ANNUAL REVIEWS

Annual Review of Entomology

Biology and Control of the Khapra Beetle, *Trogoderma granarium*, a Major Quarantine Threat to Global Food Security

Christos G. Athanassiou,[1,*] Thomas W. Phillips,[2] and Waqas Wakil[3]

[1]Laboratory of Entomology and Agricultural Zoology, Department of Agriculture Crop Production and Rural Environment, University of Thessaly, Nea Ionia, Magnesia 384 46, Greece; email: athanassiou@uth.gr

[2]Department of Entomology, Kansas State University, Manhattan, Kansas 66506-4004, USA; email: twp1@ksu.edu

[3]Department of Entomology, University of Agriculture, Faisalabad 38040, Pakistan; email: waqaswakeel@hotmail.com

Annu. Rev. Entomol. 2019. 64:131–48

First published as a Review in Advance on October 4, 2018

The *Annual Review of Entomology* is online at ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-011118-111804

*Corresponding author

Keywords

Coleoptera, Dermestidae, stored products, quarantine pest, invasive species, food safety

Abstract

The khapra beetle, *Trogoderma granarium*, is a voracious feeder of stored products and is considered one of the most important quarantine pests globally. Its ability to survive for long periods under extreme conditions facilitates its spread through international commerce, which has led to invasions of new geographic regions. The khapra beetle is an important quarantine pest for many countries, including the major wheat-producing countries the United States, Canada, Russia, and Australia, and has been classified as one of the 100 worst invasive species worldwide. This species cannot always be controlled by insecticides and other nonchemical methods that are usually effective against other pests of stored products, particularly owing to its diapausing late larval stage. It can rapidly develop at elevated temperatures and under dry conditions, which are not favorable for many major stored-product insects. We synthesize key published work to draw attention to advances in biology, detection and control of the khapra beetle, and directions to consider for future research.

INTRODUCTION

The khapra beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae), is a noxious stored-product insect that is listed as a quarantine species by the European and Mediterranean Plant Protection Organization (EPPO) and others (48, 96). The khapra beetle is endemic to India and has expanded regionally in recent centuries via human travel even though adults do not fly. Like most stored-product pests, *T. granarium* was introduced to other continents through international trade (48). The current distribution of *T. granarium* includes several countries in Africa and South Asia and a few in Europe, while the number of interceptions in countries in which khapra beetle is not established has increased steadily in recent decades (41, 48, 49, 96). The khapra beetle shares habitats with other storage pests and can overcome competition with an exceptional capacity for population growth and other life history traits. Many stored-product dermestids are scavengers in late successional stages of storage ecosystems, but the khapra beetle can be a voracious primary feeder, damaging more grain than it consumes, on staple cereal grains like wheat kept in good storage condition. Larvae of this species, particularly those in diapause, are tolerant to common insecticides and other control methods that are usually effective against most stored-product insects. The word *khapra* from Urdu and Hindi can mean carapace, tile, shard, or destroyer, all of which describe the persistence, tolerance, and destructiveness of this synanthropic pest.

There have been useful articles and regulatory compendia on the khapra beetle over the years (17, 41, 44, 87, 103). Here we review key biological features of *T. granarium* that facilitate its impact on stored products and threat as a quarantine pest of world grain supplies, its current distribution and status, recent invasion history, concerns and needs for effective diagnostic identification of intercepted specimens, the weaknesses of some traditional pest control and quarantine treatments, and our proposals for future work needed to prevent the khapra beetle from threatening security of agricultural commodities in many countries throughout the world.

BIOLOGY AND IMPACT

A broad host range contributes to the establishment and spread of *T. granarium* (4, 12, 55, 85, 88). This species can infest many durable postharvest foods with moisture content as low as 2%, it can develop over a range of temperatures, and it can remain cryptically within storage structures, sometimes in a larval diapause for many months or even years (3, 61, 92).

Life History

Optimal temperatures for development of *T. granarium* are between 20°C and 35°C (85, 87). Egg to adult development time was reported as 39–45 days at 30°C and as much as 220 days at 21°C (48). Larvae can pass through 4–8 instars depending on temperature, they can complete development in as few as 15 days at 35°C, and females have one molt more than males before pupation (31, 32, 54). Kavallieratos et al. (81) showed that population growth of *T. granarium* at 35°C was 10–250 times higher than that for other stored-product beetles. *Trogoderma granarium* can reach pest status when mean monthly temperatures are at least 20°C for four consecutive months with relative humidity (RH) <50% (59, 63), while mean monthly temperatures >27°C and RH <75% for 1–2 months will result in explosive population growth (116). There is no oviposition below 20°C, and although oviposition does not vary markedly between 27°C and 35°C, it is reduced if humidity increases (100). Thus, low RH together with high temperatures are key conditions for rapid development and establishment of this species (17). In addition to its reproductive success at low RHs under optimal temperatures, *T. granarium* is exceptionally tolerant to very high and very low temperatures, which is a rare life history characteristic among stored-product insects (126, 128).

Trogoderma granarium adults do not feed and live up to 10 days under optimal conditions. Although both sexes have fully developed wings, neither are able to fly (17, 54). Most studies report that adult females lay between 26 and 66 eggs in their short life span (29, 54, 78, 100), which is common for other short-lived stored-product beetles. However, females of *T. granarium* that emerge from diapausing larvae can have multiple matings and lay over 130 eggs per female at ideal laboratory conditions (78).

Diapause is the key characteristic in *T. granarium* biology that contributes to its longevity and invasive success (17). Fifth-instar larvae can enter a facultative diapause that can last for six years (4, 22, 31, 32, 97). Diapausing larvae can survive for long intervals without food and can make additional molts (48), though they can become active for foraging excursions to feed and then return to their quiescent state (22, 127). Diapause typically occurs under crowded conditions when temperature is less than 30°C and food is reduced. Photoperiod plays a minor role, if any (78, 97, 127), compared to that in other insects. Diapause of *T. granarium* can therefore be classified as being density dependent (32, 97). Termination of diapause comes with increased temperature, while, paradoxically, food availability is far less important or plays some role only under conditions of isolation (32, 97). Diapausing larvae are cryptic and immobilized in refuges, which is a challenge for detection and contributes to the frequency of introductions in countries with quarantine legislation (22).

Trogoderma granarium can have up to 10 generations per year, depending on food and environmental conditions. It has been calculated that at 30°C to 33°C, the population increase of *T. granarium* is 19–44 times per generation, which corresponds to 2–2.5 times per week (12, 48). This population growth is comparable to that of other major pests, but *T. granarium* has the advantage of also multiplying remarkably fast under warm and dry conditions (12, 81). Young larvae of *T. granarium* cannot damage sound grain kernels but will feed on the soft germ of the seed, while older larvae can then break apart and infest the kernel. A significant infestation can therefore occur faster when intact kernels coexist with already infested or cracked kernels and probably under conditions of coexistence with other species (12, 81).

Difficulties in Identification

Accurate identification of *T. granarium* specimens is a major challenge to quarantine personnel upon interception of dermestids at ports of entry, and it requires the taxonomic expertise of individuals specifically trained for this purpose (48, 52, 103). Moreover, the larvae of *T. granarium*, and not the adults, are the most frequently found life stage in infested commodities and in buildings and shipping vessels (96). Larvae can be identified only under a microscope, using few detailed morphological structures after special preparation, and these resources are not always available to phytosanitary authorities in some countries (52). Although identification of adults of *T. granarium* is easier than that of larvae, it too is based on very specialized features (**Figure 1**). There is also a polymerase chain reaction–based assay to separate *T. granarium* from other congeners on the basis of 16S mitochondrial DNA (101) and an immunological assay to separate species (122). Both methods were accurate for the identification of known *T. granarium*, but consistent diagnoses of other specimens were inconclusive (101, 122). Challenges to accurate identification of *T. granarium* and the crucial need for correct identification to take appropriate quarantine actions regarding this pest point to the critical need for useful taxonomic tools and more training of inspectors.

Quarantine Importance

Trogoderma granarium was listed as one of the 100 worst invasive species worldwide (89). Once the species enters a new geographic region, it can establish itself by breeding rapidly under optimum

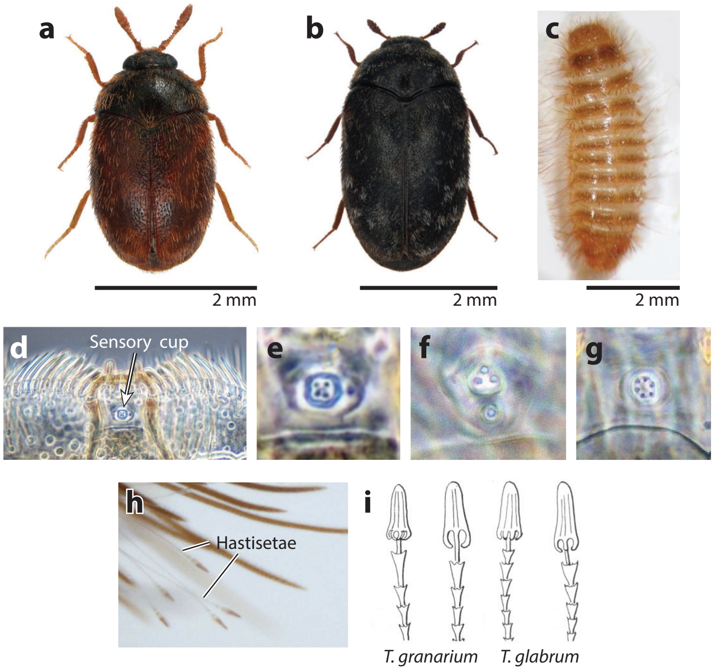

Figure 1

Some of the morphological characters used for identification of *Trogoderma granarium* and for diagnostic separation from other species of *Trogoderma*. (*a*) Adult *T. granarium* with a reddish-brown integument but with a very brown to black pronotum; (*b*) *T. glabrum* with a black integument; and (*c*) mature larva of *T. granarium*. (*d*) Larval epipharynx with a distal sensory cup (*arrow*) that has four sensory papillae (and enlarged in panel *e*), which is typical of both *T. granarium* and *T. glabrum* larvae. (*f*) Two sensory cups, one with three sensory papillae and a second small cup with just one papilla, which is found in some *T. granarium*. (*g*) Ventral view of a sensory cup with six sensory papillae that is common for *Trogoderma* species other than *T. granarium* and *T. glabrum*. The six papillae are commonly found in just one cup, but some specimens may have six papillae in a group of four and two papillae distributed among two cups. (*h*) Hastisetae among the stout dark setae of *Trogoderma* larvae. (*i*) Four morphological forms of hastisetae: those of *T. granarium* with two forms of terminal segments with apical club and those of *T. glabrum* with two forms of terminal segments and apical club. Images in panels *a* and *b* are by Charles Brodel and reproduced with permission from Reference 52; panels *d*–*h* are modified with permission from images courtesy of Charles Brodel of the United States Department of Agriculture's Animal and Plant Health Inspection Service, Plant Protection and Quarantine; panel *i* reproduced from Reference 52.

conditions and it can persist owing to its larval diapause under unfavorable conditions (30, 31, 33, 93, 118). Dermestidae in stored products typically occupy ecological niches characterized by degraded plant and animal materials, but *T. granarium* distinguishes itself with its ability to rapidly infest cereal grains in good storage conditions (21, 30, 37, 56, 76). This species is classified as an A2 quarantine organism by the EPPO, signifying that it occurs in the geographic region of the European and Mediterranean Plant Protection Organization (49). The World Trade Organization committee on Sanitary and Phytosanitary Measures prohibits the importation of infested wheat and similar grains, as well as products milled from these, to protect domestic production in an importing country and generally prevent the spread of *T. granarium*. The frequency of recorded interceptions in the United States has increased dramatically in recent years. These records likely represent true increases in khapra beetle introductions but can also be tied to increased inspection rates during the same time period (96, 121).

Host Range and Preference

Trogoderma granarium has been recorded infesting over 100 commodities (12, 55, 103) (**Supplemental Table 1**). The foods include almost all kinds of seeds; beans; nuts; other dried plant or animal products like animal feed, pet food, dried orange pulp, bread, and dried coconuts; and other substances of animal origin such as dead mice, dried blood, and dried insects (4, 12, 38, 42, 56, 67, 89, 108, 114). In India, which is the area of origin for this pest before modern international trade, *T. granarium* has been found infesting stored wheat, maize, sorghum, rice, barley, gram, pulses, pistachio nuts, coconut, and walnuts, causing more damage as a pest of wheat (108). Unlike most other dermestids, *T. granarium* prefers and can thrive on a diet of just grain and cereal products without need for any nutrients from animal products (4, 108). In general, oil seeds and dried fruits were less suitable as a larval diet than cereals and pulses were (107). Although the species is able to develop on sound grains, the presence of cracked kernels enhances its development (12). The studies cited above point to wheat as being one of the best hosts for the development of this species, but its presence in nonpreferred commodities can seriously contribute further to its geographical expansion (81).

Supplemental Material >

Damage and Losses

Infestation by *T. granarium* larvae in grain kernels negatively affects mineral quality, available carbohydrates, and protein and starch digestibility and bioavailability (72–74, 113). Newly hatched larvae feed on grain dust or broken kernels, while whole grains are attacked by fourth-instar or older larvae (42). The weight loss of infested grain and cost of necessary treatment will reduce profit at sale and rapidly make it unmarketable. Infestation levels of 75% in wheat, maize, and sorghum result in a significant reduction in crude fat, total carbohydrates, sugars, and true protein contents (69–71, 73–75, 109). Increased food consumption has been recorded in constant darkness; however, constant light accelerated development but reduced oviposition (117). Larval survival was 81% in constant darkness versus 51% in constant light for larvae reared on white rice at 28.5°C (68).

Trogoderma granarium damages many more kernels than it consumes, and it causes heavy contamination of the commodities with body parts and cast skins (96, 121). Consumption of some of these contaminants in food may cause serious health hazards (94, 103). Infestations by *T. granarium* result in a high amount of frass, much higher than that produced by other major stored-product beetle species (81). Grains in good condition (i.e., with low frass levels) may be less suitable for a rapid development of *T. granarium* populations than those with high amounts of frass (12). Certain grain characteristics such as kernel hardness and kernel size were crucial for *T. granarium* population growth (112); population growth was negatively correlated with kernel size (111). Larval infestation on the germ of grain kernels results in serious germination losses (72, 105, 111), while the presence of germ seems to enhance population growth (12).

GEOGRAPHICAL DISTRIBUTION

Trogoderma granarium is native to the Indian subcontinent, where it was first reported as a pest in 1894 (19, 102, 109). This species prefers hot and dry climates and occurs in such habitats between 35° north latitude and 35° south latitude (41, 52). These conditions prevail in certain areas of the Middle East, Africa, and South Asia where the species occurs, while it has also been found in certain specialized warm habitats in more temperate countries (e.g., infesting stored grain malt in the United Kingdom) (4, 17, 30, 109). Previous population modeling, surveillance, and risk assessment studies showed that the likelihood of *T. granarium* becoming established in Canada or other cold countries is considered low owing to ambient temperatures, but as with most stored-product insects, the potential for infestation of heated buildings with other suitable resources and conditions will always exist (8, 127). Conversely, areas such as the southwestern United States and the majority of the areas in Australia and Brazil are considered quite suitable for *T. granarium* invasion and establishment, as evidenced in the last century (17, 41, 102, 121).

Populations of the khapra beetle have become established in 34 countries in Asia, Africa, and Europe (**Figure 2**). An additional 32 countries in Europe, North and South America, and Oceania have a history of confirmed khapra beetle introductions and/or infestations that were subsequently eradicated or otherwise are no longer known to occur (**Figure 2**). All countries but two with established khapra beetle populations fall within the region between 35° N and 35° S, while many countries with documented eradications, most in Europe, fall outside that region. New reports on *T. granarium* infestations in a country can result in serious trade restrictions (17, 25, 48, 49). Scientific literature in the past 50 years reports that before the 1960s, this pest had spread to and was briefly established in all continents where grain and grain products were stored (48, 87), but these were eradicated or are no longer present (**Figure 2**). Recent summaries with regard to routine interceptions (not infestations) of the khapra beetle at ports of entry in the

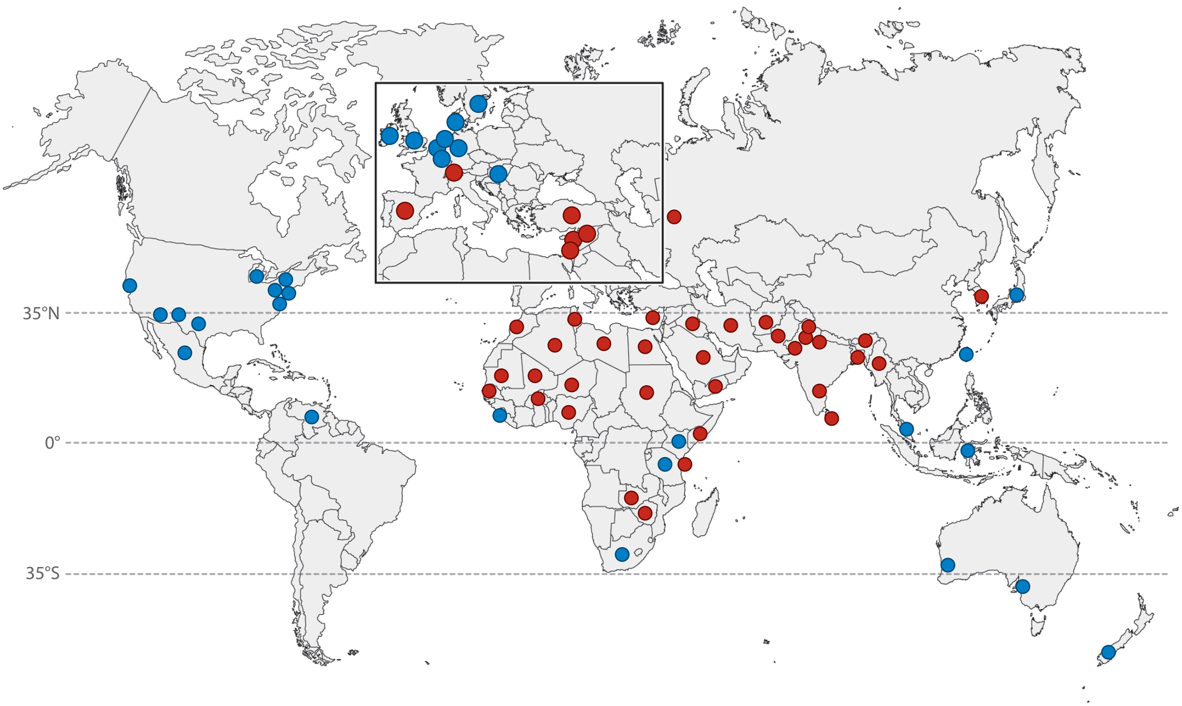

Figure 2

Map showing the current known world distribution of the khapra beetle by country, as marked with red circles. Blue circles indicate countries that had infestations of the khapra beetle beyond ports of entry during the past century and that are known to have been eradicated or for which there are no current records of occurrence. The lines for 35° north latitude and 35° south latitude encompass the geographic region most likely to support populations of the khapra beetle. Figure adapted from Reference 44 but with added records from Reference 34. A listing of countries and locations derived from the CABI Invasive Species Compendium (34) shown on this map is elaborated in **Supplemental Table 2**.

Supplemental Material >

United States coming from various countries (96, 121) showed that the sources of interceptions from 1984 to 2010 were from Asia (45%) and Middle Eastern and Northern African countries (43%), with only 1–4% originating in either Europe, Canada, Central America, Australia, or Sub-Saharan Africa, despite the fact that some of these countries had no infestations recorded as of 2014 (**Supplemental Table 2**). Over 100 countries' records of the khapra beetle from over the past 40 years are listed in **Supplemental Table 3**.

Supplemental Material >

Historical literature from India reports that *T. granarium* was found in large numbers in cargoes of wheat shipped from Karachi (now Pakistan) and Bombay (now Mumbai, India) (11). The pest steadily increased its geographic range during the twentieth century. Introduction into Britain may have been before 1916 (43, 62), with no record of damage by this pest at that time, but significant damage was recorded some years later in stored malt in Britain (30, 43) and Germany (130). In 1920, a serious infestation of *T. granarium* in an English brewery was reported where malt in storage bins was heavily infested with beetles and larvae intermingled with the empty husks (91). It was later found in linseed imported into Britain from India (95), while in 1956, the species was intercepted in the United Kingdom in a shipment of barley from South Australia on a ship that two years earlier had carried a cargo infested with *T. granarium* (15). The species was first reported in Germany in 1921 (125), while it was found in 1923 in large numbers in the malt stores of a brewery in northwestern Germany. *T. granarium* was introduced to Western Africa through the North India subcontinent (40), while it was prevalent in Japan in 1923 and in Korea in 1928 (98).

Trogoderma granarium was first recorded in the United States in October 1953 in the state of California, where it was reported in extremely high numbers in two warehouses containing wheat and barley in Tulare County and was apparently carried in with used sacks from Fresno. The introduction may have been as early as 1946 but was misidentified as the black carpet beetle, *Attagenus piceus* (Olivier) (Coleoptera: Dermestidae) [now *Attagenus unicolor* (Brahm)] (9, 20), and this is likely the first record of *T. granarium* in the Western Hemisphere (9, 10, 87). A thorough surveillance revealed the presence of *T. granarium* in other areas of the Southwest as well (59, 60, 63), which resulted in a costly eradication supported by the United States Department of Agriculture (USDA) (10, 42). By 1966, the species was successfully eradicated from California, Arizona, and New Mexico (103). After its eradication in these southwestern US states, *T. granarium* was then found in a New Jersey warehouse in 1968 and again in isolated infestations from 1980 to 1983 in California, Maryland, Michigan, New Jersey, New York, Pennsylvania, and Texas. Day & White (41) give a thorough summary of these North American introductions and eradications.

The Commonwealth of Australia issued a proclamation in 1921 under the Quarantine Act of 1908 forbidding the introduction of *Attagenus undulatus* (Motschulsky) (Coleopterea: Dermestidae), which was assumed to be the khapra beetle. Australia was then listed as a "khapra beetle country" in the late 1940s owing to this taxonomic error, and it took over 15 years of lobbying and the publication of a position statement in the *FAO Plant Protection Bulletin* to have this stigma removed (14, 15). A survey over a wide area of Australia found 30 species of dermestids but not *T. granarium*, and except for a single record from Tasmania in a cargo of barley, it had never been found within Australia apart from certain interceptions associated with shipping (41). Much of the interior of Australia, including some grain-growing areas, provide suitable conditions for this pest (17). Coastal population centers with the exception of Adelaide appear unsuitable. A risk analysis identified the entry ports of Australia where *T. granarium* introduction is most likely to occur (102). In April 2007, there was a postborder detection of *T. granarium* larvae and adults in a Western Australian residence (46). Immediate action was taken by the government and grain industry to eradicate the infestation with methyl bromide fumigation followed by a two-year trapping program to confirm eradication of the pest (45, 46).

DETECTION, TRAPPING, AND MONITORING

Detecting the presence of *T. granarium* in any context of commercial trade or any form of international and domestic transportation requires that careful and consistent routines be adopted by the relevant quarantine agency in each country. Systematic inspection of cargo, ship holds, shipping containers, and other structures for transporting agricultural commodities, as well as all passenger baggage and personal vehicles crossing borders, is the most common and first line of detecting the khapra beetle entering a country or region (66). Myers & Hagstrum (96) cited USDA–Animal and Plant Health Inspection Service information that of the 559 out of 666 specimens intercepted between 1985 and 2010 at ports of entry in the United States and identified as *T. granarium*, about half were in passenger baggage, 30% were from general cargo, and the remainder were from a variety of sources like mail and empty ship holds. Sources of these specimens coming into the United States were from 43 different countries during that same time, with the majority coming from countries in Asia, the Middle East, and North Africa. Government interceptions of the khapra beetle at or near ports of entry remain common. For example, in a recent Internet search for khapra beetle interceptions by the United States government agency Customs and Border Patrol, we found, using the search terms "CBP khapra beetle," six press releases on interceptions occurring at locations from Atlanta, Georgia, to Port Huron, Michigan, in calendar years 2016 and 2017. A nine-year history of US interceptions of the khapra beetle by the Customs and Border Patrol is tallied in **Supplemental Table 4**.

Supplemental Material >

Detection and continuous monitoring of spaces potentially infested by the khapra beetle is critical for controlling this quarantine pest as it is for the integrated pest management (IPM) of any target pest in nonquarantine contexts. Traps for the khapra beetle are very important in quarantine survey operations, and there is a history for trap and attractant development spanning many decades. The pheromones for *T. granarium* were identified as a mixture with 92% of the *Z* and 8% of the *E* isomer of 14-mehtyl-8-hexadecenal (39). This aldehyde is a female-produced sex pheromone that attracts males of *T. granarium*, and the closely related species *T. variabile* Ballion, *T. inclusum* LeConte, and *T. glabrum* (Herbst) will also respond to this same pheromone. Synthetic *Trogoderma* pheromone is used in commercial lures for traps that can detect and monitor these species inside and outside buildings. Since *T. granarium* adults do not fly, any pheromone-baited sticky traps used for flying insects would capture only species of *Trogoderma* that are not khapra beetles. Traps for walking insects placed on floors or walls can be baited with the *Trogoderma* pheromone and thus capture walking adult *T. granarium* males in addition to adults of other species (18). These floor- and wall-mounted traps are baited with both the synthetic pheromone and a small amount of a wheat germ oil–based food attractant that can enhance responses to the pheromone and serve as a food attractant for dermestid larvae as well as other stored-product insects. Floor traps are square or circular and capture insects responding to the semiochemicals that crawl up the surface of the trap and then fall into a receptacle partially filled with the food oil (104). Wall traps are mounted vertically on a wall, usually close to the ground, and take advantage of the negative geotaxis of responding beetles to climb up and into the folded paper structure of the trap and then into an oil-filled receptacle (18). The attraction of walking adults and larvae of three or more species of *Trogoderma* to these floor or wall traps requires careful taxonomic identification of specimens to determine whether *T. granarium* was captured.

Difficulties in Eradication

Once an infestation is established, it can prevail as this pest breeds rapidly in very dry foods and survive in cool conditions (30–33, 58, 93, 118). The rapid spread of *T. granarium* in several continents is an indication of the capacity of this pest to move around by several means, all anthropogenic (17, 41, 102). Diapausing *T. granarium* larvae are extremely persistent, and they are much more tolerant to pesticides than nondiapausing larvae are (23–25). The cryptic nature of both larvae and adults enables them to be transported undetected (31, 32, 126). Although an infestation may be effectively eradicated, the potential for reinfestation from subsequent introductions remains due to shipping and trade from source countries. One reason proposed for the increase of interceptions at locations far from established populations is the increasing use of metal shipping containers that carry products from country to country via multiple ships, barges, railways, and roads. Stanaway et al. (120) inspected the wooden floors of 3,001 empty shipping containers and found 1174 containers that collectively contained a total of 7,400 live and dead insects. About 300 of those containers were recorded as having one or more stored-product insects, but species identifications were not reported. Numerous interceptions of *T. granarium* in freight containers have been recorded at Australian ports (17), while refugia within the structure of containers and ship holds can protect diapausing larvae from insecticides (17, 64, 65). The case of the isolated infestation at a residence in Western Australia points to the potential for introductions by shipping containers that can put khapra beetle–free countries at risk (41). A family that relocated from the United Kingdom with the infestation of khapra beetles in their home had a shipping container deliver their household goods to Perth from England. Prior to loading in England, that specific container had visited six other countries, including three in Asia and two in the Middle East, all potential sources of the khapra beetle (41).

Eradication of *T. granarium* can be difficult and costly once a population is well established. Its ability to hide in protected locations and enter diapause can negatively affect eradication measures. The success of eradication programs can be impeded by development of resistance to commonly used residual and fumigant insecticides (28, 36, 84, 106). Nevertheless, although difficult, there are several historically recorded cases of effective eradication of *T. granarium* infestations. For instance, *T. granarium* was introduced and established in the United States several times in the last seven decades, and in all cases, it was eradicated through expensive programs that involved extensive fumigation and surveillance (96).

CONTROL

Research on chemical and nonchemical methods to control *T. granarium* is not as extensive as with other stored-product pests, probably owing to quarantine restrictions preventing access to *T. granarium* colonies by most laboratories in countries that do not have established *T. granarium* populations. Hence, there is lack of recent information on the efficacy of some key methods and new active ingredients. Research shows, however, that *T. granarium* is tolerant to many of the control measures that are usually effective for other stored-product insect species.

Chemical Insecticides

Work during the last four decades of the twentieth century evaluated residual activity of modern organophosphates (OP), pyrethroids, and other grain protectants, but the majority of these are no longer registered for use in many countries. Recent studies with registered grain protectants show that the OP insecticide pirimiphos-methyl and diatomaceous earth were more effective than pyrethroids, insect growth regulators (IGRs), and spinosad, while large larvae of *T. granarium* and *T. variabile* were more tolerant than small ones for both (13, 53, 79, 82, 129). Application of contact insecticides to surfaces in buildings can help to prevent establishment and spread of introduced *T. granarium* at ports of entry. Surface treatments of the pyrrole chlorfenapyr, OPs, and pyrethroids were far more effective than IGRs and spinosad (80). These results can be utilized further for quarantine and preshipment strategies in key export scenarios, such as treating empty containers, loading equipment, and loading structures. Methyl bromide (MB) is a very effective fumigant for quarantine treatments, and the recommended rates for the khapra beetle are usually two times higher compared with those for other stored-product pests (27) for quarantine security. The concentration required to control all *T. granarium* life stages was suggested as a concentration-time product (CTP; the product of the treatment time in hours and the gas concentration over the course of the treatment) of 600 g hm^{-3} at temperatures higher than 15°C (26). The Australian quarantine requirements were 80 g m^{-3} for 48 h at >21°C (41), corresponding to CTP of 1,700 g hm^{-3} on the basis of exponential decay of fumigant concentration and end point retention of 20% of the applied dosage. Treatment manuals of the USDA (123, 124) specify a dosage of 96 g m^{-3}, with a retention of 30 g m^{-3} at 12 h at 15–21°C, corresponding to a CTP of about 530 g hm^{-3}. Historically, dosage recommendation for controlling *T. granarium* has been based on double the normal dosage for general stored-product pest control (27). Despite the completion of its phase-out in 2015, MB remains available under a waiver for quarantine uses, but concerns about the future of this waiver continue to facilitate more research on MB alternatives. Phosphine is an effective fumigant for *T. granarium* (88) but requires longer exposure times than MB (upward of 3 days) and warm temperatures (above 25°C) (23, 24, 57).

Champ & Dyte (36) reported that some populations of *T. granarium* were resistant to malathion, lindane, methyl bromide, and phosphine, while others reported resistance to deltamethrin, dichlorvos, and pirimiphos-methyl (84, 106). Borah & Chahal (28) detected frequent resistance development to phosphine when they exposed resistant and susceptible strains of the khapra beetle to different treatments of phosphine and reported 5–12% larval mortality in a resistant strain compared to 84–94% in a susceptible strain. During a survey conducted in Pakistan, the khapra beetle was by far the most abundant pest species found in silos at three months post-phosphine fumigation; however, before treatment, its population size was lower than those of the lesser grain borer, *Rhyzopertha dominica* (Fabricius) (Coleoptera: Bostrychidae), and red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) (90).

Nonchemical Control

Extreme temperatures can be used for controlling many species of stored-product insects. *Trogoderma granarium* is perhaps the most cold-tolerant stored-product insect species known despite its subtropical origin. The time needed to kill diapausing cold-acclimated larvae at −15°C at the probit-9 level (99.9968%) was estimated to be 70 days, and the same rate of kill at −20°C would require up to 15 days (50, 126, 128). Cold tolerance of *T. granarium* might be attributed to adaptation to desiccation, which is a benefit in its typical hot and dry environments (115). Larvae of *T. granarium* are considered the most cold-tolerant life stage, while larval acclimation to cold seems to contribute more to cold tolerance than larval diapause does (128). Larval acclimation occurs after exposure to temperatures between 4°C and 15°C for several weeks (127), which corresponds to realistic scenarios in storage facilities in many parts of the world. A low-temperature quarantine treatment for *T. granarium* would therefore require an unreasonably long exposure time and would be very impractical. *T. granarium* is extremely heat tolerant (126, 128). Exposure of most insect species to 50°C is usually 100% lethal after a few hours, so heat-treatment protocols usually specify 45°C for hours to days (51). Significantly higher temperatures and longer exposure intervals are needed to control *T. granarium* (126). Diapausing larvae were found to be the most heat-tolerant life stage. The exposure time estimated from probit-9 analyses to achieve complete kill of diapausing larvae was 397 h at 45°C, 7 h at 50°C, and 1.2 h at 60°C (126). Hence, a heat treatment for *T. granarium* in a sealed and insulated chamber should be 50°C or higher for several hours, but this same minimum temperature would be extremely difficult to achieve in all parts of a building and such a temperature could not be maintained for an effective time period. The tolerance of *T. granarium* to extreme temperatures creates serious challenges to its control using standard heat and cold treatments and points to the adaptation of its diapausing larvae to survive extreme environmental conditions.

Controlled or modified atmospheres can be alternatives to conventional fumigation methods for *T. granarium*. Lindgren & Vincent (86) reported that 60–80% CO_2 was more effective against *T. granarium* compared to the application of 100% CO_2. A concentration of 60% CO_2 at 20°C or 30°C with 60% RH resulted in eggs, pupae, and adults killed within 6 days, while at the same conditions, larvae required 16 days for control (119). Purging with nitrogen to create a low-oxygen treatment has proven very effective for the control of *T. granarium*, with eggs being the most susceptible life stage, followed by larvae and pupae (5). Treatments using either high CO_2 or low O_2 at elevated temperatures can be highly effective against *T. granarium* larvae (99), and this suggests that a quarantine treatment could be developed with the use of effective fumigation chambers.

The biological control of the khapra beetle has not been widely studied, but a number of biological control agents are known to be associated with the khapra beetle. The protozoan *Mattesia trogodermae* Canning (Protozoa: Neogregarinida) is a parasite of species in the genus *Trogoderma* (35, 121), while the nematode *Steinernema masoodi* (Rhabditida: Steinernematidae) has been effective against *T. granarium* (6). *Xylocoris flavipes* (Reuter) (Hemiptera: Anthocoridae) is a cosmopolitan predator of *T. granarium* larvae (2, 110), while predatory mites are known to feed upon eggs of *T. granarium* (108). Al-Kirshi et al. (7) considered the potential of the larval parasitoid *Laelius pedatus* (Say) (Hymenoptera: Bethylidae) to control the khapra beetle in cereals. Although it is mostly found in other stored product beetle species, *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae) has been also recorded to parasitize *T. granarium* (1, 77). Several Iranian isolates of the fungus *Metarhizium anisopliae* (Metschinkoff) Sorokin (Ascomycota: Hypocreales) were pathogenic to khapra beetle adults and larvae (83), and the bacterium *Bacillus thuringiensis* Berliner (Bacilli: Bacillaceae) was very effective against khapra beetle larvae (3). Although populations of parasites and predators may play a minor role in regulating populations of the khapra beetle (16), the information on natural enemies and pathogens for the khapra beetle points to the potential for encouraging biological control in IPM systems for this pest in its endemic range.

CONCLUSIONS

Trogoderma granarium has been an important threat to global food security for decades, but there is still a great need for more information on its biology, geographic distribution, detection, and control. The beetle has a wide host range and can be introduced with international movement of people and many durable food products traveling from Asian countries with established populations. It is the ability for this species to aggressively infest bulk-stored wheat, and its absence from the major wheat-exporting countries, that makes it a serious quarantine pest. The challenge for accurate taxonomic diagnosis of this species and limitations on effective control and eradication measures contribute to quarantine insecurity. The biological adaptations of the khapra beetle, from the longevity of diapausing larvae to the cryptic nature during transport, call for additional research to develop effective prevention, detection, and control measures for this pest.

FUTURE ISSUES

Despite the fact considerable research has been carried out for *T. granarium*, the majority of the key literature was produced more than 40 years ago, and there are serious gaps in key biology issues and modern control of this species. Phytosanitary restrictions allow only some laboratories to have khapra beetle rearing for research. Suggestions for work needed in the immediate future are as follows:

1. Accurate identification of species is difficult because of variable character states in both larvae and adults that require that two or more characters are confirmed for diagnosis as *T. granarium*. There are very few diagnosticians who are trained for khapra beetle identification, and there is a critical need for quarantine agencies worldwide to train and recruit technical staff for this purpose. Phytosanitary certification prior to export should be rigorous, with diagnostic expertise both at export and in receiving countries. Research on molecular diagnostics has been promising and should continue to provide useful and effective tools.
2. Source countries for the khapra beetle remain largely in Asia and are unlikely to conduct or achieve eradication of the khapra beetle. Importing countries must not only have vigilant and expert detection programs at their ports, but also conduct routine and rigorous surveys for the khapra beetle along inland trade routes with commodity storage and processing facilities. Major grain-exporting countries like Australia, Canada, Russia, and the United States must be especially vigilant in having their ports and inland grain storage and transport systems free of the khapra beetle.
3. Research is needed for new and effective quarantine treatments and eradication strategies when infestations of the khapra beetle are discovered upon import and also for the more challenging established infestations inland of the port. Methyl bromide fumigation is a highly effective control measure that can be applied to intercepted infestations and requires only a matter of hours to apply. Methyl bromide has been banned for most nonquarantine uses in agriculture, whether postharvest or preplant, but it is allowed for quarantine use under a waiver by the Montreal Protocol for quarantine and preshipment uses. However, there is no guarantee that this waiver will continue indefinitely or that gas supplies from the few manufacturers will continue. More research on methyl bromide alternatives for quarantine treatments and in-country eradication are critical for the khapra beetle, as this pest has shown marked tolerance to common alternatives in recent research.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors are grateful to their colleagues Charles Brodel, Gregory Daglish, Paul Fields, David Hagstrum, and Scott Myers for discussions and shared information about the khapra beetle. David Hagstrum was particularly helpful with information from his website, **https://www.storedproductinsects.com**, and Charles Brodel provided valuable advice in the preparation of **Figure 1**. This article represents Kansas State Research and Extension contribution 19-068-J.

LITERATURE CITED

1. Ahmed KS. 1996. Studies of the ectoparasitoid, *Anisopteromalus calandrae* How. (Hymenoptera: Pteromalidae) as a biocontrol agent against the lesser grain borer, *Rhyzopertha dominica* (Fab.) in Saudi Arabia. *J. Stored Prod. Res.* 32:137–40
2. Ahmed KS, Khatun M, Rahman MM. 1991. Biological notes on *Xylocoris flavipes* (Reuter) (Hemiptera: Anthocoridae). *J. Asiat. Soc. Bangladeshi Sci.* 17:65–67

3. Ahmedani MS, Shaheen N, Ahmedani MY, Aslam M. 2007. Status of phosphine resistance in khapra beetle, *Trogoderma granarium* (Everts) strains collected from remote villages of Rawalpindi district. *Pak. Entomol.* 29:95–102
4. Aitken AD. 1975. *Insect travellers*. Tech. Bull. 31, Minist. Agric., Fisheries Food, London, UK
5. Al-Hadidi IK. 2002. *The life of beetles* Tribolium castaneum *(Coleoptera: Tenebrionidae) (Herbst)* and Trogoderma granarium *Everts (Coleopteran: Dermestidae) in some local wheat products and its sensitivity to low pressure, carbon dioxide and nitrogen*. Master's Thesis, Univ. Mosul, Mosul, Iraq
6. Ali SS, Sirvastava M, Shankar P. 2011. First report on susceptibility of khapra beetle (*Trogoderma granarium*) against *Stienernema masoodi* and its in vivo production. *Trends Biosci*. 4:140–41
7. Al-Kirshi A, Gabbar A, Reichmuth C, Bochow H. 1997. Potential of the larval parasitoid *Lalius pedatus* for the control of the khapra beetle *Trogoderma granarium* Everts in grain. *Mitt. Dtsch. Ges. Allg. Angew. Entomol.* 111:367–72
8. Ameen A. 2012. Trogoderma granarium *Everts, khapra beetle*. Plant Health Risk Assess. Req. 2009-51, Can. Food Insp. Agency, Plant Health Risk Assess. Unit, Plant Health Sci. Div., Ottawa, Can.
9. Armitage HM. 1954. Current insect notes. *Calif. Dep. Agric. Bull.* 43:134–36
10. **Armitage HM. 1958. The khapra beetle suppression program in the United States and Mexico. In *Proceedings of the 10th International Congress of Entomology*. Ottawa, Can.: Mortimer**

10. This study illustrates the first stages of detection and eradication program for the khapra beetle in the United States.

11. Arrow GJ. 1917. The Khapra beetle (*Trogoderma khapra*, sp. n.), an Indian grain-pest. *Ann. Mag. Nat. Hist.* 19:481–82
12. **Athanassiou CG, Kavallieratos NG, Boukouvala MC. 2016. Population growth of the khapra beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae) on different commodities. *J. Stored Prod. Res.* 69:72–77**

12. In this work, the population growth of the khapra beetle on different amylaceous commodities is presented, along with the effect on cracked kernels.

13. Athanassiou CG, Kavallieratos NG, Boukouvala MC, Mavroforos ME, Kontodimas DC. 2015. Efficacy of alpha-cypermethrin and thiamathoxam against *Trogoderma granarium* Everts (Coleoptera: Dermestidae) and *Tenebrio molitor* L. (Coleoptera: Tenebrionidae) on concrete. *J. Stored Prod. Res.* 62:101–7
14. Bailey SW. 1958. The position of khapra beetle in Australia. *FAO Plant Prot. Bull.* 6:72–73
15. Bailey SW. 1965. Air-tight storage of grain: its effect on insect pests—IV *Rhyzopertha dominica* (F.) and some other coleoptera that infest stored grain. *J. Stored Prod. Res.* 1:25–33
16. Bains SS, Battu GS, Atwal AS. 1974. Population dynamics of *Trogoderma granarium* Everts (Coleoptera: Dermestidae) in rural wheat stores in the Punjab. *Ind. J. Ecol.* 1:38–47
17. **Banks HJ. 1977. Distribution and establishment of *Trogoderma granarium* Everts (Coleoptera: Dermestidae): climatic and other influences. *J. Stored Prod. Res.* 13:183–202**

17. This paper illustrates the conditions that are suitable for the spread and establishment of the khapra beetle, emphasizing the conditions in Australia.

18. Barak AV. 1989. Development of a new trap to detect and monitor khapra beetle (Coleoptera: Dermestidae). *J. Econ. Entomol.* 82:1470–77
19. Barnes JH, Grove AJ. 1916. The insects attacking stored wheat in the Punjab and the methods of combating them, including a chapter on the chemistry of respiration. *Mem. Dep. Agric. India Chem. Ser.* 4:165–280
20. Beal R Jr. 1956. Synopsis of the economic species of *Trogoderma* occurring in the U.S. with description of a new species (Col.: Dermestidae). *Ann. Entomol. Soc. Am.* 49:559–66
21. Beal RS. 1991. Dermestidae (Bostrichoidea) (including Thorictidae, Thylodriidae). In *Immature Insects*, Vol. 2, ed. FW Stehr, pp. 434–39. Dubuque, Iowa: Kendall/Hunt Publ. Co.
22. Bell CH. 1994. A review of diapause in stored-product insects. *J. Stored Prod. Res.* 30:99–120
23. Bell CH, Hole BD, Wilson SM. 1985. Fumigant doses for the control of *Trogoderma granarium. EPPO Bull*. 15:9–14
24. **Bell CH, Wilson SM. 1995. Phosphine tolerance and resistance in *Trogoderma granarium* Everts (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 31:199–205**

24. The tolerance/resistance of khapra beetle to phosphine is studied, in conjunction with the occurrence of diapause.

25. Bell CH, Wilson SM, Banks HJ. 1984. Studies on the toxicity of phosphine to tolerant stages of *Trogoderma granarium* Everts (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 20:111–17
26. Bogs D. 1976. Effectiveness of methyl bromide against storage pests at low temperatures. *Nachrichtenblatt Pflanzenschutz DDR* 30:221–22
27. Bond EJ. 1984. *A Manual of Fumigation for Insect Control*. Rome, Italy: Food Agric. Org. U.N.
28. Borah B, Chahal CG. 1979. Development of resistance in *Trogoderma granarium* Everts to phosphine in the Punjab. *Plant Prot. Bull.* 27:77–80

29. Burges HD. 1957. Studies on the dermestid beetle *Trogoderma granarium* Everts. I. Identification and duration of the developmental stages. *Entomol. Mon. Mag.* 93:105–10
30. Burges HD. 1959. Studies on the dermestid beetle *Trogoderma granarium* Everts: III. Ecology in malt stores. *Ann. Appl. Biol.* 47:445–62
31. Burges HD. 1962. Diapause, pest status and control of the khapra beetle, *Trogoderma granarium* Everts. *Ann. Appl. Biol.* 50:614–17
32. Burges HD. 1962. Studies on the dermestid beetle *Trogoderma granarium* Everts. V. Reactions of diapause larvae to temperature. *Bull. Entomol. Res.* 53:193–213
33. **Burges HD. 1963. Studies on the dermestid beetle *Trogoderma granarium* Everts. VI. Factors inducing diapause. *Bull. Entomol. Res.* 54:571–87**

33. This study focuses on the factors that affect diapause of the khapra beetle.

34. CABI (Cent. Agric. Biosci. Int.). 2018. Trogoderma granarium (*khapra beetle*). CABI Invasive Species Compendium, Wallingford, UK, updated March 29. **https://www.cabi.org/isc/datasheet/55010**
35. Canning EU. 1964. Observations on the life history of *Mattesia trogodermae* sp. n., a schizogregarine parasite of the fat body of the khapra beetle, *Trogoderma graniarium* Everts. *J. Insect Pathol.* 6:305–17
36. Champ BR, Dyte CE. 1976. *Report of the FAO Global Survey of Pesticide Susceptibility of Stored Grain Pests*. FAO Plant Prod. Prot. Ser. 5. Rome, Italy: Food Agric. Org. U.N.
37. Christensen CM, Kaufmann HH. 1969. *Grain Storage*. Minneapolis: Univ. Minn. Press
38. Cotton RT. 1956. *Pests of Stored Grain and Grain Products*. Minneapolis, MN: Burgess Publ. Minneap.
39. Cross JH, Byler RC, Cassidy RF, Silverstein RM, Greenblatt RE, et al. 1976. Porapak-Q collection of pheromone components and isolation of (*Z*)- and (*E*)-14-methyl-8-hexadecenal, sex pheromone components, from the females of four species of *Trogoderma* (Coleoptera: Dermestidae). *J. Chem. Ecol.* 2:457–68
40. Cuperus GW, Johnson G, Morrison WP. 1992. IPM in wheat and stored grain. In *Successful Implementation of Integrated Pest Management for Agricultural Crops*, ed. A Leslie, G Cuperus, pp. 33–55. Boca Raton, FL: Lewis
41. **Day C, White B. 2016. *Khapra beetle*, Trogoderma granarium *interceptions and eradications in Australia and around the world*. Work. Paper 1609, School Agric. Res. Econ., Univ. West. Aust., Crawley, Aust.**

41. This paper provides a review of the history, and current status, of interceptions and eradications of the khapra beetle in Australia.

42. Dillon K. 1968. *Report on Visit to USA and Canada by Mr. K. Dillon, Plant Quarantine Entomologist, to Investigate All Aspects of Khapra Beetle* Trogoderma granarium. Canberra, Aust.: Plant Quar. Branch
43. Durrant JH. 1921. Insects associated with grain, etc. *R. Soc. Rep. Grain Pests (War) Comm.* 9:33–52
44. Eliopoulos PA. 2013. New approaches for tackling the khapra beetle. *CAB Rev*. 8:012
45. Emery RE, Chami M, Garel N, Kostas E, Hardie DC. 2010. The use of hand-held computers (PDAs) to audit and validate eradication of a post-border detection of khapra beetle, *Trogoderma Granarium*, in Western Australia. In *Proceedings of the 10th International Working Conference on Stored Product Protection*, pp. 1031–37. Quedlinburg, Ger.: Julius-Kühn-Archiv
46. Emery RE, Kostas E, Chami M. 2008. An urban eradication of khapra beetle in Western Australia. In *Proceedings of the 8th International Conference on Controlled Atmosphere and Fumigation in Stored Products*, pp. 694–98. Chengdu, China: Sichuan Publ. Group Sichuan Publ. House Sci. Tech.
47. Eur. Mediterr. Plant Prot. Org. 1981. Data sheets on quarantine organisms. *Bull. OEPP/EPPO Bull.* 11:1–6
48. Eur. Mediterr. Plant Prot. Org. 2013. PM 7/13 (2) *Trogoderma granarium*. *EPPO Bull*. 43:431–48
49. Eur. Mediterr. Plant Prot. Org. 2016. *A2 list of pests recommended for regulation as quarantine pests*. Trogoderma granarium. **https://gd.eppo.int/taxon/TROGGA**
50. Fields PG. 1992. The control of stored product insects and mites with extreme temperatures. *J. Stored Prod. Res.* 28:89–118
51. Fields PG, White NDG. 2002. Alternatives to methyl bromide treatments for stored-product and quarantine insects. *Annu. Rev. Entomol.* 47:331–59
52. Food Agric. Org. U.N. 2016. *DP 3*: Trogoderma granarium *Everts. ISPM 27, Annex 3. Diagnostic Protocols for Regulated Pests*. Rome, Italy: Food Agric. Org. U.N.
53. Ghimire MN, Myers SW, Arthur FH, Phillips TW. 2017. Susceptibility of *Trogoderma granarium* Everts and *Trogoderma inclusum* LeConte (Coleoptera: Dermestidae) to residual contact insecticides. *J. Stored Prod. Res.* 72:75–82
54. Hadaway AB. 1955. The biology of the dermestid beetles, *Trogoderma granarium* Everts and *Trogoderma versicolor* (Creutz). *Bull. Entomol. Res.* 46:781–96

55. **Hagstrum DW, Subramanyam B. 2009. *Stored-Product Insect Resource*. St. Paul, MN: AACC Int.**
56. Hinton HE. 1945. *A Monograph of the Beetles Associated with Stored Products*. London: Brit. Mus.
57. Hole BD, Bell CH, Mills KA, Goodship G. 1976. The toxicity of phosphine to all developmental stages of thirteen species of stored product beetles. *J. Stored Prod. Res.* 12:235–44
58. Howe RW. 1952. Entomological problems of food storage in northern Nigeria. *Bull. Entomol. Res.* 43:111–44
59. Howe RW. 1958. A theoretical evaluation of the potential range and importance of *Trogoderma granarium* Everts in North America. In *Proceedings of the 10th International Congress of Entomology*, pp. 23–28. Ottawa, Can.: Mortimer
60. Howe RW. 1963. The prediction of the status of a pest by means of laboratory experiments. *World Rev. Pest Control* 2:2–12
61. Howe RW. 1965. Losses caused by insects and mites in stored food and feeding stuffs. *Nature* 35:285–93
62. Howe RW, Freeman JA. 1955. Insect infestation of West African produce imported into Britain. *Bull. Entomol. Res.* 46:643
63. **Howe RW, Lindgren DL. 1957. How much can the khapra beetle spread in the USA? *J. Econ. Entomol.* 50:374–75**
64. Hurlock ET. 1961. Persistence of khapra beetle in ship's hold. *Pest Technol.* 3:144–46
65. Hurlock ET. 1962. New efforts at khapra beetle control. *Pest Technol.* 4:150–51
66. Int. Plant Prot. Conv. 2010. *Directory of National Plant Protection Organizations and Regional Plant Protection Organization*. Rome, Italy: Int. Plant Prot. Conv. **https://www.ippc.int/static/media/files/publication/en/2016/11/1264592888_Nppo_directory_2010.pdf**
67. Invas. Species Spec. Group. 2007. *Trogoderma granarium*. Global Invasive Species Database, updated May 31, 2007, retrieved June 25, 2018. **http://www.issg.org/database/species/ecology.asp?si=142&fr=1&sts**
68. Ismail AY, Abid UK, Mawlood NA. 1988. Effect of high temperature on the mortality of the red flour beetle *Tribolium confusum* and khapra beetle *Trogoderma granarium. Zanco* 1:35–42
69. Jood S, Kapoor AC. 1992. Effect of storage and insect infestation on protein and starch digestibility of cereal grains. *Food Chem.* 44:209–12
70. **Jood S, Kapoor AC. 1993. Protein and uric acid contents of cereal grains as affected by insect infestation. *Food Chem.* 46:143–46**
71. Jood S, Kapoor AC. 1994. Vitamin contents of cereal grains as affected by storage and insect infestation. *Plant Foods Hum. Nutr.* 46:237–43
72. Jood S, Kapoor AC, Singh R. 1992. Mineral contents of cereal grains as affected by storage and insect infestation. *J. Stored Prod. Res.* 28:147–51
73. Jood S, Kapoor AC, Singh R. 1993. Available carbohydrates of cereal grains as affected by storage and insect infestation. *Plant Foods Hum. Nutr.* 43:45–54
74. Jood S, Kapoor AC, Singh R. 1993. Biological evaluation of protein quality of sorghum as affected by insect infestation. *Plant Foods Hum. Nutr.* 43:105–14
75. Jood S, Kapoor AC, Singh R. 1996. Chemical composition of cereal grains as affected by storage and insect infestation. *Trop. Agric.* 73:161–64
76. Kantack BH, Staples R. 1969. The biology and ecology of *Trogoderma glabrum* (Herbst) in stored grains. *Res. Bull.* 232:1–24
77. Kapil RP, Chaudhary JP. 1973. Record of nine new hymenopterous parasites for Khapra beetle, *Trogoderma granarium* Everts. *Indian J. Entomol.* 35:353–55
78. Karnavar GK. 1972. Mating behaviour and fecundity in *Trogoderma granarium* (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 8:65–69
79. Kavallieratos NG, Athanassiou CG, Arthur FH. 2015. Efficacy of deltamethrin against stored-product beetles at short exposure intervals or on a partially treated rice mass. *J. Econ. Entomol.* 108:1416–21
80. Kavallieratos NG, Athanassiou CG, Barda MS, Boukouvala MC. 2016. Efficacy of five insecticides for the control of *Trogoderma granarium* Everts (Coleoptera: Dermestidae) larvae on concrete. *J. Stored Prod. Res.* 66:18–24

55. This work contains a full list of the commodities that have been found infested by the khapra beetle.

63. This article provides a historical overview on the potentials of establishment and spread of the khapra beetle in the United States.

70. This study reports some key changes in quality of commodities that are infested by the khapra beetle.

81. Under suitable conditions, the khapra beetle can compete easily with other major stored-product beetle species.

96. This chapter contains a thorough list of information on the recent interceptions of the khapra beetle in US entry ports.

101. This article presents the method for the molecular identification of the khapra beetle.

102. This study provides predictions of potential interceptions, containment, and spread of the khapra beetle in Australia based on patterns of movement of shipping containers.

81. Kavallieratos NG, Athanassiou CG, Boukouvala MC. 2017. Invader competition with local competitors: displacement or coexistence among the invasive khapra beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae), and two other major stored-grain beetles? *Front. Plant Sci.* 8:1837

82. Kavallieratos NG, Athanassiou CG, Diamantis GC, Gioukari HG, Boukouvala MC. 2017. Evaluation of six insecticides against adults and larvae of *Trogoderma granarium* Everts (Coleoptera: Dermestidae) on wheat, barley, maize and rough rice. *J. Stored Prod. Res.* 71:81–92

83. Khashaveh A, Safaralizadeh MH, Ghosta Y. 2011. Pathogenicity of Iranian isolates of *Metarhizium anisopliae* (Metschinkoff) (Ascomycota: Hypocreales) against *Trogoderma granarium* Everts (Coleoptera: Dermestidae). *Biharean Biol.* 5:51–55

84. Kumar M, Srivastava C, Garg A. 2010. In vitro selection of deltamethrin resistant strain of *Trogoderma granarium* and its susceptibility to insecticides. *Ann. Plant Prot. Sci.* 18:26–30

85. Lindgren DL, Vincent LE. 1959. Biology and control of *Tragoderma granarium* Everts. *J. Econ. Entomol.* 52:312–19

86. Lindgren DL, Vincent LE. 1970. Effect of atmospheric gases alone or in combination on the mortality of granary and rice weevils. *J. Econ. Entomol.* 63:19–26

87. Lindgren DL, Vincent LE, Krohne HE. 1955. The khapra beetle, *Trogoderma granarium* Everts. *Hilgardia* 24:1–36

88. Lindgren DL, Vincent LE, Strong RG. 1958. Studies on hydrogen phosphide as a fumigant. *J. Econ. Entomol.* 51:900–3

89. Lowe S, Browne M, Boudjelas S, De Poorter M. 2000. *100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database*. Auckland, NZ: Invasive Species Spec. Group, World Conserv. Union, Int. Union Conserv. Nat. **http://www.issg.org/pdf/publications/worst_100/english_100_worst.pdf**

90. Mahmood T, Ahmad MS, Ahmad H. 1996. Dispersion of stored grain insect pests in a wheat-filled silo. *Int. J. Pest Manag.* 42:321–24

91. Mason FA. 1921. The destruction of stored grain by *Trogoderma khapra*, Arrow. A new pest in Great Britain. *Bur. Bio-Technol. Leeds Bul.* 2:27–38

92. Mason LJ, McDonough M. 2012. Biology, behavior and ecology of stored grain and legume insects. In *Stored Product Protection*, ed. DH Hagstrum, TW Philips, G Cuperus, pp. 7–20. Manhattan, KS: Kansas State Univ.

93. Mathlein R. 1961. Studies on some major storage pests in Sweden, with special reference to their cold resistance. *Medd. Växtskyddsanst. Stockh.* 12(83):1–49

94. Morison GD. 1925. The khapra beetle (*Trogoderma granarium* Everts). *Proc. R. Phys. Soc. Edinb.* 21:10–13

95. Munro JW. 1940. *Report on a Survey of the Infestation of Grain by Insects*. London: HMSO

96. Myers SW, Hagstrum DH. 2012. Quarantine. In *Stored Product Protection*, ed. DH Hagstrum, TW Philips, G Cuperus, pp. 297–304. Manhattan, KS: Kansas State Univ.

97. Nair KSS, Desai AK. 1973. The termination of diapause in *Trogoderma granarium* Everts (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 8:275–90

98. Nakayama S. 1932. On the ecology, and especially the moults, of *Trogoderma granarium* Everts. *Jpn. Soc. Appl. Zool.* 4(3):150

99. Navarro S, Finkelman S, Sabio G, Isikber A, Dias R, Rindner M, Azrieli A. 2002. Quarantine treatment of storage insect pests under vacuum or CO_2 in transportable systems. In *Proceedings of International Conference on Alternatives to Methyl Bromide: The Remaining Challenges*, ed. T Batchelor, J Bolivar, pp. 375–79. Brussels, Belg.: Eur. Comm.

100. Odeyemi OO, Hassan AT. 1993. Influence of temperature, humidity and photoperiod on oviposition and larval development in *Trogoderma*. *Appl. Entomol. Zool.* 28(3):275–81

101. Olson RLO, Farris RE, Barr NB, Cognato AI. 2014. Molecular identification of *Trogoderma granarium* (Coleoptera: Dermestidae) using the 16s gene. *J. Pest Sci.* 87:701–10

102. Paini DR, Yemshanov D. 2012. Modelling the arrival of invasive organisms via the international marine shipping network: a khapra beetle study. *PLOS ONE* 7(9):e44589

103. Pasek JE. 1998. Khapra Beetle (*Trogoderma granarium Everts*): Pest-Initiated Pest Risk Assessment. Raleigh, NC: USDA-APHIS

104. Phillips TW, Throne JE. 2010. Biorational approaches to managing stored product insects. *Annu. Rev. Entomol.* 55:375–97
105. Pingale SV, Rao NM, Swaminathan M. 1954. Effect of insect infestation on stored grains. Studies on soft wheat. *J. Sci. Food Agric.* 5:51–54
106. Pretheep Kumar P, Mohan S, Balasubramanian P. 2010. *Insecticide Resistance—Stored-Product Insects: Mechanism and Management Strategies*. Saarbrücken, Ger.: Lambert Acad. Publ.
107. Punj GK. 1968. Dietary efficiency of natural foods for the growth and development of *Trogoderma granarium* Everts. *Bull. Grain Tech.* 6:138–42
108. Rahman KA. 1942. Insect pests of stored grain in the Punjab and their control. *Ind. J. Agric. Sci.* 12:564–87
109. Rahman KA, Sohi GS, Sapra AN. 1945. Studies on stored grain pests in the Punjab. VI. Biology of *Trogoderma granarium* Everts. *Ind. J. Agric. Sci.* 15:85–92
110. Rahman MM, Islam W, Ahmad KN. 2009. Functional response of the predator *Xylocoris flavipes* to three stored product insect pests. *Int. J. Agric. Biol.* 11:316–20
111. Rajput SA, Khanzad MS, Abro GH, Khanzada SR, Syed TS, Su W. 2015. Comparative population growth and losses cause by beetle *Trogoderama granarium* (Everts) to selected past and present wheat genotypes. *Int. J. Agron. Agric. Res.* 6:66–77
112. Rao NS, Sharma K, Samyal A, Tomar SMS. 2004. Wheat grain variability to infestation by khapra beetle, *Trogoderma granarium* Everts. *Ann. Plant Prot. Sci.* 12:288–91
113. Salunkhe DK, Chavan JK, Kadam SS. 1985. *Postharvest Biotechnology of Cereals*. Boca Rato, FL: CRC Press
114. Scholtz CH, Holm E. 1985. *Insects of Southern Africa*. Durban, S. Afr.: Butterworths
115. Sinclair BJ, Ferguson LV, Salehipour-Shirazi G, MacMillan HA. 2013. Cross-tolerance and cross-talk in the cold: relating low temperatures to desiccation and immune stress in insects. *Integr. Comp. Biol.* 53:545–56
116. Sinha RN, Utida S. 1967. Climatic areas potentially vulnerable to stored product insects in Japan. *Appl. Entomol. Zool.* 2:124–32
117. Sohi GS. 1947. Studies on stored grain pests in the Punjab. VIII. Effect of constant light and darkness on the development and reproduction of and amount of food consumed by *T. granarium* Everts. *Indian J. Entomol.* 9:143–47
118. Solomon ME, Adamson BE. 1955. The powers of survival of storage and domestic pests under winter conditions in Britain. *Bull. Entomol. Res.* 46:311–55
119. Spratt E, Dignan G, Banks HJ. 1985. The effects of high concentrations of carbon dioxide in air on *Trogoderma granarium* everts (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 21:41–46
120. Stanaway MA, Zalucki MP, Gillespie PS, Rodriguez CM, Maynard GV. 2001. Pest risk assessment of insects in sea cargo containers. *Aust. J. Entomol.* 40:180–92
121. Stibick JNL. 2007. *New Pest Response Guidelines: Khapra Beetle*. Riverdale, MD: USDA–APHIS–PPQ Emerg. Domest. Progr. **https://www.aphis.usda.gov/import_export/plants/manuals/emergency/downloads/nprg-khapra.pdf**
122. Stuart MK, Barak AV, Burkholder WE. 1994. Immunological identification of *Trogoderma granarium* Everts (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 30:9–16
123. US Dep. Agric. 2012. *Treatment Manual*. Washington, DC: US Dep. Agric. **http://www.aphis.usda.gov/import_export/plants/manuals/ports/downloads/treatment.pdf**
124. US Dep. Agric. 2016. *Plant Protection and Quarantine Treatment Manual*. Washington, DC: US Dep. Agric.
125. Voelkel H. 1924. Zur biologie und bekampfung des khaprakafers, *Trogoderma granarium* Everts. *Arb. Bio. Reichanst.* 13:129–71
126. **Wilches Correal DM. 2016. *Effects of extreme temperatures on the survival of the quarantine stored-product pest*, Trogoderma granarium *(Khapra Beetle) and on its associated bacteria*. Master's Thesis, Univ. Lethbridge, Lethbridge, Can.**
127. Wilches DM, Laird RA, Floate KD, Fields PG. 2016. A review of diapause and tolerance to extreme temperatures in dermestids (Coleoptera). *J. Stored Prod. Res.*68:50–62

126. This study demonstrates that the khapra beetle is simultaneously heat and cold tolerant, especially in its larval stage.

128. Wilches DM, Laird RA, Floate KD, Fields PG. 2017. Effects of acclimation and diapause on the cold tolerance of *Trogoderma granarium*. *Entomol. Exp. Appl*. 165:169–78
129. Yadav TD. 1987. Current status of conventional insecticides in stored product insect management in India. *Recent Adv. Res. Trop. Entomol.* 8:703–7
130. Zacher F. 1938. Verschleppung und einburgerung von vorratsschladingen. In *VII. Internationaler Kongress für Entomologie*, pp. 2919–26. Berlin: Friedrich-Wilhelms-Univ.

Annual Review of Entomology

Volume 64, 2019

Contents

Indexes

Errata

An online log of corrections to *Annual Review of Entomology* articles may be found at http://www.annualreviews.org/errata/ento