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Health Hazards Associated with Arthropod Infestation of Stored Products

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Abstract

Insects and mites are common inhabitants and accidental invaders of food, including durable commodities, and their presence can have both direct and indirect effects on human health. The most common direct effect is contamination of food with arthropod fragments and related contaminants, which may be allergenic or even carcinogenic. The most important indirect effect is that their presence can change the storage microenvironment, making durable products suitable for the rapid development of fungi and other microorganisms. Some of these fungi can produce toxins (e.g., aflatoxins) that endanger human health. Insects may actively or passively contribute to the spread of microorganisms, increasing product contamination, and they may host bacteria that have developed antibiotic resistance, contributing to their spread in food. Several species also may host, attract, or transmit tapeworms, predators, or parasitoids that may affect health. This review synthesizes research on these topics and suggests directions for future research.



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INTRODUCTION

High standards of food safety and quality are priorities in most countries. Food contamination by pathogenic microbes or rodent urine or fecal droppings is often highly publicized, but arthropod contaminants are more common (95). An analysis of 4,795 US Food and Drug Administration (FDA) detentions of imported agricultural food products showed that the most frequent problem was contamination by arthropod filth (32%), followed by low-acid canned food (12%), and microbial contamination (11%). More than a decade ago, the European Union (EU) legally established a Rapid Alert System for Food and Feed (RASFF) as an interactive EU database containing internationally important data regarding food safety and contamination violations, presence of foreign bodies, and food fraud issues. A recent analysis (24) of 1,446 food safety RASFF notifications (from the period 1992–2015) revealed that the top three reported foreign materials/bodies were arthropod pests (54.6%), glass fragments (17.4%), and metals (11.5%). Arthropod-related contamination of food may originate from the preharvest infestation of agricultural commodities, in which fruits, vegetables, and nuts are infested by the larvae of Coleoptera, Diptera, Hymenoptera, and Lepidoptera. Nevertheless, a large proportion of food contamination cases are associated with stored-product arthropods, a group that includes approximately 2,000 species (44) that are mainly classified in four taxa: Coleoptera, Lepidoptera, Psocoptera, and Acari. The two latter groups are of increasing importance worldwide (88, 123, 125). The species diversity and cosmopolitan distribution of many species enable storage pests to colonize more than 1,100 different agricultural commodities and foods (44). In contrast to field pests, these species are adapted to survive and multiply on dry food (<20% moisture) and, thereby, are able to infest and contaminate food throughout its entire production and distribution chain. In addition, they cause cross-infestations of packaged food because many storage pests can penetrate food packages. Eradicating them from inside storage and food industry facilities is difficult because they have developed resistance to many insecticides, including fumigants such as phosphine (94), and even in cases of successful eradication, they may quickly recolonize facilities by immigrating from external sources (15).

The presence of either field or storage arthropods in food is a highly sensitive and controversial issue. Attitudes about the health hazards of arthropod consumption are influenced by cultural, aesthetic, religious (e.g., kosher food, halal food), and medical considerations (42, 140). Although insects serve as food in many cultures (42), the generally accepted idea—supported by legislation in some countries—is that arthropod contaminants in stored products may negatively affect not only quality standards but also human, pet, and farm animal health (5, 42, 43, 140). Traditionally, the risks associated with storage pests in agricultural commodities are divided into four classes: physical, biological (microbial), chemical (41, 43, 140), and psychological. Dividing contaminants into a particular class is arbitrary because in many cases the distinction among the classes is not clear (92). Instead, we broadly classify the negative effects of storage pests on human food as either direct (i.e., contamination of food by arthropod fragments, carcinogenic or allergenic chemical products associated with their physiology, or direct human attack such as parasitoses of the digestive tract) (or psychological) or indirect (i.e., they modify environmental conditions to support the metabolic activity and growth of pathogenic microorganisms or they host and transmit microorganisms, including antibiotic-resistant strains).

We provide a synthesis of newly published information concerning these direct and indirect effects.

SIMPLE, NEGATIVE DIRECT EFFECTS AND INTERACTIONS

Body Fragments and Feces as Physical Contaminants and Filth

Many types of durable commodities have been found to be contaminated with parts of insect bodies, which are classified as physical contaminants or arthropod body fragments (41). Approximately 75% of semolina samples taken from the Italian semolina industry contained insect fragments (133). In a survey in Italian flour mills, most of the filth detected in samples of different types of flour was insect fragments (16). A large percentage of flour samples were found to contain fragments of different insect body parts and, to a lesser extent, other contaminants, such as rodent hairs or textile fibers (16). Various arthropods and parts of their bodies are not represented equally in food. The frequency of filth contaminants found in 5,081 flour samples collected in 75 US flour mills was as follows: insect fragments, 83%; rodent hairs, 18%; feather barbules, 3%; insect fragments of head capsules, 1.3%; mites, 0.6%; larvae, 0.3%; and psocids, 0.2% (39). Also, different species and stages vary in their contribution to this contamination. Grain-feeding insects, such as *Sitophilus oryzae*, *Sitophilus granarius*, and *Rhyzopertha dominica*, develop and feed inside grain kernels, and they are the main source of insect fragments in wheat flour (96). A single preemergent *Rhyzopertha dominica* adult in a wheat kernel contributes about 9 to 23 times as many fragments as a larva or pupa (97). The US FDA has established a Defect Action Level of 75 insect fragments per 50 g of wheat flour (34), but this level is generally higher than US mills will tolerate (37). Although Europe has mandated zero tolerance for insect fragments in food, no regular inspections are performed, and zero tolerance of infestation is considered unrealistic for standard processing conditions, given that insect fragments are detected frequently in commercial flour and semolina (16, 133). Methods for detecting contaminants are laborious, and alternative rapid methods, such as using near-infrared spectroscopy (97) and polymerase chain reaction (PCR) (91), are being developed.

Chemical Contaminants Produced by Arthropods

Chemical contamination of stored products associated with the presence of pest arthropods includes (a) carcinogens and mutagens and (b) undesirable odors. Quinones, which are produced by several stored-product beetles, including *Tribolium* spp., are carcinogens and are closely associated with allergies, dermatitis, eye disorders, and the development of papules and vesicles (93, 99). The secretions of *Tribolium castaneum* contain at least 13 different quinones (52). One adult can produce up to 50 µg of quinones, a quantity that can cause serious qualitative degradation in a commodity (27, 28, 138). The accumulation rate of quinones in rice samples was estimated to range from 0.0470 to 0.0631 µg/adult per week (51). These compounds impart an unpleasant odor to stored food, and they may be responsible for liver and spleen tumors in small vertebrates (27, 28). Their mutagenic effects on mice were still evident after contaminated flour had been cooked and consumed (27, 28). Biscuits infested by *Tribolium castaneum* contain 1,4-benzoquinone and induce neoplastic lesions in mice (27). Although quinones may endanger animal health in laboratory tests, the rate of contamination in stores is rather low, and normal infestations by *Tribolium* spp. are unlikely to result in quinone accumulation that causes serious damage to human health (51).

Mites are notorious for producing volatile chemicals that are responsible for the off-odor of mite-infested grain (136); tridecane is a major volatile odor compound produced by storage mites. Bread prepared from flour infested by *Tribolium* spp. and *Oryzaephilus surinamensis* tasted bad (120). Grain infested by *Rhyzopertha dominica* had a severe off-odor; *Tribolium castaneum* caused moderate off-odor; and *Sitophilus oryzae*, *Oryzaephilus surinamensis*, and *Cryptolestes ferrugineus* caused little or no odor (112). An aggregation pheromone of *Rhyzopertha dominica* (2-pentanol) and several

Defect Action Level: level of defects in foods that present no human health hazards, as determined by the US Food and Drug Administration

Polymerase chain reaction (PCR): technique to amplify a single copy or a few copies of a piece of DNA to generate a large number of copies of that sequence

Dermatitis: inflammation of the skin that may be accompanied by itchiness, redness, or a rash, or a combination of these

Papule: small, solid, round bump rising from the skin; a pimple

Vesicle: a colored spot on the skin that is flat, even with the surrounding skin, and contains fluid

Neoplastic: refers to abnormal growth

Keratinocyte: cells in the skin that form a barrier to infection and environmental damage

Immunoglobulin E (IgE): initiates the immune response to foreign materials, including allergens

Fibroblast: a cell involved in wound healing

Urticaria: also known as hives, is a skin rash with red, itchy bumps

Angioedema: swelling of the dermis and subcutaneous tissues; similar to urticaria, which occurs in the upper dermis

Rhinitis: inflammation of the mucous membrane in the nose

Anaphylaxis: a severe allergic reaction that may be life-threatening

other metabolites, including unsaturated free acids, are responsible for the unpleasant odor of grain infested by this species (112). Generally, it is not known whether the chemicals associated with arthropod-produced off-odors have health effects.

Allergens

Allergens are the most important direct effect on human health of stored-product pests. Although most studies focus on house dust mites and cockroaches, stored-product mites are significant allergen producers in food, and in processing facilities (85) and grain stores (124). Major allergens have been identified in the feces of several species of storage mites (31, 32) and insects (33). Exposure to infested grain dust is associated with a number of allergic symptoms (11).

Stored-product pests produce a variety of chemical compounds that cause allergic reaction in humans and domestic pets (35). Allergens of mites and cockroaches are strong activators of innate immune cells—that is, keratinocytes and airway epithelial cells (62). One example of such activity is *Blattella germanica* serine proteases, which are not IgE (immunoglobulin E)-binding compounds. Instead, the hydrolytic activity on the receptors of the innate immune cells induces the cells to start responding, and the hydrolytic activity destroys the junction between epithelial cells and changes epidermal permeability and skin barrier function (64). Inhibiting the active protease results in enzyme deactivation and the disappearance of the effect of the inactivated protease on the immune system. Homogenates from stored-product mites (i.e., *Chortoglyphus arcuatus*, *Acarus siro*, and *Lepidoglyphus destructor*) influence skin keratinocytes and fibroblast function in vitro (6).

In sensitive individuals, consuming mite-contaminated pancakes caused immediate cutaneous symptoms (urticaria, facial angioedema, or both) or exacerbated their previous respiratory disease (rhinitis, asthma, or both) (40). In some cases, this has led to reactions known as pancake anaphylaxis (12, 83, 108, 109). No anaphylactic reactions have been reported after ingesting insect-contaminated food. House dust and stored-product mites are considered among the most common arthropod species responsible for anaphylactic reactions.

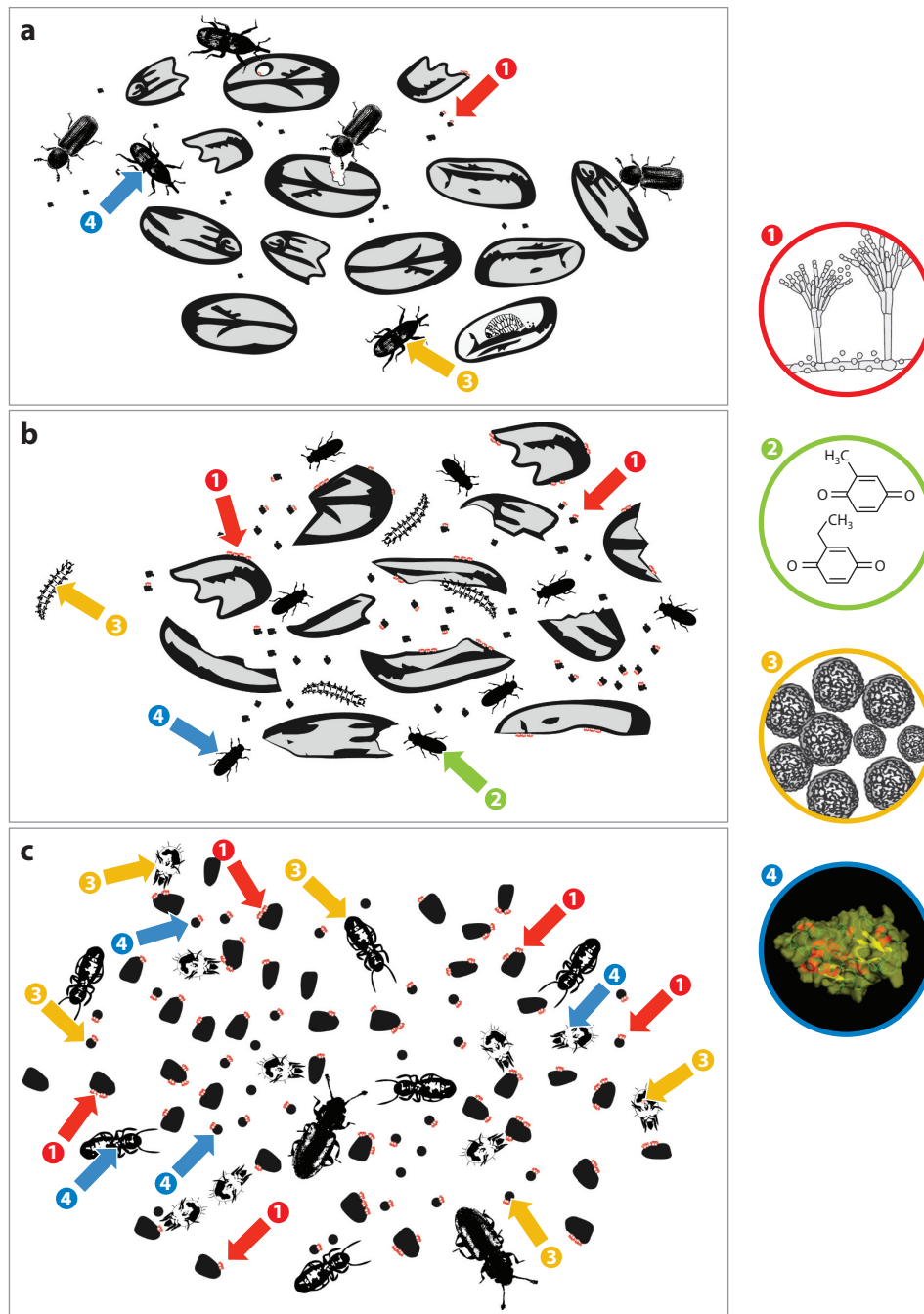
The sites of allergen production in arthropods are the digestive tract, reproductive organs, and the parenchymal tissues, glands, and muscles. This pattern suggests that some allergens are continuously produced by individuals and deposited in the environment with their feces, eggs, and gland extracts, but other allergens are present only in arthropod bodies. Although fecal or body allergens contaminate the environment when pests are present (**Figure 1**), the allergens can persist in the environment long after the pests are gone. There are indications that some allergens show high stability, with half-lives longer than 1 year in the case of house dust mites (114). A similar allergen persistence was observed in laboratory experiments with the feces of *Blattella*

Figure 1

Arthropods cause physical injury to stored grain and can contaminate the grain with substances that are hazardous to humans. (a) Primary feeders develop inside the grain and cause contamination, which is not possible to remove during grain processing. Their feeding provides entry through the grain surface for fungal infestation (❶), and fungal growth is supported by increasing grain moisture and temperature due to intensive pest respiration. (b) Secondary feeders develop outside the grain and mainly destroy the wheat germ. The *Tribolium* spp. secondary feeders contaminate the grain with benzoquinone-containing secretions (2-methyl-1,4-benzoquinone and 2-ethyl-1,4-benzoquinone) (❷). (c) Fungivorous insects and mites feed on the grain debris and fungi. Primary and secondary feeders disseminate the fungal spores on their bodies randomly, whereas fungivores can disseminate fungal spores through excretion (❸). Extracts from primary and secondary feeders contain proteins with immunoglobulin E reactivity, but most allergens (❹) are isolated from the bodies and feces of mites and psocids.

germanica and Bla g 1 and Bla g 2 allergens (33). The mild physical conditions (i.e., humidity and temperature) occurring in urban and food industry buildings lead to the long-term persistence of allergens in these environments (30).

Allergens that share similar biochemical properties and biological functions, having 67% or higher identity of amino acids, are assigned to the same group (132). The World Health



Organization and the International Union of Immunological Societies' (WHO/IUIS) Allergen Nomenclature Sub-Committee has established a system of nomenclature for allergens (<http://www.allergen.org/>). The database contains identified allergens as well as their producers, including stored-product pests: the mites *Acarus siro*, *Glycyphagus domesticus*, *Lepidoglyphus destructor*, and *Tyrophagus putrescentiae*; the psocid *Liposcelis bostrychophila*; the cockroaches *Blattella germanica* and *Periplaneta americana*; and the moth *Plodia interpunctella*. The majority of allergens in the database have been described from house dust mites; however, many of the allergens also are present in stored-product mites. Other stored-product arthropods not included in the WHO/IUIS database, despite the fact there are documented allergic IgE-mediated responses of humans to their bodies or feces, are the mites *Aleuroglyphus ovatus*, *Suidasia medanensis*, *Suidasia pontifica*, *Thyreophagus entomophagus*, *Chortoglyphus arcuatus*, and *Cheyletus eruditus* (13, 80, 86, 87, 90, 100, 101); the beetles *Tribolium confusum*, *Sitophilus granarius*, and *Sitophilus oryzae*; and the moth *Ephestia kuehniella* (7, 50, 63, 66, 76, 77, 107). Recent data show clearly that psocids also should be considered as an emerging indoor allergen source (61, 98). Hence, the list of species in the WHO/IUIS database should be expanded, given that all the species mentioned above are commonly found in stored durable products and related food items.

From a practical perspective, it is possible to distinguish allergic diseases that affect workers in work environments and those that affect residents of homes in urban or rural settings (139). In reality, workers are also exposed to work-related allergens in their homes because arthropods are brought from their work environment to their homes on their clothes. In the farm environment, stored-product mites are the most dominant allergenic pest group, followed by psocids and beetles (126). Many studies confirm that farmers are sensitive to the allergens of major arthropod pests that occur on the farm, mainly stored-product mites (82). It is likely that a mite allergy was the cause of previous attacks and the subsequent death of a man, as a result of either the ingestion of mite-contaminated food or inhalation of mite allergens in bed, or both (26). One likely method of contamination is through farmers carrying mites on their clothes from the farm into their houses. This mechanism was confirmed by tracking antigen distribution using an electrostatic dust fall collector (148). The antigens of *Acarus siro*, *Lepidoglyphus destructor*, and *Tyrophagus putrescentiae* were more frequently detected in the farm than in the urban environment (148). In the farm environment, the antigens of stored-product mites were found predominantly in changing rooms and kitchens, and house dust mite antigens were detected mainly in bedrooms (148).

Contamination of the food industry environment with specific stored-product arthropod-related allergens also has been documented (3, 50), and stored-product insects and their natural enemies are frequent pests in grain stores (8), mills (69), and bakeries (111). Case studies describe professional diseases, mainly occupational asthma in cereal workers and bakers. Cereal workers are exposed to a wide range of immunogenic substances in their working environment. Case studies reported worker hypersensitivity to *Lepidoglyphus destructor* (3), cockroaches (81), *Tribolium confusum* (2, 50), *Sitophilus granarius* (77), and *Ephestia kuehniella* (78).

Homes constitute the last stage of allergen contamination, when arthropods are introduced from contaminated food or feed, or live there as urban pests. It is hard to distinguish whether human sensitivity to allergens is caused by consuming contaminated food or by direct contact with stored-product arthropods. However, exposure to allergens from one or more sources leads to sensitization. Stored-product pests or their allergens can be present in food obtained from markets and, thereby, can infest stored food in the kitchen (84). Moreover, stored-product mite populations are common in stored cereal products in kitchens (129, 131), and in dried fruits and cheese obtained in supermarkets (17, 53). In a survey conducted in England, 30% of households contained psocids and 14% contained mites (137).

Parasitosis (Acariasis) and Irritants of Digestive Systems

In addition to their allergens contaminating food sources, mites can also infest humans and pets. The digestion of whole live insects, or large parts of insect bodies, is associated with diarrhea, with abdominal cramps, and indirectly to intestinal mycosis. When the insects involved are flies, the term myiasis is used (99, 140). Such infestations are different from those caused by parasitic mites (acariases). Acariasis is defined as a rash caused by mites, sometimes also expressed as dermatitis, that is usually accompanied by severe itching. Such reactions are often caused by *Sarcoptes* spp. or *Demodex* spp. mites burrowing in the skin or living in the sebaceous glands or hair follicles of eyelashes and eyebrows. House dust mites and some stored-product mites have been found to cause dermatitis by their presence externally on the skin, as well as to cause human acariasis of the pulmonary, intestinal, oral (resulting in anaphylaxis), urinary, optic, and vaginal systems (Figure 2) (23, 75). In a study of 1,994 patients sensitive to mites, 8% had mites in stool or urine samples, or both (74). The mites that were found in stool samples included *Acarus siro*, *Tyrophagus putrescentiae*, *Dermatophagoides farinae*, *Dermatophagoides pteronyssinus*, *Glycyphagus domesticus*, *Glycyphagus ornatus*, and *Carpoglyphus lactis*. Mites found in urine samples included *Acarus siro*, *Tyrophagus putrescentiae*, *Tyrobobus longior*, *Aleuroglyphus ovatus*, *Sancassania berlesei*, *Sancassania mycophaga*, *Suidasia nesbitti*, *Lardoglyphus konoii*, *Glycyphagus domesticus*, *Carpoglyphus lactis*, *Lepidoglyphus destructor*, *Dermatophagoides farinae*, *Dermatophagoides pteronyssinus*, *Euroglyphus maynei*, *Cosmoglyphus* (= *Sancassania*) *hughesi*, and *Tarsonemus* spp. (74). Based on sputum analyses, the highest risk of pulmonary acariases was found in those patients working in medicinal herb storehouses and in rice stores or mills (75). In a case study, living larvae of *Lasioderma serricorne* were identified in the stool of an eight-month-old baby girl who had an underdeveloped immune system (128).

Mycosis: fungal infection

Psychological Effects of Arthropods

In general, the negative reactions to insects include well-described medical phenomena like fear, phobia, and delusional parasitosis (4). There are press/web records of lawsuits regarding human depression associated with food or drink contaminated by insects (e.g., <http://www.freerepublic.com/focus/f-news/1392232/posts>) and surveys indicating that the public has negative attitudes toward pests such as cockroaches (110). This emotional sensitivity also is evident from the high rate of consumer complaints to marketing chains and food producers regarding insects and hair found in food (<http://www.agriland.ie/farming-news/live-insects-and-hair-found-in-food-among-consumer-complaints-in-2016>) and from the RASFF report analysis; in the RASFF analysis, pests were the most commonly reported foreign bodies found in food in Europe (24). Although the psychological issue is potentially of profound importance, we surprisingly were not able to trace any rigorous direct study measuring impact of storage pests on human psychological reactions.

COMPLEX INDIRECT EFFECTS AND INTERACTIONS

Arthropods may endanger food safety in indirect ways. Most importantly, insects and mites can change the humidity and temperature of stored food, creating a favorable environment for the growth of fungi and bacteria, many of which are pathogenic or toxigenic. In this dynamic environment, arthropods may not interact directly with microorganisms, but they may host fungi and bacteria in their digestive tracts and may also contribute to their spread. They also may act as vectors for pathogenic tapeworms that are not directly associated with food. The presence of storage arthropods in food also can attract predators and parasitoids, which contribute further to the physical and allergenic contamination and may attack humans directly.

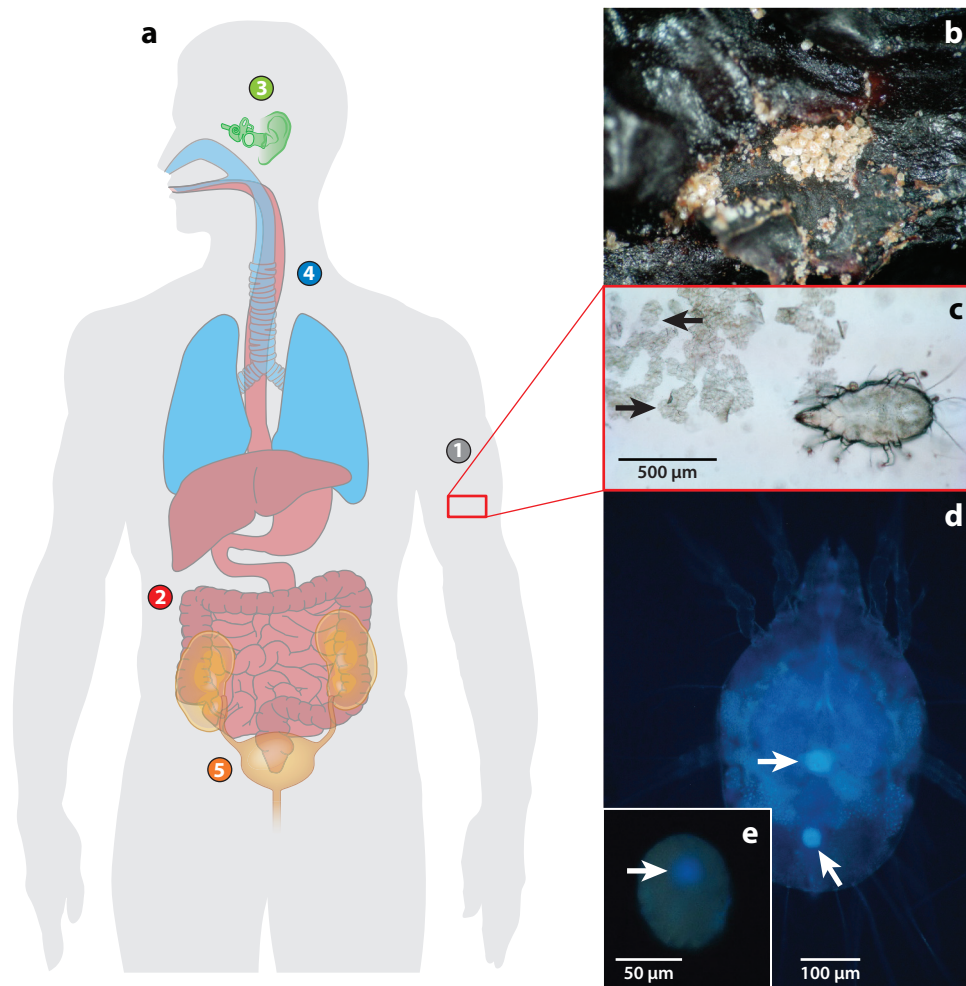


Figure 2

Acariasis is a type of parasitosis caused by the life stages of stored-product mites occurring in or on human epithelial tissues (1); by mites ingested with contaminated food products (2); by mites occurring in the ears (otic mites) (3); and by mites in the respiratory organs (4) and urogenital tract (5). Panels *a* and *c* show examples of acariases. (*a*) Mites occupying the human body. (*b*) Dried plums infested by living stadia of *Carpoglyphus lactis*, which pass through the gut and finally appear in the stool. (*c*) The presence of mites on the skin is sampled by sticky tape. *Tyrophagus putrescentiae* is shown on the tape; the arrows point to human epidermal cells, with the living mites and their feces on the surface of the epithelial cells. (*d,e*) Visualization of chymotrypsin activity by fluorescent substrate (Ala-Ala-Phe-7-amido-4-methylcoumarin). The mite bodies and feces contain proteases (trypsin, chymotrypsin, and serine protease). The proteases in contact with epithelial tissues can damage cell junctions, and when they contact a lymphocyte, they can influence the immune response by proteolytic activation of the receptors. In panel *d*, the food boli in the gut of *Lepidoglyphus destructor* are indicated by arrows. The boli show a fluorescent signal indicating substrate hydrolysis. Panel *e* shows the feces of *Aleuroglyphus ovatus*. The arrow points to active sites of substrate hydrolysis.

Environmental Changes that Favor the Growth of Microorganisms

In a stored grain mass, water and heat are produced chemically during arthropod digestion and respiration by breaking down carbohydrates, resulting in the production of water, energy, and carbon dioxide (36). When grain is managed properly, including controlling arthropod populations, arthropods have little effect on environmental conditions in the grain mass. An uncontrolled population increase of arthropod pests in grain stores may lead to significant increases in temperature and humidity, sometimes resulting in hot spots where temperatures can be as much as 50°C higher (116). In laboratory experiments, an initial population of 20 granary weevils in 200 g of triticale increased the moisture content within a month to levels at which microbial development commenced, leading to rapid deterioration of the grain (1).

Interaction with Fungi Resulting in Mycotoxin Contamination of Stored Products

Stored-product arthropods interact with stored-product fungi (118), and these interactions in stored products are influenced by temperature and moisture because both arthropods and fungi have the same optimal growth conditions, that is, temperatures from 20 to 30°C and grain moisture content higher than 14% (20). Being able to grow in the same conditions enables arthropods to feed on the fungi and fungi to be transferred by spores sticking to the arthropod's body, or by gut transfer. The transfer of fungi by arthropods can be purely mechanical or more active, depending on the feeding mode (54). Some aflatoxin-producing *Aspergillus* species and *Fusarium* species that produce deoxynivalenol (DON), trichothecenes, fumonisins, and other mycotoxins are field fungi that are mainly involved in preharvest contamination, but some fungal growth and mycotoxin production may continue postharvest. Other fungi, such as *Penicillium*, *Aspergillus*, and *Alternaria*, produce aflatoxin, ochratoxin, citrin alternariol, alternariol monomethyl ether, tenuazonic acid, iso-tenuazonic acid, altertoxins, tentoxin, altenuene, and AAL-toxins (127), and these fungi are chiefly associated with postharvest storage and may be associated with storage arthropods. An example is the infestation of stored maize in Benin by *Sitophilus oryzae*, *Tribolium castaneum*, and the fungus *Aspergillus flavus* (49). Toxigenic strains of this fungus previously were isolated from both insect species (115). The rapid growth of these insects resulted in increases in the moisture content of the grain, dust production, *Aspergillus flavus* infection, and aflatoxin accumulation. There was a negative correlation between aflatoxin content and treatment of the stored maize with insecticide (102), which clearly indicates that the arthropod presence increased the mycotoxin contamination of stored products. When mycotoxin content is measured in stored commodities at farms, there is a positive correlation between arthropod presence and mycotoxin content (102). The correlation can be explained by the favorable growth conditions for both fungi and arthropods or by the direct effect of arthropods on mycotoxin production.

Attempts to explain the relationships between stored-product arthropods and fungi led to two theories: (a) some arthropods are disseminators of fungi, and some are exterminators; and (b) some storage fungi attract arthropods and promote their population growth, but others are repellent and secrete toxins harmful to arthropods (25). These scenarios correlate with the different feeding patterns of arthropods in stored products: internal and external feeders. Internal feeders develop inside the grain kernel. Their feeding activity creates tunnels and holes inside the grain, and debris is produced during the burrowing activity. The burrowing increases the inner surface area of the grain, and the debris enhances the fungal colonization of the kernels (10). The internal feeder *Sitophilus zeamais* can transmit fungi, such as *Aspergillus flavus*, on its exoskeleton (10). External feeders feed outside grain kernels, either on debris or on the kernels themselves. These include obligate or strict fungivores, and arthropods feeding on bacteria. Many stored-product arthropods

are partly or obligatorily fungivorous; that is, they feed on fungal mycelium. The fungi provide the stored-product arthropods with nutrients, including starch, proteins, lipids, and vitamins (142). The protein content of fungi, which ranges between 13% and 44% of the total fungal mass, is generally higher than that of wheat, which has a protein content ranging only between 13% and 16% (142). In general, many stored-product beetles have greater population growth on flour or grain that is infested by fungi than on autoclaved grain, and they prefer flour infested by fungi to autoclaved flour (142, 144). Many stored-product insect species showed obligatory feeding on fungi as a secondary preference to crushed grain and grain dust (117). During feeding on fungal mycelium, fungal spores attach to the insect's exoskeleton, and, when insects move from one grain to another, the spores are mechanically transferred to different locations (58). Nevertheless, it is likely that fungi can be transferred more actively through arthropod ingestion of arthropod feces (121, 122). The risk to the fungi from such grazing is the possible overgrazing by a high density of arthropods, but they can also profit from the dispersal, and fungi can use the dead bodies of arthropods as sources of nitrogen (54).

Whether the palatability of fungi is connected to mycotoxin production has been questioned. In 2011, a hypothesis was presented suggesting that fungi can produce toxic secondary metabolites to regulate the grazers, that is, arthropods (134). The production of secondary metabolites, including mycotoxins, can be considered a defense method favored by the selective pressure of fungivorous arthropods (105). Based on this hypothesis, arthropods during feeding induce the production of defense compounds, including mycotoxins (134). The effect of mycotoxins on stored-product insects was tested by adding fungi or mycotoxin to insect diets, and the effect of mycotoxin varied with the identity of the mycotoxin and the insect species. For example, penicillic and oxalic acids were not toxic to *Tribolium confusum*, *Ephesia kuehniella*, *Lasioderma serricorne*, and *Attagenus megatoma* (141, 143). In contrast, ochratoxin A and citrinin inhibited larval growth of *Attagenus megatoma*, and citrinin and rubratoxin B inhibited growth of *Tribolium confusum* and *Lasioderma serricorne* at the 1,000 ppm level (141) or caused mortality of *Ephesia kuehniella* (143). A common fungus feeder in stored products, the hairy fungus beetle, *Typhaea stercorea*, was able to complete its life cycle on an aflatoxin-producing strain of *Aspergillus flavus* (135). Sterigmatocystin, T1 toxin, and zearalenone were lethal to *Tyrophagus putrescentiae* (104). Aflatoxin B1, citrinin, ochratoxin A, and penicillic acid were toxic to the second generation of mites reared on a diet that contained these mycotoxins (104). However, the same species of mite showed complete development and an additional increase in population on mycotoxin-producing strains of *Fusarium poae* (89, 103). Stored-product mites commonly feeding on stored grain fungi of the genera *Alternaria*, *Aspergillus*, *Cladosporium*, and *Penicillium* (118, 119) are known to be vectors of these fungi (59). Hence, several mycotoxins are partially toxic to stored-product arthropods and can cause suppressive effects on both their life cycles and population growth.

Arthropod feeding on food containing fungi can result in the dissemination of spores, which suggests that the major dissemination pathway is mechanical. Nevertheless, fungal spores occur both externally and internally in the insects' bodies (10). The feeding preferences of arthropods for fungi can change the mechanical aspects of transmission. The high rate of infection of *Aspergillus flavus* in groundnut kernels was directly associated with the feeding of the mites *Caloglyphus* spp. and *Tyrophagus* spp., which transferred the fungus (9). When grown on sterilized and *Aspergillus flavus*-contaminated maize, the fungus contributed to the growth of *Tyrophagus putrescentiae*, and vice versa, suggesting synergistic effects and mutual benefits (38). However, sterilizing the maize before inoculation enhanced *Aspergillus flavus* colonization because competition with other fungi was lacking. Rapid fungal transport into a developed fungal community of germinated barley and into stored barley after 21 days resulted in an increase in DON concentration in the barley, indicating successful colonization by *Fusarium* (56). In germinated barley, both *Acarus siro* and

Tyrophagus putrescentiae were able to transfer the mycotoxin-producing strain of *Fusarium culmorum*. After transfer, the fungus was viable and produced DON. In stored barley, the preincubation of *Tyrophagus putrescentiae* on *Fusarium poae* increased DON levels to approximately 800 and 300 µg per kg of grain for, respectively, 10 and 50 mites per 25 g of grain. The higher DON content at lower mite density is explained by the effect of mite population density; that is, the fungus was overgrazed at the high density (57).

For successful transfer, it is necessary to carry the fungi into new, uncolonized grain or other stored products. Spores of *Aspergillus* and *Penicillium* are present in the air and can be dispersed over a wide range into new habitats, including stored food products, which can be colonized without any significant contribution from stored-product arthropods (10). However, arthropod involvement can be important where arthropods infest such habitats. For example, grain debris and residues in stores can serve as sources for the colonization of stored products by insects contaminated with fungal spores (67). Interestingly, mites have different spatial patterns in comparison with insects in grain, and these patterns are not directly correlated with grain residues, which means that additional factors determine mite dispersion and these should be further explored (8, 55).

Carriers of Bacteria and Genes of Antibiotic Resistance

Stored-product arthropods interact with symbiotic and parasitic bacteria (see the sidebar, Microbiomes of Stored-Product Arthropods), which may lead to medical or veterinary effects. These effects may include the transmission of bacteria (45) and the hosting of bacteria with antibiotic-resistance genes. Bacterial symbionts may increase the resistance of pests to pesticides (65).

Gut-associated bacteria consist of both ingested bacteria and enteric bacteria and include species of major medical and veterinary importance. Bacteria also are carried on the exoskeleton of arthropods (45), and proteins associated with these bacteria may be present in feces and contribute to the epidemiology of allergens (32). The main epidemiological route for the transmission of food-borne pathogens is fecal–oral, and stored-product insects are obligatory vectors (43). Cockroaches, flies, mice, and rats are considered to be opportunistic vectors that, during food searching, can spread pathogens via their feces to food or to areas where the pathogens can be picked up by pantry pests (43, 152). Regular movement among habitats is the main method of insect-mediated transport of

MICROBIOMES OF STORED-PRODUCT ARTHROPODS

Stored-product arthropods are inhabited by bacteria that influence many physiological functions, including feeding and tolerance to predators, parasitoids, environmental stress, and pesticides. The bacteria inhabit the surface of the cuticle, internal tissues, and the gut. Some of these bacteria are ingested with food, but others are symbionts that may be vertically transmitted. One example of the latter is in *Sitophilus oryzae* in which primary bacterial symbionts living in specialized organs called bacteriocytes increase mitochondrial activity and synthesize compounds (pantothenic acid, biotin, riboflavin, phenylalanine, and tyrosine) that are poorly represented in the wheat grain on which the insect feeds. The gut microbiome is influenced by diet, as in the larvae of *Plodia interpunctella*, which have different gut microbiome compositions on protein- and carbohydrate-rich diets. The microbiome composition of populations of the stored-product mite *Tyrophagus putrescentiae* differs with mite habitat and food, and changes occur in both symbiotic and ingested bacteria. In general, the microbiomes of stored-product arthropods have been poorly studied, but they may hold the key to developing new methods for controlling and better understanding the ecology of stored-product arthropods.

bacteria of medical importance (*Enterobacteriaceae*, *Escherichia coli*, and *Listeria monocytogenes*) to human food for direct consumption. Flies visit carrion and feces, where they can pick up bacteria that are then transferred to food, and cockroaches migrate to feces and stored food, carrying bacteria on their exoskeleton and in their gut, resulting in both passive mechanical and active bacterial transfer (152). Such behavior is typical for cockroaches, but not for the rest of the stored-product pests (151).

Stored-product pests typically feed and develop inside the specific type of product that they infest, so they derive all of their food, water, and shelter from the stored food, which limits their capacity to act as vectors. Bacteria usually do not multiply in the gut of these pests. There are, however, reports suggesting that some species are able to transfer bacteria from contaminated commodities to other stored products, which is particularly important in poultry houses. *Alphitobius diaperinus* can disperse *Salmonella* spp. and *E. coli* in broiler house environments, mainly through the cuticle and gut (46, 47, 72, 150). The experimental contamination of *Alphitobius diaperinus* by *Salmonella* showed that both adults and larvae are able to produce contaminated feces up to 12 days after contamination (21). The bacteria persisted during metamorphoses in up to 20% of *Alphitobius diaperinus* adults (21). Bacterial communities isolated from *Sitophilus granarius* in grain stores included the human pathogens *Escherichia*, *Serratia*, *Streptococcus*, *Bacillus*, and *Klebsiella*. Storage beetles such as *Sitophilus oryzae*, *Sitophilus granarius*, *Tribolium castaneum*, *Oryzaephilus surinamensis*, *Rhyzopertha dominica*, *Tenebroides mauritanicus*, and *Cryptolestes pusillus* are capable of transferring *Salmonella enterica* via mechanical transmission (22), and *Sitophilus oryzae* can transmit *Salmonella enterica* from infested to clean grain on the cuticle and in the gut (60). Another study showed that the enteric bacteria in *Tribolium confusum*, *Lasioderma serricorne*, and *Stegobium paniceum* include species of the genera *Enterococcus*, *Escherichia*, and *Enterobacter* (*Cronobacter*) (145).

Tribolium confusum, *Tribolium castaneum*, *Sitophilus zeamais*, and *Trogoderma variabile* collected in mills in the United States were capable of hosting in their gut the antibiotic-resistant bacteria *Enterococcus faecium* (69). Enterococci can transfer their resistance traits to bacteria of greater clinical significance though horizontal gene transfer (18). This type of transfer can occur in the gut of insects and cattle in feedlots. *Tribolium castaneum* can successfully acquire antibiotic-resistant enterococci (*Enterococcus faecalis* OGR1RF: pCF10) from animal feed and transfer them to sterile feed (19). This is particularly important because enterococci are not food-borne pathogens, so the role of arthropods in their transfer is critical, and they represent a source of antibiotic-resistance genes in the human environment (70).

Stored-product mites are able to digest bacteria via bacteriolytic enzymes that hydrolyze the cell walls in order to use them as a food source (29); however, not all bacteria are digested, and living bacteria are passed through the digestive tract. For example, living *Bacillus cereus* bacteria produced proteolytic and chitinolytic enzymes in the mite gut, which contributed to the presence of bacterial allergens in mite feces (32). Another way that mite-transferred bacteria can contribute to allergies is by producing allergenic enterotoxins in patients suffering from house dust mite-induced atopic dermatitis (68).

Stored-Product Beetles as Vectors of Tapeworms

Hymenolepis diminuta is a tapeworm with global occurrence. Rodents are definitive hosts, and arthropods serve as intermediate hosts. There are a few reports of the parasitization of humans after accidental ingestion of infected arthropods, including a case in young children in which transmission was suggested to occur from rodent feces in grain silos, with the children ingesting contaminated insects or grain (73, 79, 130). The stored-product beetles *Tenebrio molitor* and *Tribolium* spp. are routinely used in the laboratory as intermediate hosts for the tapeworm (113).

Attracting Parasitoids and Predators that Can Also Attack Humans

One indirect negative interaction that is frequently overlooked is that food-infesting pests may attract various mite and insect parasitoids (parasitosis) and predators, which may endanger human health because they also produce allergens and can directly attack humans. Cases from Japan and South Korea describe sting dermatitis arising from the bethylid wasp *Cephalonomia gallicola*, with *Lasioderma serricorne* as the most frequent host (48, 71). Parasitic or predatory mites may also attack human skin. For example, pyemotid mites, which are ectoparasites of a large number of stored-product insects, cause rashes and itching in humans, particularly farmers and others exposed to hay (106). Health problems were reported for outbreaks of the newly reported mite *Pyemotes herfsi* in the midwestern United States (14). *Cheyletus* mites were used for biological control in empty grain stores in Central Europe, that is, parthenogenetic strains of *Cheyletus eruditus* (149), but the congener *Cheyletus malaccensis* can cause urticaria by injection of saliva in humans (146, 147).

CONCLUSIONS

Stored-product arthropods are ubiquitous in food processing and storage facilities, as well as in homes. The impact of these associations is often overlooked, especially for very small arthropods, such as psocids and mites, unless the impact of the arthropod becomes acute (such as by causing a rash or anaphylaxis). The effects of chronic associations are often poorly understood. Some of the indirect effects of stored-product arthropods are of major concern, such as their ability to modify the stored-product environment to make it more suitable for the growth of mycotoxigenic fungi, and their ability to spread antibiotic-resistant bacteria. The increasing resistance of stored-product arthropods to insecticides underscores the need to develop alternative management strategies for these pests that can adversely affect human health.

SUMMARY POINTS

1. Stored-product arthropods are common inhabitants and accidental invaders of food. Their presence can have both direct and indirect effects on human health by contaminating food with arthropod fragments and related contaminants, which may be allergenic or even carcinogenic, or by changing the storage microenvironment to make durable products suitable for the rapid development of fungi and other microorganisms, some of which produce toxins harmful to humans.
2. Contamination of stored products by Psocoptera and Acari appears to be increasingly important.
3. Stored-product arthropods are becoming more difficult to control because they have developed resistance to many insecticides, which may result in increased impacts on human health.
4. Allergen production is the most important direct effect of stored-product pests on human health, and arthropod-produced allergens are stable in the human environment.
5. Although there are frequent customer complaints to food producers and marketing chains regarding arthropod contaminations, the psychological research of customer perception is largely missing.
6. Stored-product arthropods may actively or passively contribute to the spread of microorganisms, thus increasing product contamination, and they may host bacteria that have developed antibiotic resistance, contributing to their prevalence in food.

7. Food-infesting pests may attract various mite and insect parasitoids and predators, which may endanger human health.
8. Food safety and quality are high priorities in most countries, but regulations vary. For example, the US Food and Drug Administration has Defect Action Levels for contaminants in food, including insects, but the European Union has mandated zero tolerance of insect fragments in food, although no regular inspections are performed and zero tolerance of insect infestation is considered unrealistic.

FUTURE ISSUES

1. Although many studies have documented health hazards associated with the presence of arthropods in foods, most studies focus on contaminants that the arthropods can transfer to urban and food processing environments, so there is a need for information on the effects of the presence of arthropods per se on human health.
2. Rapid and accurate methods for detecting contaminants in stored products are needed.
3. Among the major types of arthropod-associated contaminants that occur in foods are allergenic substances, and although there is a rich literature on allergens associated with stored-product mites, further characterization of allergens associated with stored-product insects is needed.
4. Research is required to understand the ability of stored-product arthropods to transmit antibiotic-resistant bacteria.
5. The effects of stored-product arthropods on the health of workers in commercial food facilities have been investigated, but additional studies are required about the health hazards associated with urban arthropod pests that occur in homes, such as psocids.
6. Realistic regulations for food quality standards must be harmonized and should be based on standardized sampling of contaminants and the assessment of risks associated with those contaminants.
7. Research is needed to evaluate the psychological impacts of the presence of arthropods in food to consumers.

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26. This case study describes the death of a 47-year-old farmer who was sensitive to mites.

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128. This case study described the presence of living larvae of *Lasioderma serricorne* in an infant's stool.

131. This study showed that stored-product mites are present almost everywhere in homes, but usually in low numbers.

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PaDIL (Pests and Diseases Image Library): <http://pbt.padil.gov.au/index.php?q=node/164>
 Hymenolepiasis: <https://www.cdc.gov/dpdx/hymenolepiasis/>

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