Population dynamics of *Tribolium castaneum* (Herbst) in wheat and wheat mixed with cracked wheat held in different types of containers

by

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ABSTRACT

The population dynamics of *Tribolium castaneum* (Herbst), red flour beetle, was studied at 30°C using long vertical columns (LVCs) (150 mm diameter and 1020 mm long) and shallow containers (SCs) (460 mm long, 660 mm wide, and 150 mm high), containing 14 kg of whole wheat or a diet made of whole wheat and cracked wheat in 19:1 ratio by mass. The moisture content of the wheat or mixed diet was 14.5% (wb). Every 4 weeks and up to 24 weeks the live and dead adults were counted in the SCs or in each section of the LVCs. Each LVC was separated into ten equal sections before removing grain from the LVC. After counting, the grains were incubated at 30°C and 70% RH for 4 wk, and emerged adults after re-incubation were counted as offspring. The adults and offspring were mainly concentrated in the top section of the LVCs, which could be due to higher mortality in the lower sections and the preference of *T. castaneum* for the surface of grain bulk. The diet influenced the population, and the insects developed better in the cracked wheat-based diet. The greater surface area of the container increased the multiplication and/ or survival of *T. castaneum.* Insects inside SCs with larger surface area and with cracked wheat-based diet, had a quicker population increase rate and larger carrying capacity than LVCs.

Keywords: *Tribolium castaneum*, red flour beetle, population dynamics, container type, diet, long vertical container, shallow container

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LIST OF ABBREVIATIONS AND SYMBOLS

LVC	Long vertical column
SC	Shallow container
SCW	Shallow container – wheat
LVC_{top}	Long vertical column – top section
SCC	Shallow container – modified diet
RH	Relative humidity (%)
SWBT	Seed wet bulb temperature (℃)
FOXO	Forkhead box O transcription factor
CWRS	Canada western red spring
PVC	Polyvinyl chloride
ASABE	American Society of Agricultural and Biological Engineers

1. INTRODUCTION

Almost one-third of the global food production is lost every year during various pre-harvest and post harvest operations, and about 10-20% of the losses accounts for food grain losses during storage (Mesterházy et al. 2020). Although the well managed storage facilities and their proper management ensures minimal (1 – 2% of production) storage losses in developed nations, the developing nations experience high levels of storage losses (20 – 50% of their production) in food grains, solely due to poorly managed storage systems (Jayas 2012).

Population dynamics studies the size and age composition of populations over time, considering various biological and environmental factors and processes causing population changes. Controlling stored-grain insects requires understanding of the insect population dynamics, as it enables their accurate prediction, insect development time estimation, and understanding the variation of individuals of each life-stage and species with respect to changing environmental conditions (Jian et al. 2018a). *Tribolium castaneum* (Herbst), red flour beetle, a secondary feeder in nature, is regarded as a ubiquitous and serious pest in stored products, owing to their cosmopolitan distribution and rapid multiplication. Their synanthropic nature, smaller size and shorter life cycle make them excellent subjects for population ecology studies (Pai 2019). Numerous studies have reported the influence of major factors on their population dynamics including grain temperature (Arthur et al. 2019b; Halliday et al. 2015; Scharf et al. 2015a), moisture content (Dars et al. 2001), climatic variability (Tripathi et al. 2021), insect density (Dukić et al. 2016), quality and quantity of food (Rustamani and Khatri 2014; Longstaff 1995), and intraspecies and interspecies interactions (Bullock et al. 2020; Hulasare et al. 2003; Goodnight and Craig 1996). Further, in recent years, emphasis has been given to larger patch size studies, thus ideally representing grain storage structures as opposed to smaller scale studies (Tripathi et al. 2021; Jian et al. 2018b). However, these studies assumed a uniform distribution of insects inside the resource patches, irrespective of the size and surface area of the patch.

Assuming a uniform distribution of *T. castaneum* inside large patches could underestimate the peak densities inside larger patches and might give an inaccurate relationship between their density and population dynamics. Infestations of *T. castaneum* are usually localized to certain locations (grain surface and edges of storage structures), due to their inactive nature (Campbell and Hagstrum 2002), movement barriers (Jian et al. 2005), aggregation due to volatiles (Jian et al. 2012), and variable goals of patch exploitation (Campbell and Hagstrum 2002). Further, the greater proportion of insects in the top grain bulks under favourable temperatures could imply that increased top surface area might have some effect on its population dynamics. A larger top surface area could be associated with relative ease in finding food and mating partners. However, it might also result in photonegative behaviour from increased exposure area to light, and complex intraspecies interactions including cannibalism and predation at high population densities. No attempts have been made to understand the population dynamics of *T. castaneum* relative to the variability of distribution and effects of top surface area on their population dynamics. Such studies are crucial for determining the probability and persistence of insect populations in grain storage structures, and designing storage structures that could limit the population growth.

The diet consumed by an insect is the key determinant for its population dynamics as it influences its development, survival, and reproduction (Skourti et al. 2020). *Tribolium castaneum* is a secondary feeder that requires a certain degree of damaged grains, with a preference for an embryo of grain and flour. Several researchers have reported the variations in digestive activity, life history, and physiology with different diets for *T. castaneum* (Naseri et al. 2017; Fabres et al.

2014; Sagheer et al. 2014). However, population dynamics studies done on *T. castaneum* in larger patches (e.g., more than a few kilograms) are limited to whole grains as diet material (Tripathi et al. 2021; Atta et al. 2020), which might have some limiting effects as *T. castaneum* is a secondary feeder. Although the effect of damaged grains and various dietary commodities on the population parameters including fecundity, development, survival and population increase of *T. castaneum* have been previously studied (Astuti et al. 2020; Dukić et al. 2016; Shafique et al. 2006; Li and Arbogast 1991;), these studies were conducted using small quantities (patch size was < 1 kg). Such small-scale studies do not ideally represent grain storage structures with residual grains, damaged grains, broken fractions, and flour dust which make excellent breeding grounds for *T. castaneum* and provide only limited information on their development and persistence in grain storage structures.

In this study the population dynamics of *T. castaneum* was studied to determine the insect density distributions in 14 kg wheat patches. Attempts were made to understand the effects of the top surface area of patches and a modified diet on their population dynamics.

2. LITERATURE REVIEW

2.1 Stored grain losses due to insects

About one-third of global food production (about 1.3 billion tonnes), which is worth US$ 1 trillion, is lost during postharvest operations every year (Gustavsson et al. 2011). Post-harvest losses can occur at multiple stages in the food supply chain, with the storage stage causing the maximum losses (Majumder et al. 2016; Aulakh et al. 2013; Bala et al. 2010). Storage losses in cereal grains include both quantitative (mass) and qualitative (nutrient and aesthetic) losses, which are governed by various biotic (insects, rodents, fungi and other pests) and abiotic factors (temperature and grain moisture content) (Abedin et al. 2012), and insect infestation is one of the major sources of the loss. Insects are the most economically significant storage pests, due to the difficulty in controlling them because of their smaller size, feeding behaviour, and ability to infest grains even before harvest. Globally, 5% of stored grain is destroyed by insects (Tipples 1995). The quantitative and qualitative damage to stored grains by insects are estimated to be around 20 – 30% in the tropical regions, and 5 – 10% in the temperate regions (Rajendran and Sriranjini 2008). Canada is the sixth largest producer (35 million tonnes (Mt) annually), and third largest exporter (23.5 Mt annually) of wheat in the world, and experiences significant losses due to stored grain insects and associated spoilage (Statistics Canada 2023; United States Department of Agriculture 2023; Canadian Grain Commission 2022; Singh et al. 2009).

Stored grain damage by insects can typically take place in the form of direct consumption of kernels, filth generation, unpleasant odour generation, webbing, depreciating the weight and quality of grains, and making them unfit for human consumption (Lal et al. 2017; Rayhan et al. 2014). Insects also reduce seed viability and germination by damaging the seed embryos (Padín et al. 2002). Further, they exploit the storage ecosystem and produce heat and water which are favourable for the growth and multiplication of harmful microflora such as fungi. Their activities increase the risk of fungal attack, mycotoxin contamination, and excess pesticide residues. The increasing awareness among consumers for clean and safe foods has led to the setting of stringent quality standards by most countries. The presence of two live insects in 1000 g of wheat, rye, or triticale grades the grain as "infested", according to the U.S. grain standards (Zayas and Flinn 1998). The Canadian grain regulations have legally defined zero tolerance for stored-food grain insects (Canada Grain Act 1975). Nevertheless, instances of infestations in farms, primary, and terminal elevators have been reported (Smith 1985). *Tribolium castaneum* is one of the most common storage insects in Western Canada and infested 30% of bins in a survey conducted across Manitoba (Madrid et al. 1990). They could considerably damage kernels and reduce germination percentage in stored wheat and reduce the baking qualities of wheat flour (Edwards et al. 1991). Infestation by *T. castaneum* on wheat grains reduces mass by about 9% in three months at 35 - 37°C, when the initial density was 0.16 insects per g of grains (Haq et al. 2005).

2.2 Common stored grain insect pests - classification

About 600 insect species are reported worldwide in stored products, out of which beetles are majorly responsible for considerable grain loss (Hill 1990). Their omnipresence could be attributed to their evolutionary adaptations (morphological, physiological, and behavioural) and human activities that transport insects from different parts of the globe to grain storage ecosystems (Ross et al. 2009). Stored grain insects are generally found within or moving within the bulk grain, processing equipment, storage structures or buildings, or other resource patches. They can live at temperatures ranging from 8 to 41°C, and inter-granular relative humidities (RH) from 1 – 99%, with the optimum ranges of temperature and RH near 30°C, and 50 – 70%, respectively (Jayas and

White 2003). Some of the major insect pests that damage stored grains include rusty grain beetle (*Cryptolestes ferrugineus* (Stephens)), red flour beetle (*Tribolium castaneum* (Herbst)), lesser grain borer (*Rhyzopertha dominica* (Fabricius)), granary weevil (*Sitophilus granarius* (Linnaeus)), and confused flour beetle (*Tribolium confusum* Jacquelin du Val). Among the major stored grain insects, *C. ferrugineus* and *T. castaneum* are regarded as the principal granivores of Western Canada. They both belong to the order Coleoptera, and are known to produce more diversified and destructive effects, in grain as both immatures and adults are capable of damage, as compared to the Lepidoptera (moths) (Upadhyay and Ahmad 2011). *Tribolium castaneum* has a higher energy consumption than *C. ferrugineus*, of about 3358 J per insect at 30°C and 70% RH, and causes more damage to stored wheat (Karunakaran et al. 2004; White 1995). Further, their cosmopolitan distribution, rapid multiplication, natural tolerance to insecticides and ability of adults and larvae to produce economic damage to a wide range of raw and processed commodities (Dal Bello et al. 2018; Skourti et al. 2019), make them the most common insect pest of stored grains, oilseeds, and food-processing facilities worldwide. Moreover, the adults of *T. castaneum* are noxious as they release toxic benzoquinones (Skourti et al. 2022), and can cause several health complications including jaundice, anaemia, and allergic skin reactions in humans (Krinsky 2019; Negi et al. 2021).

Storage pests are usually classified based on their feed and livelihood (Rees 2007), e.g., commodity feeders, fungal feeders, predators, parasitoids, and scavengers. Stored grain insect species can be also categorized on their feeding behaviour as internal and external feeders. Internal feeders are those insects that feed within the kernels, including rice weevil (*Sitophilus oryzae* (Linnaeus)), maize weevil (*Sitophilus zeamais* (Motschulsky)), lesser grain borer (*Rhyzopertha dominica* (Fabricius)), and angoumois grain moth (*Sitotroga cerealella* (Olivier)). They lay eggs on the inside or surface of grains, thus spending a part or entire larval and pupal life inside grains and emerge as adults. They cause a significant reduction in germination, which is not detectable outside (Srivastava and Subramanian 2016). They also cause physical damage to the seed and are often regarded as the most serious stored-wheat pests (Hernandez Nopsa et al. 2015). External feeders feed on the surface of grains and their products externally. Their larvae typically feed on broken grain (damaged mechanically or by other insects' infestation), grain dust, flour, and fungi. Examples of external feeders include the red flour beetle (*Tribolium castaneum*) and rusty grain beetle (*Cryptolestes ferrugineus*). The geographical distribution of stored grain insects is related to the evolutionary history and climate of the region. The global distribution of stored grain insects is also related to the dispersal and migration of these insects. Dispersal is the natural spread of part of a population away from its source at a time of high population density and it is often in response to dwindling food supply, or as a behavioural quirk coinciding with weather conditions. Migration is a larger scale movement of insect populations controlled by prevailing winds and is prominent phenomenon in the colder regions of the world. The regions most impacted by pest migrations include Canada, Japan, and North China. For instance, in Canada since large number of insects cannot survive the cold winter, they arrive in early summer from USA, breed during Canadian summer and die later in the fall after the temperature drop (Hill 1987). The tropics are characterized by little migration due to the suitability of the climate. The mechanisms of dispersal and migration coupled with the evolutionary history and climatic conditions, could explain the differences in distribution of stored grain insects across the globe. Nevertheless, the majority of stored grain insects have a cosmopolitan distribution, which could be majorly attributed to the international trade and commerce of food grains (Naveena et al. 2015). For instance, Sinha and Watters (1985) reported that about 85% of 105 stored grain insects listed have cosmopolitan distribution due to the movement of food grains across continents.

2.3 Population dynamics of stored grain insects

Population dynamics is the study of the size and age composition of populations as dynamic systems, considering various biological and environmental factors and processes causing population changes over time. Population dynamics enables the estimation of insect development time and variation of individuals of each life stage and species under varying environmental conditions (Jian et al. 2018a). Further, population dynamic studies help develop alternative pest management tools including biological control, natural chemical control, and genetic control as a lack of information on pest populations may hamper the development of these management tools (Campbell and Arbogast 2004). Understanding the population dynamics and the factors influencing them will thereby help properly manage the stored-grain insects, without much reliance on insecticides and pesticides that are associated with the risk of contaminating the food grains and the environment. The factors influencing the population dynamics of stored grain insects include various physical, insect and resource parameters encompassing insect species and developmental stage, time, temperature, moisture content of food grains, amount and quality of food, oviposition sites, insect density, number of mated females, patch size, interspecies interactions, age, and diseases. The sections below detail how the above-mentioned factors influence the population of various stored grain insects.

2.3.1 Insect species/ stages

Different insect species in the stored grain ecosystem vary greatly in their activity periods, damaging potential, biology, behavior, temperatures, longevity, moisture requirements and reproductive potential. The biology, life history traits, behavior and ecology of various stored grain insect species are extensively reported in literature (Edde 2012; Mason and McDonough 2011; Imura 1989). Also, different insect types contribute to population fluctuations and species succession through their complex interactions among their roles as fungivores, granivores, predators, or parasites (Wallace and Sinha 1981; Sinha 1973). Each storage insect species and its different life stages exhibit different damaging potentials on stored grains based on their energy budget. For example, *S. granarius* can remove the maximum gross energy from food grains, *O. surinamensis* assimilates food energy most efficiently, *R. dominica* is the most wasteful feeder, and *T. castaneum* is the most adaptive and prolific (Sinha 1982). Further, in a stored grain ecosystem, for a certain time a given insect species has an unlimited supply of developmental substrate and no natural enemies. The suitability of the environmental conditions determines the insect population trends. Different insect types respond to physical environmental factors in different ways. For example, in a study involving five major storage insects (*R. dominica*, *T. castaneum*, *C. ferrugineus*, *S. oryzae*, *O. surinamensis*) it has been found that different species grew at different rates in response to temperature and moisture conditions during storage (Hagstrum and Flinn 1990). Likewise, different species exhibit variable cold susceptibility depending on their behavioral, physiological, and biochemical adaptations to cold (Fields 2001). Similarly, stored grain insects have variable tolerance levels to the modified atmosphere, in terms of O_2 and CO_2 concentrations, where species including *R. dominica*, *S. granarius*, are most tolerant (could withstand <1% O_2 and 60 – 80% CO_2 in air for 3 – 5 weeks) and species including *P. interpunctella*, *S. cerealella*, *Oryzaephilus* spp., and *Ephestia* spp. are the least tolerant (could withstand <1% O_2 and 60 – 80% CO_2 in air for 1 – 5 d (Annis 1987; Bell 2014). Certain behavior attributes that influence population, include flight, mating, oviposition, hatching of eggs, larval development rates, foraging, pupation, and adult eclosion, which are based on the diurnal variations and temperatures (Bell 2014), and vary with species. For instance, oviposition in species including *E. elutella* (Bell 1981), *E. kuehniella* (Bell 1981), *R. dominica* (Aslam et al. 1994) and *O. surinamensis* (Bell and Kerslake 1986) is stimulated by the daily onset of darkness, whereas for species like *P. interpunctella* it is influenced by both light and temperature (Lovitt and Soderstrom 1973).

Similarly, different life stages exhibit variable levels of tolerance to changes in ambient conditions. For example, various stored product insects exhibit stage-specific susceptibility to elevated temperatures; the younger larvae (for *T. castaneum*, *S. paniceum*) (Hulasare et al. 2010; Mahroof et al. 2003), the older larvae (*P. interpunctella*, *T. confusum*) (Mahroof and Subramanyam 2006; Boina and Subramanyam 2004) and the egg stages (for *L. serricorne*) (Yu et al. 2011) are considered most heat tolerant stages among various species. Susceptibility to cold temperatures is also affected by the developmental stage. Likewise, for increasing levels of CO_2, larval stage exhibits least tolerance in *O. surinamensis*, whereas adult stage is the least tolerant for *Lasioderma serricorne* and *Stegobium paniceum* (Moses et al. 2015). Understanding the tolerance levels of each species and insect stage to various abiotic stresses, is crucial for use in bioassays and devising strategies that completely control infestations.

Therefore, insect species/ stage is the first major factor influencing population dynamics, owing to their variations in damaging potential, activity periods, behavior, biology, optimum growth conditions, biological interactions, responses to fluctuating ambient conditions, and adaptation strategies.

2.3.2 Temperature

Stored grain insects are ectotherms whose internal temperature fluctuate with the environment's temperature The optimal temperature maximizes the metabolic rate, growth rate, locomotion, and reproduction, improving growth, and survival. The temperature influences the population dynamics of stored grain insects through its impact on development time, fecundity, survival, movement, and spatial distribution (Arthur et al. 2019b; Mason and McDonough 2011; Jian et al. 2002a; Flinn and Hagstrum 1998).

In general, the lower development threshold for the majority of stored grain insects is approximately 18℃ (Howe 1965). The optimum temperature for growth and development for most stored grain insects is approximately 25 – 35℃, whereas 18 – 25℃ or 33 – 35℃ enables complete development and offspring production (Fields 1992). In a study by Tripathi et al. (2021) it was reported that increasing temperatures (from 26 to 34℃) significantly increased the offspring number and increased peak adult densities. Similar results were reported by Eastham and McCully (1943) on weevils where increasing temperatures (20 – 27.5℃) resulted in higher oviposition rates. The population increase at higher temperatures, within the optimum range, could be attributed to the increased rate of metabolism, reproductive potential, rapid egg production and higher relative humidity associated with higher temperatures. With higher relative humidity, there is a reduction in water loss through the insect cuticles thus resulting in higher survival rates (Salin et al. 1999). Further, the combined effects of higher temperature and relative humidity make the grains softer causing insects to consume more food and increase their population and density (Jian et al. 2018b; Throne 1991). Higher temperature and relative humidity also result in mould growth, which is advantageous for mould-consuming species like *C. ferrugineus* (Sinha 1965).

Temperatures less than 13°C or greater than 35°C, will halt the development of most insects and cause eventual death. It has been reported that lowering the grain temperatures from 20 to 14°C enables slower population growth and reduces the fitness of most stored grain insects, and temperatures below 14°C can result in the death of insect species, particularly in immature stages (Banks and Fields 1994). The delayed development could be due to a reduction in water activity and relative humidity at lower temperatures (Ziegler et al. 2016). However, insects could get acclimated to colder temperatures when exposed to gradually declining temperatures, which increases their chance of survival by 2-10 times (Fields 1992). The cold acclimation of insects could be prevented through rapid cooling of commodities, in the application of low temperatures for insect control. Control strategies involving ice nucleating bacteria, a potent nucleator (either ingested by storage insects or exposure), could raise the freezing point, and reduce the cold hardiness of insects including *C. ferrugineus* and other beetle species (Lee et al. 1992; Fields 1991). Similarly, exposure to high temperatures of about 5°C above the optimum temperature for population will halt the development of insects and cause eventual death. The temperature, duration of exposure, species, stage of development, acclimation, and relative humidity could determine the survival of insects at higher temperatures and the majority of species will not survive > 24 h at 40°C, 12 h at 45°C, and 5 min at 50°C (Fields 1992). It is reported that for each temperature there is a cumulative period of thermal stress and after the critical exposure time, an additional few minutes or hours at that temperature will result in the killing of all the adults (Jian et al. 2002b). However, grain storage ecosystems are exposed to fluctuating temperature conditions naturally, resulting in the acclimation of insects to these temperatures and thus impacting their survivorship. Physiological acclimation or heat hardening can improve the survival of insects at temperature of 40 – 50°C, and the survival varies among different developmental stages of insects.

Acclimation strategies could be in the form of expression of heat shock proteins and sorbitol (protects insects from heat shock), and biogenic amines. However, they offer thermal protection but could also result in reproductive impairment. For instance, in *T. castaneum,* the expression of the Hsp83 gene at 40℃ for 1 h offers protection from heat stress. Hsp83 is also involved in oogenesis during ovarian maturation; the increased expression of Hsp83 under heat stress, could also imply that relatively lower expression in the ovary resulting in slower ovarian development (Xu et al. 2010). Therefore, it can be concluded that acclimation involves both resource allocation trade-offs and costly behavioral avoidance mechanisms demanding time and resources, thereby compromising development, and reproduction (González-Tokman et al. 2020). Knowledge of mechanisms underlying cold and heat acclimation in stored grain insects, and methods to block them is crucial since it would help synergize the control strategies under extreme temperature conditions. Synergistical approach could greatly increase the stress response and result in higher mortality rates (Kim et al. 2015).

The objective of thermal control methods for controlling stored grain insect populations is to bring grain temperature at levels where the finite rate of increase of population is reduced to zero (Evans 1982). The rate of insect population growth in a stored grain bulk is strongly influenced by both the grain temperature and moisture content (Desmarchelier 1988). Low temperature aeration could sufficiently kill the insects in temperate regions (like Canada and Europe) characterized by sufficiently low ambient temperatures during winter months. However, in the warmer regions (Australia, parts of the United States, Spain, Italy, China, India, the Middle East, Northern and Southern Africa, parts of South America), characterized by large daily temperature variations (low temperature at night, warm temperature at day), aeration to cool down the grains to a lower dry bulb temperature than the ambient dry bulb temperature, would incur high running costs. Under such situations, considering the threshold grain or seed wet bulb temperature, that maintains the insect population growth rate at zero, would help determine the corresponding moisture content and seed dry bulb temperature for aeration (Wilson and Desmarchelier 1994). Seed wet bulb temperature (SWBT) refers to the wet bulb temperature of intergranular air and there exists a correlation between the SWBT and the population growth rate of major stored grain insects, due to the influence of microclimate of interstitial air upon the rate of population growth. The threshold SWBT for the major stored grain insects have been reported by Wilson and Desmarchelier (1994). The dry bulb temperatures, corresponding to SWBT are very close to ambient temperatures when the grains are harvested in warmer conditions (low moisture content). The advantages of using SWBT in warmer climates include ease of aeration when the system needs to cool the grain from warm harvest temperature to a dry bulb temperature that is closer to ambient temperature, minimization of grain rewarming when aeration is stopped and limited moisture migration as there is only a small temperature difference between the interior of grain bulk and mean ambient temperature (Wilson and Desmarchelier 1994). It is also worth noting that the SWBT and seed dry bulb temperature is very close to wet seed, and therefore using dry bulb temperature to control insects at cool climates is effectively the same as using SWBT control. Hence, maintaining the grain mass at the target wet bulb temperature by adopting the optimum aeration strategy would therefore ensure population increase is zero, until the temperature or moisture content increases (Banks and Fields 1994). Further, using SWBT models could help determine the effect of different aeration conditions on the intrinsic growth rate and population increase of diverse insect species (Ranjbaran and Emadi 2015).

2.3.3 Time

Stored product insect populations are significantly influenced by the storage period (Gnonlonfin et al. 2008) because their development and multiplication under environmental conditions need time. The general trend of stored grain insect population with respect to time is characterized by an initial population stasis, followed by a period of continual increase till reaching peak density and then fall over time. The initial stasis period of a species is generally determined by its developmental time under the given environmental condition. The initial stasis periods of various stored grain insects were reported in the literature, and were 30 to 33 days for *C. ferrugineus,* and 35 to 38 days for *T. castaneum* (Hagstrum and Throne 1989). Following the period of continual increase which is attributed to the high quality and quantity of food and reduced competition (Smith 1966). Insects in a stored grain ecosystem (bulk storage) are assumed to grow exponentially as they initially have unlimited food resources, and therefore lack density dependence (Aspaly et al. 2007) because they can migrate to other locations. The exponential growth trend with continuous breeding could be explained using the equation:

$$N_t / N_0 = e^{rt} \qquad (1)$$

Where N_t represents the population number at time t, N_0 presents the initial population number, t is the time period, and r is the innate or intrinsic increase rate. Many authors have determined the innate rate of increase of a population in an unlimited environment and under constant conditions. The population growth rate or net rate of reproduction of various storage insects, at any given temperature and relative humidity can be hence estimated from equation 1.

One possible trend after the continuous increase, is fall in insect number or density giving a peak number or density. This reduction in growth rate after attainment of peak density could be possibly due to the decline of possible niches with time, increasing competition, starvation, cannibalism, depleted resources, increased time for searching for food, and reduced fecundity and longevity. However, there are instances where the insect does not attain peak density due to unfavorable ambient conditions (temperature). Whether the population continually increase or attains a peak density over time is related to various patch (quality and quantity of food, temperature, grain moisture content, relative humidity, volume) and insect attributes (rate of growth, number of eggs laid, adult longevity, insect movement, competition, accumulation of waste substances) (Jian et al. 2018b). For example, small habitat patches (< 50 g grains) reach peak density faster than large patches (14 kg) for *C. ferrugineus* and *T. castaneum* (Tripathi et al. 2021). Nevertheless, in a grain bin insect populations rarely attain their peak density due to unlimited resources, movement and emigration, and temperature fluctuations (Jian et al. 2018b). For example, in commercial grain elevators in Kansas, USA, less than 20% of bins contained economically significant insect densities (> 2 insects/ kg) (Flinn et al. 2010). In those bins, with insect densities >2 insects/ kg, often due to migration of insects from heavily infested moved to adjacent bins.

2.3.4 Moisture content

The stored-grain insect pests depend on their food supply for water intake. The general observation is that up to a certain level the rate of development of stored grain insects increases with the increase in the moisture content of the food grains, by favouring insect activity and reproduction. The most favorable grain moisture ranges from 12-15% for insect development (Upadhyay and Ahmad 2011).

It has been reported that moisture content has a greater impact on population growth than temperature, with increasing moisture from 10 to 14% at 32℃ resulting in increased population growth by 20 times over 365 days for *Rhyzopertha dominica* in wheat samples (Flinn and Hagstrum 1990). Similar results were reported for *C. ferrugineus* where the number of eggs laid significantly increased when the moisture content of wheat was increased from 14% to 18% (Jian and Jayas 2009). The increase in insect population with high grain moisture content could be correlated to the higher rate of respiration (Hayma 2003), and the increase in temperature (Lee 2000) at elevated moisture contents. Dampened grains could be more easily consumed by insects than relatively dry grains (Surtees 1964). In high moisture diets, more of the water available in the food is utilized for the growth of the insects than to maintain the water content in the insect body. High grain moisture and associated high temperature also act as a precursor for the growth and proliferation of fungi, resulting in the rapid deterioration of grains (Danso et al. 2017; Ekechukwu and Norton 1999). The development of fungi makes the environment preferable for the growth and development of mould consuming species like *C. ferrugineus* and *C. pusillus* (Arbogast 1991; Wright and Burroughs 1983).

Most insects cannot survive in extremely dry conditions. However, storage beetles are capable of breeding on grains containing floury dust, and broken kernels irrespective of its moisture content (Cotton and Ashby 1952). Generally, moisture content below 9% hits the insect survival and reproduction inside grains (Upadhyay and Ahmad 2011). Low moisture content (below 11%) induces stress which could result in a reduction in progeny and adult weight, causing death in weevils (Sedlacek et al. 1991). The decline in insect population at reduced moisture contents could be attributed to the reduced water activity and speed of enzymatic biochemical reactions (Ziegler et al. 2021). Further, lower moisture contents prevent fungal development and chances of infestation by mold-consuming species. However, practically in grain bulks, the peripheral parts are prone to take up moisture from the air, damp floors, and walls making them more susceptible to infestations (Athanassiou et al. 2003, 2001; Burrell and Havers 1976; Solomon 1946). This results in the development of surface pests even in dry commodities, which could be minimised by reducing the bulk moisture content. Also, combining the cooling regime with a top-dressing of pesticide is recommended to ensure reduced infestations on the surface of bulk grain bins (Armitage et al. 2002).

In stored grains, the moisture content, temperature, and equilibrium relative humidity are interrelated. When considering the storage potential and insect activity; however, the equilibrium relative humidity (or water activity) is more important than moisture content, as it estimates the availability of water for insects and microbes and indicates the biological activity of the stored commodity (Pixton and Warburton 1971). Therefore, I summarize the minimum and maximum water activity that support the survival of various stored grain insects at any given temperature in Table 1.

Table 1. Minimum and maximum water activities for the survival of various stored grain insects

Insect	**Commodity**	**MC_{min} (%)**	**MC_{max} (%)**	**T (°C)**	**a_{wmin}**	**a_{wmax}**	**Reference**
R. dominica	Wheat	8	14	38	0.30	0.75	Edde (2012)
T. castaneum	Wheat	12	36	40	0.30	0.90	Howe (1956)
S. zeamais	Maize	8	-	30	0.30	-	Okelana and Osuji (1985)
S. oryzae	Wheat	11.2	14	15	0.60	0.73	Evans (1982)
T. confusum	Wheat	7	35	37.5	0.10	0.90	Howe (1960)
O. surinamensis	Oats	6	35	30	0.12	0.96	Arbogast (1976)

MC_{min} – Minimum moisture content for survival (%).
MC_{max} – Maximum moisture content for survival (%).
T – Temperature (°C).
a_{wmin} – minimum water activity for survival.
a_{wmax} – maximum water activity for survival.

2.3.5 Food

2.3.5.1 Amount of food

Stored grain insects are considered opportunists (Athanassiou and Arthur 2018), and the food availability is a crucial factor for their survival. The majority of stored grain insects can develop and reproduce on a wide range of whole and processed foods, except those species which develop entirely within the grains. It has been also reported that the increasing availability of food increases female fecundity and grain infestation until saturation (Fava and Burlando 1995) by providing more room for insect multiplication. However, in grain storage structures, in between grain shipments and when cleaned, viable resources exhaust, and food deprivation occurs naturally. Starvation in stored grain insects are characterized by imbalanced energy metabolism, and biological processes like migration and reproduction, and susceptibility to multiple stressors (cold, desiccation) simultaneously (Scharf et al. 2016). The insects respond to food deprivation in two ways: (1) behavioral responses such as diapause, cannibalism, reduced fecundity, retrogressive moulting, migration to food-rich places, and death feigning behavior and (2) regulating the metabolism of biochemical substances through physiological countermeasures to improve the insects' ability to endure hunger (Zhang et al. 2019).

Starvation induces a trade-off between survival and reproduction, where the primary focus is survival whereas maintenance and reproduction are held until favorable conditions (food) are restored. *Trogoderma granarium* is known for its ability to enter larval diapause, characterized by suppressed growth and development which help them withstand starvation (Shivananjappa et al. 2020). Stored grain insects including *T. castaneum*, *R. dominica*, produce fewer progeny with increasing starvation period, either due to starvation, aging or a combination of both (Daglish 2006). It could be an example of reducing reproductive investment under starvation conditions to increase somatic cell maintenance. The depletion of food reserves results in another reproductive strategy, oosorption (reabsorption of eggs) occurs while egg is still in the ovariole, interrupting vitellogenesis and destruction of oocyte. This has been reported for various storage insects of orders Lepidoptera and Coleoptera (Perez-Mendoza et al. 2004). Level of hunger could be considered a primary factor for cannibalism in stored grain insects, as hunger triggers searching behavior, increases foraging time and increases the chances of intraspecific encounters (Parajulee and Phillips 1995). *Trogoderma granarium* undergoes a phenomenon of retrogressive moulting when deprived of food (Shivananjappa et al. 2023). Retrogressive moulting is characterized by the shedding of larval skin periodically causing reduction in size, such that immature larvae moult remains a larva of smaller mass and size thereby reducing their energy requirement for survival. Migrating insects like *R. dominica, L. serricorne* initiate flight as a response to starvation (Shinoda and Fujisaki 2001; Barrer et al. 1993) . Starvation imposes severe water stress on *S. zeamais*, which they compensate for by changing their humidity responses by orienting themselves towards environments that allow them to reverse their water deficit (Weston and Hoffman 1992). However, starvation stress could negatively impact the flight endurance of insects, by decreasing the speed and angular velocity of beetles with increasing hunger (Nguyen 2008).

Under starvation conditions, trehalose in insect blood is primarily used as source of energy (Tang et al. 2014). For instance, reduced trehalose content was observed in *T. granarium* larvae undergoing starvation (Mohammadzadeh and Izadi 2018). Trehalose extended the starvation survival in *T. castaneum*, and could act as a metabolism modifier in protecting them from death (Xu et al. 2013). As starvation intensifies, glycogen gets converted to trehalose and released into blood, therefore both levels of glycogen and trehalose decrease, and are restored when the insect relieves hunger stress (Morya et al. 2010). Further, the ability of an insect to survive starvation is dependent on the ratio of triglycerides to lipids in the body (Laparie et al. 2012; Renault et al. 2002). Stored lipid resources are utilized through reduced glucose oxidation and increased lipid oxidation and fatty acid mobilization (Zhang et al. 2019). It is also reported that insects undergoing starvation stress, initiate a series of antistress mechanisms such as regulation of expression of related genes, synthesis of anti-stress substances and regulation of catabolism of energy substances in the body to prolong regular growth and development (Buckemüller et al. 2017). For instance, in *T. castaneum*, starvation increased the expression of forkhead box O (FOXO) transcription factor at both mRNA and protein levels, imparting tolerance to prolonged starvation by regulating metabolic and transcriptional responses. FOXO activity is crucial in maintaining glycogen, triglycerides, glucose and trehalose levels under starvation conditions (Zhang et al. 2022). Hence, stored grain insects have evolved diverse adaptive strategies or responses to tolerate periods of food shortage and can survive long periods with little or no food. The starvation tolerance of major storage insects in terms of insect lifespan without food are summarized in Table 2.

Table 2. Starvation tolerance of major stored grain insects in terms of lifespan at 30 – 35°C.

Insect species	**Lifespan**	**Reference**
R. dominica	4 – 18 d	Swain (1975)
T. castaneum	35 d	Daglish (2006)
S. cerealella (larvae)	2.1 d	Agah (1961)
S. oryzae	14 d	Daglish (2006)
P. truncatus	9 d	Edde and Phillips (2006)

2.3.5.2 Quality of food

Stored grain is the principal diet of storage pests, and its quality is a key determinant of their population. Stored grain insects are adapted to develop and reproduce on dry foods, owing to their ability to utilize their own metabolic water, a by-product of the breakdown of fats and carbohydrates (Fraenkel and Blewett 1944). The food preferences of stored-grain insects are the result of long-term evolution (Yongxue et al. 2003), and depend upon the feeding behavior of the insects. The relative growth rates and growth efficiencies of insects are reflected by the quality of food consumed by them (Slansky Jr 1985). The major food quality parameters that influence the population are the following:

1. **Grain kernel size:** Kernel size plays a crucial role in the oviposition strategy of grain weevils where larger kernels are preferred for egg-laying (Campbell 2002).
2. **Moisture content:** Feeding on food with increased moisture content hastens the developmental rates and increases the body size of stored grain insects (Baker and Loschiavo 1987).
3. **Germ content:** Stored grain insects thrive more efficiently and longer in diets containing ground wheat and germ, as it is easier to consume and requires expending less energy (White and Bell 1993).
4. **Physical condition of grain:** Stored grain insects find it difficult to infest grains containing husk due to the protection offered by husk (Arthur et al. 2019b). Further, the presence of dockage is critical for secondary feeding storage insects surviving only in the presence of dockage (White 1995).
5. **Nutritional suitability:** The proportions by weight of major nutrient categories including amino acids, carbohydrates, fatty acids, minerals, vitamins, and sterol in the diet influences the insect population by impacting larval growth (Singh 1977).
6. **Presence of fungi:** The presence of fungi in stored grains is an indicator of deteriorated quality, and is suitable for species that feed on fungi (White 1995). However, the presence of fungi has limiting effects on grain weevils by reducing reproduction and by inducing sublethal effects on larvae (Sedlacek et al. 1991).

7. **Conditioning by conspecifics:** Conditioning of grain and grain products by conspecifics results in the quality deterioration of food supply in the form of contamination from dead insect bodies, waste products, frass, and dust (Fleurat-Lessard 2002), increased fatty acid content, and uric acids (Mason and McDonough 2011), which make it relatively less preferable for grain beetles (Ziegler 1978).

These parameters impact the population by influencing various population growth parameters, progeny production patterns, development period from egg to adult, mating behavior trends (Benyi and Gall 1981), interspecies interactions (Shah et al. 2021), the extent of cannibalism (Craig 1986) and insect distribution patterns.

2.3.6 Oviposition sites

Oviposition is the process of laying eggs. Oviposition is characterized by two different sets of behaviors: pre-oviposition and post-oviposition. Pre-oviposition behavior involves all parameters and actions involved in the selection of an oviposition site and the oviposition process. The post-oviposition involves various strategies that ensure the proper development, protection from environmental stresses, devices for attaching the eggs to substrate, and defence from would-be predators (Lancaster and Downes 2013). For the successful exploitation of a grain storage environment by an insect pest, it is necessary to find suitable oviposition sites when they are in short supply and spread over a wide area (Cox and Collins 2002). The orientation of insects towards an oviposition site is based on primary host-derived or secondary conspecific-insect-derived chemical cues (Mohandass et al. 2007). The oviposition sites of the major stored grain insects are summarized in Table 3.

Table 3. Oviposition sites for major stored grain insects. Insects typically lay eggs singly or in clusters on these sites.

Insect species	Oviposition sites	Preferred substrates	Reference
Tribolium castaneum	Flour patches near edge of storage structures.	All traditional grain flours, with high fibre and protein contents	Campbell and Hagstrum (2002) Gerken and Campbell (2020)
Cryptolestes ferrugineus	Splits and cracks in the grain.	Grain debris and kernels of cereals such as wheat, barley, rye, oats	Mason and McDonough (2011)
Rhyzopertha dominica	Grains with crevices and rough surfaces	Broken grains, with suitable moisture content, previously infested flours	Breese (1963) Chanbang et al. (2008)
Sitophilus granarius	Inside the grain	Clean grains of wheat	Nawrot et al. (2010)
Oryzaephilus surinamensis	Usually out of sight in some crevice in food supply.	Finely ground flour, intact grain kernels, non-grain products like dry fruits and nuts	Awadalla et al. (2021); Back and Cotton (1927)
Sitotroga cerealella	Exterior of the grains and prefers substrates with smaller crevice heights.	Whole grains of corn, wheat, sorghum	Mason and McDonough (2011)
Plodia interpunctella	Vicinity of food source and substrates containing conspecific secretions. Physical contact with substrate is essential to elicit oviposition.	Wheat bran, almonds, walnut, wheat, broken maize	Mohandass et al. (2007)
P. truncatus	Within the grains in blind-ending tunnels bored at right angles to the main feeding tunnel.	Soft wheat, pulses, ground nut, dried tubers, artificial grains of compacted cereal flour.	Vowotor et al. (1998)

The suitability of an oviposition site for stored grain insects is related to environmental conditions of temperature and relative humidity (Waterhouse et al. 1971), patch quality (Campbell and Hagstrum 2002), grain moisture content (Mason and McDonough 2011), and various physical and chemical characteristics of the grains (Awadalla et al. 2021). Each stored grain insect has their optimum range of temperature and relative humidity suitable for their oviposition, summarized in Table 4. With respect to patch quality, storage insects prefer to oviposit on cleaner patches than patches which are previously exploited (Ziegler 1976). Previously exploited patches might contain eggs, pheromones (Suzuki 1980), cuticular quinone and hydrocarbon secretions (Howard 1987; Markarian et al. 1978) which could contribute to negative fitness consequences in the form of larval cannibalism and competition (Park, 1965, 1974), and therefore are not preferred for oviposition. Further, the nutritional composition and volatile compounds present in the food grains also influence the suitability of oviposition (Fabres et al. 2014). The absence of nutrients in balanced proportions results in problems in egg-laying, failure in ecdysis, and cuticular colour changes whereas high quality diets promote more robust and heavier individuals with higher fecundity and fertility (Chapman 1998). Grain physical characteristics including grain size, shape, and hardness, play a crucial role in the oviposition of primary feeders (Awadalla et al. 2021; Mwenda et al. 2019), whereas the level of milling determines the oviposition in secondary feeders (Campbell and Runnion 2003; Throne and Culik 1989).

The absence of suitable oviposition sites results in reduced oviposition rates (Breese 1960). However, females do not exhibit complete restraint in egg laying in the absence of suitable oviposition, i.e., oviposition rate fell from ten eggs per female per day to four eggs per female per day in the complete absence of oviposition sites. It has been reported that *Rhyzopertha dominica* focuses on fewer oviposition sites preferring a short period of intense oviposition even in the presence of multiple sites (Breese 1963). Similarly, *Sitotroga cerealella* does not necessarily require grains as a stimulant for egg laying, and will oviposit even between strips of cardboard (Richardson 1925).

Table 4. Optimum temperature and relative humidity conditions for oviposition by major stored grain insects

Insect species	Temperature (℃)	Relative humidity (%)	Reference
Tribolium castaneum	35	70	Abdelsamad et al. (1988)
Cryptolestes ferrugineus	35	90	Currie (1967)
Cryptolestes pusillus	32.5	90	Currie (1967)
Rhyzopertha dominica	30 ± 2	75 ± 5	Deshwal et al. (2018)
Sitophilus oryzae	30	75	Singh et al. (1974)
Sitotroga cerealella	25 – 30	65 – 80	Boldt (1974)
Plodia interpunctella	30	80	Mbata (1985)
Trogoderma granarium	33 – 37	65	Rizwan et al. (2018); Yadav and Srivastava (2017)

Knowledge of oviposition sites is crucial because, understanding how each insect species responds to volatile, chemical, or textural cues associated with different food grains and their products would aid in the management of mixed storage sites, where more than one grain-based product is stored. It is advisable to store a higher value product near a "bait" product of lower value, that has more risk of infestation than the higher value product. This behavioral management of insect pests ensures that the higher value product is not infested, and need not be treated for any infestation (Gerken and Campbell 2020).

2.3.7 Insect density

Increasing population densities of stored grain insects result in their regulation by inducing a lower reproduction rate, higher mortality rate, or a combination of these, whereas with decreasing population densities the converse is true. The regulating effects of insect populations under higher densities could be through competitions, intra and interspecific interactions, regulation through modification of environment (conditioning) or through genetic feedback mechanisms. The regulatory effects are present across the life history of insects regardless of their growth stage. For instance, larvae reared under crowding conditions produce stunted adults of reduced fecundity, whereas adults crowding could influence their feeding, rest, copulation and oviposition (Crombie 1942). Some of the major effects of high insect densities are discussed below.

2.3.7.1 Competition

Competition for oviposition sites

Competition for oviposition sites has the most limiting effects on the population, as it is the most important factor in reducing fecundity. The density dependent competition for oviposition sites is more severe among the females, although male densities does contribute to the competition by feeding on the grains in which the females oviposit. Each insect species has their own maximum density beyond which the oviposition starts to fall and eventually reaches zero. For instance, population densities above 0.25 beetles per grain, 0.50 beetles per grain, and 1 moth per grain reduced the fecundity in *R. dominica*, *O. surinamensis*, and *S. cerealella*, respectively (Crombie 1942). The competition for oviposition is evident in the form of no egg production, adults fleeing to escape crowding, or preference to lay eggs at locations other than grains at locations of high densities (egg dumping). High insect densities could upset the oviposition rhythm, and the females behave as if competition for grains is becoming severe, thereby reducing the percentage of eggs oviposited on grains (Crombie 1947). The diminishing egg production could be either due to delayed oviposition, resorption of matured oocytes or egg number and size adjustment (Moore and Attisano 2011). Delayed oviposition might be somewhat advantageous as it allows time for the adults to find unoccupied oviposition sites in the future. Further, certain stored grain insect species can adjust their egg number and size, according to the availability of oviposition sites, by partitioning of vitellogenesis such that the yolk precursor molecules are integrated into fewer larger eggs or many smaller eggs (Teixeira et al. 2016). The egg dumping behavior or preference to lay eggs at substrates other than grains in grain beetles could be due to the egg retaining in the oviduct for too long, resulting from the inability to halt oogenesis and oviposition once the process is triggered (Messina et al. 2007; Roberts and Schmidt 2004; Minkenberg et al. 1992; Wilson and Hill 1989). It could also be an adaptive strategy that prepares females for the subsequent availability of oviposition sites.

Competition for food

The effect of competition for food grains at high densities is translated into two forms: a reduction in feeding rate and a reduction in insect fecundity. The initial increase in densities, results in decreased feeding rate even when food supplies are not deficient, due to competition and interruption by other insects. However, as densities increase further, severe competition for food grains occur, and the resulting starvation results in reduced fecundity. This effect was observed in *R. dominica* where the feeding rate was reduced at densities above 8 beetles per grain, whereas densities above 16 beetles per grain resulted in a starvation induced reduction in fecundity (Crombie 1942). Competition for food is not limited to adults, but also includes larval competition which could result in (a) larval and pupal mortality; (b) reduced size of larvae, pupae and adults consequently causing reduced fecundity and oviposition; (c) changes in the rate of development of immature stages and in adult longevity; (d) changes in sex ratio; and (e) movement of individuals out of the area of competition (Vowotor et al. 1998). When there is competition for food, *R. dominica* larvae would attack each other directly after encounters within the grains and supernumerary individuals are either killed or forced to migrate (Crombie 1944). Incidences of larval density associated mortality have been reported for storage insects like *R. dominica* (Crombie 1944) and *Cryptolestes* species (Ashby 1961). Further, larval competition is regarded as more intense in internal feeding granivores that cannot migrate and are forced to grow and develop on grain chosen by the mother for oviposition (e.g., bruchid and curculionid species), than other internal feeding granivores which migrate (e.g., *R. dominica*, *S. cerealella*) and choose their development site (Giga and Smith 1991).

Competition for mating partners

It has been reported that an increase in densities of *Sitophilus* spp. resulted in an increase in the amount of male fighting (fights per male per 0.5 h) for potential female mating partners. The female copulation frequency was observed to be maximum at the density of 2 males per female, and with further increase in male density per female, the copulation frequency decreased due to competition for female mating partners (Crombie 1942). Males also attack other males engaged in the act of copulation in the absence of females. Conversely, moderate levels of competition are regarded beneficial for insect fitness and insects could perform better in stressful environments. For instance, males becoming more sexually aggressive would increase offspring numbers in certain seed weevils and would thus impact the population dynamics (Teixeira and Zucoloto 2012; Wilson et al. 2007).

2.3.7.2 Conditioning

Crowding of stored grain insects induces changes in the available food, resulting in its conditioning. The conditioned media might contain eggs, larval exuviae, feces and various chemical substances that harm the population. The exocrine glands of stored grain insects secrete a toxic mixture of methyl-, ethyl-, and methoxy-quinones, which prompts the ceasing of oviposition in species like *Tribolium* (Sonleitner 1961), *O. surinamensis* (Mignon et al. 1996), and

R. dominica. Further, the adults developing on such depleted diet, can induce poisoning effects, and therefore they tend to be less fecund (Arthur et al. 2019b). Conditioning of media also impacts the larval stage of the population, by reducing its weight, prolonging its development period, and retarding its development in *Tribolium* species (Park 1938). Although conditioning of media is a mechanism of competition, consumption of the conditioned media (accumulation of waste materials, silk, pheromones, frass) might promote growth in times of very low food availability in certain secondary storage pests like *C. cautella* (Jones et al. 1990). This is because, conditioned media might contain some residual nutrients, which could be extracted, but at a greater cost than unconditioned media.

2.3.7.3 Intraspecies interactions

The effects of high population densities are not just limited to competition, but also the resultant complex intraspecific interactions, which directly impact the population size and composition. Interactions among conspecifics at high densities are mediated via chemical cues like dodecanal, cuticular, hydrocarbons and hydrocarbon components secreted by the Dufour gland of the insects (Collatz et al. 2009; Howard and Pérez-Lachaud 2002; Howard 1998; Howard and Infante 1996). With respect to stored-grain insects, the major interspecies interactions are regarded to be combined effects of resource limitation, crowding (Sonleitner 1961; Rich 1956) and cannibalism between various life stages (Holditch and Smith 2020). Several instances of intraspecific interactions in stored grain insects impacting the population have been reported (Mathias et al. 2015; Vowotor et al. 1998; Giga and Smith 1991; Park et al. 1974; Ashby 1961;). For example, Hulasare et al. (2003) found that *Tribolium* spp. eggs, pupae and callow adults experienced mortality greater than 90% due to predation by larvae and adults of the same species. Similarly, higher densities of eggs per grain in *S. granarius* results in larval cannibalism. The potential costs of cannibalism include the risk of injury to the aggressor, the loss of inclusive fitness due to the consumption of genetically related individuals, and the eventual acquisition of parasites or pathogens (Bolívar-Silva et al. 2018). These effects result in increased immature mortality, disrupted reproductive behavior (Hardy and Goubault 2007; Gómez et al. 2005), reduced oviposition (Ziegler 1978) and fecundity (Rich 1956), and increased development time (Bancroft 2001), thus influencing the population negatively. However, it is difficult to conclude if the effect of cannibalism is potentially negative or positive for the population. This is because, although larval cannibalism results in injuries and loss of inclusive fitness, it reduces further competition, searching time and favours fitter individuals. Further, cannibalism also increases the genetic diversity in these insects because of consuming genetically related individuals (Bolívar-Silva et al. 2018). Studies have also shown that cannibalistic populations of *T. castaneum* thrive in stressful environment because of egg cannibalism. This implies that although cannibalism is a consequence of high insect density, it could permit colonization and range expansion (Via 1999).

Stored grain insects are also known to avoid intraspecies competition by resorting to various strategies, either due to adaptive or selective traits. For instance, certain stored grain insects including *C. chinensis,* under limited resources, devise their egg distribution pattern according to "ideal free distribution model", an adaptive trait (Chung et al. 1995). This means that the eggs are distributed onto the grains such that all the offspring have an equal probability of access to food, thus preventing competition. This behavior is an adaptive trait, as it is a consequence of the change in its environment (limitation of resources) (Teixeira and Zucoloto 2012). Similarly, under conditions of competition, it has been noted that genotypes tend to be constantly selected, such that food is recognized quickly, new diets are included, nutritional utilization is improved, increasing metabolic rate and overall resource utilization efficiency, which is a selective trait.

However, these selective traits might have some trade-offs including slower development time, lower levels of reproduction and lower resistance to environmental stresses (Teixeira et al. 2009). This could imply it is rather easier for the stored grain insects to follow adaptive traits (adapt to available resources and competitive conditions and available resources), than relying on selective traits (inclusion of new diet and diet preference hierarchy) as the process is slower (Teixeira et al. 2008).

2.3.7.4 Reduced longevity

Increasing population density is associated with increased energy expenditure in insect locomotion in response to aggregation pheromones, engaging in mating activities, and production of eggs and sperms which could reduce insect lifespan. Further, aggressive male sexual behavior at higher densities is also regarded as a crucial factor in reducing the lifespan of grain beetles (Spratt 1980). Higher densities are also associated with impaired future reproductive success in stored grain beetles, owing to their negative effect on the body weight of insects (Assie et al. 2008).

2.3.8 Number of mated females

Most stored grain insects reproduce more or less continuously under favorable environmental conditions. The female individuals of stored-grain insects are capable of breeding enormously and multiply in short duration under favorable conditions because, 1) both female and male can mate multiple times, 2) females can store sperms and do not need to mate in the future; and 3) mating can increase insect fitness. Therefore, mating disruption using synthetic pheromones can suppress mating which results in reduced eggs (Jones 1998).

Multiple mating is a widespread behavior in stored grain beetles and weevils (Campbell 2005; Lewis and Iannini 1995). It has been reported that multiple mating significantly increases female fecundity (Lewis and Austad 1994). Multiple mating in females is desirable in terms of material benefits such as extra sperm or male-derived substances and genetic benefits (Campbell 2005). The genetic benefits derived from multiple mating comprise improving previous copulations by mating with males of higher quality (Thornhill and Alcock 2013; Olsson et al. 1996; Simmons 1987), limiting the risk of genetic incompatibility (Zeh and Zeh 1996, 1997), inbreeding avoidance (Tregenza and Wedell 2002; Madsen et al. 1992), manipulating offspring paternity (Edvardsson and Arnqvist 2000), increasing genetic diversity (Baer and Schmid-Hempel 1999) and genetic bet-hedging (Watson 1991). The genetic benefits ensure greater likelihood of carrying insecticide-resistance genes and thereby increasing the survival of the insect population (Ridley et al. 2016).

Mated females of stored grain insects can store sperms which could be used for many weeks to produce offspring. Several researchers report sperm transfer and storage in flour beetles (Lewis et al. 2005; Lewis and Jutkiewicz 1998; Qazi et al. 1998, 1996). It has been reported that mated females of *T. castaneum* have control over the sperm movement from the site of deposition in the bursa copulatrix to storage in spermatheca by means of the muscular contraction of their reproductive tract (Qazi et al. 1998). The females continue using sperm stored in spermatheca to fertilize their eggs for about 140 days following a single mating (Qazi et al. 1996). This enables the initiation of infestation by the mated females themselves, and the enhanced movement of genetic material adds to the gene flow. Hence, the ability to initiate an infestation by a single female possibly contributes to an increase in population (Ridley et al. 2016). For instance, *R. dominica* populations in between study areas (storages and fields away from storages) displayed high degree of connectivity, due to the dispersal (flight) of mated individuals of potential fecundity. About 95% of these dispersing females of *R. dominica* were mated, and store sperm for multiple weeks, and they can produce an average of 242 offspring, whereas the average number of eggs *R. dominica* produces in a lifetime is 200-500. Further, the more males the dispersing females' mate before dispersal, the more likely she is to carry insecticide resistant genes (Ridley et al. 2016). Similar results have been reported for *T. castaneum,* where the females mated when they dispersed and had an average fecundity of 105 (± 13) offspring per mated female (Ridley et al. 2011). The relationship between mating and fitness can be positive or negative. Multiple mating is associated with an increased risk of predation, physical damage, transmission of infection, reduction of female lifespan, and time lost for feeding and oviposition (Campbell 2005). Further, the presence of long-lasting sexual interactions might have concurred to boost the evolution of population-level behavioral asymmetries in insects (Benelli et al. 2017; Frasnelli 2013). However, multiple mating enhances female fecundity and numerous other benefits including sperm replenishment, hydration, and nutrition effects. Lower rate of mating in females, efficiently reduced the costs of mating, whereas a higher rate of mating maximized the benefits of mating. Hence mating at an intermediate rate is thought to maximize the fitness of most female insects.

2.3.9 Patch size

A habitat patch is defined as a distinct area of fixed contour, spatial, and configuration, where the species grow in population and find its resources (Atkins et al. 2019). The patch for storage insects is a grain patch, a complex combination of its food and space, which means that either food or space or both could be a limiting factor for population, depending on its availability. The patch size influences the insect population by impacting the resource availability, oviposition, movement behavior, crowding behavior, and insect density. Female grain beetles reportedly evaluate the patch size and adjust the number of eggs they lay, and thereby optimizing the number of adults emerging from the patch (Campbell and Runnion 2003). Large patches like grain storage bins are characterized by more resources, more room for oviposition and multiplication, increased freedom for movement and locating resources, reduced chances of competition, and relative difficulty in finding mating partners at lower insect densities (Jian et al. 2018b). Larger patches are also characterized by larger residence times for grain beetles, which could be due to the deepness of resource patches (flour) resisting their movement. Further, they might mark larger patches with aggregation pheromones, which ensures the acceptance of these patches in future encounters (Romero et al. 2010). Smaller patches are associated with limited food resources, limited living volume, increased crowding (Halliday et al. 2015), cannibalism by adults and larvae on eggs (Sonleitner 1961), and reduced oviposition rates in females.

The effect of patch size on insect populations in grain storage bins is regarded as negligible if the grains are maintained at safe temperature and moisture conditions. To elucidate, the effect of patch size as a determinant of resource availability is negligible on the population since they have ample resources and insects are free to move to preferred locations within bins when resources exhaust at a location (Jian et al. 2018b). It implies that crowding behavior, if any in grain bins, could be therefore an effect of movement rather than resource limitation. Crowding in grain bins as an effect of insect movement could be characterized by insect fighting, lower egg dispersal, higher chances of egg damage, and higher larval mortality due to cannibalism and trampling by larvae and adults due to insects walking on eggs (Suresh et al. 2001; White and Bell 1990; Smith 1966). These events could ensure that insects rarely reach their peak density inside large grain patches. Further, the insects not attaining their peak density indicates that the conditioning of grains over time is of little importance considering the scale of grain patch. These conclusions were based on large patch size studies on the population of *C. ferrugineus* by Jian et al. (2018b), who reported that patch size did not affect the insect population dynamics at temperatures of ≤ 30°C. Similar results have been reported by (Tripathi et al. 2021) for *T. castaneum* populations, where insects inside larger patches did not attain their peak density, ruling out the possible effects of patch size on population dynamics in storage bins. It has been also proven that changes in patch size by manipulating the depth of storage structures will affect the population dynamics of *Tribolium* species, due to their non-uniform distribution along depth (Tripathi et al. 2021; McDonald 1968). These indicate that patch size might not be a limiting factor for population dynamics in a grain storage bin.

2.3.10 Interspecies interactions

2.3.10.1 Symmetric and asymmetric outcomes

With respect to stored grain insects, Nansen et al. (2009) emphasized the importance of interspecies interactions reporting that single-species studies do not represent actual conditions of stored-grain ecosystems where multi-species infestations and resultant interspecific associations are prevalent. The factors that influence interspecies interactions in stored grain insects include the insect species involved, initial population densities of the insect species (Hayles et al. 2014), the quantity of food available, type of food material (Lefkovitch 1968), presence of fungi (Sinha 1968), and relative time of arrival of each species, also known as priority effects (Holditch and Smith 2020). In a storage environment, the outcomes of an interspecies interaction are determined by the context, species identity and abiotic conditions. Interspecies interactions might have positive and negative impacts on the population of stored grain insects, where the area of positive effects is relatively underexplored.

Interspecies interactions could be regarded as symmetric (positive) when it results in coexistence (White and Sinha 1980), involved species have similar microhabitat preferences (Nansen et al. 2009), habitat modification by primary pest, and grain damage induced by feeding and reproduction of one species is beneficial for the other species (Edde 2012). Changes in the abiotic conditions (temperature, moisture content and their gradients) in a grain storage ecosystem might result in spatial segregation of interacting species. It could result in habitat partitioning and enable coexistence of these species under certain abiotic conditions. Temperature is an important abiotic factor determining the competitive outcome between storage insects, where the competitive superiority of one species over the other is dependent on the temperature. For instance, the competition advantage of *C. ferrugineus* over *C. pusillus* is not very intense at low temperatures (20℃) (White et al. 1995). Similar results have been reported for *T. granarium, R. dominica* and *S. oryzae* interactions at low temperatures (25℃), with no evidence of larval interference and cannibalism due to resource partitioning (Kavallieratos et al. 2017). Also, *P. truncates* and *S. zeamais* co-exist in the temperature range of 25 – 30℃ (Quellhorst et al. 2020). Another example of positive association is reported between *R. dominica* and *T. castaneum*, where both species responded positively to each other's presence due to habitat modification and similar microhabitat preferences, as *R. dominica* lives inside the kernels whereas *T. castaneum* lives outside (Nansen et al. 2009). However, contradictory results have been reported for the interaction of the same species by Cui et al. (2006) where *T. castaneum* impeded the reproductive rate of *R. dominica*, possibly due to food resource depletion and omnivorous *T. castaneum* consuming the immatures of *R. dominica* and diet (Jagadeesan et al. 2013), particularly when the studies were carried out with limited space and food resource conditions, indicating a negative consequence of interspecies interactions. Communities within a resource patch can coexist along with conventional niche partitioning and absence of competition when the species differ in their resource utilization, behavior and time partitioning. This model of coexistence is based on the principle that two species can coexist in a community, if one species is a superior competitor and other is a superior colonizer (Vidan et al. 2020). Some instances include the interactions between colonizers (*R. dominica* and *S. oryzae*) and secondary consumers (*C. ferrugineus, T. castaneum* and *O. surinamensis)* (Trematerra et al. 2015; Arbogast and Mullen 1988). Several studies have reported beneficial effects on such interactions due to modifying growth substrate (wheat) and ecological niche (Arbogast and Mullen 1988; LeCato 1975; Kabir 1966). Similarly, the increase in moisture content associated with weevil activity, favors softening of wheat and mold growth, which in turn aids in habitat and mate-finding and foraging (Davis et al. 2013), thus synergizing the activity of secondary pests that feed on fungi (*C. ferrugineus*). However, this effect is not always true, as there are instances where secondary feeder (*L.* serricorne) gets suppressed owing to non-competitive exclusion by primary feeder (exclusion between relatively unrelated beetles) (*S. oryzae*) (Lefkovitch 1968) and certain fungal metabolites are capable of repelling insects (Magan et al. 2003).

The major asymmetric (negative) effects of interspecies interactions on insect populations include cannibalism and predation (Hulasare et al. 2003), interference competition (direct interaction between foraging species) (Nansen et al. 2009), exploitative competition (indirect effect through exploitation or depletion of resources) (Jagadeesan et al. 2013; Begon et al. 1986), and impeded reproduction (Cui et al. 2006). Further, the outcome of an interspecific interaction could be negative based on the relative time of arrival of each species and the overall competitive outcome is termed as priority effects. The priority effects between *T. castaneum* and *T. confusum* were evaluated by Holditch and Smith (2020). Often the species which has priority entry to the grain storage ecosystem has larger population than later arriving species, due to the production of ample eggs, minimal predation costs from larval and adult stages of later arriving species. Further modification of the storage environment (release of toxic metabolites) limits the later arriving species (Fukami 2015). Climate changes at global level, can result in changes in the growth and development cycles of insect pests and their interactions (Moses et al. 2015). The consequences of such changes could favor one pest species over another in a grain storage ecosystem. Some examples of the asymmetrical outcomes of interspecies interactions are presented in Table 5.

The negative effects of interspecies interactions could be effectively exploited for the regulation and control of insect populations within grain storage ecosystems. The benefits of species employed for biological control include short life cycles, high reproductive capacity, the ability to attack small-sized storage pests, and ease of removal from grain mass using normal cleaning procedures (Schöller et al. 2006). The major insect predators used for the biological control of various stages of stored grain insects are summarized in Table 6.

Despite the benefits of biological control methods, the associated cost, lack of ample understanding of the population dynamics of pests, and integration of biological control approach with pest monitoring and sanitation programs remain challenging (Schöller et al. 2006). The development of efficient release guidelines in terms of a number of insects to be released and timing of release is also crucial since the same storage pest may be found in a wide variety of storage systems. Further, knowledge of both the host and enemy phenology under a variety of environmental conditions is crucial for optimizing the timing of the release of the biological control insect (Schöller 2010), as their effectiveness is impacted by abiotic factors like temperature and humidity.

Table 5. Asymmetric interspecies interactions in various stored grain insects

Interacting species	Growth conditions	Effects	Possible reasons	Reference
S. oryzae *R. dominica* *T. castaneum*	Sorghum	- - +	Ecological niche modification by primary feeders escalating the activity of secondary feeder.	Kabir (1966)
S. granarius *S. oryzae* *S. zeamais*	Rice	- + +	Differences in life table characteristics (oviposition and development time) Changes in grain characteristics.	Athanassiou et al. (2017)
T. castaneum *C. ferrugineus*	Wheat	- +	Cannibalism and predation on eggs and larvae of *T. castaneum,* whereas immatures of *C. ferrugineus* were protected by developing under seed coat.	Hulasare et al. (2003); Suresh et al. (2001)
S. zeamais *P. truncatus*	Maize, ≥ 25°C	- +	Higher optimum growth temperature of *P. truncatus* than *S. zeamais*	Quellhorst et al. (2020)
R. dominica *S. oryzae* *T. granarium*	Wheat, ≥ 30°C	- - +	Competition among the beetles Modification of diet by co-occurring species Better adaptation of *T. granarium* to warmer temperatures	Athanassiou et al. (2016, 2017)
E. cautella *P. interpunctella*	Bran based diet	- +	Competitive exclusion Reduced oviposition in *E. cautella* females due to exudates from heterospecifics.	Cameron et al. (2007)

'+' and '–' indicates positive and negative outcome of interaction, respectively. Positive outcomes indicate favorable effects on population growth and negative outcomes indicate adverse effects on population growth when multiple species interact.

Table 6. Biological control organisms used to control various stored grain insects

Species	Insect species controlled	Host stage	Reference
Xylocoris flavipes	*T. confusum, S. zeamais, T. castaneum, S. granarius, L. serricorne, P. interpunctella, S. cerealella*	Immature stages of beetles and moths	Schöller et al. (2018)
Thecolax elegans	*R. dominica, S. oryzae, S. cerealella*	Larval stages of various coleopteran and moths	Adarkwah et al. (2019)
Anisopteromalus calandrae	*S. granarius, S. zeamais. R. dominica, S. paniceum, L. serricorne*	Late larval stages and early pupal stages of beetles inside seeds and cocoons	Schöller et al. (2018); Shin et al. (1994)
Habrobracon hebetor	*P. interpunctella, E. kuehniella, E. elutella, C. cautella*	Larvae of stored product moths	Schöller (2010)
Lariophagus distinguendus	*S. oryzae, S. granarius, R. dominica, S. paniceum*	Larvae, prepupae and pupal stages of beetles in seeds and cocoons	Schöller et al. (2006)
Trichogramma spp.	*P. interpunctella, S. cerealella, E. cautella, E. kuehniella*	Egg stage	Grieshop et al. (2009); Steidle et al. (2001)
Cephalonomia tarsalis	*O. surinamensi, O. mercator*	Larvae of grain beetles	Collatz and Steidle (2008)

2.3.10.2 Interference

Reproductive interference is a consequence of incomplete species recognition in the reproductive process and refers to the negative interspecific sexual interactions that affect the fitness of males and females adversely (Gröning and Hochkirch 2008; White et al. 1995; Kuno 1992; Bull 1991). Reproductive interference is likely to happen at various reproductive stages between closely related species and sometimes between distantly related species, engaging in reproductive interactions (Chow-Fraser and Maly 1988). These interactions can be a result of signal interference, disrupted mate searching, heterospecific rivalry, mate choice errors, misplaced courtship, mating attempts, or copulation (Shuker and Burdfield-Steel 2017). The effects of reproductive interference include sexual harassment (McLain and Pratt 1999), reduced opportunity to mate with conspecifics (Hochkirch et al. 2007), competitive exclusion (Kishi et al. 2009), reduced fecundity (Birch et al. 1951; Lloyd and Park 1962), damage to the female genitalia (Sota and Kubota 1998), gamete dumping (Lessios and Cunningham 1990), and hybridization (Garcia-Vazquez et al. 2002; Kubota and Sota 1998; Pfennig 2007). These effects result in a reduction in the population growth rate of one species due to resource exploitation or interference by another species (Reznick et al. 2002), accelerating the extinction of species with lower population density if the interference is symmetrical (Kishi et al. 2009). For instance, in a study involving *Callosobruchus chinensis* and *Callosobruches maculatus,* it has been reported that an increasing number of heterospecific males resulted in reduced fecundity and longevity of *C. maculatus* females, resulting in species exclusion (Kishi et al. 2009). Similar results have been reported by various researchers for *T. castaneum* females housed with *T. confusum* male, resulting in reduced fecundity and longevity of *T. castaneum* due to the asymmetric promiscuity of males of the species (Lloyd and Park 1962; Birch et al. 1951). Heterospecific mating in closely related carabid beetles caused a rupture in the vaginal membranes in females, broke genital parts in males, and reduced fertilization rates (Sota and Kubota 1998). Similar results have been reported for interspecific mating between grain beetles *T. confusum* males and *T. castaneum* females, i.e., the damage of genitalia of *T. castaneum* females (Graur and Wool 1985). Thus, sexual harassment associated with interspecific mating imposes high fitness costs, which could potentially limiting habitat use by ecologically similar species (McLain and Pratt 1999).

However, reproductive interference is largely overlooked owing to the lack of detectable evidence, even though studies on hybridization and resultant genetic invasion have been reported (Gröning and Hochkirch 2008). It is interesting to note that although asymmetric reproductive interference has negative effects on the population growth of one species, reproductive interference itself reduces the chance of reproductive interference by promoting spatial segregation of the interacting species. Rationally, as a consequence of reproductive interference, resource partitioning is expected between closely related species, minimizing negative interactions between those species (Hochkirch et al. 2007).

2.3.11 Age

2.3.11.1 Maternal age

Parental age effects can be defined as the age-related changes whose expression is witnessed in the progeny of the aging parents. They play an integral role on the progeny of the next generation by influencing the evolution of components of the life cycle and life history strategies (Soliman 1987). Maternal age refers to the time during which an insect oviposits egg, and several studies have reported that the rate of oviposition and fecundity of mated female beetles is affected by the age of female beetles only (Chahal and Simwat 1975; Simwat and Chahal 1975; Raychaudhuri and Butz 1965; Erdman 1964; Park et al. 1964). Maternal age also influences offspring survival, development time, and mass at birth and maturity (Zehnder et al. 2007). The age-related maternal effects could be either adaptive or non-adaptive or detrimental to the offspring's fitness, with the majority being detrimental thereby impacting offspring fitness and population negatively.

The majority of increased age-related maternal effects are detrimental to offspring fitness, owing to maternal constraint or a maternal trade-off between maternal and offspring fitness

(Marshall and Uller 2007). In stored grain insects, typically older mothers lay smaller eggs that are less viable and take longer to develop. Production of trophic eggs in *Tribolium* species is considered a form of parental care, where certain progeny has no other purpose than to serve as food for their siblings or closely related conspecifics (Alabi et al. 2008). Further, it has been reported for *S. oryzae* that the offspring of younger females had a longer lifespan and greater fitness compared to those produced by older females (Opit and Throne 2007). Similar results were reported for *C. chinensis* where the egg sizes, unitary egg sizes, egg number, and reproductive effort significantly decreased with increasing maternal age (Rahman et al. 2021). It could be explained by the "Lansing effect" where offspring produced by older parents have reduced longevity (Zehnder et al. 2007). The lower initial resource allocation to eggs by older mothers, the genesis of pleiotropic genes in parents which negatively impacts offspring as they age and harmful mutations in the gametes of older parents could be regarded as the mechanisms for the 'Lansing effect' (Singh and Omkar 2009; Priest et al. 2002). Reduction in performance and impaired starvation tolerance in offspring are also regarded as the negative effects of aging. The impaired starvation tolerance could be reasoned by the carry-over effect from the larval stage as starvation is largely dependent on larval fat cells that persist to the adult age (Aguila et al. 2007), with the parental age negatively impacting the larval fat body. However, there is a limited impact of parental age on the thermal tolerance of the offspring because, to a greater extent, thermal tolerance is impacted by other factors like growth or acclimation temperature (Scharf et al. 2015b).

If the parent insects could predict the future conditions of their offspring and adjust their egg-laying appropriately, then the age-related parental effects could be adaptive (Halle et al. 2015). The transfer of epigenetic modification to the offspring is a consequence of aging and is of adaptive nature, which is observed in the form of offspring diapauses and flight polymorphisms. Studies have shown that older females often produce offspring that diapauses more frequently than those produced by younger females (Hockham et al. 2001; Mousseau 1991), as these diapauses are triggered by the environmental conditions experienced by the parental generations. Similarly, in some insects the environment experienced by the mother is the primary determinant of progeny's flight phenotype. The production of dispersing progeny reportedly increases with maternal age in seed beetle *C. maculatus*, is possibly because they use seasonal or ephemeral resources, environmental cues such as crowding, temperature or photoperiod as predictable indicators of future habitat deterioration and impending food shortage (Fox and Mousseau 1998).

2.3.11.2 Old age

The performance of living organisms worsens with age because old age is usually associated with increased mortality, less intense reproduction, and reduced fitness including learning and locomotion (Simon et al. 2006; Hughes and Reynolds 2005; Novoseltsev et al. 2003; Ridgel et al. 2003). Stored-grain insects also undergo change in morphological, physiological, biochemical, behavioral, and pathological parameters as they age (Soliman 1987). The major effects of old age on the stored grain insect population include reduction in starvation tolerance (Ducoff et al. 1970), increase in the rate of oxygen sensitivity (Lee and Ducoff 1983), changes in cannibalism rate (Takahashi and Yamamoto 1972), decline in emigration tendency (Ritte and Agur 1977; Ziegler 1976), reduced refugee-seeking behavior, increased resistance to diseases (Keymer 1982; Kelly et al. 1967), impaired cold tolerance, and lower body mass (Halle et al. 2015). For example, in adults of *T. castaneum* and *T. confusum* undergoing complete starvation the survival time decreased with ageing (Ducoff et al. 1970). This reduction in starvation tolerance could be possibly due to the reduced body mass, amount of body fat, and nutritional reserves in old age. Similarly, continuous decline in thermal tolerance was reported for *T. castaneum* with age, which could be attributed to the reduced body mass at advanced age. However, the effects of ageing on body mass of *T. castaneum* could be strain-specific (Halle et al. 2015) as not all studies report a decrease in body mass with age (Soliman 1987). In a study on *T. confusum*, it has been reported that the oxygen sensitivity increased with the age of the beetles; however, did not affect the longevity of the insects (Lee and Ducoff 1983). Further, a continuous decline in the emigration tendency was also reported for *T. castaneum* and *T. confusum* (Ziegler 1976). This decline in emigration tendency with age could be attributed to several causes including degeneration of cell organelles, decline in glycogen reserves, genetically programmed expression of deleterious changes in respiratory enzymes and lack of protein synthesis after maturation (Perez-Mendoza et al. 2011). Similarly, in a study on *C. ferrugineus*, it has been reported that the refuge seeking behavior tended to be lower in older beetles compared to younger beetles, possibly due to their reduced response to pheromones and abundant oviposition sites in the grain filled refuges (Cox et al. 1990).

Another interesting aspect with respect to aging in *T. confusum* and *T. castaneum* is their reduced susceptibility to infection and improved immune capabilities (Vogelweith et al. 2017; Keymer 1982). In a study conducted on *T. castaneum*, an age-related improvement in the baseline constitutive immune response was reported. However, the increase in immune function essentially did not translate into higher-post infection survivorship, probably due to other aspects of senescence that make older individuals more susceptible to infections (Khan et al. 2016a). It has been reported that the propensity of *T. castaneum* to destroy eggs increases with age, reaching a maximum around 105 d, and later falls off as old age is attained. Thus, old age has predominantly limited effects on the population of insects due to associated fitness costs and cannibalism effects.

Understanding the age-related changes in stored-grain insect populations requires knowledge about the changes that cause and control the aging process. It is, therefore, necessary to relate the observable changes to their biochemical basis and thereby manipulate the ageing process physiologically and genetically (Soliman and Lints 1982). Areas concerning growth, nutrition, ultrastructural changes, and behavior need further investigation to understand the age-related changes in stored-grain insects (Soliman 1987).

2.3.12 Diseases

The incidence of diseases in stored grain beetles declines their population (Rashki et al. 2019; Onstad and Maddox 1990). Disease-causing fungal, protozoan, viral, and bacterial infections have major implications on the growth, differentiation, sexual behavior, and evolution of stored grain insects, thereby influencing their population dynamics (Hurd 1993). The major disease-causing pathogens in stored grain insect hosts are summarized in Table 7. These effects are evident in reduced reproductive output, offspring survivorship, and longevity (Kumano et al. 2010). Various parameters are used to indicate these reproductive disturbances including the ability to lay viable eggs (Mercer and Wigley 1987), the incidence of locked matings (Gaugler and Brooks 1975), frequency of mating (Armstrong and Bass 1986), fecundity, and egg viability. The reduction in fecundity could be attributed to nutritional deprivation (Malone 1987), depletion of fat and protein reserves due to microsporidial infection of insect fat bodies (Thompson and Sikorowski 1979), reduced vitellogenin production (Gaugler and Brooks 1975), and massive germ cell destruction (Sajap and Lewis 1988). Further, protozoan diseases result in reduced longevity and prolonged larval period due to the induction of a juvenile hormonal effect causing larval-pupal and pupal-adult intermediate forms influencing population growth and differentiation (Rabindra et al. 1981). Therefore, pathogens can be effectively utilized for biological control of stored-grain insects alone or in combination with selective insecticides (Batta and Kavallieratos 2018).

Table 7. Major disease-causing pathogens in stored grain insects

Pathogenic species	Insect hosts
Nosema whitei	*Tribolium castaneum*
	Tribolium confusum
Farinocystic tribolii	*Tribolium castaneum*
	Tribolium confusum
	Tribolium garnhami
Mattesia ***spp.***	*Sitophilus zeamais*
	Rhyzopertha dominica
	Plodia interpunctella
	Cryptolestes ferrugineus
	Oryzaephilus surinamensis
Adelina ***spp.***	*Tribolium castaneum*
	Rhyzopertha dominica
Gregarina ***spp.***	*Tribolium castaneum*
	Tenebrio molitor
	Plodia interpunctella
Beauveria bassiana	*Rhyzopertha dominica*
	Oryzaephilus surinamensis
	Cryptolestes ferrugineus
	Tribolium castaneum
Lymphotropha tribolii	*Tribolium castaneum*

2.4 Life cycle and morphology of *T. castaneum*

T. castaneum undergoes a complete metamorphosis comprising four stages of life cycle: egg, larva, pupa and adult (Fig. 1). The development time is influenced by environmental (temperature, RH, and food) and genetic factors. Under optimal conditions of food, temperature, and relative humidity, the life cycle may be as short as 3 – 4 weeks; however, it might vary among different strains of the species (Pai 2019). The optimum temperature and RH for their growth and development is 30 - 37℃ and 70% RH (Singh and Prakash 2015). Temperatures approaching the optimum ranges significantly accelerate the immature development time, resulting in the faster emergence of larvae or pupae compared to sub-optimal conditions (Skourti et al. 2019). The life cycle commences when mature female adults lay eggs between or on the stored product. At optimal conditions, embryogenesis in *T. castaneum* lasts 3.5 to 5 days, followed by larval and pupal stages lasting 2 to 3 weeks and 5 – 6 days, respectively (Pai 2019). Adults generally have a lifespan of 1 to 6 months in laboratory conditions, although they may live up to more than 3 years. The adult beetles are highly prolific, with an average lifetime fecundity of more than 300 eggs (Kumar et al. 2018; Campbell and Runnion 2003); however, fecundity drops after 3-4 months due to the using up of their germ cells.

The eggs of *T. castaneum* are white-colored, translucent, sticky, slender and cylindrical in appearance. Their stickiness often causes them to be coated with flour or stick to the walls of the storage containers (Devi and Devi 2015). The larvae are worm-like, yellowish brown in colour, measuring about 1 mm in length. They have six to seven instar stages and become well sclerotized and 4-5 mm long when fully grown. The larval instars can be fairly distinguished from each other due to the certain unique characteristics (Devi and Devi 2015). The duration of larval period is influenced by food type, availability, and quality and on the prevailing conditions of temperature and humidity (Haines 1991). The pupae are white in color, dorsally covered with fine hairs, has dark wings, well-developed eyes, and sclerotized legs (Abdullahi et al. 2019). The pupae carry gin traps, laterally on each abdominal segment, which are outgrowths with strong sclerotized teeth. Although pupae are quiescent, they exhibit wriggling movement, which moves the gin traps of two abdominal segments relative to each other. Beetles can be sexed at pupal stage, where female pupae have larger genital papillae (two finger-like structures anterior to the pointed urogomphi) than male pupae, when viewed under a microscope. The adult beetles are 2.3–4 mm in length, red-brown colored, oblong and have a flat body. The adults have functional hind wings, used in flight.

Distinguishing the sexes is also possible at adult stage, as forelimbs of male adults have a gland, absent in females (Pointer et al. 2021). Nevertheless, sexing the beetles at the pupal stage is easier as they are relatively immobile (Sreeramoju et al. 2016).

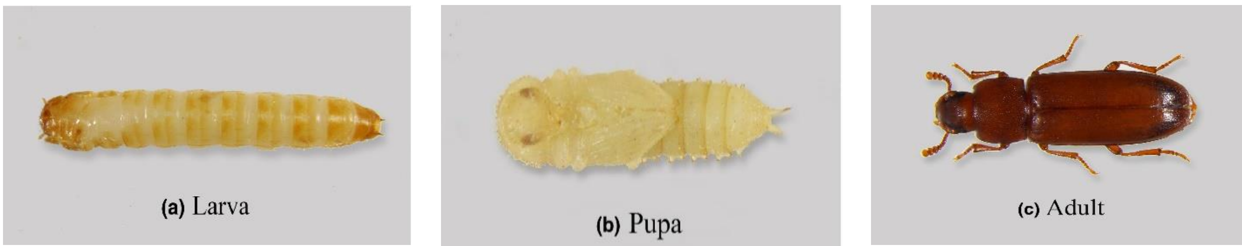

Fig. 1. Different life stages of *T. castaneum* (Source: Khan et al. (2016b), re-used under open access license CC BY 4.0 2023)

2.5 Knowledge gap and objectives

Researchers have reported on the various factors influencing the population dynamics of *T. castaneum* including grain temperature (Arthur et al. 2019b; Halliday et al. 2015; Scharf et al. 2015a), moisture content (Dars et al. 2001), insect density (Dukić et al. 2016), climatic variability (Tripathi et al. 2021), patch size (Tripathi et al. 2021), intra and interspecies interactions (Bullock et al. 2020; Hulasare et al. 2003; Goodnight and Craig 1996), diet type and quality (Arthur et al. 2019a; Khalid et al. 2019; Dukić et al. 2016), and geometry (volume and surface area) of the grain bulk (Garcia et al. 1990; McDonald 1968). However, the majority of this research was based on small scale experiments (with grain quantity < 1 kg) mostly performed on whole wheat, and therefore yield results which are limited in scope of application to bulk grain storage and for a secondary feeding insect like *T. castaneum*. There is a lack of published literature about the influence of diet and surface area on the population dynamics of *T. castaneum*, a secondary feeding pest under large scale storage conditions.

The objectives of this study are:

1. To determine the density distribution of *T. castaneum* in 14 kg wheat patches.
2. To understand the effect of a cracked wheat-based diet on the population dynamics of *T. castaneum.*
3. To understand the effect of top surface area on the population dynamics of *T. castaneum.*

3. MATERIALS AND METHODS

3.1 Wheat

About 800 kg of hard red spring wheat (variety: CS Daybreak, CWRS Grade-1) was procured at once from Pitura Seed Service Ltd., Altona, Manitoba. The moisture content of the wheat was measured by using ASABE standard (ASABE Standards 2016) and was 12.0% (wet basis). The moisture content of the wheat was adjusted to 14.5% by adding 29.2 mL of distilled water per kg of wheat. The wheat and added distilled water were tumbled for 30 min in a tumbler type batch mixer with 75 kg capacity for evenly distributing the water. The conditioned wheat was stored in sealed plastic bags at the room temperature for two weeks. The desired amount of the conditioned wheat was cracked by using a grinding mill (Model 4E Grinding mill, QCG systems LLC, Phoenixville, PA, USA). The wheat and cracked wheat were disinfected by freezing at -15°C for three weeks before using.

3.2 Rearing and sexing of insects

The insects were reared in a mixture of wheat flour and brewer's yeast (19:1 ratio by mass) at 30°C and 70 ± 5% RH. Adults were separated from the laboratory colony culture by sieving and aspirating with a laboratory vacuum pump. About 100 adults were introduced into a jar containing 2 kg of rearing media and incubated at 30°C and 70% RH to allow mating and egg-laying for five days. The jar was closed with a screen lid covered with a layer of filter paper enabling air exchange. The adults from the jar were then sieved out five days later, and the rearing media containing eggs were incubated at the rearing condition for 21 d. Pupae were separated from the culture and the sex of the pupae was determined by checking pupal genital papillae under a microscope (Halstead 1963). About 700 pupae were sexed. The sexed female and male pupae were separately kept in glass vials containing 30 g rearing media, with each vial containing 10 pupae. These vials were incubated at 30℃ and 70% RH. Once the adults emerged from these vials, they were sieved out and separately kept in glass jars containing rearing media at the rearing condition for 10 d. These 10-day old adults were used for this study.

3.3 Grain containers

Two types of grain containers were used: long vertical PVC columns (LVC) (Fig. 2) and shallow containers (SCs) (Fig. 3). The LVC was the same as used by Tripathi et al. (2021) and had a 150 mm inner diameter and was 1.2 m long. To count the insect number inside each section of a LVC, each section was cut halfway along its cross-section at nine places which made 10 sections by inserting nine metal plates in the cut slots. Each section was 90 mm long. During the experimental period, the slots were sealed with duct tape. Each LVC was filled with 14 kg of whole wheat, before introducing the sexed adults. The shallow containers (SC) were transparent plastic containers with transparent lids. Holes of 50 mm diameter were drilled onto these lids, and these holes were covered by one layer of filter paper to ensure the exchange of air between the inside and outside of each container, while restricting the entry of insects and mites from the outside. The inner dimension of each SC was 660 mm long, 460 mm wide, and 150 mm high. The shallow containers were used to study two growth substrates: whole wheat and a mixed diet made of whole wheat and cracked wheat (19:1 ratio by mass). The containers used to study whole wheat were filled with 14 kg of whole wheat each and were referred to as SCWs in this study. The containers used to study the mixed diet were filled with 14 kg of the mixed diet and were referred to as SCCs in this study. The columns and containers were cleaned and disinfected using soap and hot water before loading the growth substate. After loading the substrate, a lining of Teflon (Fluon, PTFE-

30LX Insect barrier) was applied along the top inner walls of the columns (about 10 mm) and containers (about 10 mm) to prevent insects from escaping.

Fig. 2. Long vertical columns (LVCs) used in the experiment.

Fig. 3. Shallow containers (SCs) used in the experiment.

3.4 Experimental procedure

The entire experiment was conducted inside an environmental chamber (C1010, CONVIRON, Winnipeg, Manitoba, Canada) set at 30°C and 70% RH. All the columns and containers filled with wheat or mixed diet were placed inside the environmental chamber. Once the grain reached 30°C, three pairs of 10-day old virgin female and male adults were introduced into each column or container. The LVCs were then closed with a layer of mesh nylon cloth that was secured with elastic bands. The SCs were covered with their lids. A total of 18 LVCs, 18 SCWs, and 18 SCCs were prepared. The 18 LVCs were kept vertically, so the insect population dynamics in each section of the column in a vertical direction could be determined. The surface area of the grain inside each LVC was 0.0177 m^2. The 18 SCWs and 18 SCCs were placed horizontally, and the grain inside each SC had a surface area of 0.3036 m^2. The insect population dynamics in whole wheat or cracked wheat diet with a larger surface area were determined in these SCs. Insect numbers inside each LVC or SC were counted every 4 wk. At each counting time, three LVCs, three SCWs, and three SCCs were removed from the environmental chamber. For sampling each section of LVC, nine semi-circular metallic plates were inserted into the cut slots after the duct tapes were removed. The wheat from the first section was removed first, and then the next section was emptied. The process was repeated to empty all ten sections of each LVC. The growth substrate inside the SCs was removed entirely once. The removed growth substrates from the LVCs and SCs were sieved with a sieve (#10, 2 mm opening for whole wheat; and #14, 1.4 mm opening for mixed diet) on a shaker (AS400, Retsch GmbH, Haan, North Rhine-Westphalia, Germany) for 3 min. The separated adults from the growth substrate were counted using a laboratory aspirator. The live and dead adult numbers (adults with no movement of legs when touched) were recorded. The counted adults were discarded, and the growth substrate containing larvae, pupae, eggs, and dockage were incubated at 30℃ and 70% RH for 4 wk. The grains corresponding to different sections of the LVCs were carefully returned back in their order into the LVCs, after securing the sampling slots with duct tapes. The adults were counted from LVCs and SCs after the incubation and were recorded as the offspring at the first sieving time. The sampling method for the LVCs was the same as for the first sieving time. The experiment was terminated when the insect numbers inside the last LVC and SC were determined (at 24 wk).

3.5 Data analysis

The adults (live and dead) numbers and offspring numbers were combined and termed as 'all insect numbers'. A statistical software (R Core Team 2023) was used for all statistical analysis. All insect density, live adult density, offspring density and dead adult density (insect number per kg of grain) were computed. The densities inside each LVC were calculated for the entire column as well as for each section.

Kruskal-Wallis test was performed to find if there is any statistically significance difference between insect densities along the various sections of LVCs at each storage time. To find whether the surface area of grain bulk influenced the population dynamics, comparison of insect densities and adult mortalities between the SCWs and the top section of LVCs and the entire LVC were conducted using the non-parametric Wilcoxon signed rank test, as the insect densities and mortality failed the normality test. To find whether the diet material influenced the population dynamics, comparison between the insect densities and mortality in SCWs and SCCs were done. All the statistical tests were conducted at 95% confidence level.

The population increase rate for insects (all insects and adults) at a given storage time were calculated as:

All insects' increase rate = $\frac{N_{t+1}}{N_t}$

Where, N_{t+1} and N_t are the all insect number at the current and previous times, respectively. The same method was used for calculating the adult increase rate.

4. RESULTS

4.1 Density and mortality of *T. castaneum* population in vertical columns

The adults and offspring of *T. castaneum* showed variations in their density and mortality along the length of the LVCs (Fig. 4). The adult densities were always the highest in the topmost sections across all the storage times, the offspring densities were the highest in the topmost sections in most of the time, while adult mortality were not (Fig. 4). Results of Kruskal – Wallis test indicated that there were significant differences ($\chi^2(9) = 23.72$, $p < 0.01$) in adult density at different sections of the LVCs by the end of 4th week of storage. However, no significant difference was recorded for adult densities at the other storage times (Table 8). This lack of significance was caused by the variations among replicates because total insect number in different columns had big difference (Fig. 5). For example, in 12 wk, the total insect number in the three LVC was 287, 30 and 82, respectively. Towards the later storage times, adult densities dispersed throughout the lower sections of LVCs, more offspring were counted in the top sections, and higher mortality was recorded in the bottom sections. The higher mortality in the bottom sections might explain the lower live insect numbers in those sections. Despite the higher offspring densities in the topmost sections in the later weeks of storage, the lack of significant difference might be due to variation among replicates (Fig. 6).

Table 8. Comparison of insect densities at different sections of LVCs and different storage times

Storage time (wk)	Adult density (adult/kg)		Offspring density (offspring/kg)	
	χ^2	*p*	χ^2	*p*
4	23.72	0.004*	5.83	0.75
8	10.30	0.32	13.11	0.15
12	5.28	0.80	5.83	0.75
16	6.75	0.66	15.65	0.07
20	6.85	0.65	13.96	0.12
24	5.62	0.77	11.46	0.24

Comparison of insect densities between different sections of LVC (Kruskal-Wallis test at α = 0.05 level) and different storage times. The χ^2 and *p* are χ^2 and *p* values of the *Kruskal – Wallis test* (N = 3, df = 9), respectively.

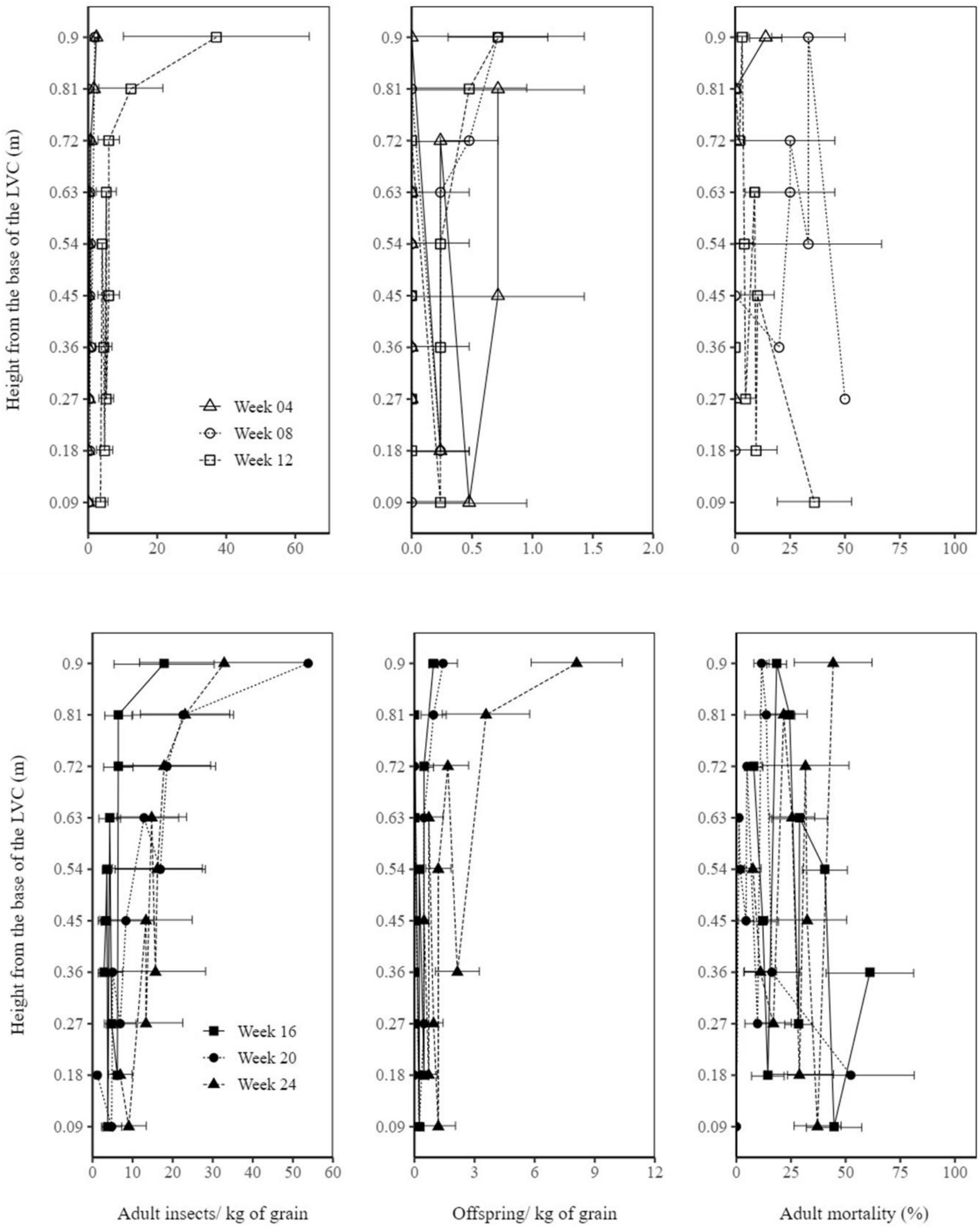

Fig. 4. Density (adult and offspring) and adult mortality in different sections of LVCs (Long vertical columns) at various storage times.

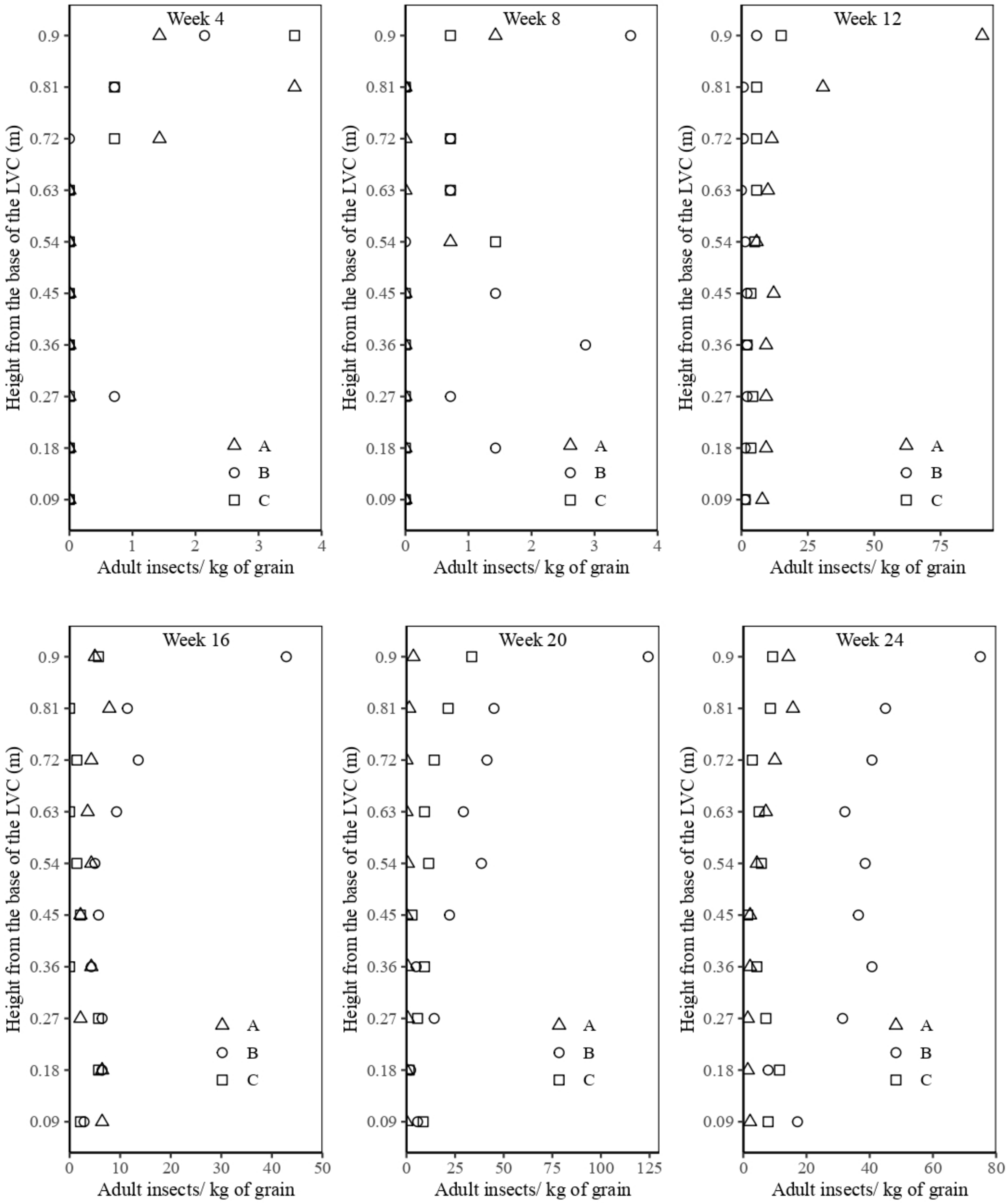

Fig. 5. Adult densities in different sections of LVCs at different storage times. A, B, and C represent the three different replications.

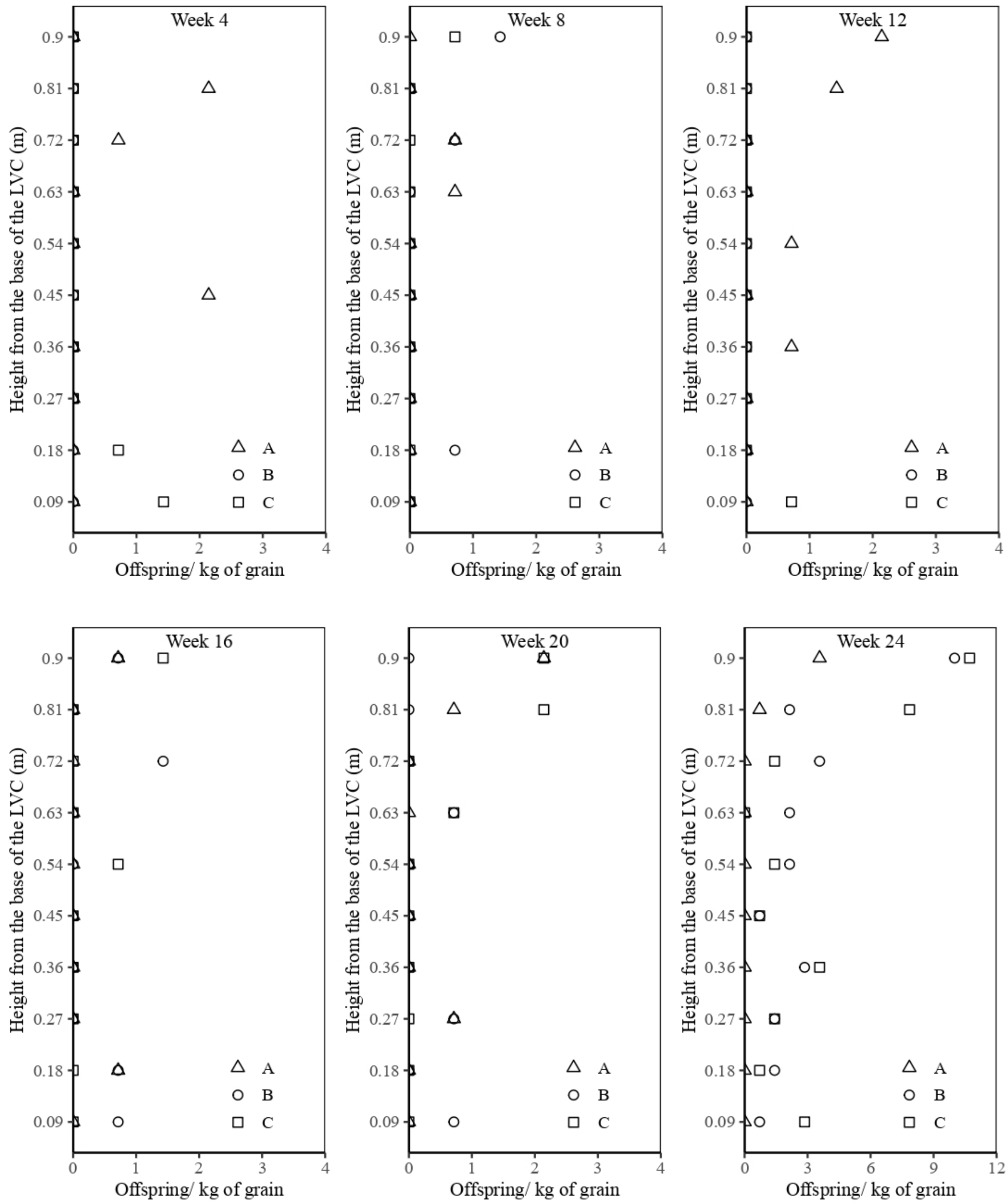

Fig. 6. Offspring densities in different sections of LVCs at different storage times. A, B, and C represent three different replications.

4.2 Density and mortality of *T. castaneum* in shallow containers

Insect densities (all adults and offspring) inside the SCCs were higher than inside SCWs for most of the storage times (Fig. 7, Table A1). It was observed that SCWs had higher adult mortality than SCCs, except for the initial weeks of storage. These results indicated that *T. castaneum* multiplies and develops better in cracked wheat than in whole wheat, and higher mortality in whole wheat bulk might be one of the reasons for the low insect density.

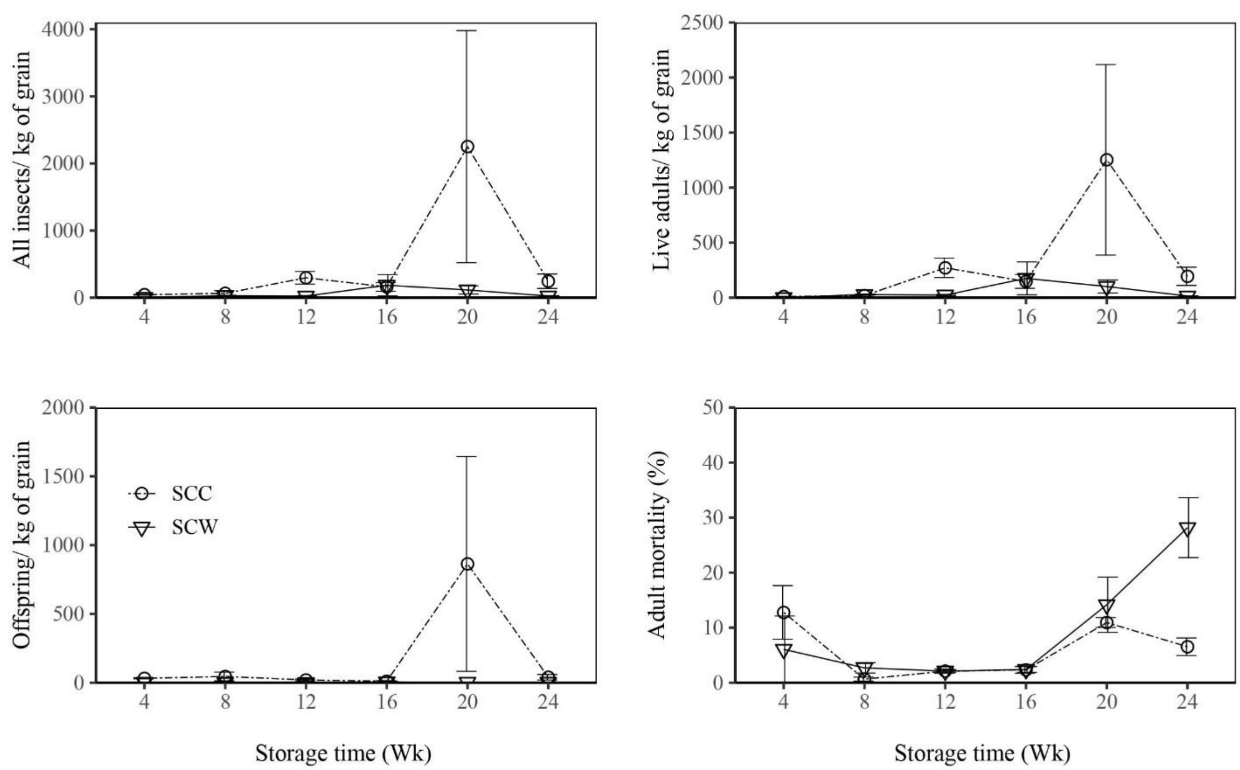

Fig. 7. Insect densities (live adults and offspring) and adult mortality in SCWs (Shallow container filled with wheat) and SCCs (Shallow container filled with mixed diet) at different storage times.

4.3 Effect of diet on population dynamics

No significant difference was observed between all and adult insect densities and mortality values between *T. castaneum* reared on whole wheat and modified diet (Table 10). The no-difference was mainly caused by the no-differences at the beginning and the end of the storage time (Fig. 7). The offspring densities inside the SCWs and SCCs, exhibited significant difference (Table 9). At the end of the storage time, higher mortality (more than 30%) occurred in the whole wheat after the insect density reached peak, so the insect density reduced. Therefore, diet influenced the population dynamics of *T. castaneum.*

Table 9. Effect of diet and top surface area on the insect densities and mortality of *T. castaneum*

Comparison [a]	All insect density (insect/kg)		Adult density (adult/kg)		Offspring density (offspring/kg)		Adult mortality (%)	
	z^b	p^b	z^b	p^b	z^b	p^b	z^b	p^b
LVC – SCW	-2.15	0.03*	-1.67	0.09	-2.15	0.03*	-1.67	0.09
LVC_{top} –SCW	-0.77	0.44	-0.77	0.43	-0.40	0.68	-1.67	0.09
SCW – SCC	-1.86	0.06	-1.23	0.22	-2.15	0.03*	-0.77	0.43
LVC - SCC	-2.15	0.03*	-2.15	0.03*	-2.15	0.03*	-1.67	0.09
LVC_{top} – SCC	-2.15	0.03*	-2.15	0.03*	-2.15	0.03*	-2.15	0.03*

[a] Comparison between different treatments by conducting Wilcoxon signed rank tests at α = 0.05 level. LVC, SCW, SCC and LVC_{top} indicated the insect density inside long vertical columns, shallow container filled with wheat, shallow container filled with modified diet and top section of the long vertical columns, respectively, were used in the comparison.

[b] The *z* and *p* are *z* and *p* statistic values of the Wilcoxon signed rank test (*N* = 6), respectively.

4.4 Effect of top surface area on population dynamics

All insect and offspring densities and mortality inside the entire LVCs and SCWs were significantly different. No significant difference was observed when the insect densities and mortality values inside top section of LVCs and in the entire SCWs were compared (Table 9). Insects (adults and offspring) in SCWs attained peak density (16^{th} wk) sooner than in the entire

LVCs (24th wk) and in the top section of LVCs (20th and 24th wk, respectively for adult and offspring density). The top section of LVCs (20th wk) also reached peak adult density sooner than the entire LVCs (24th wk). The sooner attainment of peak density could imply that a larger surface area might provide some benefit for insect growth and development because mortality in the sections with larger area was low before insect density reached peak.

The population increase rate within the entire LVCs and top section of LVCs was different from that of SCWs and SCCs (Fig. 8). At 4 wk, insects in the SCCs had significantly higher increase rate, than any other treatment conditions. This result indicates that the combination of larger surface area and a modified diet is advantageous for insect multiplication and/ or survival rate in less than 4 wk. At 8 wk, insects in any containers had the same population increase rate except that in the SCW, which had a significantly higher increase rate, implying increased surface area could benefit *T. castaneum* population, regardless of the diet material. The population in whole wheat declined at 12 wk, and peaked at 16 wk, and then declined. In the cracked wheat, the population had three peaks of population increase rate at 4, 12, and 20 wk. The third peak was the highest than any other periods and treatment (Fig. 8). The substantially high initial increase rate and highest peak could indicate that cracked wheat with a larger surface area could provide a larger carrying capacity of insect population than any other treatment, even though there were fluctuations in the population increase rates for all the treatments (Fig. 8). After 8 wk, all insects and adults in the LVCs and top section increased with a maximum increase rate (10.23 and 11.58, respectively) in 12 wk, then declined, followed by another increase (2.06 and 2.64, respectively) at 20 wk, and then declined. The second peak in the LVC was smaller than that in SCC and SCW. This result indicated that whole wheat with a small surface area had a smaller carrying capacity of insect population due to a larger mortality in the bottom sections of the LVCs. Therefore, whole wheat plus cracked wheat in a larger surface container could have a quicker population increase rate and larger carrying capacity than any other treatments tested in this study.

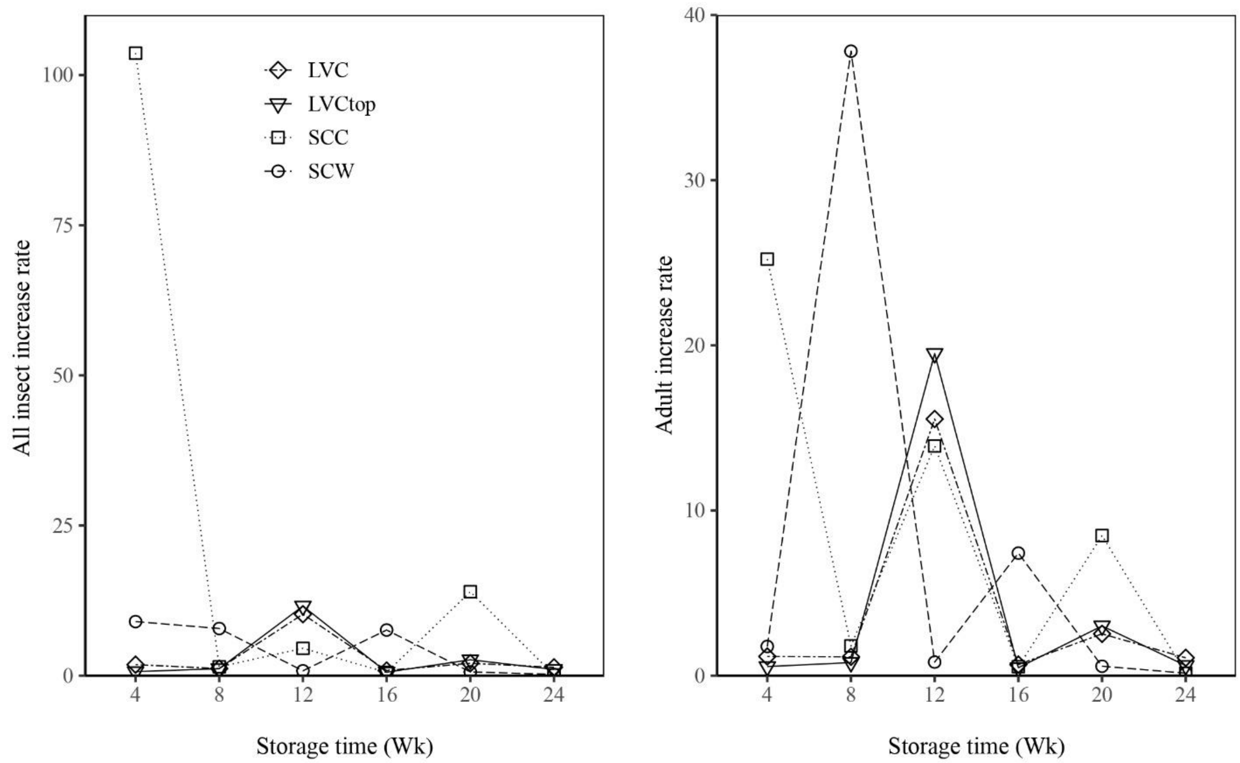

Fig. 8. All and adult insects increase rate under different experimental conditions in different storage times. LVC, LVCtop, SCC and SCW are long vertical columns, top section of the LVC, shallow container filled with modified diet, and shallow container filled with wheat, respectively.

5. DISCUSSIONS

5.1 Density distribution of *T. castaneum* population

The distribution of *T. castaneum* in a food patch may depend on various factors including temperature, moisture content, insect density, insect age, insect sex, patch size, patch quality, and variable goals of patch exploitation (Jian 2019; Campbell and Hagstrum 2002). Individuals of *T. castaneum* are reported to have highly clumped distribution at low and medium densities (Jian et al. 2012). When insect densities became higher, it resulted in overcrowding, which forced insects to disperse to bottom sections of the LVCs (Fig. 4). The offspring densities were relatively uniform throughout the different sections of LVCs during the first 12 wk of storage. These results suggested that adults moved down and laid eggs in the bottom sections. After 12 wk, more adults and offspring were found in the top sections, adult mortality was also higher in the bottom sections (Fig. 4). Therefore, higher mortality in the bottom sections of the vertical columns with small surface area might be one of the main reasons for the higher insect number at the top sections of the vertical columns. Researchers suggested that *T. castaneum* preferred and were most likely to be found in the surface of wheat bulk, due to the barrier effect of the smaller intergranular spaces in wheat bulk (Jian et al. 2005, 2012; Ogden 1970). Other reasons for the lower densities could be lower oviposition (Halliday et al. 2019; Sonleitner and Gutherie 1991) and higher cannibalism by the active life stages (adults and larvae) (Young 1970; Lloyd and Park 1962). Though low oviposition and higher cannibalism should be similar in both top and bottom sections of the vertical columns. Therefore, the preference of the top sections plus higher mortality in the deep grain might result in the top clumped distribution in grain bins.

5.2 Effect of diet on the population dynamics

The adequacy of a diet at behavioral, digestive, and metabolic levels is determined by the differences in intake, digestibility and efficiency of conversion of food to body substance (Waldbauer and Bhattacharya 1973). Cracked wheat has the inherent advantage of exposed germ portion, and germ portion is regarded extremely suitable for *Tribolium* spp. The consumption of germ in the cracked wheat further ensures low food intake and high overall efficiency owing to the high digestibility and efficient utilization of the digested portion (Waldbauer and Bhattacharya 1973). Further, cracked wheat is easier to consume and therefore insects expend less energy and time, thus thrive longer (White and Bell 1993). Conversely, secondary insects reared in undamaged whole grain kernels have reduced fecundity, lower survival, and delayed development times. Previous studies have reported that whole grains produce less number of pupae compared to cracked wheat and flour (Ahmad et al. 2012). These facts are supported by the results in this study which showed a higher insect number in the cracked wheat than that in whole wheat before peak density was reached (Fig. 5). During the entire storage time, except for the first 4 wk, higher mortality in whole wheat than in cracked wheat was recorded (Fig. 5). The higher mortality on whole wheat could be due to the difficulty in feeding and extracting nutrients, due to the harder outer layer of wheat kernels. The difficulty in consumption might result in difficulty in the maintenance of life of beetles after eclosion (Sokoloff et al. 1966), which could be a reason for high mortality. On attaining the peak density, the mortality was approximately 30% in the SCWs as against 5% in the SCCs, and therefore higher mortality might be the main reason for lower insect densities inside the SCWs. Apart from higher mortality, the effects of crowding (Peters and Barbosa 1977), cannibalism of immatures by adults (Li and Arbogast 1991), reduction in overall lifespan (Spratt 1980), diet depletion (Arthur et al. 2019b), and overall weight loss of insects (Assie et al. 2008) might also contribute to the reduction in insect densities.

5.3 Effect of top surface area on the population dynamics

Researchers in the past, have reported growth medium in larger shallow surfaces had a significantly greater number of *T. castaneum* adults than that in small surface deep orientation (Garcia et al. 1990). They concluded that the surface area of the growth medium has strong effect on the productivity of *T. castaneum*. Many adult interactions take place particularly in the surface of the medium (Sonleitner 1961), and greater surface area could imply relative ease of finding mating partners and resources. Increased surface area could be seen as more efficient utilization of available resources (Wool and Mendlinger 1981). The results of our study confirmed those conclusions because LVCs, characterized by smaller surface area, had a smaller carrying capacity of insect population due to their higher mortality. The SCWs characterized by higher surface area had the highest population increase rate at 8 wk, than any other treatments. Further, SCCs characterized with a larger surface area and cracked wheat diet, had a significantly higher increase rate at 4 wk and had its third population peak density significantly higher than any other treatments, indicating larger carrying capacity. The combination of benefits associated with the cracked wheat (ease of consumption, high digestibility, efficient utilization of digested portion and high overall efficiency), and the larger surface area (relative ease of finding partners and resources), might have favoured the multiplication of *T. castaneum*, thus resulting in quicker population increase rate and higher carrying capacity in the SCCs.

6. CONCLUSIONS

This study has led to the following conclusions:

1. Adults and offspring concentrated in the top section of the vertical columns, due to the higher mortality in the lower sections of the columns.
2. *Tribolium castaneum* multiply and develop better in cracked wheat than in whole wheat, and higher mortality in whole wheat bulk might be one of the reasons of the low insect density.
3. Whole wheat plus cracked wheat in a larger surface container had a quicker population increase rate and larger carrying capacity than any other treatments tested in this study.
4. Preference for top grain plus higher mortality in the deep grain might result in the top clumped distribution in grain bins for *T. castaneum*.

7. REFERENCES

Abdelsamad, R.M., E.A. Elhag and Y.M. Eltayeb. 1988. Studies on the phenology of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) in the Sudan Gezira. *Journal of Stored Products Research* 24(2): 101–105. https://doi.org/10.1016/0022-474X(88)90038-0.

Abdullahi, G., R. Muhamad and H. Sule. 2019. Biology, host range and management of red flour beetle *Tribolium castaneum* (Herbst)(Coleoptera: Tenebrionidae): a review. *Taraba Journal of Agricultural Research* 7(1): 48–64. https://www.researchgate.net/profile/Gambo-Abdullahi/amp

Abedin, M.Z., M.Z. Rahman, M.I.A. Mia and K.M.M. Rahman. 2012. In-store losses of rice and ways of reducing such losses at farmers' level: An assessment in selected regions of Bangladesh. *Journal of the Bangladesh Agricultural University* 10(1): 133–144. https://doi.org/10.3329/jbau.v10i1.12105.

Adarkwah, C., D. Obeng-Ofori, E. Opuni-Frimpong, C. Ulrichs and M. Schöller. 2019. Predator-parasitoid-host interaction: biological control of *Rhyzopertha dominica* and *Sitophilus oryzae* by a combination of *Xylocoris flavipes* and *Theocolax elegans* in stored cereals. *Entomologia Experimentalis et Applicata* 167(2): 118–128. https://doi.org/10.1111/EEA.12760.

Agah, A.A. 1961. The biology of *Sitotroga cerealella*: with special reference to food and the effects of extreme physical conditions. Imperial College London.

Aguila, J.R., J. Suszko, A.G. Gibbs and D.K. Hoshizaki. 2007. The role of larval fat cells in adult *Drosophila melanogaster*. *Journal of Experimental Biology* 210(6): 956–963. https://doi.org/10.1242/jeb.001586.

Ahmad, F., G.H. Walter and S. Raghu. 2012. Comparative performance of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) across populations, resource types and structural forms of those resources. *Journal of Stored Products Research* 48: 73–80. https://doi.org/10.1016/J.JSPR.2011.09.005.

Alabi, T., J.P. Michaud, L. Arnaud and E. Haubruge. 2008. A comparative study of cannibalism and predation in seven species of flour beetle. *Ecological Entomology* 33(6): 716–726. https://doi.org/10.1111/J.1365-2311.2008.01020.X

Andreadis, S.S. and C.G. Athanassiou. 2017. A review of insect cold hardiness and its potential in stored product insect control. *Crop Protection* 91: 93–99. https://doi.org/10.1016/j.cropro.2016.08.013

Annis, P. 1987. Towards rational controlled atmosphere dosage schedules: a review of current knowledge. In *Proc. 4th Int. Work. Conf. Stored-Product Protection*. https://cir.nii.ac.jp/crid/1572543025490151680 (2023 /4/4)

Arbogast, R. 1991. Beetles: coleoptera. *Ecology and Management of Food-Industry Pests. FDA Technical Bulletin* 4: 131–176.

Arbogast, R.T. 1976. Population parameters for *Oryzaephilus surinamensis* and *O. mercator*: Effect of relative humidity. *Environmental Entomology* 5(6): 738–742. https://doi.org/10.1093/EE/5.4.738.

Arbogast, R.T. and M.A. Mullen. 1988. Insect succession in a stored-corn ecosystem in southeast Georgia. *Annals - Entomological Society of America* 81(6): 899–912. https://doi.org/10.1093/aesa/81.6.899.

Armitage, D.M., D.A. Cook and D.E. Baxter. 2002. Farm-scale experiments to compare infestation and quality changes in malting barley stored at three moisture contents. *Journal of the Institute of Brewing* 108(2): 178–186. https://doi.org/10.1002/j.2050-0416.2002.tb00538.x.

Armstrong, E. and L.K. Bass. 1986. Effects of infection by *Nosema whitei* on the mating frequency and fecundity of *Tribolium castaneum*. *Journal of Invertebrate Pathology* 47(3): 310–316. https://doi.org/10.1016/0022-2011(86)90101-1.

Arthur, F.H., B.A. Hale, L.A. Starkus, A.R. Gerken, J.F. Campbell and T. McKay. 2019a. Development of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) on rice milling components and by-products: Effects of diet and temperature. *Journal of Stored Products Research* 80: 85–92. https://doi.org/10.1016/j.jspr.2018.11.001.

Arthur, F.H., K.L. Hartzer, J.E. Throne and P.W. Flinn. 2015. Susceptibility of *Tribolium castaneum* (Coleoptera: Tenebrionidae) and *Trogoderma inclusum* (Coleoptera: Dermestidae) to cold temperatures. *Journal of Stored Products Research* 64: 45–53. https://doi.org/10.1016/J.JSPR.2015.07.006.

Arthur, F.H., L.A. Starkus, A.R. Gerken, J.F. Campbell and T. McKay. 2019b. Growth and development of *Tribolium castaneum* (Herbst) on rice flour and brown rice as affected by time and temperature. *Journal of Stored Products Research* 83: 73–77. https://doi.org/10.1016/J.JSPR.2019.04.005.

ASABE Standards. 2016. S352.2: Moisture Measurement - Unground Grain and Seeds, ASABE, St. Joseph, MI.

Ashby, K.R. 1961. The population dynamics of *Cryptolestes ferrugineus* (Stephens) (Col., Cucujidae) in flour and on Manitoba wheat. *Bulletin of Entomological Research* 52(2): 363–379. https://doi.org/10.1017/S0007485300055462.

Aslam, M., D. Hagstrum and B. Dover. 1994. The effect of photoperiod on the flight activity and biology of *Rhyzopertha dominica* (Coleoptera: Bostrichidae). *Journal of the Kansas Entomological Society* 107–115. https://www.jstor.org/stable/25085494

Aspaly, G., V. Stejskal, S. Pekár and J. Hubert. 2007. Temperature-dependent population growth of three species of stored product mites (Acari: Acaridida). *Experimental and Applied Acarology* 42(1): 37–46. https://doi.org/10.1007/S10493-007-9074-1.

Assie, L.K., Y. Brostaux and E. Haubruge. 2008. Density-dependent reproductive success in *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae). *Journal of Stored Products Research* 44(3): 285–289. https://doi.org/10.1016/j.jspr.2008.02.007.

Astuti, L.P., Y.E. Lestari, R. Rachmawati and Mutala'liah. 2020. Preference and development of *Tribolium castaneum* (Herbst, 1797) (Coleoptera: Tenebrionidae) in whole grain and flour form of five corn varieties. *Biodiversitas Journal of Biological Diversity* 21(2). https://doi.org/10.13057/BIODIV/D210218

Athanassiou, C.G. and F.H. Arthur. 2018. *Recent Advances in Stored Product Protection*. https://doi.org/10.1007/978-3-662-56125-6.

Athanassiou, C.G., N.G. Kavallieratos and M.C. Boukouvala. 2016. Population growth of the khapra beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae) on different commodities. *Journal of Stored Products Research* 69: 72–77. https://www.sciencedirect.com/science/article/pii/S0022474X16300297

Athanassiou, C.G., N.G. Kavallieratos and J.F. Campbell. 2017. Competition of three species of *Sitophilus* on rice and maize. *PLOS ONE* 12(3): e0173377. https://doi.org/10.1371/JOURNAL.PONE.0173377

Athanassiou, C.G., N.G. Kavallieratos, N.E. Palyvos and C.T. Buchelos. 2003. Three-dimensional distribution and sampling indices of insects and mites in horizontally-stored wheat. *Applied Entomology and Zoology* 38(3): 413–426. https://doi.org/10.1303/aez.2003.413.

Athanassiou, C.G., N.E. Palyvos, P.A. Eliopoulos and G.T. Papadoulis. 2001. Distribution and migration of insects and mites in flat storage containing wheat. *Phytoparasitica* 29: 379–392. https://doi.org/10.1007/BF02981856.

Atkins, J.L., G.L. Perry and T.E. Dennis. 2019. Effects of mis-alignment between dispersal traits and landscape structure on dispersal success in fragmented landscapes. *Royal Society Open Science* 6(1).

Atta, B., M. Rizwan, A.M. Sabir, M.D. Gogi and K. Ali. 2020. Damage potential of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) on wheat grains stored in hermetic and non-hermetic storage bags. *International Journal of Tropical Insect Science* 40: 27–37. https://doi.org/10.1007/s42690-019-00047-0

Aulakh, J., A. Regmi, J.R. Fulton and C.E. Alexander. 2013. Estimating post-harvest food losses: Developing a consistent global estimation framework. In *Proceedings of the Agricultural & Applied Economics Association's 2013 AAEA & CAES Joint Annual Meeting*, Washington, DC, USA.

Awadalla, H.S., R. Narciso, C. Guedes and A.S. Hashem. 2021. Feeding and egg-laying preferences of the sawtoothed grain beetle *Oryzaephilus surinamensis*: Beyond cereals and cereal products. *Journal of Stored Products Research* 93: 101841. https://doi.org/10.1016/j.jspr.2021.101841

Back, E.A. and R.T. Cotton. 1927. Biology of the Saw-Toothed Grain Beetle, *Oryzaephilus surinamensis* Linne. *Journal of Agricultural Research* 33: 1–6.

Baer, B. and P. Schmid-Hempel. 1999. Experimental variation in polyandry affects parasite loads and fitness in a bumble-bee. *Nature* 397(6715): 151–154. https://doi.org/10.1038/16451

Baker, J. and S. Loschiavo. 1987. Nutritional ecology of stored-product insects. *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates. John Wiley & Sons, London, New York* 321–344.

Bala, B.K., M.A. Haque, M.A. Hossain and S. Majumdar. 2010. Post Harvest Loss and Technical Efficiency of Rice, Wheat and Maize Production System: Assessment and Measures for Strengthening Food Security. Bangladish Agricultural University.

Bancroft, J.S. 2001. Intraspecific interaction and mechanisms of population regulation in experimentally limited habitat. *Environmental Entomology* 30(6): 1061–1072. https://doi.org/10.1603/0046-225X-30.6.1061.

Banks, J. and P. Fields. 1994. Physical Methods for Insect Control in Stored-Grain Ecosystems. In *Stored Grain Ecosystems*, 353. CRC Press.

Barrer, P.M., N.T. Starick, R. Morton and E.J. Wright. 1993. Factors influencing initiation of flight by *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae). *Journal of Stored Products*

Research 29(1): 1–5. https://doi.org/10.1016/0022-474X(93)90013-T.

Batta, Y.A. and N.G. Kavallieratos. 2018. The use of entomopathogenic fungi for the control of stored-grain insects. *International Journal of Pest Management* 64(1): 77–87. https://doi.org/10.1080/09670874.2017.1329565.

Begon, M., J.L. Harper and C.R. Townsend. 1986. *Ecology. Individuals, Populations and Communities*. Blackwell scientific publications.

Bell, C. 1981. The influence of light cycle and circadian rhythm on oviposition in five pyralid moth pests of stored products. *Physiological Entomology* 6(3): 231–239. https://doi.org/10.1111/J.1365-3032.1981.TB00267.X

Bell, C.H. 2014. A review of insect responses to variations encountered in the managed storage environment. *Journal of Stored Products Research* 59: 260–274. https://doi.org/10.1016/J.JSPR.2014.06.004.

Bell, C.H. and P.R. Kerslake. 1986. A circadian rhythm influencing foraging behaviour in the saw-toothed grain beetle *Oryzaephilus surinamensis*. *Physiological Entomology* 11(1): 1–6. https://doi.org/10.1111/J.1365-3032.1986.TB00384.X

Benelli, G., D. Romano, C. Stefanini, N.G. Kavallieratos, C.G. Athanassiou and A. Canale. 2017. Asymmetry of mating behaviour affects copulation success in two stored-product beetles. *Journal of Pest Science* 90: 547–556. https://doi.org/10.1007/s10340-016-0794-z.

Benyi, K. and G.A.E. Gall. 1981. Genotype-environment interaction effects on reproductive performance in *Tribolium castaneum*. *Theoretical and Applied Genetics* 59: 123–128. https://doi.org/10.1007/BF00285903.

Birch, L.C., T. Park and M.B. Frank. 1951. The Effect of Intraspecies and Interspecies Competition on the Fecundity of Two Species of Flour Beetles. *Evolution* 116–132. https://doi.org/10.2307/2405763.

Boina, D. and B. Subramanyam. 2004. Relative Susceptibility of *Tribolium confusum* Life Stages Exposed to Elevated Temperatures. *Journal of Economic Entomology* 97(6): 2168–2173. https://academic.oup.com/jee/article-abstract/97/6/2168/2218207

Boldt, P.E. 1974. Effects of Temperature and Humidity on Development and Oviposition of *Sitotroga cerealella* (Lepidoptera: Gelechiidae). *Journal of the Kansas Entomological Society* 47(1): 30–36. https://www.jstor.org/stable/25082618

Bolívar-Silva, D.A., N.M.P. Guedes and R.N.C. Guedes. 2018. Larval cannibalism and fitness in the stored grain weevils *Sitophilus granarius* and *Sitophilus zeamais*. *Journal of Pest Science* 91: 707–716. https://doi.org/10.1007/s10340-017-0921-5

Breese, M.H. 1960. The infestibility of stored paddy by *Sitophilus sasakii* (Tak.) and *Rhyzopertha dominica* (F.). *Bulletin of Entomological Research* 51(3): 599–630. https://doi.org/10.1017/S000748530005519X.

Breese, M.H. 1963. Studies on the oviposition of *Rhyzopertha dominica* (F.) in rice and paddy. *Bulletin of Entomological Research* 53(4): 621–637. https://doi.org/10.1017/S0007485300048379

Buckemüller, C., O. Siehler, J. Göbel, R. Zeumer, A. Ölschläger and D. Eisenhardt. 2017. Octopamine underlies the counter-regulatory response to a glucose deficit in honeybees (*Apis mellifera*). *Frontiers in Systems Neuroscience* 11: 63. https://doi.org/10.3389/FNSYS.2017.00063/BIBTEX.

Bull, C.M. 1991. Ecology of parapatric distributions. *Annual Review of Ecology and Systematics* 22(1): 19–36. https://doi.org/10.1146/annurev.es.22.110191.000315.

Bullock, M., G. Legault and B.A. Melbourne. 2020. Interspecific Chemical Competition Between *Tribolium castaneum* and *Tribolium confusum* (Coleoptera: Tenebrionidae) Reduces Fecundity and Hastens Development Time. *Annals of the Entomological Society of America* 113(3): 216–222. https://doi.org/10.1093/AESA/SAAA001

Burrell, N. and S. Havers. 1976. Effects of cooling on mite infestations in bulk grain. *Annals of Applied Biology*.

Cameron, T.C., H.J. Wearing, P. Rohani and S.M. Sait. 2007. Two-species asymmetric competition: effects of age structure on intra-and interspecific interactions. *Journal of Animal Ecology* 76: 83–93. https://www.jstor.org/stable/4125097

Campbell, J.F. 2002. Influence of Seed Size on Exploitation by the Rice Weevil, *Sitophilus oryzae*. *Journal of Insect Behavior* 15(3).

Campbell, J.F. 2005. Fitness Consequences of Multiple Mating on Female *Sitophilus oryzae* L. (Coleoptera: Curculionidae). *Environmental Entomology* 34(4): 833–843. https://doi.org/10.1603/0046-225X-34.4.833

Campbell, J.F. and R.T. Arbogast. 2004. Stored-product insects in a flour mill: Population dynamics and response to fumigation treatments. *Entomologia Experimentalis et Applicata* 112(3): 217–225. https://doi.org/10.1111/j.0013-8703.2004.00197.x.

Campbell, J.F. and D.W. Hagstrum. 2002. Patch exploitation by *Tribolium castaneum*: Movement patterns, distribution, and oviposition. *Journal of Stored Products Research*

38(1): 55–68. https://doi.org/10.1016/S0022-474X(00)00042-4.

Campbell, J.F. and C. Runnion. 2003. Patch exploitation by female red flour beetles, *Tribolium castaneum*. *Journal of Insect Science* 3(1). https://doi.org/10.1093/JIS/3.1.20

Canada Grain Act. 1975. Canada grain regulations. *Canada Gazette* Part II 10(No. 14): 1708–1839.

Canadian Grain Commission. 2022. Archive of Canadian grain exports (annual). https://www.grainscanada.gc.ca/en/grain-research/statistics/canadian-grain-exports-annual/.

Chahal, G. and G. Simwat. 1975. Development of *Tribolium castaneum* Herbst larvae on different foods, their survival under starvation and longevity of the adults at various temperatures and relative humidities. *Tribolium Inf. Bull.* 18: 83–84.

Chanbang, Y., F.H. Arthur, G.E. Wilde and J.E. Throne. 2008. Hull characteristics as related to susceptibility of different varieties of rough rice to *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae). *Journal of Stored Products Research* 44(3): 205–212. https://doi.org/10.1016/J.JSPR.2007.10.003.

Chapman, R. 1998. *The Insects: Structure and Function*. Cambridge university press.

Chow-Fraser, P. and E.J. Maly. 1988. Aspects of mating, reproduction, and co-occurrence in three freshwater calanoid copepods. *Freshwater Biology* 19(1): 95–108. https://doi.org/10.1111/j.1365-2427.1988.tb00331.x.

Chung, S., W. Choi and M. Ryoo. 1995. Egg laying decision of adzuki bean weevil (Coleoptera: Bruchidae): Effects of seed size and egg distribution pattern on a seed. *Korean Journal of Entomology*. https://agris.fao.org/agris-search/search.do?recordID=KR19970077027

Collatz, J. and J.L.M. Steidle. 2008. Hunting for moving hosts: *Cephalonomia tarsalis*, a parasitoid of free-living grain beetles. *Basic and Applied Ecology* 9(4): 452–457. https://doi.org/10.1016/J.BAAE.2007.04.002.

Collatz, J., T. Tolasch and J.L.M. Steidle. 2009. Mate finding in the parasitic wasp *Cephalonomia tarsalis* (Ashmead): More than one way to a female's heart. *Journal of Chemical Ecology* 35: 761–768. https://doi.org/10.1007/s10886-009-9659-8.

Cotton, R. and W. Ashby. 1952. Insect pests of stored grains and seed. In *Insects, The 1952 Yearbook of Agriculture*, 629–639. US Department of Agriculture Washington.

Cox, P.D. and L.E. Collins. 2002. Factors affecting the behaviour of beetle pests in stored grain, with particular reference to the development of lures. *Journal of Stored Products Research* 38(2): 95–115. https://doi.org/10.1016/S0022-474X(01)00010-8.

Cox, P.D., W.E. Parish and M. Ledson. 1990. Factors affecting the refuge-seeking behaviour of *Cryptolestes ferrugineus* (Stephens)(Coleoptera: Cucujidae). *Journal of Stored Products Research* 26(3): 169–174.

Craig, D.M. 1986. Stimuli governing intraspecific egg predation in the flour beetles, *Tribolium confusum* and *T. castaneum*. *Population Ecology* 28(2): 173–183. https://doi.org/10.1007/BF02515448.

Crombie, A. 1942. The Effect of Crowding Upon the Oviposition of Grain-Infesting Insects. *Journal of Experimental Biology* 19(3): 311–340. https://doi.org/10.1242/jeb.19.3.311.

Crombie, A. 1944. On intraspecific and interspecific competition in larvae of graminivorous insects. *Journal of Experimental Biology* 20(2): 135–151.

https://journals.biologists.com/jeb/article-abstract/20/2/135/4813

Crombie, A.C. 1947. Interspecific Competition. *The Journal of Animal Ecology* 16(1): 44. https://doi.org/10.2307/1506.

Cui, J., Y. Deng, J. Wang, L. Yang, Z. Yang and T. Jiang. 2006. Effects of interspecific competition on the population dynamics of four stored grain insect pests. *Zoological Research* 27(3): 275–280.

Currie, J.E. 1967. Some effects of temperature and humidity on the rates of development, mortality and oviposition of *Cryptolestes pusillus* (Schönherr) (Coleoptera, Cucujidae). *Journal of Stored Products Research* 3(2): 97–108. https://doi.org/10.1016/0022-474X(67)90019-7.

Daglish, G.J. 2006. Survival and reproduction of *Tribolium castaneum* (Herbst), *Rhyzopertha dominica* (F.) and *Sitophilus oryzae* (L.) following periods of starvation. *Journal of Stored Products Research* 42(3): 328–338. https://doi.org/10.1016/J.JSPR.2005.04.003.

Dal Bello, G.M., C.B. Fusé, N. Pedrini and S.B. Padín. 2018. Insecticidal efficacy of *Beauveria bassiana*, diatomaceous earth and fenitrothion against *Rhyzopertha dominica* and *Tribolium castaneum* on stored wheat. *International Journal of Pest Management* 64(3): 279–286. https://doi.org/10.1080/09670874.2017.1397300

Danso, J.K., E.A. Osekre, N. Manu, G.P. Opit, P. Armstrong, F.H. Arthur, J.F. Campbell and G. Mbata. 2017. Moisture content, insect pests and mycotoxin levels of maize at harvest and post-harvest in the Middle Belt of Ghana. *Journal of Stored Products Research* 74: 46–55. https://doi.org/10.1016/j.jspr.2017.08.007.

Dars, F., M.A. Rustamani, R.D. Khuhro and H.B. Baloch. 2001. Effect of wheat grain moisture on infestation of red flour beetle, *Tribolium castaneum* (Herbst.). *Pakistan Journal of Zoology* 33(3): 189–192.

Davis, T.S., T.L. Crippen, R.W. Hofstetter and J.K. Tomberlin. 2013. Microbial volatile emissions as insect semiochemicals. *Springer* 39(7): 840–859. https://doi.org/10.1007/s10886-013-0306-z

Deshwal, R., P. Gupta, V. Vaibhav, N. Kumar and A. Kumar. 2018. Biology of lesser grain borer (*Rhyzopertha dominica* Fab.), under different temperature and humidity at laboratory condition. *Journal of Entomology and Zoology Studies* 6(4): 364–368.

Desmarchelier, J. 1988. The relationship between wet-bulb temperature and the intrinsic rate of increase of eight species of stored-product Coleoptera. *Journal of Stored Products Research* 24(2): 107–113. https://www.sciencedirect.com/science/article/pii/0022474X88900392

Devi, M.B. and N.V. Devi. 2015. Biology of rust-red flour beetle, *Tribolium castaneum* (Herbst)(Coleoptera: Tenebrionidae). *Biological Forum* 7(1): 12–15. https://www.cabdirect.org/cabdirect/abstract/20153254870

Ducoff, H.S., A.P. Vaughan and J.L. Crossland. 1970. Sensitivity to starvation as an index of physiological age in *Tribolium*. *Experimental Gerontology* 5(3): 233–240. https://doi.org/10.1016/0531-5565(70)90043-4.

Dukić, N., A. Radonjić, J. Lević, R. Spasić, P. Kljajić and G. Andrić. 2016. The effects of population densities and diet on *Tribolium castaneum* (Herbst) life parameters. *Journal of Stored Products Research* 69: 7–13. https://doi.org/10.1016/J.JSPR.2016.05.007.

Eastham, L. and S.B. McCully. 1943. The Oviposition Responses of *Calandra Granaria* Linn. *Journal of Experimental Biology* 20(1): 35–42. https://doi.org/10.1242/jeb.20.1.35.

Edde, P.A. 2012. A review of the biology and control of *Rhyzopertha dominica* (F.) the lesser grain borer. *Journal of Stored Products Research* 48: 1–18. https://doi.org/10.1016/J.JSPR.2011.08.007.

Edde, P.A. and T.W. Phillips. 2006. Longevity and pheromone output in stored-product Bostrichidae. *Bulletin of Entomological Research* 96(6): 547–554. https://doi.org/10.1079/BER2006456

Edvardsson, M. and G. Arnqvist. 2000. Copulatory courtship and cryptic female choice in red flour beetles *Tribolium castaneum*. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267(1443): 559–563. https://doi.org/10.1098/RSPB.2000.1037

Edwards, J.P., J.E. Short and L. Abraham. 1991. Large-scale evaluation of the insect juvenile hormone analogue fenoxycarb as a long-term protectant of stored wheat. *Journal of Stored Products Research* 27(1): 31–39. https://doi.org/10.1016/0022-474X(91)90030-G.

Ekechukwu, O. V. and B. Norton. 1999. Review of solar-energy drying systems II: An overview of solar drying technology. *Energy Conversion and Management* 40(6): 615–655. https://doi.org/10.1016/S0196-8904(98)00093-4.

Eliopoulos, P.A., G.Z. Prasodimou and A. V. Pouliou. 2011. Time–mortality relationships of larvae and adults of grain beetles exposed to extreme cold. *Crop Protection* 30(8): 1097–1102. https://doi.org/10.1016/J.CROPRO.2011.04.017.

Erdman, H. 1964. Sexual precocity of the male flour beetle, *Tribolium castaneum* Herbst, and the influence of temperatures on reproduction during early adult life. *The Canadian Entomologist* 96(4): 656–659.

Evans, D.E. 1982. The influence of temperature and grain moisture content on the intrinsic rate of increase of *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae). *Journal of Stored Products Research* 18(2): 55–62. https://doi.org/10.1016/0022-474X(82)90003-0.

Fabres, A., J. de Campos Macedo da Silva, K.V.S. Fernandes, J. Xavier-Filho, G.L. Rezende and A.E.A. Oliveira. 2014. Comparative performance of the red flour beetle *Tribolium castaneum* (Coleoptera: Tenebrionidae) on different plant diets. *Journal of Pest Science* 87(3): 495–506. https://doi.org/10.1007/S10340-014-0569-3.

Fava, A. and B. Burlando. 1995. Influence of female age and grain availability on the ovipositional pattern of the wheat weevil *Sitophilus granarius* (Coleoptera: Curculionidae). *European Journal of Entomology* 92: 421.

Fields, P. 1991. The cold-hardiness of *Cryptolestes ferrugineus* and the use of ice nucleation-active bacteria as a cold-synergist. In *International working conference on stored-product protection*, 1183–1192. Bordeaux, France.

Fields, P.G. 1992. The control of stored-product insects and mites with extreme temperatures. *Journal of Stored Products Research* 28(2): 89–118. https://doi.org/10.1016/0022-474X(92)90018-L.

Fields, P.G. 2001. Control of Insects in Post-Harvest: Low Temperature. *Physical Control Methods in Plant Protection* 95–107. https://doi.org/10.1007/978-3-662-04584-8_6

Fleurat-Lessard, F. 2002. Qualitative reasoning and integrated management of the quality of stored grain: A promising new approach. *Journal of Stored Products Research* 38(3): 191–218. https://doi.org/10.1016/S0022-474X(01)00022-4.

Flinn, P. and D. Hagstrum. 1998. Distribution of *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) in response to temperature gradients in stored wheat. *Journal of Stored Products Research* 34(2–3): 107–112.

Flinn, P.W. and D.W. Hagstrum. 1990. Simulations comparing the effectiveness of various stored-grain management practices used to control *Rhyzopertha dominica* (Coleoptera: Bostrichidae). *Environmental Entomology* 19(3): 725–729. https://doi.org/10.1093/ee/19.3.725.

Flinn, P.W., D.W. Hagstrum, C. Reed and T.W. Phillips. 2010. Insect population dynamics in commercial grain elevators. *Journal of Stored Products Research* 46(1): 43–47. https://doi.org/10.1016/j.jspr.2009.09.001.

Fox, C. and T. Mousseau. 1998. Maternal Effects As Adaptations for Transgenerational Phenotypic Plasticity in Insects. *Maternal Effects as Adaptions* 159–177. https://books.google.com/books/about/Maternal_Effects_As_Adaptations.html?id=JuARTAPwNzUC

Fraenkel, G. and M. Blewett. 1944. The utilisation of metabolic water in insects. *Bulletin of Entomological Research* 35(2): 127–139. https://doi.org/10.1017/S0007485300017351.

Frasnelli, E. 2013. *Brain and behavioral lateralization in invertebrates*. *Frontiers in Psychology*, 2013. https://doi.org/10.3389/fpsyg.2013.00939.

Fukami, T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46: 1--23.

Garcia-Vazquez, E., P. Moran, J. Perez, J.L. Martinez, J.I. Izquierdo, B. De Gaudemar and E. Beall. 2002. Interspecific barriers between salmonids when hybridisation is due to sneak mating. *Heredity* 89(4): 288–292. https://doi.org/10.1038/sj.hdy.6800134.

Garcia, C., M.A. Toro and J.S.F. Barker. 1990. Individual and group selection for productivity in *Tribolium castaneum*. *Theor Appl Genet* 79: 256–260.

Gaugler, R.R. and W.M. Brooks. 1975. Sublethal effects of infection by *Nosema heliothidis* in the corn earworm, *Heliothis zea*. *Journal of Invertebrate Pathology* 26(1): 57–63. https://doi.org/10.1016/0022-2011(75)90169-X.

Gerken, A.R. and J.F. Campbell. 2020. Oviposition and Development of *Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae) on Different Types of Flour. *Agronomy* 10(10): 1593. https://doi.org/10.3390/AGRONOMY10101593

Giga, D.P. and R.H. Smith. 1991. Intraspecific Competition in the Bean Weevils *Callosobruchus maculatus* and *Callosobruchus rhodesianus* (Coleoptera: Bruchidae). *Source: Journal of Applied Ecology* 28(3): 918–929.

Gnonlonfin, G.J.B., K. Hell, A.B. Siame and P. Fandohan. 2008. Infestation and population dynamics of insects on stored cassava and yams chips in benin, west Africa. *Journal of Economic Entomology* 101(6): 1967–1973. https://doi.org/10.1603/0022-0493-101.6.1967.

Gómez, J., J.F. Barrera, J.C. Rojas, J. Macias-Samano, J.P. Liedo, L. Cruz-Lopez and M.H. Badii. 2005. Volatile compounds released by disturbed females of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae): A parasitoid of the coffee berry borer

Hypothenemus hampei (Coleoptera: Scolytidae). *Florida Entomologist* 88(2): 180–187. https://doi.org/10.1653/0015-4040(2005)088[0180:VCRBDF]2.0.CO;2.

González-Tokman, D., A. Córdoba-Aguilar, W. Dáttilo, A. Lira-Noriega, R.A. Sánchez-Guillén and F. Villalobos. 2020. Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. *Biological Reviews* 95(3): 802–821. https://doi.org/10.1111/brv.12588

Goodnight, C.J. and D.M. Craig. 1996. The effect of coexistence on competitive outcome in *Tribolium castaneum* and *Tribolium confusum*. *Evolution* 50(3): 1241–1250. https://doi.org/10.1111/J.1558-5646.1996.TB02364.X.

Graur, D. and D. Wool. 1985. Undirectional interspecific mating in *Tribolium castaneum* and *T. confusum*: evolutionary and ecological implications. *Entomologia Experimentalis et Applicata* 38(3): 261–265. https://doi.org/10.1111/j.1570-7458.1985.tb03528.x.

Grieshop, M.J., P.W. Flinn and J.R. Nechols. 2009. Biological Control of Indianmeal Moth (Lepidoptera: Pyralidae) on Finished Stored Products Using Egg and Larval Parasitoids. *Journal of Economic Entomology* 99(4): 1080–1084. https://doi.org/10.1603/0022-0493-99.4.1080.

Gröning, J. and A. Hochkirch. 2008. Reproductive interference between animal species. *The Quarterly Review of Biology* 83(3): 257--282.

Gustavsson, J., C. Cederberg, U. Sonesson, R. van Otterdijk and A. Meybeck. 2011. *Global Food Losses and Food Waste: Extent, Causes and Prevention, Rome: Food and Agriculture Organisation of the United Nations*. Philosophical Transactions of the Royal Society B: Biological Sciences.

Hagstrum, D.W. and P.W. Flinn. 1990. Simulations Comparing Insect Species Differences in Response to Wheat Storage Conditions and Management Practices. *Journal of Economic Entomology* 83(6): 2469–2475. https://doi.org/10.1093/jee/83.6.2469.

Hagstrum, D.W. and J.E. Throne. 1989. Predictability of Stored-Wheat Insect Population Trends from Life History Traits. *Environmental Entomology* 18(4): 660–664. https://doi.org/10.1093/EE/18.4.660

Haines, C. 1991. Insects and arachnids of tropical stored products: their biology and identification (a training manual). https://agris.fao.org/agris-search/search.do?recordID=GB9590021

Halle, S., A. Nowizki and I. Scharf. 2015. The consequences of parental age for development, body mass and resistance to stress in the red flour beetle. *Biological Journal of the Linnean Society* 115(2): 305–314. https://doi.org/10.1111/bij.12501.

Halliday, W.D., I. Slevan-Tremblay and G. Blouin-Demers. 2019. Do Female Red Flour Beetles Assess both Current and Future Competition during Oviposition? *Journal of Insect Behavior* 32(3): 181–187. https://doi.org/10.1007/S10905-019-09723-Y/METRICS

Halliday, W.D., A.S. Thomas and G. Blouin-Demers. 2015. High temperature intensifies negative density dependence of fitness in red flour beetles. *Ecology and Evolution* 5(5): 1061–1067. https://doi.org/10.1002/ece3.1402.

Halstead, D.G.H. 1963. External sex differences in stored-products Coleoptera. *Bulletin of Entomological Research* 54(1): 119–134. https://doi.org/10.1017/S0007485300048665

Haq, T., N.F. Usmani and T. Abbas. 2005. Screening of plant leaves as grain protectants against

Tribolium castaneum during storage. *Pak. J. Bot* 37(1): 149–153.

Hardy, I. and M. Goubault. 2007. Wasp fights: understanding and utilizing agonistic bethylid behaviour. *Biocontrol News and Information* 28: 11–15.

Hayles, J., L. Johnson and D. Losic. 2014. Interspecific interactions between beetles in multi-species infestations. In *11th International Working Conference on Stored Product Protection*, 166–179. https://doi.org/10.14455/DOA.res.2014.35.

Hayma, J. 2003. *The Storage of Tropical Agricultural Products*. Agromisa Foundation.

Hernandez Nopsa, J.F., G.J. Daglish, D.W. Hagstrum, J.F. Leslie, T.W. Phillips, C. Scoglio, S. Thomas-Sharma, G.H. Walter and K.A. Garrett. 2015. Ecological Networks in Stored Grain: Key Postharvest Nodes for Emerging Pests, Pathogens, and Mycotoxins. *BioScience* 65(10): 985–1002. https://doi.org/10.1093/biosci/biv122.

Hill, D. 1987. *Agricultural Insect Pests of Temperate Regions and Their Control*. CUP Archive.

Hill, L.D. 1990. *Grain Grades and Standards: Historical Issues Shaping the Future*. Chicago: Illinois: University of Illinois Press.

Hochkirch, A., J. Gröning and A. Bücker. 2007. Sympatry with the devil: Reproductive interference could hamper species coexistence. *Journal of Animal Ecology* 76(4): 633–642. https://doi.org/10.1111/j.1365-2656.2007.01241.x.

Hockham, L.R., J.A. Graves and M.G. Ritchie. 2001. Variable maternal control of facultative egg diapause in the bushcricket ephippiger ephippiger. *Ecological Entomology* 26(2): 143–147. https://doi.org/10.1046/j.1365-2311.2001.00312.x.

Holditch, Z. and A.D. Smith. 2020. Priority determines *Tribolium* competitive outcome in a food-limited environment. *PLoS ONE* 15(7): e0235289. https://doi.org/10.1371/journal.pone.0235289.

Howard, R.W. 1987. Chemosystematic studies of the Triboliini (Coleoptera: Tenebrionidae): phylogenetic inferences from the defensive chemicals of eight *Tribolium* spp., *Palorus ratzeburgi* (Wissmann), and *Latheticus oryzae* Waterhouse. *Annals of the Entomological Society of America* 80(3): 398–405.

Howard, R.W. 1998. Ontogenetic, reproductive, and nutritional effects on the cuticular hydrocarbons of the host-specific ectoparasitoid *Cephalonomia tarsalis* (Hymenoptera: Bethylidae). *Annals of the Entomological Society of America* 91(1): 101–112. https://doi.org/10.1093/aesa/91.1.101.

Howard, R.W. and F. Infante. 1996. Cuticular hydrocarbons of the host-specific ectoparasitoid *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae) and its host the coffee berry borer (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 89(5): 700–709. https://doi.org/10.1093/aesa/89.5.700.

Howard, R.W. and G. Pérez-Lachaud. 2002. Cuticular hydrocarbons of the ectoparasitic wasp *Cephalonomia hyalinipennis* (Hymenoptera: Bethylidae) and its alternative host, the stored product pest *Caulophilus oryzae* (Coleoptera: Curculionidae). *Archives of Insect Biochemistry and Physiology* 50(2): 75–84. https://doi.org/10.1002/arch.10034.

Howe, R.W. 1956. The effect of temperature and humidity on the rate of development and mortality of *Tribolium castaneum* (Herbst) (Coleopteram, Tenebrionidae). *Annals of Applied Biology* 44(2): 356–368. https://doi.org/10.1111/J.1744-7348.1956.TB02128.X

Howe, R.W. 1960. The effects of temperature and humidity on the rate of developent and the mortality of *Tribolium Confusum* Duval (Coleoptera, Tenebrionidae). *Annals of Applied Biology* 48(2): 363–376. https://doi.org/10.1111/j.1744-7348.1960.tb03532.x.

Howe, R.W. 1965. A summary of estimates of optimal and minimal conditions for population increase of some stored products insects. *Journal of Stored Products Research* 1(2): 177–184. https://doi.org/10.1016/0022-474X(65)90018-4.

Hughes, K.A. and R.M. Reynolds. 2005. Evolutionary and mechanistic theories of aging. *Annual Review of Entomology* 50: 421–445. https://doi.org/10.1146/annurev.ento.50.071803.130409.

Hulasare, R., B. Subramanyam, P. Fields and A. Abdelghany. 2010. Heat treatment: a viable methyl bromide alternative for managing stored-product insects in food-processing facilities. *Julius-Kühn-Archiv* 425: 661. https://doi.org/10.5073/jka.2010.425.096

Hulasare, R.B., N.D.G. White, D.S. Jayas and C.J. Demianyk. 2003. Intra- and interspecific interactions among *Tribolium castaneum* and *Cryptolestes ferrugineus* in stored wheat at different insect densities. *Phytoprotection* 84(1): 19–26. https://doi.org/10.7202/007441AR.

Hurd, H. 1993. Reproductive Disturbances Induced by Parasites and Pathogens of Insects. In *Parasites and Pathogens of Insects*, 87–105. https://doi.org/10.1016/B978-0-08-091649-1.50009-8.

Imura, O. 1989. Life histories of stored-product insects. In *Bruchids and legumes. Proc. 2nd international symposium*, 257–269. Okayama, Japan. https://doi.org/10.1007/978-94-009-2005-7_27/COVER (2023 /3/31)

Jagadeesan, R., M.K. Nayak, K. Dawson, V. Byrne and P.J. Collins. 2013. Dietary media for mass rearing of rusty grain beetle, *Cryptolestes ferrugineus* (Stephens) and flat grain beetle, *Cryptolestes pusillus* (Schonherr) (Coleoptera: Cucujidae). *Journal of Stored Products Research* 55: 68–72. https://doi.org/10.1016/j.jspr.2013.08.004.

Jayas, D.S. 2012. Storing Grains for Food Security and Sustainability. *Agricultural Research* 1: 21–24. https://doi.org/10.1007/s40003-011-0004-4.

Jayas, D.S. and N.D.G. White. 2003. Storage and drying of grain in Canada: low cost approaches. *Food Control* 14(4): 255–261. https://doi.org/10.1016/S0956-7135(03)00014-8.

Jian, F. 2019. Influences of Stored Product Insect Movements on Integrated Pest Management Decisions. *Insects* 10(4): 100. https://doi.org/10.3390/INSECTS10040100

Jian, F. and D.S. Jayas. 2009. Detecting and responding to resource and stimulus during the movements of *Cryptolestes ferrugineus* adults. *Food and Bioprocess Technology* 2: 45–56. https://doi.org/10.1007/s11947-008-0144-0.

Jian, F., D.S. Jayas, P.G. Fields and N.D.G. White. 2018a. Modelling of population dynamics of insects in any ecosystem with several distributions of insect development: A Review. In *Proceedings of the 12th International Working Conference on Stored Product Protection (IWCSPP)*, 100–107. Berlin, Germany. https://doi.org/10.5073/JKA.2018.463.026.

Jian, F., D.S. Jayas, P.G. Fields, N.D.G. White, H. Zhang and P. Tang. 2018b. Demography of rusty grain beetle in stored bulk wheat: Part I, population dynamics at different temperatures and grain bulk sizes. *Environmental Entomology* 47(2): 244–255. https://doi.org/10.1093/ee/nvy019.

Jian, F., D.S. Jayas and N.D.G. White. 2002a. Movement of adult rusty grain beetles, *Cryptolestes ferrugineus* (Coleoptera: Cucujidae), in wheat in response to 5°C/m temperature gradients at cool temperatures. *Journal of Stored Products Research* 39(1): 87–101. https://doi.org/10.1016/S0022-474X(02)00024-3.

Jian, F., D.S. Jayas and N.D.G. White. 2005. Movement of *Tribolium castaneum* (Coleoptera: Tenebrionidae) Adults in Response to Temperature Gradients in Vertical and Horizontal Wheat and Corn Columns. *Journal of Economic Entomology* 98(4): 1413–1419. https://doi.org/10.1603/0022-0493-98.4.1413

Jian, F., D.S. Jayas, N.D.G. White and W.E. Muir. 2002b. Temperature and geotaxis preference by *Cryptolestes ferrugineus* (Coleoptera: Laemophloeidae) adults in response to 5°C/m temperature gradients at optimum and hot temperatures in stored wheat and their mortality at high temperature. *Environmental Entomology* 31(5): 816–826. https://doi.org/10.1603/0046-225X-31.5.816.

Jian, F., R. Larson, D.S. Jayas and N.D.G. White. 2012. Three Dimensional Temporal and Spatial Distribution of Adults of *Tribolium castaneum* (Coleoptera: Tenebrionidae) in Stored Wheat Under Different Temperatures and Adult Densities. *Agricultural Research* 1: 165–174. https://doi.org/10.1007/s40003-012-0015-9.

Johnson, J.A. and K.A. Valero. 2003. Use of Commercial Freezers to Control Cowpea Weevil, *Callosobruchus maculatus* (Coleoptera: Bruchidae), in Organic Garbanzo Beans. *Journal of Economic Entomology* 96(6): 1952–1957. https://doi.org/10.1093/JEE/96.6.1952.

Jones, A.E., W.S.C. Gurney, R.M. Nisbet and D.M. Gordon. 1990. Food Degradation as a Mechanism of Intraspecific Competition among the Larvae of Secondary Stored-Product Pests. *Functional Ecology* 4(5): 629. https://doi.org/10.2307/2389730.

Kabir, S.M.H. 1966. Interactions in stored grain of of populations of *Sitophilus zea-mais*, Motschulsky, *Rhyzopertha dominica* (Fabricius) and *Tribolium castaneum* (Herbst). Texas A and M University, College Station, TX.

Karunakaran, C., D.S. Jayas and N.D.G. White. 2004. Identification of wheat kernels damaged by the red flour beetle using X-ray images. *Biosystems Engineering* 87(3): 267–274. https://www.sciencedirect.com/science/article/pii/S1537511003002290

Kavallieratos, N.G., C.G. Athanassiou, R.N.C. Guedes, J.D. Drempela and M.C. Boukouvala. 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? *Frontiers in Plant Science* 8: 1837. https://doi.org/10.3389/FPLS.2017.01837/FULL

Kelly, R.J., D.M. O'Brian and F.F. Katz. 1967. The incidence and burden of *Hymenolepis diminuta* cysticercoids as a function of the age of the intermediate host, *Tribolium confusum*. *Journal of the New York Entomological Society* 19–23.

Keymer, A. 1982. The dynamics of infection of *Tribolium confusum* by *Hymenolepis diminuta*: the influence of exposure time and host density. *Parasitology* 84(1): 157–166.

Khalid, M., A. Rasul, F. Jabeen, A. Rasool and R. Munir. 2019. Red flour beetle *Tribolium castaneum*(Tenebrionidae, Coleoptera): Population dynamics, screening of *Wolbachia* in different regions and cereal foods of Pakistan. *Pakistan Entomologist* 41(1): 13–20. www.pakentomol.com

Khan, I., A. Prakash and D. Agashe. 2016a. Immunosenescence and the ability to survive bacterial infection in the red flour beetle *Tribolium castaneum*. *Journal of Animal Ecology*

85(1): 291–301. https://doi.org/10.1111/1365-2656.12433.

Khan, I., A. Prakash and D. Agashe. 2016b. Divergent immune priming responses across flour beetle life stages and populations. *Ecology and Evolution* 6(21): 7847–7855. https://doi.org/10.1002/ECE3.2532

Kim, H., Y.S. Yu and K.Y. Lee. 2015. Differential induction of heat shock protein genes to the combined treatments of heat with diatomaceous earth, phosphine or carbon dioxide on *Plodia interpunctella*. *Entomological Research* 45(6): 332–338. https://doi.org/10.1111/1748-5967.12139.

Kishi, S., T. Nishida and Y. Tsubaki. 2009. Reproductive interference determines persistence and exclusion in species interactions. *Journal of Animal Ecology* 78(5): 1043–1049. https://doi.org/10.1111/j.1365-2656.2009.01560.x.

Krinsky, W.L. 2019. Beetles (Coleoptera). *Medical and Veterinary Entomology* 129–143. https://doi.org/10.1016/B978-0-12-814043-7.00009-1.

Kubota, K. and T. Sota. 1998. Hybridization and Speciation in the Carabid Beetles of the Subgenus *Ohomopterus* (Coleoptera, Carabidae, Genus *Carabus*). *Researches on Population Ecology* 40: 213–222. https://doi.org/10.1007/BF02763406.

Kumano, N., N. Iwata, T. Kuriwada, K. Shiromoto, D. Haraguchi, C. Yasunaga-Aoki and T. Kohama. 2010. The neogregarine protozoan *Farinocystis* sp. reduces longevity and fecundity in the West Indian sweet potato weevil, *Euscepes postfasciatus* (Fairmaire). *Journal of Invertebrate Pathology* 105(3): 298–304. https://doi.org/10.1016/j.jip.2010.08.003.

Kumar, H., M. Panigrahi, S. Chhotaray, V. Bhanuprakash, R. Shandilya, A. Sonwane and B. Bhushan. 2018. Red flour beetle (*Tribolium castaneum*): From population genetics to functional genomics. *Veterinary World* 11(8): 1043. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6141300/

Kuno, E. 1992. Competitive exclusion through reproductive interference. *Researches on Population Ecology* 34: 275–284. https://doi.org/10.1007/BF02514797.

Lal, M., B. Ram and P. Tiwari. 2017. Botanicals to Cope Stored Grain Insect Pests: A Review. *International Journal of Current Microbiology and Applied Sciences* 6(6): 1583–1594. https://doi.org/10.20546/ijcmas.2017.606.186.

Lancaster, J. and B.J. Downes. 2013. Oviposition and eggs. In *Aquatic Entomology*, 173–189. OUP Oxford.

Laparie, M., V. Larvor, Y. Frenot and D. Renault. 2012. Starvation resistance and effects of diet on energy reserves in a predatory ground beetle (*Merizodus soledadinus*; Carabidae) invading the Kerguelen Islands. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 161(2): 122–129. https://doi.org/10.1016/J.CBPA.2011.09.011.

LeCato, G.L. 1975. Species composition influencing insect population growth and weight loss of stored rice, wheat, and corn. *Journal of the Kansas Entomological Society* 48: 224--231.

Lee, R.E., J.M. Strong-Gunderson, M.R. Lee, I. Mo and E.C. Davidson. 1992. Ice-nucleating active bacteria decrease the cold-hardiness of stored grain insects. *Journal of Economic Entomology* 85(2): 371–374. https://academic.oup.com/jee/article-abstract/85/2/371/813362

Lee, S. 2000. Low-temperature damp corn storage with and without chemical preservatives. The University of Guelph.

Lee, Y.J. and H.S. Ducoff. 1983. Age and sensitivity to oxygen in the flour beetle, *Tribolium confusum*. *Mechanisms of Ageing and Development* 22(2): 97–103. https://doi.org/10.1016/0047-6374(83)90102-1.

Lefkovitch, L.P. 1968. Interaction between four species of beetles in wheat and wheatfeed. *Journal of Stored Products Research* 4(1): 1–8. https://doi.org/10.1016/0022-474X(68)90023-4.

Lessios, H.A. and C.W. Cunningham. 1990. Gametic incompatibility between species of the sea urchin *Echinometra* on the two sides of the Isthmus of Panama. *Evolution* 44(4): 933–941. https://doi.org/10.1111/j.1558-5646.1990.tb03815.x.

Lewis, S.M. and S.N. Austad. 1994. Sexual selection in flour beetles: The relationship between sperm precedence and male olfactory attractiveness. *Behavioral Ecology* 5(2): 223–224. https://doi.org/10.1093/BEHECO/5.2.223.

Lewis, S.M. and J. Iannini. 1995. Fitness consequences of differences in male mating behaviour in relation to female reproductive status in flour beetles. *Animal Behaviour* 50(5): 1157–1160. https://doi.org/10.1016/0003-3472(95)80031-X.

Lewis, S.M. and E. Jutkiewicz. 1998. Sperm precedence and sperm storage in multiply mated red flour beetles. *Behavioral Ecology and Sociobiology* 43(6): 365–369. https://doi.org/10.1007/S002650050503

Lewis, S.M., A. Kobel, T. Fedina and R.W. Beeman. 2005. Sperm stratification and paternity success in red flour beetles. *Physiological Entomology* 30(3): 303–307. https://doi.org/10.1111/J.1365-3032.2005.00450.X.

Li, L. and R.T. Arbogast. 1991. The effect of grain breakage on fecundity, development, survival, and population increase in maize of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae). *Journal of Stored Products Research* 27(2): 87–94. https://doi.org/10.1016/0022-474X(91)90017-7.

Lloyd, M. and T. Park. 1962. Mortality Resulting from Interactions between Adult Flour Beetles in Laboratory Cultures. *Physiological Zoology* 35(4): 330–347. https://doi.org/10.1086/physzool.35.4.30155430.

Longstaff, B.C. 1995. An experimental study of the influence of food quality and population density on the demographic performance of *Tribolium castaneum* (Herbst.). *Journal of Stored Products Research* 31(2): 123–129. https://doi.org/10.1016/0022-474X(94)00045-U.

Lovitt, A.E. and E.L. Soderstrom. 1973. Effect of varying light and temperature cycles on the ovipositional response of malathion-treated Indian meal moth adults. *Journal of Economic Entomology* 66(1): 167–170. https://academic.oup.com/jee/article-abstract/66/1/167/2211294

Maceljski, M. 1973. Contribution of the morphology and ecology of *Sitophilus zeamais* Motsch. in Yugoslavia. *J. Stored Prod. Res* 9: 225–234.

Madrid, F.J., N.D.G. White and S.R. Loschiavo. 1990. Insects in stored cereals, and their association with farming practices in Southern Manitoba. *The Canadian Entomologist* 122(3): 515–523. https://doi.org/10.4039/ENT122515-5

Madsen, T., R. Shine, J. Loman and T. Håkansson. 1992. Why do female adders copulate so frequently? *Nature 1992 355:6359* 355(6359): 440–441. https://doi.org/10.1038/355440a0

Magan, N., R. Hope, V. Cairns and D. Aldred. 2003. Post-harvest fungal ecology: Impact of fungal growth and mycotoxin accumulation in stored grain. *European Journal of Plant Pathology* 109: 723–730.

Mahroof, R. and B. Subramanyam. 2006. Susceptibility of *Plodia interpunctella* (Lepidoptera: Pyralidae) developmental stages to high temperatures used during structural heat treatments. *Bulletin of Entomological Research* 96(6): 539–545. https://doi.org/10.1079/BER2006454

Mahroof, R., B. Subramanyam, J.E. Throne and A. Menon. 2003. Time-Mortality Relationships for *Tribolium castaneum* (Coleoptera: Tenebrionidae) Life Stages Exposed to Elevated Temperatures. *Journal of Economic Entomology* 96(4): 1345–1351. https://doi.org/10.1093/JEE/96.4.1345

Majumder, S., B.K. Bala, F.M. Arshad, M.A. Haque and M.A. Hossain. 2016. Food security through increasing technical efficiency and reducing postharvest losses of rice production systems in Bangladesh. *Food Security* 8: 361–374. https://doi.org/10.1007/s12571-016-0558-x.

Malone, L.A. 1987. Longevity and fecundity of Argentine stem weevils, *Listronotus bonariensis* (Coleoptera: Curculionidae), infected with *Microsporidium itiiti* (Protozoa: Microspora). *Journal of Invertebrate Pathology* 50(2): 113–117. https://doi.org/10.1016/0022-2011(87)90110-8.

Markarian, H., G.J. Florentine and J.J. Pratt. 1978. Quinone production of some species of *Tribolium*. *Journal of Insect Physiology* 24(12): 785–790. https://doi.org/10.1016/0022-

1910(78)90096-3.

Marshall, D.J. and T. Uller. 2007. When is a maternal effect adaptive? *Oikos* 116(12): 1957–1963. https://doi.org/10.1111/j.2007.0030-1299.16203.x.

Mason, L. and M. McDonough. 2011. Biology, Behavior, and Ecology of Stored Grain and Legume Insects. In *Stored Product Protection*, 13–20.

Mathias, D., A. Taofic, H. Eric and F. Fr&ederic. 2015. Oviposition strategy of *Sitophilus zeamais* Motsch. (Coleoptera: Curculionidae) in relation to conspecific infestation. *African Journal of Agricultural Research* 10(4): 301–307. https://doi.org/10.5897/AJAR2013.8304

Mbata, G.N. 1985. Some physical and biological factors affecting oviposition by *Plodia interpunctella* (Hubner) (Lepidoptera: Phycitidae). *International Journal of Tropical Insect Science* 6(5): 597–604. https://doi.org/10.1017/S1742758400009176

McDonald, D.J. 1968. The Response of *Tribolium Confusum* to Variations in the Volume of Its Environment. *Ecology* 49(6): 1166–1168. https://doi.org/10.2307/1934504.

McLain, D.K. and A.E. Pratt. 1999. The cost of sexual coercion and heterospecific sexual harassment on the fecundity of a host-specific, seed-eating insect (Neacoryphus bicrucis). *Behavioral Ecology and Sociobiology* 46: 164–170. https://doi.org/10.1007/s002650050606.

Mercer, C.F. and P.J. Wigley. 1987. A microsporidian pathogen of the poroporo stem borer, *Sceliodes cordalis* (Dbld) (Lepidoptera: Pyralidae). I. Description and identification. *Journal of Invertebrate Pathology* 49(1): 93–101. https://doi.org/10.1016/0022-2011(87)90130-3.

Mertz, D.B. 1969. Age-Distribution and Abundance in Populations of Flour Beetles. I. Experimental Studies. *Ecological Monographs* 39(1): 1–31. https://doi.org/10.2307/1948563.

Mertz, D.B. 1975. Senescent decline in flour beetle strains selected for early adult fitness. *Physiological Zoology* 48(1): 1–23.

Messina, F.J., J.L. Morrey and M. Mendenhall. 2007. Why do host-deprived seed beetles 'dump' their eggs? *Physiological Entomology* 32(3): 259–267. https://doi.org/10.1111/J.1365-3032.2007.00579.X

Mesterházy, Á., J. Oláh and J. Popp. 2020. Losses in the Grain Supply Chain: Causes and Solutions. *Sustainability* 12(6): 2342. https://doi.org/10.3390/SU12062342

Mignon, J., E. Haubruge, V. Liénard, C. Gaspar and G. Lognay. 1996. Mortality in *Oryzaephilus surinamensis* following short-term exposure to conditioned kernels by high-density culture. *Entomologia Experimentalis et Applicata* 80(3): 555–557. https://doi.org/10.1111/J.1570-7458.1996.TB00972.X

Minkenberg, O.P.J.M., M. Tatar and J.A. Rosenheim. 1992. Egg Load as a Major Source of Variability in Insect Foraging and Oviposition Behavior. *Oikos* 65(1): 134. https://doi.org/10.2307/3544896.

Miyatake, T. 2001. Effects of starvation on death-feigning in adults of *Cylas formicarius* (coleoptera: brentidae). *Annals of the Entomological Society of America* 94(4): 612–616. https://doi.org/10.1603/0013-8746(2001)094[0612:EOSODF]2.0.CO;2.

Mohammadzadeh, M. and H. Izadi. 2018. Cooling rate and starvation affect supercooling point and cold tolerance of the Khapra beetle, *Trogoderma granarium* Everts fourth instar larvae (Coleoptera: Dermestidae). *Journal of Thermal Biology* 71: 24–31. https://doi.org/10.1016/J.JTHERBIO.2017.10.007.

Mohandass, S., F.H. Arthur, K.Y. Zhu and J.E. Throne. 2007. Biology and management of *Plodia interpunctella* (Lepidoptera: Pyralidae) in stored products. *Journal of Stored Products Research* 43(3): 302–311. https://doi.org/10.1016/J.JSPR.2006.08.002.

Moore, P.J. and A. Attisano. 2011. Oosorption in response to poor food: complexity in the trade-off between reproduction and survival. *Ecology and Evolution* 1(1): 37–45. https://doi.org/10.1002/ECE3.4

Morya, K., S. Pillai and P. Patel. 2010. Effect of powdered leaves of *Lantana camara*, *Clerodendrum inerme* and *Citrus limon* on the rice moth, *Corcyra cephalonica*. *Bulletin of Insectology* 63(2): 183–189.

Moses, J.A., D.S. Jayas and K. Alagusundaram. 2015. Climate Change and its Implications on Stored Food Grains. *Agricultural Research* 4(1): 21–30. https://doi.org/10.1007/S40003-015-0152-Z.

Mousseau, T.A. 1991. Geographic Variation in Maternal-Age Effects on Diapause in a Cricket. *Evolution* 1053–1059. https://doi.org/10.2307/2409710.

Mwenda, E.T., J.H. Ringo and E.R. Mbega. 2019. The implication of kernel phenology in convening resistance to storage weevil and varietal development in sorghum. *Journal of Stored Products Research* 83: 176–184. https://doi.org/10.1016/j.jspr.2019.06.010

Nansen, C., P. Flinn, D. Hagstrum, M.D. Toews and W.G. Meikle. 2009. Interspecific associations among stored-grain beetles. *Journal of Stored Products Research* 45(4): 254–260. https://doi.org/10.1016/j.jspr.2009.04.005.

Naseri, B., E. Borzoui, S. Majd and S. Mozaffar Mansouri. 2017. Influence of Different Food Commodities on Life History, Feeding Efficiency, and Digestive Enzymatic Activity of *Tribolium castaneum* (Coleoptera: Tenebrionidae). *Journal of Economic Entomology* 110(5): 2263–2268. https://doi.org/10.1093/JEE/TOX236

Naveena, N., S. Subramanya and S. Setty. 2015. Diversity and distribution of stored grain insects among the Soliga Tribal settlements of Biligirirangana Hills, Karnataka, India. *Journal of Stored Products Research* 62: 84–92. https://www.sciencedirect.com/science/article/pii/S0022474X15300023

Nawrot, J., M. Gawlak, J. Szafranek, B. Szafranek, E. Synak, J.R. Warchalewski, D. Piasecka-Kwiatkowska, W. Błaszczak, T. Jeliński and J. Fornal. 2010. The effect of wheat grain composition, cuticular lipids and kernel surface microstructure on feeding, egg-laying, and the development of the granary weevil, *Sitophilus granarius* (L.). *Journal of Stored Products Research* 46(2): 133–141. https://doi.org/10.1016/J.JSPR.2010.02.001.

Negi, A., A. Pare, L. Manickam and M. Rajamani. 2021. Effects of defect action level of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) fragments on quality of wheat flour. *Journal of the Science of Food and Agriculture* 102(1): 223–232. https://doi.org/10.1002/jsfa.11349

Nguyen, D.T. 2008. Effects of starvation period on the locomotory response of *Rhyzopertha dominica* (F.). *Journal of Stored Products Research* 44(1): 100–102. https://doi.org/10.1016/J.JSPR.2007.06.007.

Novoseltsev, V.N., J.A. Novoseltseva and A.I. Yashin. 2003. What does a fly's individual fecundity pattern look like? The dynamics of resource allocation in reproduction and ageing. *Mechanisms of Ageing and Development* 124(5): 605–617. https://doi.org/10.1016/S0047-6374(03)00061-7.

Ogden, J.C. 1970. Aspects of Dispersal in *Tribolium* Flour Beetles. *Physiological Zoology* 43(2): 124–131. https://doi.org/10.1086/PHYSZOOL.43.2.30155521.

Okelana, F.A. and F.N.C. Osuji. 1985. Influence of relative humidity at 30°C on the oviposition, development and mortality of *Sitophilus zeamais* Motsch. (Coleoptera: Curculionidae) in maize kernels. *Journal of Stored Products Research* 21(1): 13–19. https://doi.org/10.1016/0022-474X(85)90054-2.

Olsson, M., R. Shine, T. Madsen, A. Gullberg and H. Tegelstrom. 1996. Sperm selection by females. *Nature 1996 383:6601* 383(6601): 585–585. https://doi.org/10.1038/383585a0

Onstad, D.W. and J. V. Maddox. 1990. Simulation model of *Tribolium confusum* and its pathogen, *Nosema whitei*. *Ecological Modelling* 51(1–2): 143–160. https://doi.org/10.1016/0304-3800(90)90062-L.

Opit, G.P. and J.E. Throne. 2007. Influence of maternal age on the fitness of progeny in the rice weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae). *Environmental Entomology* 36(1): 83–89. https://doi.org/10.1603/0046-225X(2007)36[83:IOMAOT]2.0.CO;2.

Padín, S., G. Dal Bello and M. Fabrizio. 2002. Grain loss caused by *Tribolium castaneum*, *Sitophilus oryzae* and *Acanthoscelides obtectus* in stored durum wheat and beans treated with *Beauveria bassiana*. *Journal of Stored Products Research* 38(1): 69–74. https://doi.org/10.1016/S0022-474X(00)00046-1.

Pai, A. 2019. *Tribolium*. *Encyclopedia of Animal Behavior* 231–241. https://doi.org/10.1016/B978-0-12-809633-8.01216-4.

Parajulee, M.N. and T.W. Phillips. 1995. Survivorship and Cannibalism in *Lyctocoris campestris* (Hemiptera: Anthocoridae): Effects of Density, Prey Availability, and Temperature. *Journal of Entomological Science* 30(1): 1–8. https://doi.org/10.18474/0749-8004-30.1.1

Park, T. 1938. Studies in population physiology. VIII. The effect of larval population density on the postembryonic development of the flour beetle, *Tribolium confusum* Duval. *Journal of Experimental Zoology* 79(1): 51–70. https://doi.org/10.1002/JEZ.1400790105.

Park, T., P.H. Leslie and D.B. Mertz. 1964. Genetic Strains and Competition in Populations of *Tribolium*. *Physiological Zoology* 37(2): 97–162. https://doi.org/10.1086/physzool.37.2.30152328.

Park, T., J.R. Ziegler, D.L. Ziegler and D.B. Mertz. 1974. The cannibalism of eggs by *Tribolium* larvae. *Physiological Zoology* 47(1): 37--58.

Perez-Mendoza, J., J.F. Campbell and J.E. Throne. 2011. Influence of Age, Mating Status, Sex, Quantity of Food, and Long-Term Food Deprivation on Red Flour Beetle (Coleoptera: Tenebrionidae) Flight Initiation. *Journal of Economic Entomology* 104(6): 2078–2086. https://doi.org/10.1603/EC11140

Perez-Mendoza, J., J.E. Throne and J.E. Baker. 2004. Ovarian physiology and age-grading in the rice weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae). *Journal of Stored Products Research* 40(2): 179–196. https://doi.org/10.1016/S0022-474X(02)00096-6.

Peters, T.M. and P. Barbosa. 1977. Influence of population density on size, fecundity, and developmental rate of insects in culture. *Annual Review of Entomology* 22(1): 431–450.

Pfennig, K.S. 2007. Facultative mate choice drives adaptive hybridization. *Science* 318(5852): 965–967. https://doi.org/10.1126/science.1146035.

Pixton, S.W. and S. Warburton. 1971. Moisture content/relative humidity equilibrium of some cereal grains at different temperatures. *Journal of Stored Products Research* 6(4): 283–293. https://doi.org/10.1016/0022-474X(71)90041-5.

Pointer, M.D., M.J. Gage and L.G. Spurgin. 2021. Tribolium *beetles as a model system in evolution and ecology*. *Heredity,* 2021. https://doi.org/10.1038/s41437-021-00420-1.

Priest, N.K., B. Mackowiak and D.E.L. Promislow. 2002. The role of parental age effects on the evolution of aging. *Evolution* 56(5): 927–935. https://doi.org/10.1111/j.0014-3820.2002.tb01405.x.

Qazi, M.C.B., J.R. Aprille and S.M. Lewis. 1998. Female role in sperm storage in the red flour beetle, *Tribolium castaneum*. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 120(4): 641–647. https://doi.org/10.1016/S1095-6433(98)10081-8.

Qazi, M.C.B., J.T. Herbeck and S.M. Lewis. 1996. Mechanisms of Sperm Transfer and Storage in the Red Flour Beetle (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of America* 89(6): 892–897. https://doi.org/10.1093/AESA/89.6.892

Quellhorst, H., C.G. Athanassiou, A. Bruce, E.D. Scully and W.R. Morrison. 2020. Temperature-Mediated Competition between the Invasive Larger Grain Borer (Coleoptera: Bostrichidae) and the Cosmopolitan Maize Weevil (Coleoptera: Curculionidae). *Environmental*

Entomology 49(1): 255–264. https://doi.org/10.1093/ee/nvz151.

R Core Team. 2023. R: A Language and Environment for Statistical ComputingVienna, Austria, 2023. https://www.r-project.org/.

Rabindra, R.J., M. Balasubramanian and S. Jayaraj. 1981. The effects of Farinocystis tribolii on the growth and development of the flour beetle *Tribolium castaneum*. *Journal of Invertebrate Pathology* 38(3): 345–351. https://doi.org/10.1016/0022-2011(81)90100-2.

Rahman, M.A., F. Zohora, M. Mohanta, A. Saha and M. Rahman. 2021. Maternal age induced changes in the reproductive traits of the bruchid beetle, *Callosobruchus chinensis* (L.)(Coleoptera: Bruchidae). *International Journal of Entomology Research* 6(5): 189–195.

Rajendran, S. and V. Sriranjini. 2008. Plant products as fumigants for stored-product insect control. *Journal of Stored Products Research* 44(2): 126–135.

Ranjbaran, M. and B. Emadi. 2015. A mathematical model of commodity wet-bulb temperature (CWBT) for grain storage applications. *Biosystems Engineering* 139: 128–135. https://www.sciencedirect.com/science/article/pii/S1537511015001531

Rashki, M., S. Ghayeb and L. S. 2019. Application of Wheat Cultivars and Pathogenic Fungus Combination against the Lesser Grain Borer, *Rhyzopertha dominica* (Col.: Bostrichidae) and the Red Flour Beetle *Tribolium castaneum* (Col.: Tenebrionidae). *Egyptian Academic Journal of Biological Sciences. A, Entomology* 12(1): 121–130. https://doi.org/10.21608/eajbsa.2019.26723.

Raychaudhuri, A. and A. Butz. 1965. Aging. I. Effects of parental age on the life cycle of *Tribolium confusum* (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of*

America 58(4): 535–540.

Rayhan, M.Z., S. Das, R. Sarkar, S.K. Adhikary, S.N. Tania, M.M. Islam and M.G. Rabbani. 2014. Bioefficacy of neem , mahogoni and their mixture to protect seed damage and seed weight loss by rice weevil in storage. *J Biodivers Environ Sci* 5(1): 582–589.

Rees, D. 2007. *Insects of Stored Grain: A Pocket Reference*. CSIRO publishing.

Renault, D., F. Hervant and P. Vernon. 2002. Comparative study of the metabolic responses during food shortage and subsequent recovery at different temperatures in the adult lesser mealworm, *Alphitobius diaperinus* (Coleoptera: Tenebrionidae). *Physiological Entomology* 27(4): 291–301. https://doi.org/10.1046/J.1365-3032.2002.00299.X

Reznick, D., M.J. Bryant and F. Bashey. 2002. r- and K-selection revisited: The role of population regulation in life-history evolution. *Ecology* 83(6): 1509–1520. https://doi.org/10.1890/0012-9658(2002)083[1509:raksrt]2.0.co;2.

Rich, E.R. 1956. Egg Cannibalism and Fecundity in *Tribolium*. *Ecology* 37(1): 109–120. https://doi.org/10.2307/1929674.

Richardson, C.H. 1925. *The Oviposition Response of Insects*. US Department of Agriculture.

Ridgel, A.L., R.E. Ritzmann and P.L. Schaefer. 2003. Effects of aging on behavior and leg kinematics during locomotion in two species of cockroach. *Journal of Experimental Biology* 206(24): 4453–4465. https://doi.org/10.1242/jeb.00714.

Ridley, A.W., J.P. Hereward, G.J. Daglish, S. Raghu, P.J. Collins and G.H. Walter. 2011. The spatiotemporal dynamics of *Tribolium castaneum* (Herbst): adult flight and gene flow. *Molecular Ecology* 20(8): 1635–1646. https://doi.org/10.1111/J.1365-294X.2011.05049.X

Ridley, A.W., J.P. Hereward, G.J. Daglish, S. Raghu, G.A. McCulloch and G.H. Walter. 2016. Flight of *Rhyzopertha dominica* (Coleoptera: Bostrichidae)-A spatio-temporal analysis with pheromone trapping and population genetics. *Journal of Economic Entomology* 109(6): 2561–2571. https://doi.org/10.1093/jee/tow226.

Ritte, U. and Z. Agur. 1977. Variability for dispersal behavior in a wild population of *Tribolium castaneum*. *Tribolium Inf Bull* 20: 122–131.

Rizwan, M., Mansoor-ul-Hassan, A. Aslam, D. Majeed, M. Jafir, M.K. Malik and M. Usman. 2018. Effects of temperature and relative humidity on the development of *Trogoderma granarium* (cole- optera: dermestidae) under laboratory conditions. *International Journal of Entomology Research* 3(4): 9–12.

Roberts, H.L. and O. Schmidt. 2004. Lifetime egg maturation by host-deprived *Venturia canescens*. *Journal of Insect Physiology* 50(2–3): 195–202. https://www.sciencedirect.com/science/article/pii/S0022191003002506

Romero, S.A., J.F. Campbell, J.R. Nechols and K.A. With. 2010. Movement behavior of red flour beetle: response to habitat cues and patch boundaries. *Environmental Entomology* 39(3): 919–929. https://academic.oup.com/ee/article-abstract/39/3/919/448198

Ross, P.R., S.R. Pugazhvendan, K. Elumalai and M. Soundararajan. 2009. Repellent Activity of Chosen Plant Species Against *Tribolium castaneum*. *World Journal of Zoology* 4(3): 188–190. https://www.researchgate.net/publication/238738088

Rustamani, M.A. and I. Khatri. 2014. Population fluctuation of red flour beetle, *Tribolium castaneum* (Herbst.)(Coleoptera: Tenebrionidae) on different cereal foods in laboratory. *Pakistan Journal of Zoology* 46(6). https://www.researchgate.net/publication/280556569

Sagheer, M., Mansoor-ul-Hassan, M. Bilal, M. Najam-ul-Hassan, F. Zafar Ahmad Khan, S. Raza Haidri and M. Farhan. 2014. Nutritional indices of *Tribolium castaneum* (herbst) and its response to plant extracts in relation to three types of flours. *International Journal of Agronomy and Agricultural Research (IJAAR)* 4: 51–56.

Sajap, A.S. and L.C. Lewis. 1988. Histopathology of transovarial transmission of *Nosema pyrausta* in the European corn borer, *Ostrinia nubilalis*. *Journal of Invertebrate Pathology* 52(1): 147–153. https://doi.org/10.1016/0022-2011(88)90114-0.

Salin, C., P. Vernon and G. Vannier. 1999. Effects of temperature and humidity on transpiration in adults of the lesser mealworm, *Alphitobius diaperinus* (Coleoptera: Tenebrionidae). *Journal of Insect Physiology* 45(10): 907–914. https://doi.org/10.1016/S0022-1910(99)00067-0.

Scharf, I., H. Braf, N. Ifrach, S. Rosenstein and A. Subach. 2015a. The effects of temperature and diet during development, adulthood, and mating on reproduction in the red flour beetle. *PLoS ONE* 10(9): 0136924. https://doi.org/10.1371/journal.pone.0136924.

Scharf, I., N. Galkin and S. Halle. 2015b. Disentangling the Consequences of Growth Temperature and Adult Acclimation Temperature on Starvation and Thermal Tolerance in the Red Flour Beetle. *Evolutionary Biology* 42: 54–62. https://doi.org/10.1007/s11692-014-9298-z.

Scharf, I., Y. Wexler, H.A. Macmillan, S. Presman, E. Simson and S. Rosenstein. 2016. The negative effect of starvation and the positive effect of mild thermal stress on thermal tolerance of the red flour beetle, *Tribolium castaneum*. *Science of Nature* 103(3): 1–10. https://doi.org/10.1007/S00114-016-1344-5/METRICS

Schöller, M. 2010. Biological control of stored-product insects in commodities, food processing facilities and museums, Section: Non-Chemical Control. In *10th International Working Conference on Stored Product Protection*, 596–605. https://doi.org/10.5073/jka.2010.425.167.165 (2023 /1/9)

Schöller, M., P.W. Flinn, M.J. Grieshop and E. Zdarkova. 2006. Biological control of stored product pests. In *Insect Management for Food Storage and Processing*, 67--87. AACC International St. Paul, Minnesota.

Schöller, M., S. Prozell, P. Suma and A. Russo. 2018. Biological control of stored-product insects. *Recent Advances in Stored Product Protection* 183–209. https://doi.org/10.1007/978-3-662-56125-6_9/COVER

Sedlacek, J.D., R.J. Barney, B.D. Price and M. Siddiqui. 1991. Effect of Several Management Tactics on Adult Mortality and Progeny Production of *Sitophilus zeamais* (Coleoptera: Curculionidae) on Stored Corn in the Laboratory. *Journal of Economic Entomology* 84(3): 1041–1046. https://doi.org/10.1093/jee/84.3.1041.

Shafique, M., M. Ahmad and M.A. Chaudry. 2006. Feeding Preference and Development of *Tribolium castaneum* (Herbst.) in Wheat Products. *Pakistan J. Zool* 38(1): 27–31.

Shah, J.A., T. Vendl, R. Aulicky and V. Stejskal. 2021. Frass produced by the primary pest *Rhyzopertha dominica* supports the population growth of the secondary stored product pests *Oryzaephilus surinamensis*, *Tribolium castaneum,* and *T. confusum*. *Bulletin of Entomological Research* 111(2): 153–159. https://doi.org/10.1017/S0007485320000425

Shin, S.S., Y.S. Chun and M.I. Ryoo. 1994. Functional and numerical responses of *Anisopteromalus calandrae* and *Lariophagus distinguendus* (Hymenoptera: Pteromalidae) to the various densities of an alternative host, *Callosobruchus chinensis*. *Korean Journal of Entomology (Korea Republic)*. https://agris.fao.org/agris-search/search.do?recordID=KR9502585

Shinoda, K. and K. Fujisaki. 2001. Effect of adult feeding on longevity and fecundity of the cigarette beetle, *Lasioderma serricorne* F. (Coleoptera: Anobiidae). *Applied Entomology and Zoology* 36(2): 219–223. https://doi.org/10.1303/AEZ.2001.219.

Shivananjappa, S., P. Fields, R.A. Laird and K.D. Floate. 2020. Contributions of diet quality and diapause duration to the termination of larval diapause in khapra beetle, *Trogoderma granarium* (Coleoptera: Dermestidae). *Journal of Stored Products Research* 85: 101535. https://doi.org/10.1016/J.JSPR.2019.101535.

Shivananjappa, S., K.D. Floate, P.G. Fields and R.A. Laird. 2023. Retrogressive moulting in khapra beetle, *Trogoderma granarium* (Coleoptera: Dermestidae). *Physiological Entomology*. https://doi.org/10.1111/PHEN.12404

Shuker, D.M. and E.R. Burdfield-steel. 2017. Reproductive interference in insects. *Ecological Entomology*. https://doi.org/10.1111/een.12450.

Simmons, L.W. 1987. Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (De Geer). *Behavioral Ecology and Sociobiology* 21(5): 313–321. https://doi.org/10.1007/BF00299969

Simon, A.F., D.T. Liang and D.E. Krantz. 2006. Differential decline in behavioral performance of *Drosophila melanogaster* with age. *Mechanisms of Ageing and Development* 127(7): 647–651. https://doi.org/10.1016/j.mad.2006.02.006.

Simwat, G. and B. Chahal. 1975. Effect of the age of *Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae) on the rate of egg laying and fecundity (India). *Bulletin of Grain Technology*.

Singh, C.B., D.S. Jayas, J. Paliwal and N.D.G. White. 2009. Detection of insect-damaged wheat kernels using near-infrared hyperspectral imaging. *Journal of Stored Products Research* 45(3): 151–158. https://doi.org/10.1016/J.JSPR.2008.12.002.

Singh, K., N.S. Agrawal and G.K. Girish. 1974. The oviposition and development of *Sitophilus oryzae* (L.) in different high-yielding varieties of wheat. *Journal of Stored Products Research* 10(2): 105–111. https://doi.org/10.1016/0022-474X(74)90017-4.

Singh, K. and Omkar. 2009. Effect of parental ageing on offspring developmental and survival attributes in an aphidophagous ladybird, *Cheilomenes sexmaculata*. *Journal of Applied Entomology* 133(7): 500–504. https://doi.org/10.1111/j.1439-0418.2008.01356.x.

Singh, P. 1977. *Artificial Diets for Insects, Mites, and Spiders*. 1st edition. Springer New York, NY. https://doi.org/10.1007/978-1-4684-8349-9.

Singh, S. and S. Prakash. 2015. Effect of Temperature and Humidity on the Culture of *Tribolium castaneum*, Herbst (Coleoptera: Tenebrionidae) in the laboratory. *International Journal of Scientific and Research Publications* 5(7): 1–6. https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=6f9b175df5b6715a40aec51b173fd65925d33c18#page=476

Sinha, R. 1973. Interrelations of physical, chemical, and biological variables in the deterioration of stored grains. In *Grain Storage: Part of a System*, 15–47. Avi publishing Company Wesport, CT, USA.

Sinha, R. and F. Watters. 1985. Insect pests of flour mills, grain elevators, and feed mills and their control..

Sinha, R.N. 1965. Development of *Cryptolestes ferrugineus* (Stephens) and *Oryzaephilus mercator* (Fauvel.) on seed-borne fungi. *Entomologia Experimentalis et Applicata* 8(4): 309–313. https://doi.org/10.1111/j.1570-7458.1965.tb00867.x.

Sinha, R.N. 1968. Adaptive Significance of Mycophagy in Stored-Product Arthropoda. *Evolution* 785–798. https://doi.org/10.2307/2406903.

Sinha, R.N. 1982. Food losses through energy transfer from cereal grains to stored-product insects. *Food and Nutrition Bulletin* 4(2).

Skourti, A., N.G. Kavallieratos and N.E. Papanikolaou. 2019. Laboratory evaluation of development and survival of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) under constant temperatures. *Journal of Stored Products Research* 83: 305–310. https://doi.org/10.1016/J.JSPR.2019.07.009.

Skourti, A., N.G. Kavallieratos and N.E. Papanikolaou. 2020. Suitability of Semolina, Cracked Wheat and Cracked Maize as Feeding Commodities for *Tribolium castaneum* (Herbst; Coleoptera: Tenebrionidae). *Insects* 11(2). https://doi.org/10.3390/insects11020099

Skourti, A., N.G. Kavallieratos and N.E. Papanikolaou. 2022. Demographic responses of *Tribolium castaneum* (Coleoptera: Tenebrionidae) to different temperatures in soft wheat flour. *Journal of Thermal Biology* 103: 103162. https://doi.org/10.1016/j.jtherbio.2021.103162.

Slansky Jr, F. 1985. Food consumption and utilization. *Comprehensive Insect Physiology*, *Biochemistry and Pharmacology* 4: 88–163.

Smith, L.B. 1966. Effect of crowding on oviposition, development and mortality of *Cryptolestes ferrugineus* (Stephens) (Coleoptera, Cucujidae). *Journal of Stored Products Research* 2(2): 91–104. https://doi.org/10.1016/0022-474x(66)90014-2.

Smith, L.B. 1970. Effects of cold-acclimation on supercooling and survival of the rusty grain beetle, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Cucujidae), at subzero temperatures. *Canadian Journal of Zoology* 48(4): 853–858. https://doi.org/10.1139/Z70-149.

Smith, L.B. 1985. Insect infestation in grain loaded in railroad cars at primary elevators in southern Manitoba, Canada. *Journal of Economic Entomology* 78(3): 531–534.

Sokoloff, A., I. Franklin, L. Overton and F. Ho. 1966. Comparative studies with *Tribolium* (Coleoptera, Tenebrionidae)—I: Productivity of *T. castaneum* (Herbst) and *T. confusum* Duv. on several commercially-available diets. *Journal of Stored Products Research* 1(4): 295–311.

Soliman, M.H. 1987. Ageing and parental age effects in *Tribolium* (Review). *Archives of Gerontology and Geriatrics* 6(1): 43–60. https://doi.org/10.1016/0167-4943(87)90038-0.

Soliman, M.H. and F. Lints. 1982. Influence of preimaginal constant and alternating temperatures on growth rate and longevity of adults of five genotypes in *Tribolium castaneum*. *Mechanisms of Ageing and Development* 18(1): 19–31.

Solomon, M.E. 1946. Tyroglyphid mites in stored products. Ecological studies. *Annals of Applied Biology* 33(1): 82–97. https://doi.org/10.1111/j.1744-7348.1946.tb06279.x.

Sonleitner, F.J. 1961. Factors Affecting Egg Cannibalism and Fecundity in Populations of Adult *Tribolium castaneum* Herbst. *Physiological Zoology* 34(3): 233–255. https://doi.org/10.1086/physzool.34.3.30152701.

Sonleitner, F.J. and J. Gutherie. 1991. Factors affecting oviposition rate in the flour beetle *Tribolium castaneum* and the origin of the population regulation mechanism. *Population Ecology* 33(1): 1–11. https://doi.org/10.1007/BF02514569

Sota, T. and K. Kubota. 1998. Genital lock-and-key as a selective agent against hybridization. *Evolution* 52(5): 1507–1513. https://doi.org/10.1111/J.1558-5646.1998.TB02033.X.

Spratt, E.C. 1980. Male homosexual behaviour and other factors influencing adult longevity in *Tribolium castaneum* (Herbst) and *T. confusum* Duval. *Journal of Stored Products Research* 16(3–4): 109–114. https://doi.org/10.1016/0022-474X(80)90006-5.

Sreeramoju, P., M. Prasad and V. Lakshmipathi. 2016. Complete study of lifecycle of *Tribolium castaneum* and its weight variations in the developing stages. *International Journal of Plant and Animal Environmental Sciences* 6(1): 95–100.

Srivastava, C. and S. Subramanian. 2016. Storage insect pests and their damage symptoms: an overview. *Indian Journal of Entomology* 78: 53–58. https://doi.org/10.5958/0974-8172.2016.00025.0.

Statistics Canada. 2023. Estimated areas, yield, production, average farm price and total farm value of principal field crops, in metric and imperial units. Table: 32-10-0359-01. https://doi.org/https://doi.org/10.25318/3210035901-eng.

Steidle, J.L.M., D. Rees and E.J. Wright. 2001. Assessment of Australian *Trichogramma* species

(Hymenoptera: Trichogrammatidae) as control agents of stored product moths. *Journal of Stored Products Research* 37(3): 263–275. https://doi.org/10.1016/S0022-474X(00)00027-8.

Suresh, S., N.D.G. White, D.S. Jayas and R.B. Hulasare. 2001. Mortality resulting from interactions between the red flour beetle and the rusty grain beetle. *Proceedings of the Entomological Society of Manitoba* 57: 11–18.

Surtees, G. 1964. Laboratory studies on dispersion behaviour of adult beetles in grain. VIII. Spontaneous activity in three species and a new approach to analysis of kinesis mechanisms. *Animal Behaviour* 12(2–3): 374–377. https://doi.org/10.1016/0003-3472(64)90027-2.

Suzuki, T. 1980. 4, 8-dimethyldecanal: The aggregation pheromone of the flour beetles, *Tribolium castaneum* and *T. confusum* (coleoptera: Tenebrionidae). *Agricultural and Biological Chemistry* 44(10): 2519–2520. https://doi.org/10.1080/00021369.1980.10864359.

Swain, W.R. 1975. Cold tolerance in relation to starvation of adult *Rhyzopertha dominica* (Coleoptera: Bostrichidae). *The Canadian Entomologist* 107(10): 1057–1061. https://doi.org/10.4039/Ent1071057-10

Takahashi, F. and Y. Yamamoto. 1972. Upper limit of the population growth of *Tribolium confusum* Duval. *Kontyú* 40(2): 55–64.

Tang, B., Z. Qin, Z.K. Shi, S. Wang, X.J. Guo, S.G. Wang and F. Zhang. 2014. Trehalase in *Harmonia axyridis* (Coleoptera: Coccinellidae): Effects on beetle locomotory activity and the correlation with trehalose metabolism under starvation conditions. *Applied Entomology* *and Zoology* 49(2): 255–264. https://doi.org/10.1007/S13355-014-0244-4/FIGURES/5

Teixeira, I.R. do V., A.R. Barchuk and F.S. Zucoloto. 2008. Host preference of the bean weevil *Zabrotes subfasciatus*. *Insect Science* 15(4): 335–341. https://doi.org/10.1111/J.1744-7917.2008.00218.X.

Teixeira, I.R. do V., L.A. Beijo and A.R. Barchuk. 2016. Behavioral and physiological responses of the bean weevil *Zabrotes subfasciatus* to intraspecific competition. *Journal of Stored Products Research* 69: 51–57. https://doi.org/10.1016/J.JSPR.2016.06.003.

Teixeira, I.R.V., A.R. Barchuk, L. Medeiros and F.S. Zucoloto. 2009. Females of the weevil *Zabrotes subfasciatus* manipulate the size and number of eggs according to the host seed availability. *Physiological Entomology* 34(3): 246–250. https://doi.org/10.1111/J.1365-3032.2009.00682.X.

Teixeira, I.R.V. and F.S. Zucoloto. 2012. Intraspecific competition in *Zabrotes subfasciatus*: Physiological and behavioral adaptations to different amounts of host. *Insect Science* 19(1): 102–111. https://doi.org/10.1111/J.1744-7917.2011.01425.X

Thompson, A.C. and P.P. Sikorowski. 1979. Effects of *Nosema heliothidis* on fatty and amino acids in larvae and pupae of the bollworm, *Heliothis zea*. *Comparative Biochemistry and Physiology -- Part A: Physiology* 63(3): 325–328. https://doi.org/10.1016/0300-9629(79)90597-8.

Thornhill, R. and J. Alcock. 2013. *The Evolution of Insect Mating Systems*. Harvard University Press. Harvard University Press. https://doi.org/10.4159/HARVARD.9780674433960/HTML.

Throne, J.E. 1991. Rusty Grain Beetle (Coleoptera: Cucujidae) Oviposition in Cracked and Whole Corn. *Journal of Entomological Science* 26(1): 183–187. https://doi.org/10.18474/0749-8004-26.1.183.

Throne, J.E. and M.P. Culik. 1989. Progeny production and duration of development of rusty grain beetles, *Cryptolestes ferrugineus* (Stephens)(Coleoptera: Cucujidae), on cracked and whole corn. *Journal of Entomological Science* 24(1): 150–155.

Tipples, K. 1995. Quality and nutritional changes in stored grain. In *Stored Grain Ecosystems*, eds. D. Jayas; N. White and W. Muir, 325–351. Marcel Dekker New York.

Tregenza, T. and N. Wedell. 2002. Polyandrous females avoid costs of inbreeding. *Nature 2002 415:6867* 415(6867): 71–73. https://doi.org/10.1038/415071a

Trematerra, P., R. Ianiro, C.G. Athanassiou and N.G. Kavallieratos. 2015. Behavioral interactions between *Sitophilus zeamais* and *Tribolium castaneum*: the first colonizer matters. *Journal of Pest Science* 88(3): 573–581. https://doi.org/10.1007/S10340-014-0633-Z/METRICS

Tripathi, R., D.S. Jayas, F. Jian and V.A.D. Hervet. 2021. Population dynamics of red flour beetle (*Tribolium castaneum* (Herbst)) under different temperatures and patch sizes. *Journal of Stored Products Research* 94: 101865. https://doi.org/10.1016/j.jspr.2021.101865.

United States Department of Agriculture. 2023. Crop Explorer - Wheat. https://ipad.fas.usda.gov/cropexplorer/Default.aspx.

Upadhyay, R.K. and S. Ahmad. 2011. Management Strategies for Control of Stored Grain Insect Pests in Farmer Stores and Public Ware Houses. *World Journal of Agricultural Sciences*

7(5): 527–549.

Via, S. 1999. Cannibalism facilitates the use of a novel environment in the flour beetle, *Tribolium castaneum*. *Heredity* 82(3): 267–275. https://doi.org/10.1038/sj.hdy.6884820.

Vidan, E., E. Quinn, A. Trostanetsky, A. Rapaport, J. Doron, A. Harush, M. Kostyukovsky and D. Gottlieb. 2020. How do similar community dynamics yield different population dynamics and spatial distributions of species? *Journal of Stored Products Research* 87: 101621. https://doi.org/10.1016/j.jspr.2020.101621.

Vogelweith, F., S. Foitzik and J. Meunier. 2017. Age, sex, mating status, but not social isolation interact to shape basal immunity in a group-living insect. *Journal of Insect Physiology* 103: 64–70. https://doi.org/10.1016/j.jinsphys.2017.10.007.

Vowotor, K.A., W.G. Meikle and J.N. Ayertey. 1998. Intraspecific competition in larvae of the larger grain borer, *Prostephanus Truncatus* (Horn) within maize grains. *Insect Science and Its Application* 18(3): 171–175. https://doi.org/10.1017/S1742758400023365/METRICS

Waldbauer, G.P. and A.K. Bhattacharya. 1973. Self-selection of an optimum diet from a mixture of wheat fractions by the larvae of *Tribolium confusum*. *Journal of Insect Physiology* 19(2): 407–418. https://doi.org/10.1016/0022-1910(73)90115-7.

Wallace, H. and R. Sinha. 1981. Causal factors operative in distributional patterns and abundance of fungi: a multivariate study. *Mycology Series*.

Waterhouse, F.L., A.K. Onyearu and T.G. Amos. 1971. Oviposition of *Tribolium* in Static Environments Incorporating Controlled Temperature and Humidity Gradients. *Oikos* 22(1): 131. https://doi.org/10.2307/3543374.

Watson, P.J. 1991. Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). *Animal Behaviour* 41(2): 343–360. https://doi.org/10.1016/S0003-3472(05)80486-5.

Weston, P.A. and S.A. Hoffman. 1992. Influence of Starvation, Dehydration, and Humidity Differential on Humidity Responses of *Sitophilus zeamais* (Coleoptera:Curculionidae). *Environmental Entomology* 21(6): 1345–1350. https://doi.org/10.1093/EE/21.6.1345

White, N.D. 1995. Insects, mites and insecticides in stored-grain ecosystems. In *Stored Grain Ecosystems*, 123--168. Marcel Dekker: New York, NY, USA.

White, N.D.G. and R.J. Bell. 1990. Relative fitness of a malathion-resistant strain of *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) when development and oviposition occur in malathion-treated and untreated wheat kernels. *Journal of Stored Products Research* 26(1): 23–37. https://doi.org/10.1016/0022-474X(90)90034-P.

White, N.D.G. and R.J. Bell. 1993. Effects of mating status, sex ratio, and population density on longevity and offspring production of *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Cucujidae). *Experimental Gerontology* 28(6): 617–631. https://doi.org/10.1016/0531-5565(93)90051-E.

White, N.D.G., C.J. Demianyk, H. Kawamoto and R.N. Sinha. 1995. Population growth of *Cryptolestes ferrugineus* and *C. pusillus* (Coleoptera: Cucujidae) alone, or in competition in stored wheat or maize at different temperatures. *Cambridge.Org* 85: 425–429. https://doi.org/10.1017/S0007485300036154

White, N.D.G. and R.N. Sinha. 1980. Principal component analysis of interrelations in stored-wheat ecosystems infested with multiple species of insects. *Population Ecology* 22(1): 33–

50. https://doi.org/10.1007/BF02513534

Wilson, K. and L. Hill. 1989. Factors affecting egg maturation in the bean weevil *Callosobruchus maculatus*. *Physiological Entomology* 14(1): 115–126. https://doi.org/10.1111/J.1365-3032.1989.TB00943.X

Wilson, R.S., E. Hammill and I.A. Johnston. 2007. Competition moderates the benefits of thermal acclimation to reproductive performance in male eastern mosquitofish. *Proceedings of the Royal Society B: Biological Sciences* 274(1614): 1199–1204. https://doi.org/10.1098/RSPB.2006.0401

Wilson, S.G. and J.M. Desmarchelier. 1994. Aeration according to seed wet-bulb temperature. *Journal of Stored Products Research* 30(1): 45–60. https://doi.org/10.1016/0022-474X(94)90271-2.

Wool, D. and S. Mendlinger. 1981. Genetical and Ecological Consequences of Subdivision in *Tribolium* Populations. *The Journal of Animal Ecology* 50(2): 421. https://doi.org/10.2307/4064.

Wright, V.F. and R. Burroughs. 1983. Mold-Damaged Grain Sorghum as a Diet for Three Stored-Grain Beetles (Coleoptera)1. *Environmental Entomology*. https://doi.org/10.1093/ee/12.2.558.

Xu, J., Z. Sheng and S.R. Palli. 2013. Juvenile Hormone and Insulin Regulate Trehalose Homeostasis in the Red Flour Beetle, *Tribolium castaneum*. *PLOS Genetics* 9(6): e1003535. https://doi.org/10.1371/JOURNAL.PGEN.1003535

Xu, J., J. Shu and Q. Zhang. 2010. Expression of the *Tribolium castaneum* (Coleoptera:

Tenebrionidae) hsp83 gene and its relation to oogenesis during ovarian maturation. *Journal of Genetics and Genomics* 37(8): 513–522. https://doi.org/10.1016/S1673-8527(09)60071-0.

Yadav, S.K. and C. Srivastava. 2017. Effect of temperature and food on the biology of khapra beetle, *Trogoderma granarium* Everts. *Journal of Entomology and Zoology Studies JEZS* 5(3): 1015–1019. https://www.researchgate.net/publication/320311369

Yongxue, D., Z. Zhimo and L. Longshu. 2003. Research advance of environmental factors on stored grain insects. *Grain Storage* 1: 5–12.

Young, A.M. 1970. Predation and Abundance in Populations of Flour Beetles. *Ecology* 51(4): 602–619. https://doi.org/10.2307/1934040.

Yu, C., B. Subramanyam, P.W. Flinn and J.A. Gwirtz. 2011. Susceptibility of *Lasioderma serricorne* (Coleoptera: Anobiidae) Life Stages to Elevated Temperatures Used During Structural Heat Treatments. *Journal of Economic Entomology* 104(1): 317–324. https://doi.org/10.1603/EC10067

Zayas, I. and P.W. Flinn. 1998. Detection of insects in bulkwheat samples with machine vision. *Transactions of the ASAE* 41(3): 883. https://elibrary.asabe.org/abstract.asp?aid=17206

Zeh, J.A. and D.W. Zeh. 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 263(1377): 1711–1717. https://doi.org/10.1098/RSPB.1996.0250

Zeh, J.A. and D.W. Zeh. 1997. The evolution of polyandry II: postcopulatory defenses against genetic incompatibility. *Proceedings of the Royal Society of London. Series B: Biological*

Sciences 264(1378): 69–75. https://doi.org/10.1098/RSPB.1997.0010

Zehnder, C.B., M.A. Parris and M.D. Hunter. 2007. Effects of maternal age and environment on offspring vital rates in the oleander aphid (Hemiptera: Aphididae). *Environmental Entomology*. https://doi.org/10.1603/0046-225X(2007)36[910:EOMAAE]2.0.CO;2.

Zhang, D.W., Z.J. Xiao, B.P. Zeng, K. Li and Y.L. Tang. 2019. Insect behavior and physiological adaptation mechanisms under starvation stress. *Frontiers in Physiology* 10(MAR). https://doi.org/10.3389/FPHYS.2019.00163/FULL.

Zhang, N., X. Meng, H. Jiang, H. Ge, Y. Zheng, K. Qian and J. Wang. 2022. Metabolic and transcriptional responses to starvation are regulated by FOXO in the red flour beetle, *Tribolium castaneum*. *Physiological Entomology* 47(4): 209–218. https://doi.org/10.1111/PHEN.12390

Ziegler, J.R. 1976. Evolution of the migration response: emigration by *Tribolium* and the influence of age. *Evolution*. https://doi.org/10.1111/j.1558-5646.1976.tb00935.x.

Ziegler, J.R. 1978. Dispersal and Reproduction in *Tribolium*: the Influence of Initial Density. *Environmental Entomology* 7(1): 149–156. https://doi.org/10.1093/ee/7.1.149.

Ziegler, V., L.J. Marini, C.D. Ferreira, I.A. Bertinetti, W.S.V. Da Silva, J.T.S. Goebel, M. De Oliveira and M.C. Elias. 2016. Effects of temperature and moisture during semi-hermetic storage on the quality evaluation parameters of soybean grain and oil. *Semina:Ciencias Agrarias*. https://doi.org/10.5433/1679-0359.2016v37n1p131.

Ziegler, V., R.T. Paraginski and C.D. Ferreira. 2021. Grain storage systems and effects of moisture, temperature and time on grain quality - A review. *Journal of Stored Products*

Research. https://doi.org/10.1016/j.jspr.2021.101770.

APPENDIX

Table A110. Insect density (all, adult, and offspring) and adult mortality (%) in experimental containers at 30℃ and 70% RH

Storage period (wk)	Experimental container*	All insect density	Adult density	Offspring density	Adult mortality (%)
4	LVC	0.78 ±0.20	0.50 ± 0.08	0.23 ± 0.14	9.72 ± 5.00
4	SCW	3.85 ± 1.61	0.76 ± 0.27	3.00 ± 1.67	6.06 ±6.06
4	SCC	44.42 ± 5.54	10.80 ± 0.99	31.85 ± 3.86	12.76 ± 4.87
8	LVC	0.92 ± 0.39	0.57 ± 0.28	0.16 ± 0.06	29.52 ± 5.79
8	SCW	30.02 ± 4.21	28.80 ± 4.59	0.50 ± 0.20	2.69 ± 0.94
8	SCC	65.07 ± 39.87	19.50 ± 8.50	45.38 ± 31.87	0.64 ± 0.37
12	LVC	9.50 ± 5.60	8.88 ± 5.47	0.19 ± 0.15	9.44 ± 4.30
12	SCW	24.38 ± 6.79	23.64 ± 6.54	0.26 ± 0.19	2.10 ± 0.25
12	SCC	296.45 ± 94.32	271.26 ± 88.11	19.95 ± 6.15	2.10 ± 0.38
16	LVC	8.07 ± 2.93	5.95 ± 2.49	0.23 ± 0.06	27.05 ± 4.13
16	SCW	185.52 ± 158.59	175.59 ± 149.80	5.92 ± 5.39	2.39 ± 0.53
16	SCC	161.09 ± 65.35	147.69 ± 62.53	10.66 ± 4.50	2.33 ± 0.61
20	LVC	16.64 ± 10.03	15.09 ± 9.40	0.40 ± 0.04	12.18 ± 5.44
20	SCW	115.02 ± 61.04	101.50 ± 59.25	2.83 ± 0.31	14.16 ± 5.02
20	SCC	2251.09 ± 1728.80	1252.72 ± 865.32	863.16 ± 780.50	10.93 ±0.89
24	LVC	23 ± 10.96	16.30 ± 10.09	2.07 ± 0.82	29.03 ± 11.80
24	SCW	25.07 ± 5.77	15.07 ± 1.83	3.57 ± 2.21	28.17 ± 5.44
24	SCC	245.30 ± 107.38	194.11 ± 82.84	39.66 ± 20.08	6.53 ± 1.59

*LVC, SCW and SCC indicate Long vertical columns, Shallow container – wheat and Shallow container – modified diet, respectively.