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Sustainable farming of the mealworm *Tenebrio molitor* for the production of food and feed

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Abstract: The farming of edible insects is an alternative strategy for the production of protein-rich food and feed with a low ecological footprint. The industrial production of insect-derived protein is more cost-effective and energy-efficient than livestock farming or aquaculture. The mealworm *Tenebrio molitor* is economically among the most important species used for the large-scale conversion of plant biomass into protein. Here, we review the mass rearing of this species and its conversion into food and feed, focusing on challenges such as the contamination of food/feed products with bacteria from the insect gut and the risk of rapidly spreading pathogens and parasites. We propose solutions to prevent the outbreak of infections among farmed insects without reliance on antibiotics. Transgenerational immune priming and probiotic bacteria may provide alternative strategies for sustainable insect farming.

Keywords: edible insects; immune priming; insect mass rearing; probiotics; *Tenebrio molitor*.

1 Introduction

Alternative food and feed sources are needed for the continually growing world population, particularly the increasing demand for protein-rich food and livestock feed [1–3]. Reducing meat-based diets will be beneficial for environmental, health and economic factors [4]. Current feed protein sources such as soybean and fishmeal are imported into the European Union (EU) and the

cost is expected to increase [5]. Alternatives are therefore required to reduce the EU's economic dependence on imports [6]. Furthermore, large amounts of food and nonprofitable side streams from industrial processes are currently wasted [7], but this could be used as feed for insects, which can convert diverse waste streams into protein. Edible insects are therefore gaining attention among the research community: in 2007, the search term “edible insects” recovered 12 publications listed in PubMed, but this had increased to more than 40 publications in 2016. More than 2000 edible insect species are known worldwide, but only a few are produced commercially [8, 9]. These species show diverse nutritional profiles but insects are generally considered as good alternative protein sources for humans, livestock and aquaculture, which can be produced in an environmentally sustainable manner, although several potential safety issues have been raised [3, 10–14].

In this review, we focus on the yellow mealworm beetle *Tenebrio molitor*. The larvae of this species (known as mealworms) are often used as pet food, and they offer a promising alternative protein-rich animal feed [3, 15]. Mealworms are not only suitable as animal feed but they are also considered ideal for human nutrition and have even been recommended as a bioregenerative life support system for space missions [16, 17]. Industrial companies such as Ynsect (Paris, France) produce tons of mealworm biomass per week and have become leaders in the large-scale farming of this insect. *Tenebrio molitor* is also well known as a model organism for studies of innate immunity, and a complete mitochondrial genome sequence has been published [18–21]. *Tenebrio molitor* is closely related to the flour beetles *Tribolium castaneum* and *Tribolium confusum*, which are widely used as model organisms to study insect development and immunity, with a complete genome sequence published for *T. castaneum*. Much more background knowledge is therefore available for *T. molitor* than other edible insects, allowing the utilization of this knowledge to develop state-of-the-art mass rearing management systems. This article will first consider the potential benefits and risks of mealworms as food and feed, followed by the proposition of measures to exploit the benefits and overcome the risks.

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2 The benefits of mealworms as food and feed

2.1 Excellent nutritional value

The nutritional components of mealworms can be classified as “high in” and “source of” according to the thresholds for World Health Organization and Food and Agriculture Organization of the United Nations food labels [13, 22] (Figure 1A–D). Mealworms have a high content of protein (13.68–22.32 g/100 g edible portion) and fat (8.90–19.94 g/100 g edible portion) and also provide considerable amounts of polyunsaturated fatty acids [13]. Mealworms are also categorized as a source of zinc and are high in magnesium, but they contain only low levels of calcium [13]. Furthermore, mealworms can be labeled as a source of niacin and as high in pyridoxine, riboflavin, folate and vitamin B₁₂ [13]. The nutritional profile of mealworms has been compared with conventional meats, revealing that mealworms have a significantly higher nutritional value than beef and chicken and are not significantly less nutritionally balanced [23]. They also provide a good source of all essential amino acids [11].

2.2 Good alternative to fish meal and soybean meal as feed for livestock and aquaculture

The nutrient profile of mealworms is similar to that of fish and soybean meal, and so is the essential amino acid

profile (Figure 1H), so mealworms provide a good alternative livestock feed [28]. Several poultry diet studies have shown that the replacement or partial replacement of fish or soybean meal with mealworms resulted in similar or even slightly better growth performance and digestibility [29–31]. Similar to soybean meal, the limiting essential amino acid in mealworms is methionine [32]. The low calcium levels in mealworms can be avoided by feeding the larvae on calcium-enriched diets [33, 34]. Furthermore, mealworms have been tested in various aquaculture settings and up to 25% of the traditional feed can be replaced without compromising the yields achieved on the standard diet, whereas higher proportions of mealworm had a negative effect [27, 35–37]. For shrimp farming, the complete replacement of fish meal with mealworms resulted in an increase in body weight and lipid content [38]. Furthermore, the supplementation of weaning pig diets with up to 6% pulverized mealworm improved growth performance and nutrient digestibility [39]. Further research is required to optimize the dietary proportion of mealworms to achieve the best yields. Nevertheless, current results suggest that mealworms could often replace or partially replace fish and soybean meal as livestock feed, which would reduce the EU's dependence on imported feed because the insects can be reared locally.

2.3 Environmentally sustainable production for human food

The mass rearing of animals has a negative environmental impact by producing large amounts of greenhouse gas

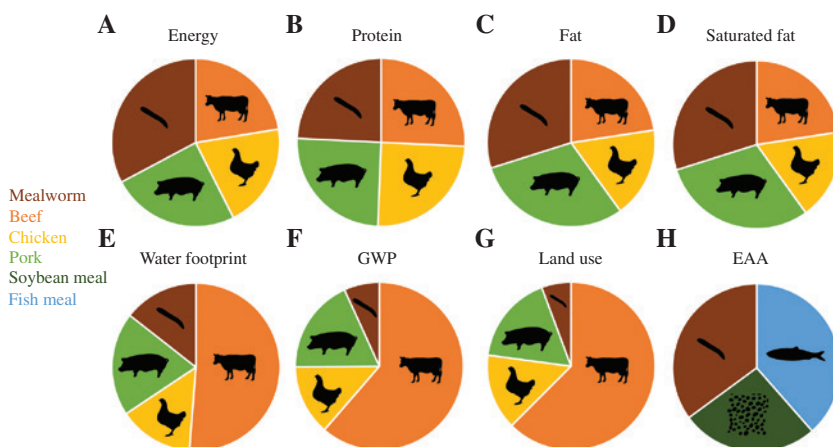


Figure 1: Nutritional values and sustainability of mealworms and conventional food/feed. (A–D) The nutritional value of a 100-g edible portion of mealworms compared with various livestock meats. (E–G) The comparative effect of mealworms and livestock on the environment, presented as water footprint per edible ton, global warming potential (GWP) for each 1 kg edible portion, and land use for each 1 kg edible portion. (H) Essential amino acid (EAA) comparison of mealworms and classic feeds such as soybean and fish meal. Values adapted from Payne et al. [23], de Vries and de Boer [24], Miglietta et al. [25], Oonincx and de Boer [26], and Sánchez-Muros et al. [27].

and ammonia, and using large amounts of water, energy and land. The water footprint per edible ton of mealworms is 4341 m³/t, which is comparable to that of chicken meat and 3.5 times lower than that of beef (Figure 1E) [25]. The energy used to produce 1 kg of fresh mealworms is similar to that used in the production of beef and pork, but the land area required was much less compared with beef, chicken and pork [26]. The production of ammonia and greenhouse gasses (CO₂, N₂O and CH₄) was significantly lower for mealworms compared with livestock (Figure 1F) [40]. Mealworms also require less land for the production of 1 kg of edible protein compared with livestock (Figure 1G) [13].

Another parameter to consider when rearing animals is the feed conversion efficiency. When provided with an optimal diet, mealworms convert feed as efficiently as poultry, and the nitrogen use efficiency is higher than traditional livestock [41]. Furthermore, high-protein diets improve larval survival and reduce the duration of development [41]. Mealworms can therefore be reared in a more environmentally sustainable manner than livestock in addition to achieving similar nutritional values, supporting their use as a protein source for human food.

3 The risks of edible insects as food and feed

3.1 Microbial contamination

Microbial safety and shelf life are influenced by the microbial load of the original product [42]. Mealworms are used as food and feed without removing the gut, so any microbes therein (including pathogens) are transmitted to livestock and human consumers. The microbial profile of commercially reared mealworms has been investigated using both culture-dependent and culture-independent methods. Several culture-based studies that measured the number of microbial colony forming units (CFUs) revealed that freeze-dried or fresh mealworms contain large numbers of aerobic bacteria (up to 8 log CFU/g) when the larvae are pulverized. This is higher than the recommended values for minced meat, which is considered comparable (EC 1441/2007) [43–47]. The pulverized larvae also contained 7.2 log CFU/g enterobacteria, 3.6 log CFU/g endospores, and up to 5.3 log CFU/g yeast and fungi [43, 45, 46]. The log CFU/g values decreased to less than two when the larvae were not completely pulverized before measuring the microbial load [48], but this could reflect the trapping of microbes in the gut, which would prevent

their cultivation, although they would still be found in the final product.

Even so, the high microbial load in the mealworms did not include typical food-borne pathogens such as *Salmonella* spp. or *Listeria monocytogenes* [43–47]. A short heating or blanching step significantly reduced the total bacterial load as well as the enterobacteria count [43, 49]. The mealworm cuticle is also covered with microbes due to the larvae eating and defecating in the same environment (Mitschke, personal communication), but the effects of surface sterilization have not been investigated. Culture-independent next-generation sequencing has been used to analyze the mealworm microbiota and define the operational taxonomic units (OTUs). In one study, the mealworms were dominated by three bacterial phyla that are common in insects: Proteobacteria (35.9%), Firmicutes (31.1%) and Actinobacteria (26.9%) [50]. Overall, the genus *Propionibacterium* was the most abundant OTU (22.2%). These are Gram-positive rod-shaped bacteria with probiotic properties in humans, although some species are opportunistic pathogens [51, 52]. Another study found that the three dominant bacterial phyla were Tenericutes (44.2%), Proteobacteria (39.22%) and Firmicutes (13.09%), and the genus *Spiroplasma* was the most abundant OTU (44.1%) [48]. A third study confirmed the dominance of Tenericutes (36.6%), Proteobacteria (34.1%), and Firmicutes (26.2%), and at the genus level also *Spiroplasma* (38.7%) [53]. Members of the genus *Spiroplasma* are small, helical, motile and wall-less bacteria [54]. These species promote male-killing to yield extreme female-biased sex ratios in insects and can also cause diseases in mammals, including humans [55–58]. However, *Spiroplasma* spp. can also increase the fitness of insect hosts by acting as mutualists and protecting the host against pathogens [59].

Reproductive manipulators such as *Spiroplasma*, *Wolbachia* and *Rickettsia*, which are known to infect a wide variety of insects, could disrupt breeding programs during the mass rearing of insects and could act as pathogens in livestock or human consumers. However, these bacteria cannot be eliminated entirely due to their potential protective effects. More research is therefore needed to understand the relationship between the insect host and its symbionts and pathogens, with the aim of fine-tuning this balance according to human needs.

3.2 Parasites and prions

The cestode *Hymenolepis diminuta*, commonly known as the rat tapeworm, uses a variety of insects as intermediate

hosts, including the mealworm beetle. The parasite develops in the host's hemocoel and inhibits its reproductive success [60, 61]. Infected mealworms consumed by the definitive host (usually rodents, but also livestock and humans) thus transmit the parasite, resulting in enteritis, anorexia and gut irritation [62, 63]. The single-cell parasite *Gregarina niphandrodes* primarily infects arthropods, and although the infection of mealworms does not influence the population dynamics, it does reduce the lifespan of the adult beetle [64, 65].

Prion diseases (transmissible spongiform encephalopathies) are fatal neurodegenerative diseases affecting both humans and livestock [66, 67]. Insect-specific prions have not yet been described, but the uptake of prions when insects consume prion-containing food of animal origin cannot be ruled out [68].

To the best of our knowledge, there is no documented evidence thus far of infections during the mass rearing of mealworms. However, the risk cannot be completely excluded because analogous situations have arisen in other insects, such as densovirus infections during the commercial rearing of the house cricket *Acheta domesticus* [69]. Invertebrate pathogens are encountered more frequently in mass rearing systems, often due to overcrowding and stress, such as microsporidian infections in mites reared commercially for pest control [70].

3.3 Antibiotic use

The mass rearing of livestock often involves the confinement of animals in crowded conditions where they are bred and managed for maximum yield, with a negative effect on their health and immune system [71]. Antibiotics are therefore used as growth promoters and prophylactics, which has led to an explosive increase in the prevalence of antibiotic-resistant bacteria, threatening livestock and human health [71, 72]. Although the use of antibiotics to promote growth is restricted in the EU [73], even the therapeutic use of antibiotics has resulted in the spread of antibiotic-resistant bacteria among livestock [74, 75].

The microbiota of the mealworm beetle is vulnerable to antibiotics, which reduce the bacterial diversity as well as the bacterial load, but it is stable against environmental factors [53]. Furthermore, sterile mealworms perform poorly, suggesting that the microbiota is required for the efficient digestion and detoxification of plant secondary products [76]. In other insects, antibiotic use can shorten the development time as well as reduce the number of eggs [77–79]. Although the treatment of edible insects with antibiotics could solve some of the problems discussed

previously, the benefits are outweighed by the negative side effects in addition to the known problem of increasing the spread of antibiotic-resistant pathogens.

3.4 Pesticides and toxins

The mass rearing of insects for feed and food could result in the accumulation of hazardous chemicals, such as heavy metals, dioxins and flame-retardants originating in contaminated insect diets. Commercial mealworms have been tested for a range of chemical contaminants and the levels were similar to or lower than those found in livestock meat [80]. However, contaminated waste streams as feed could promote the accumulation of pesticides, as shown in an experiment in which mealworms were fed on pesticide-contaminated diets for 48 h [81]. A 24-h starvation phase after exposure and before sampling reduced the concentration of pesticides with lower $\log(K_{ow})$ values (representing their solubility in water and lipids [82]) but pesticides with high $\log(K_{ow})$ values were excreted less efficiently [81].

Food contaminated with cadmium, lead, or arsenic did not influence the development time, dry matter content, or survival time of mealworms, and may therefore remain undetected if the insects are not tested at regular intervals [83]. The larvae accumulated high levels of arsenic, intermediate levels of cadmium, and low levels of lead but were able to excrete arsenic slowly when transferred to a noncontaminated diet [83].

These data suggest that feed quality should be checked carefully when using industrial side streams to rear mealworms to avoid the accumulation of toxins, and that insect stocks should also be checked regularly because the effect of accumulating toxins may not be apparent immediately in the breeding facility. Furthermore, a starvation step before harvesting the larvae may achieve partial detoxification, albeit potentially at the expense of slightly lower nutritional quality.

3.5 Allergens

Food allergy is defined as an adverse immunological response to a dietary protein [84]. There are only a few studies reporting the potential allergy risk posed by mealworms or insects in general. However, mealworm proteins cross-reacted in vitro with IgE produced by patients allergic to house dust mites and crustaceans, in response to tropomyosin, a well-known allergen in arthropods [85, 86]. A recent double-blind placebo study in humans

showed that mealworm allergy is most likely in patients allergic to shrimp, with a potentially severe outcome [87].

Therefore, mealworms and additives derived from them must carry an allergy warning. Heat processing and in vitro digestion reduces the allergic reaction but does not eliminate it completely [85]. The feeding of freeze-dried mealworm powder to rats in a safety assessment study did not show any adverse effects, toxicity, or allergy [88]. Furthermore, insects may carry specific molds that cause allergic reactions [14]. This would not only affect mealworm consumers but also workers in the production facilities, as described in the animal feed industry [89].

3.6 Consumer acceptance

The acceptance of entomophagy (the consumption of insect-based food by humans) is influenced by price, taste, availability, and established cultural preferences [90–92]. Humans tend to avoid unfamiliar food and it is advisable to address perceptions that insect-based foods are unpalatable [93]. Processing mealworms into conventional foods, such as burgers and tortillas, increased consumer acceptance [46, 94]. Further strategies to increase consumer acceptance include the provision of more information about the benefits of insect foods while dealing openly with the potential risks [12].

The acceptance of insect-based livestock feed is much higher than the acceptance of insect-based food because insects are already part of the natural food chain in poultry and freshwater fish [95]. Consumers will also be influenced by the cost of feed. Currently, feed based on the lesser mealworm (*Alphitobius diaperinus*) is 15 €/kg [96], which is far higher than soybean meal (0.33 €/kg) and fish meal (1.22 €/kg) (indexmundi.com/, accessed December 2016). However, the cost of fish and soybean meal will

increase in the future, whereas the cost of insect meal will decline [95], thus encouraging the production and consumption of insects.

4 Solutions and recommendations

To market edible insects successfully, selling the promises laid out previously must go hand in hand with openly addressing the risks. Consumers are becoming increasingly aware of organic farming and animal welfare issues, and they will only accept high-quality products that they consider “clean”. It is therefore advisable to apply the same food standards to insects as apply to livestock, and to follow similar hygiene regulations (Box 1). Furthermore, breeders should not repeat the mistakes made in livestock management by using antibiotics and other pharmaceutical products without specific necessity. Nevertheless, breeders must deal responsibly with the risk of spreading infections, and we recommend alternative preventive approaches such as probiotics or transgenerational immune priming (as discussed in later sections). Other aspects of mass rearing for edible insects can be imported from the rearing of sterile insects for pest control. Mass rearing can lead to changes in a number of phenotypic traits due to artificial diets, strong laboratory adaptation, and/or inbreeding depression [97].

4.1 Carrying capacity and population density

Mealworm larvae are naturally attracted to each other and will form dense clusters [98, 99]. As discussed previously, rearing mealworms under suboptimal conditions increases the risk of infections [100, 101]. The optimal growth temperature is 25 °C–27.5 °C, resulting in a

Box 1: EU regulations governing edible insects.

2001	EU legislation prohibits the use of dead insects or processed insects in feed but feeding with live insects is allowed (EC 999/2001)
2002	There are no specific regulations covering edible insects for human consumption, so the production of edible insects should follow the requirements of general food laws (EC 178/2002)
2003	EU legislation bans the use of antibiotics as growth promoters (EC 1831/2003)
2004	The production of edible insects should follow general good hygiene and production requirements (EC 852-854/2004)
2007	The production of edible insects should follow general good hygiene and production requirements (EC 852-854/2004)
2013	The use of insect meal in aquaculture diets will be allowed in the EU starting from January 2018 (EC 56/2013)
2014	Some countries in the EU tolerate the marketing of whole insects for human consumption. The Belgian Federal Agency for the Safety of the Food Chain (FASFC) advised producers in April 2014 (SHC 9160) to refer to hygiene criteria for comparable products (EC 1441/2007)
2015	Insects and their parts will be considered as Novel Food in the EU from 1 January 2018 (EC 2015/2283) thus introducing a more efficient authorization process for insect products

development period lasting 80.0–83.7 days involving 15–17 larval instars [102, 103]. Individual food consumption and larval weight depend on the larval density, i.e. increasing the larval density from 12 to 96 larvae per square decimeter reduced the biomass produced per gram of feed by approximately 22% [104] (see Figure 2 for similar findings in *T. confusum*). Reproductive output per female declined as the adult density and age increased, and the highest reproductive output was with 2–3 weeks after eclosion [106]. High larval density increases the metabolic heat and thus the rearing temperature, which has sublethal effects on the population [104, 107].

It is important to find the optimal density that balances space, food conversation, and productivity during mass rearing, aiming to produce mealworms with a high nutritional value reared in as little time and space as possible using low-cost feed. Adjusting the population density to match the environmental space is a relatively easy measure, which can be applied in all facilities, and this should be the first method used to address the risks of overcrowding.

4.2 Probiotics

Probiotic bacteria increase the fitness of the host [108, 109]. They are widely used to improve the growth, survival, and health of livestock and farmed fish [110–115],

as well as for the prevention and treatment of gastrointestinal tract infections in humans [116, 117]. Probiotic bacteria produce antimicrobial compounds, inhibit virulence genes in pathogens, modulate epithelial barrier functions, and stimulate the host immune system [118]. EU restrictions on the prophylactic use of antibiotics have encouraged the development of alternative strategies to prevent infections during the mass rearing of insects, and the addition of probiotic bacteria to the diet is one such approach [73]. Further research in this field is needed to see how mealworms respond to probiotic bacteria in terms of resistance to infection and growth performance. Bacteria that are probiotic in one species can act as pathogens in another, so the prescreening of bacteria before large-scale application is advisable. For example, *Pseudomonas aeruginosa* is probiotic in the tropical freshwater fish rohu (*Labeo rohita*) and in western king prawns (*Penaeus latissulcatus*) but is a pathogen in humans [119, 120].

The inclusion of probiotic bacteria in mealworm diets is also beneficial because the larvae are processed without removing the gut so the residual microbiota is carried over to the final consumer. The microbiota accounts for up to 10% of the total insect biomass [121]. Probiotic bacteria increase the nutritional value of mealworms because they are known to produce health-promoting metabolites such as B vitamins [122, 123]. The manipulation of the mealworm microbiota could therefore be exploited to benefit the insect host (e.g. by allowing the degradation

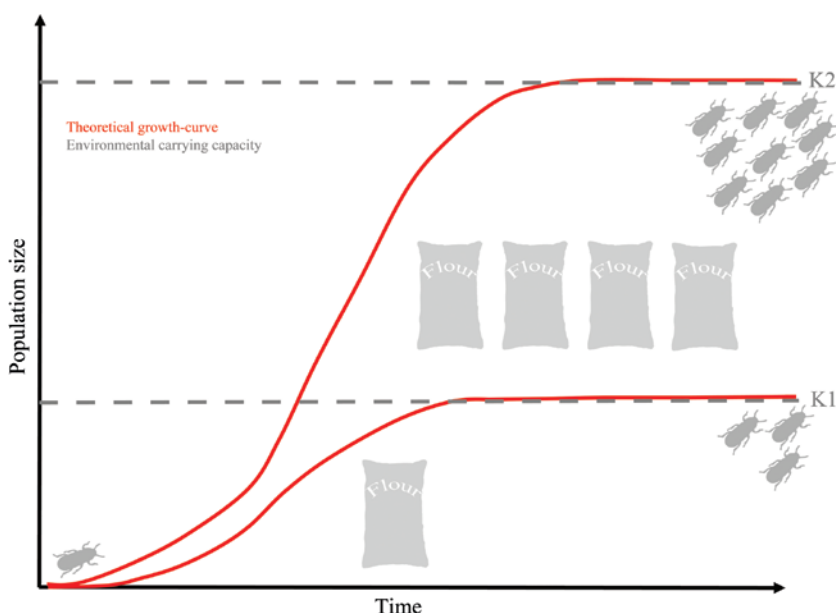


Figure 2: The population growth, measured as population density, does not scale linearly with an increasing environment (flour sacks). If the environment becomes four times larger, population size only becomes three times larger due to intraspecific competition for resources and the spreading of infections. Adapted and modified from Park [105].

of nondigestible feed components such as keratin) and the consumer (e.g. by allowing the production of specific nutrients).

Probiotic effects have already been observed in some studies. For example, chickens fed on a diet supplemented with mealworms contained lower numbers of *Escherichia coli* and *Salmonella* spp. after an infection due to a more effective immune system [124]. This may reflect the consumption of the larval microbiota as well as chitin, which can act as a prebiotic in aquacultures [125, 126]. Whereas probiotics are microbes that confer health benefits on the host, prebiotics are substances that induce the growth or activity of probiotic microbes [127]. The addition of probiotic bacteria to mealworm diets would therefore generate an insect-based feed that contained both prebiotics and probiotics for livestock and human consumers, as well as increasing the performance of the insects during rearing (Figure 3).

4.3 Immune priming and transgenerational immune priming

Tenebrio molitor has a typical arthropod innate immune system, although phenotypic evidence also indicates adaptive and memory-like functions [100, 128]. Whereas immune priming increases host resistance to pathogens during second and subsequent encounters, transgenerational immune priming allows the offspring of the host to

benefit from the same resistance even on their first encounter with the pathogen (Figure 3) [129–133]. However, individual immune priming by systemic injection would prove difficult in mass-reared insects due to their relatively small size and great number. In this context, the broad database available for other tenebrionid beetles is valuable because *T. castaneum* is considered as a model organism for the investigation of immune priming [134–136]. One advantage of *T. castaneum* is that oral priming is possible by adding pathogens or a corresponding supernatant directly to the diet [137]. The gut microbiota in *T. castaneum* plays an important role in immune priming, but a cold shock applied to the parents is required for transgenerational immune priming [138, 139]. A similar cold shock approach could be used in mass-reared mealworms, i.e. the parental beetles could be primed by reducing the rearing temperature and the more resistant offspring generation could then be used as food or feed, and for the production of proteins. In shrimp farming, vaccine-like approaches to combat the white spot syndrome virus (WSSV) have been reported as being very successful [140, 141]. Vaccination with inactivated viruses or recombinant virus proteins lead to an improved survival rate upon WSSV infection [142–144]. The application of transgenerational immune priming to reduce disease outbreaks has also been considered in the aquaculture industry [145].

The specific mechanism of (transgenerational) immune priming in insects is not fully understood [132]. One assumption is that antimicrobial peptides (AMPs) are

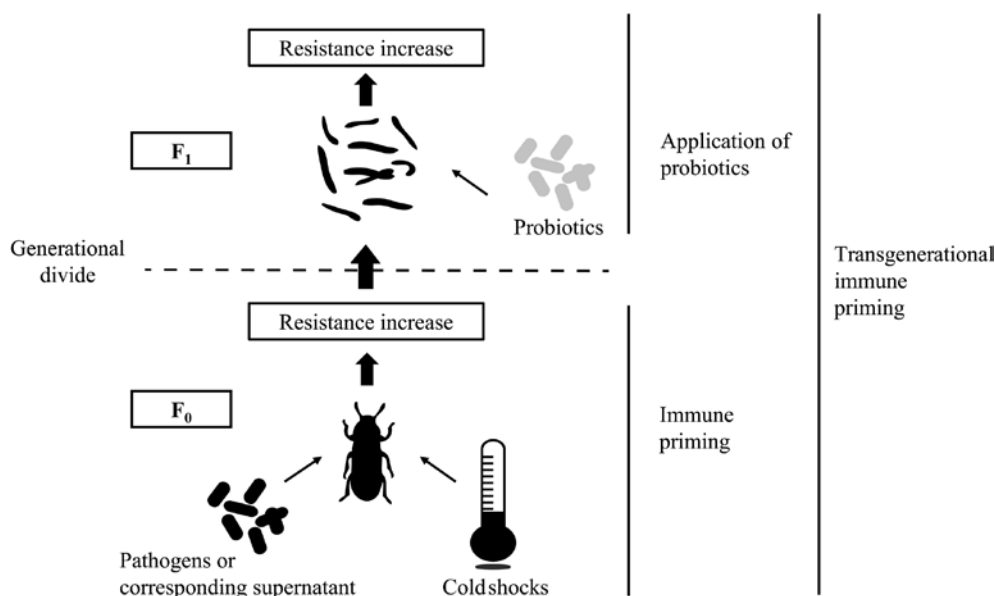


Figure 3: Improving the resistance to pathogens of mass-reared mealworms by (transgenerational) immune priming and the administration of probiotic bacteria.

involved in this seemingly more specific immune response in insects [146]. *Tenebrio molitor* produces a wide range of AMPs constitutively at local sites or in response to infection [19]. AMPs, as a general class of molecules, show a broad spectrum of antimicrobial activity, but specific AMPs range from broadly active to highly specific against particular pathogens [147, 148]. Therefore, selective (transgenerational) immune priming would provide a good alternative to antibiotics in addition to avoiding their unwanted effects. Furthermore, because the entire mealworm is utilized for food and feed, any AMPs triggered by (transgenerational) immune priming would probably remain active, with a beneficial effect in the livestock or human consumers.

4.4 The role of the cuticle in immunity

The first line of defense against pathogens in mealworm beetles is the cuticle [149]. Melanin is involved in the melanization and sclerotization of the cuticle, and is an indicator of the investment in the immune system [93, 150]. Cuticle darkness in the adult beetle correlates with pathogen resistance [93, 151]. Darker beetles have a thicker cuticle and stronger melanin staining than tan beetles [152]. Furthermore, melanin offers protection against UV damage and is involved in wound repair [153]. In an experimental evolution experiment, darker beetles had denser hemocytes and produced more phenoloxidase, characteristics that correlate with resistance [154]. Beetles reared at a higher density showed more resistance towards entomopathogenic fungi and a higher degree of melanization [93]. Density-dependent prophylaxis is not unique to mealworm beetles but can also be observed in other insects reared at high densities, potentially addressing the higher risk of spreading pathogens in dense colonies [155, 156]. One way to take advantage of the darkening of the cuticle is the selection of darker beetles for reproduction, which would enhance pathogen resistance at the population level.

5 Conclusion

Mealworms are economically among the most important farmed insects produced for food and feed. They have excellent nutritional characteristics and they can be reared in an environmentally sustainable manner. As an alternative human food, mealworms address the potential risks associated with edible insects because

the relatively high microbial load can be reduced during processing by applying a heat treatment step, offering an excellent alternative to the application of antibiotics. More elegantly, the gut microbiota can be manipulated by the administration of probiotic bacteria, to benefit the insect during rearing and to achieve beneficial carry-over effects for the consumer. The fitness of *T. molitor* can also be increased by transgenerational immune priming induced by cold shock, and direct immune priming induced by the inclusion of specific pathogens or supernatants in the diet. Finally, the selection of darker beetles increases the general level of innate resistance in the population.

In conclusion, the measures recommended for the sustainable mass rearing of mealworms, especially the administration of probiotics and the application of (transgenerational) immune priming, help prevent infections in the mass culture in addition to simultaneously achieving beneficial carry-over effects for the consumer. Experimental evidence for these direct effects is already available, but the potential carry-over effects require further investigation.

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