to both growth and composition (51). The environmental impact of maintaining these temperatures for efficient growth also remains to be established.

Food Sources

The specific nutritional requirements of insects are not yet completely described. Insufficient or excess nutrients provided during the rearing phase may result in suboptimal growth, environmental concerns, and financial losses. Most insects have similar nutritional requirements owing to the uniformity in their chemical compositions and metabolic capabilities (12), with most potential production species being solid feeders. Hence, feeding behavior influences production requirements. Most insects eat discrete meals, separated by relatively long periods of nonfeeding (10), leading to the question of whether they need ab libitum or twice-a-day feeding. The optimal feeding regimen will result in maximum biomass production and minimum waste.

Flexibility in food sources could allow for use of alternative or waste sources that cannot be used directly in human or livestock diets. Importantly, insects can be raised on biowaste (52) or plant material that cannot be used for human consumption (53), and this biotransformation of organic matter or waste into edible insect mass is seen as highly efficient (53) and sustainable. Those species requiring perishable food sources will need a more frequent supply, as storage is an issue, particularly in comparison to the use of dry-based foods, such as wheat bran, that can be stored (40).

As with any production system, there are limitations. For example, cricket production is constrained by high feed costs, overcrowding, and inbreeding (37), whereas there are no major constraints in the mealworm farming process apart from moisture-attracting fungal pathogens (37). Achieving optimum production is complicated, and although some important production qualities for farming have been identified, further work is needed to define specific requirements for a mass-production system. **Figure 1** provides an overview of the wide range of factors associated with insect production.

NUTRITIONAL VALUE OF DIFFERENT INSECT SPECIES IN ANIMAL FEED AND HUMAN FOOD

Interest in insects as food and feed has largely centered on their potential role as nutrient concentrators, associated with their ability to grow on relatively low-quality diets and assimilate high-quality protein and a range of other essential nutrients. The nutritional value of insects varies depending on the species and their diet and development stage. In general, they are a good source of energy, high-quality protein, and PUFA (54), as well as a range of readily available vitamins and minerals (55).

Table 1 describes the nutrient content of the 10 insect species most commonly considered as possible food and feed sources, with energy contents being comparable to other protein-rich sources, such as soya. The content of individual nutrients is further discussed below.

Protein Content and Quality

On a dry-matter basis, protein is the main component of insects, followed by fat (42). The relative amount of protein can vary substantially, with crude protein content ranging from 23% to 76%,

Table 1 Nutritional composition (%) and energy content (MJ/kg) of commonly used insects in food and feed on a DM basis

Order	Common name	Latin name	Crude protein (% DM)	Total fat (% DM)	Fiber (% DM)	Ash (% DM)	Energy (MJ/kg DM)	Sources
Coleoptera	Yellow mealworm	*Tenebrio molitor*	46–54	25–36	2–5	3–4	27	60, 65, 127–129
	Superworm	*Zophobas morio*	47	44	ND	8	ND	130
Diptera	Black soldier fly	*Hermetia illucens* (larvae meal)	34–42	25–58	7	4–20	22–24	52, 60, 128, 131
	Housefly	*Musca domestica* (maggot meal)	51–60	25–28	6–7	11–20	20–23	52, 62, 132
	Housefly	*Musca domestica* (pupae meal)	71–76	14–16	15–16	7–8	20–24	52, 62
Lepidoptera	Silkworm	*Bombyx mori* (pupae meal)	23	14	ND	1	10	133
	Greater wax moth	*Galleria mellonella*	39	51–59	9	2–3	ND	56, 134
Orthoptera	House cricket	*Acheta domesticus*	59–72	10–23	5	5	ND	56, 128, 135
	Tropical house cricket	*Gryllodes sigillatus*	70	18	4	5	19	65
	Desert locust	*Schistocerca gregaria*	76	13	3	3	18	65
Soybean meal (for comparison)			55	2	4	7	20	136

Abbreviations: DM, dry matter; ND, no data.

the highest content being in the adult locust (**Table 1**). In general, insects compare well to traditional protein sources, such as soybean meal and fishmeal. However, a significant proportion of the protein is chemically bound within the exoskeleton and, as such, may not be bioavailable (56). Furthermore, the exoskeleton contains the nitrogen-containing polysaccharide chitin, meaning that the total protein content of insects is potentially overestimated when measured based on nitrogen content. Rather than the usual nitrogen-to-protein conversion factor of 6.25 (57), a value of 5.60 may be more appropriate for a range of insect species (58). Alternatively, the protein content of insects could be reevaluated by subtracting the nitrogen found in the chitin exoskeleton.

Insects are generally regarded as a good source of EAAs. The EAA content (milligrams per gram of protein) of commonly reared insect species is shown in **Figure 2**, alongside that of soya protein. Although the specific amounts of EAAs vary between species and developmental stages, in general, they compare well to traditional protein sources used in animal feed, as well as high-quality sources of protein consumed by humans, such as meat, dairy, and fish (8).

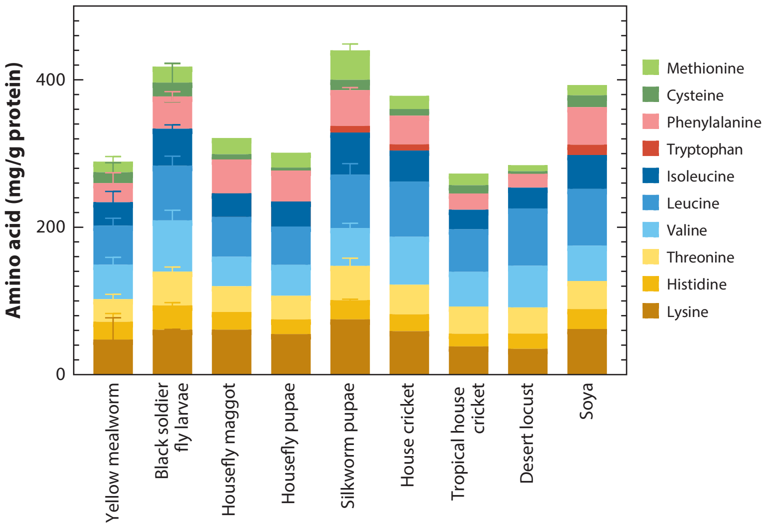

Figure 2

Mean amino acid contents (mg/g crude protein) of commonly used insects in food and feed. Essential amino acids are grouped: sulphur (*greens*), aromatic (*reds*), branched (*blues*), and others (*yellows*). Insects are grouped according to their taxonomic order. Latin names are shown in **Table 1**. Mean values calculated from the following studies obtained from the literature: yellow mealworm ($n = 2$), black soldier fly larvae ($n = 4$), housefly maggot ($n = 1$), housefly pupae ($n = 1$), silkworm pupae ($n = 2$), house cricket ($n = 1$), and desert locust ($n = 1$). Error bars indicate standard deviation. Insect data from 52, 60, 64, 65, 137–140; soya data from 136.

Protein digestibility has not been fully evaluated for all insect species but has been suggested to range from 77% to 98% for 78 different species across a range of orders (59). For *T. molitor* and *Hermetia illucens*, apparent protein digestibility has been reported as 60% and 51%, respectively (60). As discovered via in vitro digestion techniques, the crude protein digestibility of *T. molitor* and *H. illucens* appears to be negatively correlated with their chitin content (61). Pretorius (62) fed broilers with corn-based diets that were supplemented with 50% fly larvae or pupae meal and found increased total tract digestibility for crude protein and individual amino acids with the pupae meal.

Fat and Fatty Acid Contents

As **Table 1** shows, the amount of fat associated with insects can vary substantially both within and between species. In general, on a dry-matter basis, larval invertebrates have a higher fat content than adult species (56). Fat is present in different forms, with triacylglycerol and phospholipids accounting for 80% and 20% of the total, respectively (53). The increased fat content of insect meal compared with fishmeal or soybean meal suggests it may be necessary to remove at least some of the fat before use in animal feeds (52). The resulting oil could then be used as a supplemental ingredient (52). Reported fatty acid compositions of various insect species are summarized in **Figure 3**. In general, insects contain a range of saturated and monounsaturated fatty acids and PUFA, similar to that of other animal species. The main saturated fatty acid is palmitic acid (C16:0), with more variable amounts of stearic acid (C18:0). Oleic acid (C18:1) is the main monounsaturated fatty acid, though some species also appear to accumulate significant amounts of palmitoleic acid (C16:1). In general, insects are relatively rich in the n-6 PUFA, linoleic

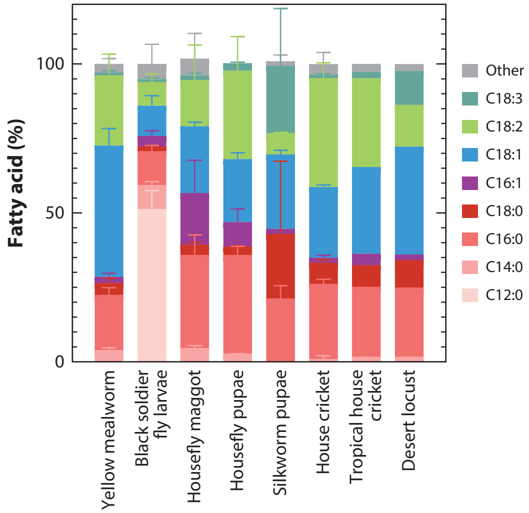

Figure 3

Mean fatty acid composition (% of total fatty acids) of commonly used insects in food and feed on a dry-matter basis. Fatty acids are grouped into saturated, monounsaturated, polyunsaturated, and others. Insects are grouped according to their taxonomic order. Latin names appear in **Table 1**. Error bars indicate standard deviation (52, 62, 64, 65, 128, 129, 131, 132, 140–146).

acid (n-6 C18:2), with smaller amounts of n-3 alpha-linolenic acid (C18:3). However, there is little evidence to suggest that insects can synthesize the longer-chain n-3 PUFAs, such as eicosapentaenoic (C20:5) and docosahexanoic (C22:6) acids, associated with oily fish. Both the total amount of fat and the fatty acid composition of various insect species can be manipulated by altering the diet. For example, Fasel et al. (63) showed that including PUFA-rich sources in mealworm diets can markedly increase their PUFA content.

Mineral and Vitamin Contents

Insect micronutrient and vitamin compositions vary across species and orders, as well as seasonally, and are dependent on the feed provided (53). The literature available for individual species also varies widely (8), which may be due to analysis being undertaken at different insect life stages. In general, insects contain sufficient levels of minerals to meet the dietary requirements of most animals (56). Insects can provide significant amounts of calcium, magnesium, manganese, phosphorus, and selenium (42), with noticeably high iron and zinc levels (8). Black soldier fly larvae have higher calcium and phosphorus contents (58) compared with yellow mealworms, which have higher potassium and sodium contents (52, 65). Insects also contain high levels of the B vitamins, riboflavin (B2), panthothenic acid (B5), and biotin but are lacking in vitamin A (26), vitamin C, niacin (B3), thiamine (B1) (42), and vitamin D (66). Vitamin B12 levels are highest in yellow mealworms compared with other species (8).

Dietary Fiber Contents

Insects are comparable to traditional livestock in their nutritional composition, but their physiology has a greater impact on nutrient content, particularly fiber content (55). Insects can contain up to 10% fiber (67), the most common form being chitin (8), but also amino acid cuticular proteins (68). The highest amount is found in housefly pupae (**Table 1**).

As indicated previously, chitin is a nitrogen-based carbohydrate found in the exoskeleton of most insects as a long-chain polymer of *N*-acetyl glucosamine. Chitin contents range from 2.7 to 49.8 mg/kg on a fresh-weight basis and 11.6 to 137.2 mg/kg on a dry-matter basis across seven different species (68). It is unclear whether chitin can be considered a positive or negative component of insects with regard to their use in food or feeds. Some evidence suggests beneficial antioxidant, anticancer, and anti-inflammatory properties of chitin and metabolites (69). However, chitin may also have antinutritional effects because it can bind various macromolecules, potentially making them inaccessible for digestion in the gut.

USE OF INSECTS IN ANIMAL FEEDS

Insects have been highlighted to have a suitable nutrient composition for inclusion in feed for livestock and aquaculture (the farming of fish, crustaceans, and other aquatic animals) production systems. Livestock and aquaculture production provide high-quality protein sources for human consumption; however, aspects of both production systems are currently considered to be unsustainable. Compound feed is supplied to all livestock species, with 45% of this feed supporting global poultry production (70). This demand for compound feed is expected to intensify the burden on land-based crop production (71), particularly for soya and rapeseed. Currently, these plants are the main source of protein used in livestock diets, often fortified with synthetic amino acids for those that are limiting (72). Although soybean has a high-quality digestible protein and amino acid composition (73), production is considered unsustainable, due to increasing deforestation required to meet demands for intensive livestock production (74). As such, there is increasing uncertainty about the future of soya to meet increasing demands for protein (75).

In the future, non-ruminant (pig and poultry) production is expected to grow at a faster rate than that of ruminants (75), which will require a large quantity of highly digestible, high-quality protein (74) with a suitable amino acid composition. To the best of our knowledge, studies published to date on the use of insects in the feed are restricted to non-ruminant species (see **Supplemental Table 1**). This may be due to their rapid digestion in the rumen, with very little useful by-pass protein.

Supplemental Material >

Studies on the Use of Insects in Poultry Feeds

Poultry will naturally eat insects when foraging, but currently this is not used in commercial indoor production systems. Soybean is now the main protein source in broiler feed that is either fully or partially replaced by insects, with supplementation varying from 5% dry weight to up to approximately 35% with complete replacement (60, 76–79). Broilers fed a diet in which soya was completely replaced with mealworms showed no growth effects (79), but differing effects on feed-conversion ratio (FCR) (kilograms of feed intake per kilograms of body weight gain) have been reported. Some studies observed an improvement (i.e., decrease) in FCR (79), but others showed no difference when mealworms partially replaced soya (77) or completely replaced gluten meal (76). Black soldier fly larvae have also been used with no effects on body weight gain or feed consumption (78) and were found to be more digestible than mealworms, with a higher apparent digestibility coefficient for ether extract, in a comparative study (60), although both were good sources of apparent metabolizable energy and digestible amino acids. Housefly maggots have also been used in broiler chick diets, resulting in similar or improved growth rates (80). Supplementation at an inclusion level of between 10% and 15% improved broiler chicken growth performance and product quality, but with no improvement in FCR (81).

Fewer studies have investigated the inclusion of insects not in the larval stage. Use of house crickets as a complete replacement for soybean had no effects on weight gain (82). Addition of methionine and arginine supplements to the feeds significantly improved FCR (82), suggesting that the amino acid composition of each batch of insects might need to be checked prior to their use in diet formulations.

In laying hens, black soldier fly larvae had a negative effect on live weight, feed intake, and apparent nutrient digestibility when used to completely replace soybean (83, 84). Interestingly, gut physiology and microbiome appeared to be affected, as inclusion of black soldier fly larvae in the diet resulted in a higher villi height in the duodenum, but lower villi height in the ileum and jejunum (83), and increased positive diversity in the microbial population of the gut microbiome (84).

Studies on the Use of Insects in Pig Feeds

Fewer studies have investigated the effects of insects in pig diets. In piglet diets, full soybean replacement with either full-fat or partially defatted black soldier fly prepupae showed no differences in body weight gain and feed intake (85). Additionally, the inclusion of partially defatted black soldier fly larvae meal, up to 10% of the diet, had no negative effects in weaned piglets (86), with inclusion in adult pig feeds having no impact on meat quality (87). Partial replacement of dried plasma in the diet with up to 50% black soldier fly prepupae actually improved performance in early-weaned pigs (88). Similarly, in weaned pigs, partial replacement of soya with mealworms was found to increase body weight gain, feed intake, and crude protein digestibility (89). In contrast, ileal protein digestibility of full-fat black soldier fly prepupae was reduced compared with control feeds (85), and apparent ileal digestibility of lysine, histidine, and arginine was higher with mealworm replacement compared with black soldier fly (90), suggesting that mealworms are more digestible than black soldier fly prepupae.

Studies on the Use of Insects in Aquaculture

Global fish consumption is increasing alongside consumption of traditional livestock (91). As a consequence, aquaculture increased from 12% of world fish production in 1984 to 46% in 2009 (91). However, aquaculture feeds currently rely heavily on fishmeal, derived from smaller fish, which is unsustainable due to increasing pressure on wild fish stocks (92). Fishmeal is a high-quality-protein (60–72%) feed ingredient, but fish diets are also frequently supplemented with fish oil, which has high levels of long-chain omega-3 fatty acids (93). As already discussed, insects are poor sources of these fatty acids, but future work on the manipulation of fatty acid composition, perhaps by genetic manipulation, may enhance their capacity to synthesize them.

Previous aquaculture studies have rarely shown any negative effects of including insect meal as a replacement for fishmeal, making it a viable option if an alternative source of omega-3 fatty acids can be found. Defatted black soldier fly larvae have been fed to rainbow trout (*Oncorhynchus mykiss*) at levels up to 40% without negative effects on survival, growth performance, or condition factor (a measure of fish health) (94). Similarly, increasing levels of black soldier fly larvae in European seabass (*Dicentrarchus labrax*) (95) or replacement of fishmeal in juvenile barramundi (*Lates calcarifer*) (96) or Atlantic salmon (*Salmo salar*) (97) diets had no effects on growth performance or feed utilization. Indeed, complete (100%) replacement actually increased EEA contents in the whole barramundi fish body (96), and the inclusion of protein and oil produced from black soldier fly larvae also had no negative effects on Atlantic salmon (*S. salar*) (98). Likewise, there were no effects on growth performance or marketable indices when mealworms replaced fishmeal up to 25% in sea bream (*Sparus aurata*) diets (99) or were added at 10% of Nile tilapia (*Oreochromis niloticus*) diets

(100). In contrast, feeding mirror carp (*Cyprinus carpio* var. *specularis*) a fermented meal containing silkworm pupae to replace fishmeal had no negative effects up to 40 g/kg, but higher amounts (80 or 120 g/kg) resulted in reduced growth, feed utilization, and crude lipid content (101).

USE OF INSECTS AS HUMAN FOOD

Humans appear to have been consuming insects throughout history, with evidence of consumption available from fossils in caves in the United States (53) right through to more modern times (102). Despite many insect species historically being primarily considered pests, they represent a potential contributor to global food security and sustainability challenges (53). Entomophagy, the consumption of insects (103), is a traditional practice in 113 countries worldwide (53) and is particularly common in Asian, African, and Central and Southern American cultures (102). Humans consume more than 2,000 species of insect, including beetles (31% of those consumed); caterpillars (18%); wasps, bees, and ants (15%); crickets, grasshoppers, and locusts (13%); true bugs (11%); and termites, dragonflies, and others (12%) (6). However, nutritional values for most remain to be determined (53).

In the Western world, insects are rarely considered as a food source for humans (6). A major factor is consumers' negative attitudes toward insects (104). Foods not normally consumed by Western societies are frequently viewed with suspicion and disgust (102). This rejection clearly has effects on global food availability (104). In fact, owing to the influence of the Western world, there has been a decline in traditional insect consumption as part of the human diet in other parts of the world (6, 104).

Hence, a major challenge is to change the insect-phobic perception of Western societies into one in which insects are appreciated as a sustainable source of food (104). Therefore, the use of insects as a food source needs to be reevaluated, particularly in relation to the positive aspects of environmental impact and nutritional value, instead of focusing on the level of abnormality and disgust (105). Importantly, there is clearly an increasing global interest in the value added by use of insect products or ingredients instead of consumption of the whole insect. Examples include the recent development of cricket-based protein bars, flour, and cookies (6) and the production of burgers and nuggets with 16% mealworm flour in the Netherlands (6). Incorporating insects into already-popular processed products is an easier route to persuade people to consume edible insects. With increased interest in vegan and vegetarian diets in many Western countries, it will be interesting to see how such consumers view insect consumption.

SAFETY CONCERNS OF USING INSECTS IN ANIMAL FEED AND HUMAN FOOD

Both endogenous and exogenous risk factors contribute to safety concerns associated with consuming insects as an alternative source of nutrients (42). Belluco et al. (67) highlighted four main risks associated with insect consumption: microbial, parasitic, allergenic, and chemical. Biosecurity is an important concern with regard to using insects, because foreign species are potentially introduced into countries, increasing the risk of escape and subsequent impact on food chains of natural ecosystems. Regulations on the use of insects in either feed or food differ between countries (106).

Pathogenic Risk

Because insects are an intermediate in the food chain, they could act as a vector to transmit pathogens to livestock and fish species. This is of particular concern given the recent coronavirus disease 2019 (COVID-19) pandemic. Although van Huis et al. (8) suggested that insects are low risk in terms of transmitting infections, very little work has actually been published on this. One of the main safety concerns relates to using insects in feed and food without removing the gut, therefore potentially passing their microbial load on to the livestock or human consumer (8, 107).

Higher levels of spore-forming bacteria and *Enterobacteriaceae* have been reported in crushed mealworms and crickets (44), again suggesting that not removing the gut may increase risk. For example, *Escherichia coli* has been shown to be transmitted by houseflies into the gut of cattle (108). A potential way to reduce this microbial load in the gut would be to starve the insects prior to culling and processing. Boccazzi et al. (109) found that the black soldier fly microbiota was influenced by diet, so diet could also be an important factor in determining the microbial and parasitic risk of insects. Mealworms raised in an aseptic environment, or treated with antibiotics, have been shown to have no bacteria or fungi in their gut load (110). But this has practical implications, because mass production of insects in an aseptic environment will increase production costs, as would antibiotic use, which could also lead to greater antibiotic resistance. Processing, such as washing followed by thorough heating, could significantly reduce the risk of bacteria-borne disease (111) and may also reduce the risk of parasites (107).

Allergenic Risk

Food allergy is defined as an abnormal response arising from a specific immune reaction that occurs after exposure to a specific food. Arthropods, including crustaceans, arachnids, and insects, cause allergic reactions, which is of concern when considering including insects in the human diet. Ribeiro et al. (112) reviewed several studies on potential cross-reactivity following human consumption of insects. For example, immunoglobulins (e.g., IgE) from patients who were allergic to crustaceans showed binding affinity to proteins from three species of mealworms (*T. molitor*, *Zophobas atratus*, and *A. diaperinus*) (113), suggesting that they would promote an allergic response. Furthermore, this was not prevented by heat processing of the mealworms (113). Cross-reactivity to crickets has also been found in patients who have known allergies to prawns (114). However, there has been little work on whether insects could also cause allergic responses in livestock species that would potentially have negative effects on production. There is also concern that people working in direct, frequent contact with insects could develop allergies (115).

Chemical Risk

Owing to their accumulation of pesticides and other chemicals used on plants (used as feed), potential chemical safety risks could be associated with insect consumption. Raising insects on untreated plants would be one solution, but this may increase production costs. Further, frequent consumption of some specific insect-related chemicals, such as metabolic steroids (testosterone and dihydrotestosterone) found in the Dysticidae family of beetles, by humans or livestock could result in growth abnormalities, edema, or fertility issues (67). Some insects (e.g., bees and ants) produce natural toxins as a defense mechanism; therefore, these types of insects are not currently being investigated for use in livestock feeds (67).

Insects can also accumulate heavy metals (67). For instance, grasshoppers were found to accumulate mercury and cadmium (116), and black soldier flies grown on heavy metal–supplemented feed accumulated cadmium, though lead and zinc were suppressed to a level lower than the food supplied (117). Importantly, Ping et al. (118) found significantly higher levels of lead in the livers of chickens fed on insect larvae. Alongside heavy metals, there are also worries about organic contaminants, including PCB (polychlorinated biphenyl), DDT (dichlorodiphenyltrichloroethane), and dioxin compounds, some of which are used as insecticides. However, Poma et al. (119) found that the levels were lower than those found in other animal products.

Legislation and Ethics

The legislation relating to insect consumption varies between countries, with no global consensus. Indeed, many countries do not consider insects as food, although the European Union introduced new legislation in 2015 and 2017 (120, 121) to provide a legal framework, with insects included as a "novel food." In Europe, the use of animal proteins in pig and poultry diets is prohibited (122) owing to bovine spongiform encephalitis and other transmissible spongiform encephalopathies. Of note, insects are considered incapable of expressing prions (123), which may be due to their primitive nervous system. However, the production of insects fed on waste streams, which might include slaughterhouse waste products and animal manure, could potentially act as a vector to transmit prions either to livestock or to humans.

Additionally, there are ethical concerns about entomophagy with respect to rearing conditions and consumption, including diverse points of view about welfare, ethical rules, and social contexts (124), which could potentially come under the existing legislation for livestock (124, 125). Indeed, the European legislation regarding animal use for farming now includes invertebrates (126), and some countries have recently introduced their own legislation. For example, the Austrian Animal Protection Act (APA 2004) states that insect rearing and manipulation must not result in any avoidable pain, distress, or harm (124). Hence, clear and consistent legislation is needed to regulate the safe use of insects for both livestock feed and human food.

CONCLUSIONS

Insects represent an alternative source of protein and other nutrients for farmed livestock and aquatic species and, indeed, for humans. Many studies indicate that insects may be a more sustainable alternative to conventional feed ingredients for livestock. However, key challenges must be tackled by establishing (*a*) feed sources for the insects that cannot be directly used as livestock feed or human food, (*b*) cost-effective production and processing systems for insects, (*c*) clear safety policies, and (*d*) ethical working practices and mechanisms to conquer cultural barriers. Although there is increased interest in directly incorporating insects into the human food chain, further health concerns need to be addressed, as well as the nonacceptance of the consumption of insects in many populations. In addition, the potential use of genetic manipulation technologies to optimize growth and nutritional composition of insects represents a promising approach that is yet to be explored, but one that will ultimately require public acceptance.

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