INFLUENCE OF TEMPERATURE, RELATIVE HUMIDITY AND INTERSPECIFIC COMPETITION ON THE POPULATION GROWTH DYNAMICS OF THREE PESTS OF STORED PRODUCT, *Oryzaephilus surinamensis* (L.), *Sitophilus oryzae* (L.) AND *Tribolium castaneum* (Herbst)

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By

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RH	Relative humidity
CP	Cuticular permeability
TBW	Total body water
SE	Standard error
OGT	Optimum growth temperature

PENGARUH SUHU, KELEMBAPAN RELATIF DAN PERSAINGAN INTERSPESIFIK KE ATAS DINAMIK PERKEMBANGAN POPULASI TIGA PEROSAK HASIL SIMPANAN, *Oryzaephilus surinamensis* (L.), *Sitophilus oryzae* (L.) DAN *Tribolium castaneum* (Herbst)

ABSTRAK

Kesan suhu, kelembapan relatif dan persaingan interspesifik ke atas dinamik perkembangan populasi tiga perosak hasil simpanan, *Oryzaephilus surinamensis* (Linnaeus), *Sitophilus oryzae* (Linnaeus) dan *Tribolium castaneum* (Herbst) telah dikaji. Ketiga-tiga spesies ini dipelihara dalam linkungan julat suhu 26-40°C serta kelembapan relatif 7-85%. Anggaran suhu perkembangan optima bagi *O. surinamensis*, *S. oryzae* dan *T. castaneum* masing-masing adalah dalam lingkungan 29.61-33.96, 27.63-27.91 dan 29.92-33.53°C, tertakluk kepada kelembapan relatif. *T. castaneum* mempunyai suhu maut yang paling tinggi (40°C), disusuli oleh *O. surinamensis* (38°C) dan *S. oryzae* (36°C). *S. oryzae* tidak dapat hidup pada kelembapan relatif yang terlampau rendah (7%) di bawah semua suhu yang diuji. Kelembapan relatif yang tinggi secara umumnya memanfaatkan perkembangan populasi ketiga-tiga spesies ini. Dalam usaha untuk menerangkan reaksi ketiga-tiga spesies ini terhadap kelembapan relatif, kajian imbangan air telah dijalankan. Jumlah kandungan badan air, kadar kehilangan air dan ketelapan kutikel *O. surinamensis*, *S. oryzae* dan *T. castaneum* menunjukkan tiada perbezaan yang ketara di antara satu sama lain, menandakan kehilangan air dari kutikel bukanlah punca utama *S. oryzae* dewasa tidak dapat hidup pada kelembapan relatif rendah yang melampau. Ketiga-tiga spesies ini seterusnya didedahkan kepada persaingan interspesifik pada suhu

yang berbeza (20, 25, 30 dan 35°C). Suhu mempunyai kesan yang ketara ke atas keputusan persaingan interspesifik. *Oryzaephilus surinamensis* secara konsisten merupakan spesies yang dominan pada semua suhu yang dikaji kecuali 20°C. Pada 20°C, bilangan *O. surinamensis* telah diatasi apabila digabungkan dengan sama ada *S. oryzae* atau *T. castaneum.* Namun begitu, *T. castaneum* sentiasa mengatasi *S. oryzae* apabila kedua-dua spesies ini wujud bersama, tanpa mengira suhu yang dikaji. Kadar perkembangan populasi ketika (*instantaneous population growth rate*) (r_i) *S. oryzae* telah dikurangkan dengan banyak oleh *T. castaneum*. *O. surinamensis* juga mempunyai nilai r_i yang lebih rendah apabila dipelihara bersama dengan *T. castaneum*. *Tribolium castaneum* dipelihara sama ada dengan *O. surinamensis* atau *S. oryzae* mempunyai nilai r_i yang ketara lebih tinggi. Implikasi serta kepentingan kajian ini terhadap pefahaman tentang kelimpahan, taburan dan status perosak bagi ketiga-tiga perosak hasil simpanan ini telah dibincangkan.

INFLUENCE OF TEMPERATURE, RELATIVE HUMIDITY AND INTERSPECIFIC COMPETITION ON THE POPULATION GROWTH DYNAMICS OF THREE PESTS OF STORED PRODUCT, *Oryzaephilus surinamensis* (L.), *Sitophilus oryzae* (L.) AND *Tribolium castaneum* (Herbst)

ABSTRACT

The effects of temperature, relative humidity and interspecific competition on the population growth dynamics of three pests of stored product, *Oryzaephilus surinamensis* (Linnaeus), *Sitophilus oryzae* (Linnaeus) and *Tribolium castaneum* (Herbst) were investigated. These three species were reared under a range of temperatures (26-40°C) and relative humidities (RH) (7-85%). The estimated optimum growth temperature for *O. surinamensis*, *S. oryzae* and *T. castaneum* ranged from 29.61-33.96, 27.63-27.91 and 29.92-33.53°C, respectively, depending on RH. Lethal temperature of *T. castaneum* was the highest (40°C), followed by *O. surinamensis* (38°C) and *S. oryzae* (36°C). *S. oryzae* were unable to survive at extreme low RH (7%) at all temperatures tested. High RHs were generally beneficial to the population growth of all three species. In an attempt to elucidate the reaction of these species towards RH, water balance studies were carried out. Total body water content, water loss rate and cuticular permeability of *O. surinamensis*, *S. oryzae* and *T. castaneum* showed no significant difference from each other, implying that cuticular water loss was not the major cause of adult *S. oryzae* failed to survive at extreme low RH. These three species were then subjected to interspecific competition under different temperatures (20, 25, 30 and 35°C). Temperature has significant effect ($p < 0.05$) on the outcome of the interspecies competition.

Oryzaephilus surinamensis was consistently the dominant species at all temperatures tested except 20°C. At 20°C, *O. surinamensis* were outnumbered when combined with either *S. oryzae* or *T. castaneum.* However, *T. castaneum* always outcompete *S. oryzae* when both species occurred together, irrespective of temperatures tested. The instantaneous population growth rate (r_i) of *S. oryzae* was greatly reduced by *T. castaneum*. *Oryzaephilus surinamensis* also had slightly lower r_i value when reared together with *T. castaneum*. *Tribolium castaneum* reared together with either *O. surinamensis* or *S. oryzae* had significantly higher r_i value. The implications and the importance of these findings in the understanding of the abundances, distributions and pest status of these three pests of stored product are discussed.

CHAPTER 1

GENERAL INTRODUCTION

Food insecurity has always been an issue revolving in many parts of the world, especially in developing countries. This condition most of the time is related to the availability of food (FAO, 2014). What is even worse is that many countries, especially in impoverished region, are unable to produce enough food to sustain the amount of food consumed by the people (FAO, 2012). Another major factor that leads to this phenomenon is the rising world population (Evans, 2009; Godfray et al., 2010). In 2014, the world population has reached an alarming number of 7.2 billion people and it is predicted to rise about 31% to reach a whopping 9.7 billion people by 2050 (Population Reference Bureau, 2014).

Events of unusual and extreme climate patterns associated with climate change have further impaired agricultural production to meet the increasing demand for food resulted from world population boom (Gregory and Ingram, 2000; Gregory et al., 2005; Parry et al., 2005). Moreover, substantial fraction of food is destroyed by insects during pre- and post-harvest period. Damages of food in the post-harvest should not be underestimated even though greater losses often occurred during pre-harvest period (Pimental, 1976). Stored agricultural products such as grains, pulses and flour are highly susceptible to insect attack, which can cause significant loss of food through insect feeding activities (Irabagon, 1959; Campbell and Sinha, 1976; Demianyk and Sinha, 1987). Infested foodstuffs also degrade in quality and may cause the commodity to be rejected by consumers (Gorham, 1979; Demianyk and Sinha, 1987).

Temperature and humidity are two important environmental factors which play a vital role in determining the population size of stored product insects (Birch, 1953; Howe, 1956b). Different temperature and relative humidity range favours population growth of different species of stored product insects. At optimum condition, insect pests are able to multiple rapidly and subsequently cause more damages to the commodities (Howe, 1965). Changes in climate could also cause shifting in distribution of insects and pest status as well (Masters et al., 1998; Harrington et al., 2001; Bale et al., 2002; Estay et al., 2009).

Interspecific competition is another factor that is known to influence insect population growth. Stored product insects are often confined within an environment or ecosystem which has limited space. Coexistence of multiple stored product insect species in a closed environment with limited resources accentuates the interaction and competition among different species, where “winner” species would thrive and the “loser” would diminish and probably even extinct (Lefkovitch, 1968; LeCato, 1975a; LeCato, 1975c; Nansen et al., 2009; Cui et al., 2006; Athanassiou et al., 2014). Competition outcomes vary with the physical environment (Park, 1954; Park, 1962; Fujii, 1967; Giga and Canhao, 1993; White et al., 1995).

To ensure success in managing stored product insects, these factors must be taken into account when developing pest control approaches. The knowledge of the physiology and biology of the stored product insects under the influence of different environmental conditions aids in gauging the diversity and the extent of infestations, and also in developing non-chemical control methods, such as manipulation of storage condition and heat disinfestation (Beckett, 2011). On the other hand, the understanding of the interspecific interactions among stored product insects are important in predicting population trends and also in developing pest control approaches that focus not only on one but multiple species that coexist in the commodities.

Unfortunately, such studies are mostly dated back in early half of the nineteenth century, and are lack of comprehensiveness. In response to this problem, this research aspired to provide more updated and more extensive data involving these population regulating factors. With *Oryzaephilus surinamensis* (L.) (saw-toothed grain beetle), *Sitophilus oryzae* (L.) (rice weevil) and *Tribolium castaneum* (Herbst) (red flour beetle) selected as the test species in this study, the influence of temperature, relative humidity and interspecific competition on population growth dynamics of pests of stored product were evaluated with the following specific objectives:

- To study population growth at different temperature and relative humidity combinations, and subsequently predict the optimum growth temperature at different RH.

- To measure the water balance of the three selected pests of stored product.

- To assess the effect of interspecies competition on population growth at four different temperatures.

CHAPTER 2

LITERATURE REVIEW

2.1 Stored Product Insects

Beetles (Order: Coleoptera), moths (Order: Lepidoptera) and psocids (Order: Psocoptera) are the most common insect pests of stored products. Other insects such as wasps (Order: Hymenoptera), flies (Order: Diptera), cockroaches (Order: Blattodea) and silverfish (Order: Thysanura) are usually predators, parasitoids or accidental pests (Hill, 1990; Walker, 1992; Rees, 2004).

Stored product insects can be classified into a few categories. Primary pests are insects that feed and reproduce on whole grains. These insects are destructive because they bore holes and cavities in grains during feeding. Milled products are unsuitable for primary insects, unless these products are compressed or processed into solid forms. Examples include *Sitotroga cerealella*, *Rhyzopertha dominica*, *Cryptolestes* spp., *Sitophilus* spp. and bruchids (Golebiowska, 1969; Campbell and Sinha, 1976; Demianyk and Sinha, 1987; Shazali, 1987; Umeozor, 2005; Baidoo et al., 2010). Insects that feed only on grains damaged or broken by primary pests or during handling and processing of grains are known as secondary pests. They prefer to feed on milled and processed food products. The damage caused by feeding of secondary pests is usually not easily identifiable and is usually difficult to measure. Examples include *Tribolium* spp., *Oryzaephilus* spp. and *Cryptolestes* spp (LeCato and McCray, 1973; Sinha and Watters, 1985; Trematera et al., 2000). Also, there are other insect pest categories such as fungus feeders, predators, parasitoids, scavengers and other accidental pests (Hill, 1990; Walker, 1992; Rees, 2004; Hagstrum et al., 2012).

2.2 Economic Importance of Stored Product Insects

The small body size of stored product insects allows them to move around through gaps in between grains and also cracks and crevices of the storage, thus enabling them to exploit the unique environment of the food storage facilities. Because of this feature, they are not easily detectable. They have high tolerance towards dry and water-restricted environment, just as the condition of a dry food storage facility. In order to take advantage of the transient food resource, they have the ability to multiply their populations very fast. Most of the economically important stored product insects are found all over the world, especially in the tropical regions, predominantly owing to international trading activities and globalization (Sinha and Watters, 1985; Walker, 1992; Rees, 2004).

Insect infestation on stored food products can cause serious economic losses. They are able to cause various damages that lead to loss in quantity, quality and subsequently result in rejection by consumers. They cause significant weight losses to stored food through direct feeding. These pests can also reduce grains to small fragments and dust (Demianyk and Sinha, 1987; Campbell and Sinha, 1976; White and Demianyk, 1996). Heat and moisture are released when the insects are feeding, which can facilitate the establishment of moulds and lead to more serious deterioration (Cofie-Agblor et al., 1995). In addition, they also contaminate food products with their faeces, secretions, exoskeleton casts and dead bodies, rendering the stored food products to be unpalatable. Stored product insect infestation is also known to be able to affect seed germination (Herford, 1961; Howe, 1962a; Bronswijk and Sinha, 1971; Gorham, 1979; Rajendran and Parveen, 2005).

In Malaysia, the main types grain stored are paddy and milled rice, which usually stored in bag and or in bulk. The most common insect pests that are found in stored paddy are *Sitophilus* spp., *Rhvzopertha dominica* and *Sitotroga cerealella*. On the other hand, insect species that infest milled rice are *Sitophilus oryzae* and *Tribolium castaneum*. Under humid tropical weather, stored grains are highly susceptible to various factors that lead to deterioration, especially insect infestation. Studies have reported that insects have caused approximately 3-7% of weight loss in paddy and 5-14% in milled rice (Muda, 1985).

2.3 Saw-toothed Grain Beetle

Scientific classification

Phylum : Arthropoda

Class : Insecta

Order : Coleoptera

Family : Silvanidae

Binomial name: *Oryzaephilus surinamensis* (Linnaeus, 1758)

2.3.1 Morphology and Identification

Oryzaephilus surinamensis (Plate 2.1) is small, greatly flattened and its sides are parallel. It is brownish in colour and its length is about 2.5 to 3 mm. It has a pair of antennae that are short and clubbed. The most distinctive feature of this species is the six tooth-like lateral projections at each side of the prothorax (Sinha and Watters, 1985; Hill, 1990; Rees, 2004). *Oryzaephilus surinamensis* is very often being misidentified as *O. mercator*. To differentiate these two species, one can observe the area of the head behind the eye or the length of the temple. The length of the temple of *O. surinamensis* is much longer than *O. mercator* (Howe, 1956a).

The larva of *Oryzaephilus surinamensis* has an elongated and flattened body (campodeiform), and its legs are well-developed. It is whitish in colour but the head capsule and the last segment of the abdomen may be pigmented. A fully grown larva is about 4 to 5 mm in length. The pupa is concealed in a coccoon-like structure constructed from food particles (Sinha and Watters, 1985; Rees, 2004). Sexing of *O. surinamensis* can be done by observing the hind legs of the beetles. Males have a spine at each trochanter, femur and tibia of the hind legs. Females do not have such feature (Bousquet, 1990) (Plate 2.2).

2.3.2 Life Cycle

The shortest developmental period of *O. surinamensis* takes 20 days under optimum conditions. An adult female is able to produce 375 eggs per month in average. The eggs take 4 to 12 days to hatch. The larva has 2 to 4 instars which take approximately 13 days to develop, when reared on wheatfeed and at 30°C. Pupa normally requires 5 to 15 days before emerging as adult. Adult has long lifespan and

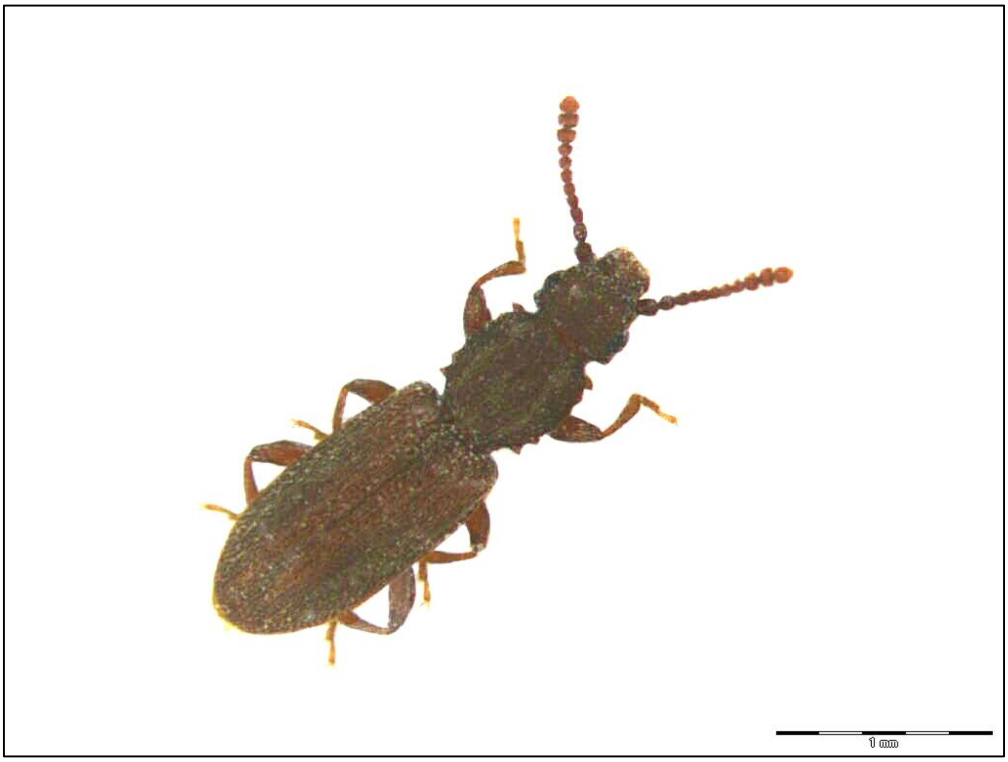
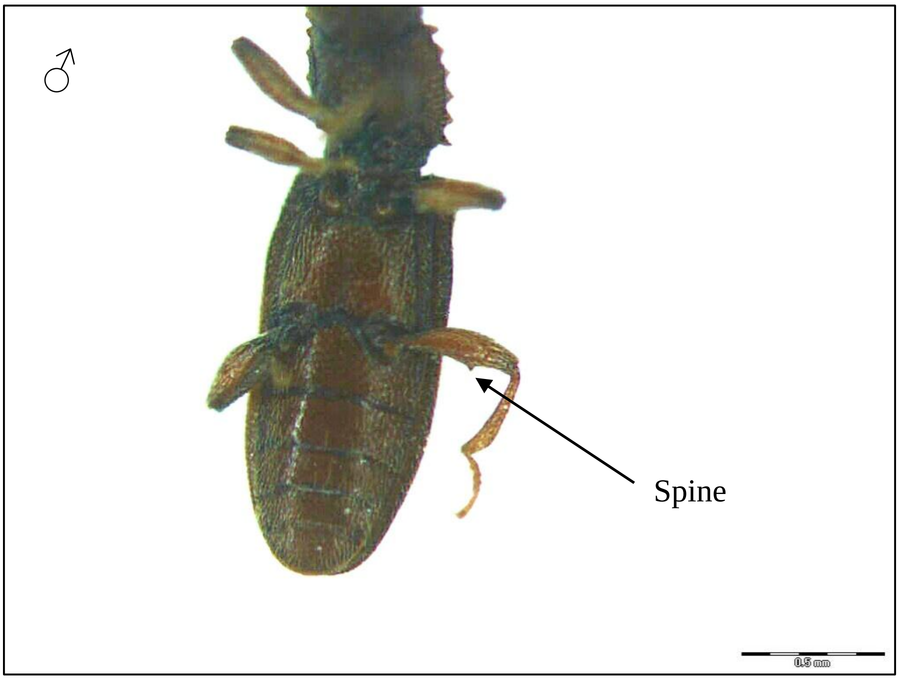


Plate 2.1: Adult *Oryzaephilus surinamensis*.



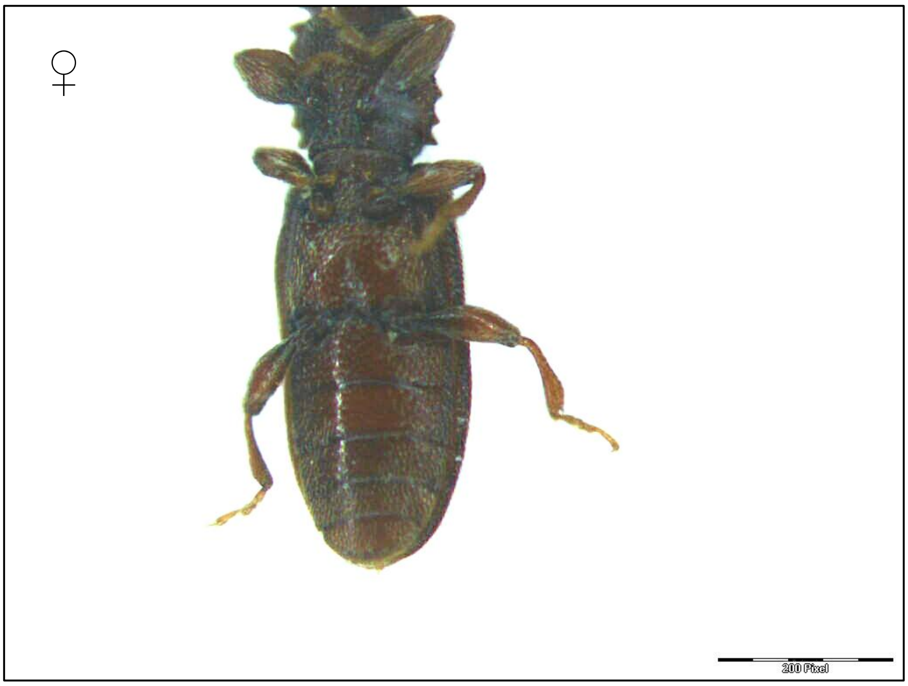


Plate 2.2: Adult male *O. surinamensis* has a spine at the femur of the hind legs (♂). Such spine is absent in female (♀).

it feeds throughout its lifetime. It is reported that the adult can live about 6 to 8 months at warm tropical conditions and up to several years in cool temperate climates (Howe, 1956a; Rees, 2004; Hagstrum et al., 2012).

2.3.3 Feeding Behaviour

Oryzaephilus surinamensis is distributed worldwide, at both tropical and temperate regions. It is a pest of stored grains, particularly milled and processed commodities. Usually, it is categorised as a secondary pest (Olsen, 1981). This species damages commodities by direct consumption. The larva attacks intact grains and it can also excavate into damaged grains. It feeds specifically on the germ area of the grains. It is also known to be able to damage product packaging. Infestations are often being overlooked due to its small size and high mobility that make the insect difficult to be noticed. Because of these features, it is able to hide in crack and crevices in storage facilities, making it difficult to be reached and controlled by insecticides (Hill, 1992; Rees, 2004). This species has been reported to be resistant to several insecticides (Lee and Lees, 2001).

2.4 Rice Weevil

Scientific classification

Phylum : Arthropoda

Class : Insecta

Order : Coleoptera

Family : Curculionidae

Binomial name: *Sitophilus oryzae* (Linnaeus, 1763)

2.4.1 Morphology and Identification

Sitophilus oryzae (Plate 2.3) is a destructive pest that has a characteristic snout at its head. It is brownish to blackish in colour and is about 2.5 to 4 mm long. Each of the elytra of adult *S. oryzae* has two yellow markings and its pronotum has punctures that are circular in shape. This characteristic helps to differentiate between this species and *S. granarius*, which has almost similar morphology but it has no markings on its elytra and has oval shaped punctures on its pronotum instead. The larva is whitish in colour and is without legs (apodous). It is immobile and is concealed within grain. The length of a fully-grown larva is about 4mm (Sinha and Watters, 1985; Hill, 1992; Rees, 2004). The size of the grains where the larva developed in may influence the size of the emerged adult insect (Russell, 1962).

To sex adult *S. oryzae*, it can be done by observing the snout or rostrum. Male adult has a rather short and broad snout. The holes along the snout are prominent and irregular in shape, thus making the snout looking rugged. In contrary, female has comparatively longer and narrower snout with small and regular holes along the snout and not touching each other, thus making the snout looking smooth (Rees, 2004) (Plate 2.4).

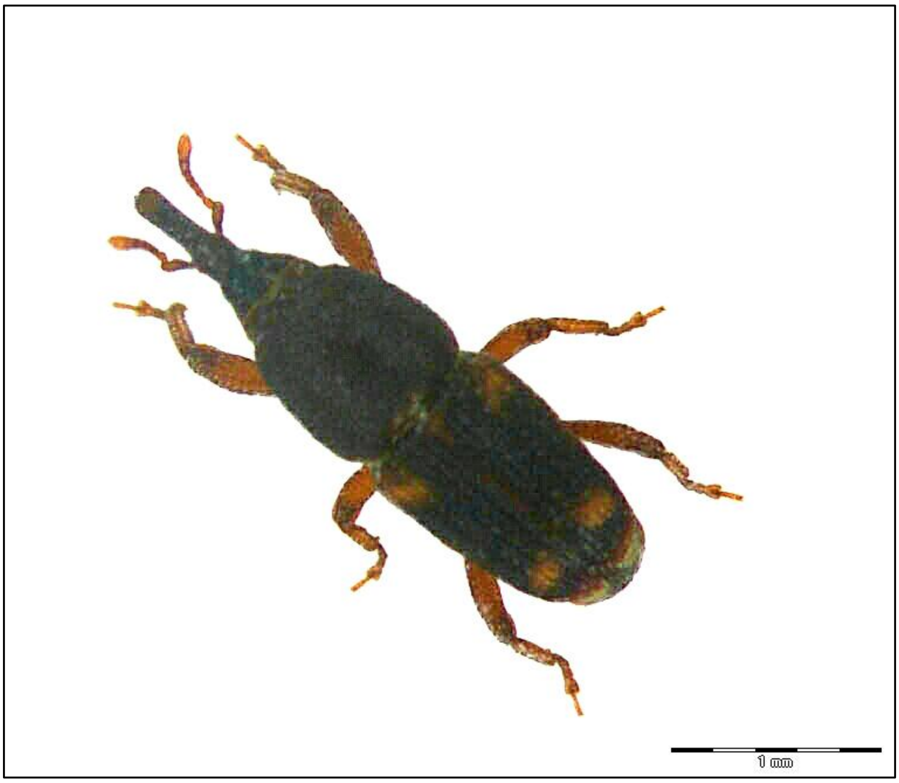


Plate 2.3: Adult *Sitophilus oryzae*.

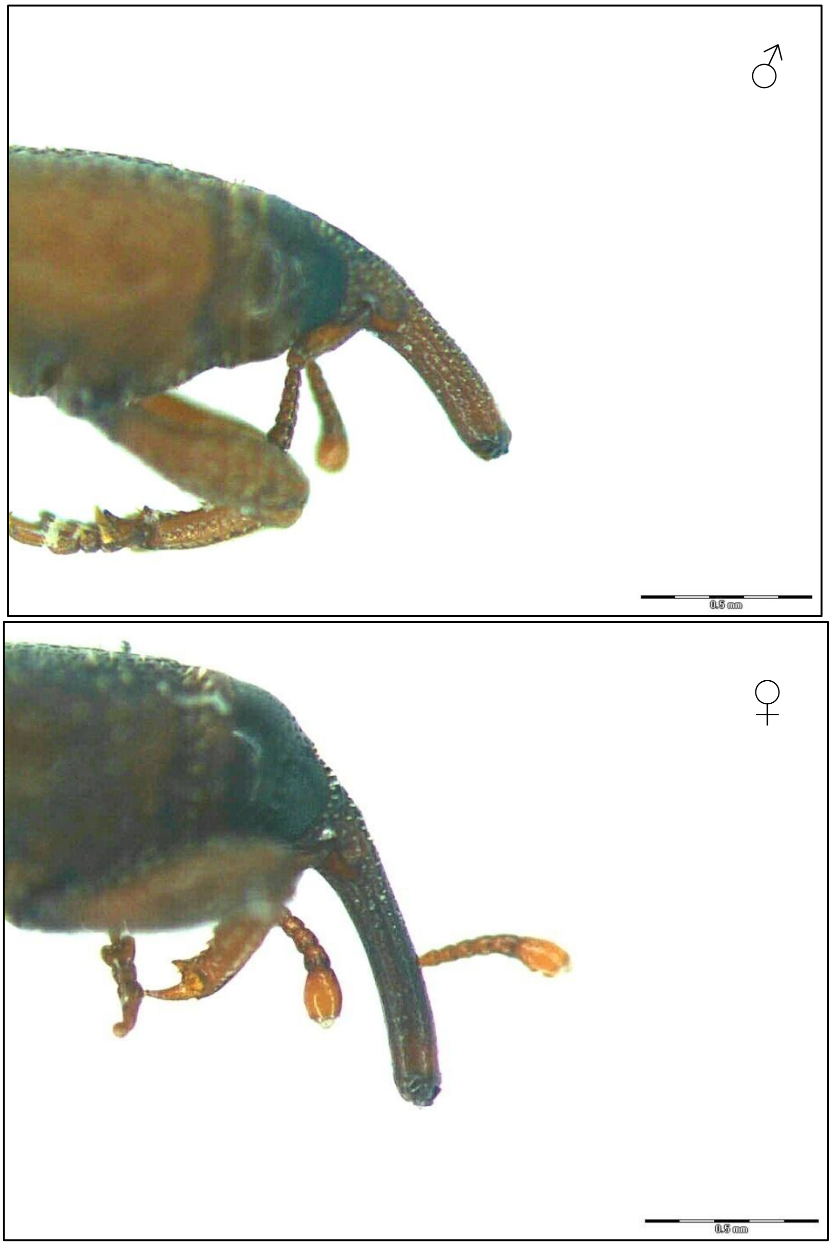


Plate 2.4: Adult male *S. oryzae*'s snout is short, broad and rough looking (♂). Female has a longer, narrower and smoother looking snout (♀).

2.4.2 Life Cycle

Its developmental period is 25 days under optimum conditions of 30°C and 70% relative humidity (Rees, 2004). However, its development may vary according to the surroundings, where lower temperature and humidity can extend its developmental period (Hagstrum and Leach, 1973; Evans, 1982; Ryoo and Cho, 1988; Beckett et al., 1994). Apart from that, developmental rate is also dependent on the food the insect has consumed (Ungsunantwiwat and Mills, 1985; Hagstrum and Milliken, 1988; Trematerra et al., 1996). Female weevil lays eggs throughout its adult life. Female adult makes hole on the grain and lays egg in it. The opening is then sealed with waxy secretion. Each hole only contains one egg (Sharifi, 1972; Hill, 1990; Rees, 2004). One female can lay about 150 to 300 eggs and it takes approximately six days to hatch when the ambient temperature is at 25°C.

Larva excavates a tunnel into the grain and consumes the internal of the grain. It has four instars which take about 25 to 100 days to develop, depending on the environmental conditions. Larva then pupates inside the grain. When mature, the adult consumes the internal of the grain to exit and leaves a jagged emergence hole, which is a distinctive damage by this species (Sinha and Watters, 1985; Hill, 1992; Rees, 2004). Adult has long lifespan of 3 to 6 months, depending on the environmental conditions.

2.4.3 Feeding Behaviour

This species are active insects, usually during the day, and it can fly. *Sitophilus oryzae* are widely distributed around the globe, but are abundant particularly in the tropical region. They are primary pests of stored grains (whole cereal grains), especially wheat and rice. They are also known to infest dried pasta, flour and other starchy food. Some strains of this species have been reported to attack pulses. Both adult and larva cause significant damage to commodities. Larva cause large cavities inside grains through feeding. Newly emerging adult leaves behind prominent jagged emergence hole. The adult then continues to cause more damage, by consuming grains that have been damaged previously (Irrabagon, 1959; Sinha and Watters, 1985; Ungsunantwiwat and Mills, 1985; Baker, 1988; Hill, 1992). Weevils infested grains are found to be easily spoilt due to excessive moisture and heat produced by the infestations which alter the environment suitable for mould growth and emergence of other pest species, which subsequently promotes further quality loss (Howe, 1962a; Cofie-Agblor et al., 1995). Thus, they are of high economic importance.

2.5 Red Flour Beetle

Scientific classification

Phylum : Arthropoda

Class : Insecta

Order : Coleoptera

Family : Tenebrionidae

Binomial name: *Tribolium castaneum* (Herbst, 1797)

2.5.1 Morphology and Identification

Adult *Tribolium castaneum* (Plate 2.5) is small in size and it is elongated and flat in shape. It is reddish brown in colour and about 3 to 4 mm in length. It has wings and is a good flyer. Larva has long and cylindrical body (elateriform), with leathery cuticle and relatively short legs. Larva is active and lives and moves freely within the stored food products (Sinha and Watters, 1985; Hill, 1992).

Tribolium castaneum is often being mistaken with *T. confusum*. They can be distinguished by the features of the eyes and the antennae. The gap between the eyes of *T. castaneum* when observed from below is narrower than that of *T. confusum*. Besides that, *T. castaneum* has distinctive three segmented antennal club, whereas the antennae segments of *T. confusum* widen gradually towards the tip. In addition to that, *T. confusum* also differs from *T. castaneum* where it usually grows better in cooler climates (Sinha and Watters, 1985; Rees, 2004). To distinguish the sex of *Tribolium* beetle, it can be done at the pupal stage. Female has a pair of minuscule genital papillae at the last segment of the ventral posterior end. On the contrary, the genital papillae of the male have shrunken to obscure elevations (Park, 1934) (Plate 2.6).

2.5.2 Life Cycle

The optimum environmental conditions for successful population growth are 32-35°C and 70-75% relative humidity (Sinha and Watters, 1985). Under optimum condition, *T. castaneum* requires period as short as 20 days to develop completely. Adults can live for a long time, about 6 months and can go up to 2 to 3 months in cooler climates (Hill, 1992). Developmental rate and fecundity of *T. castaneum* are

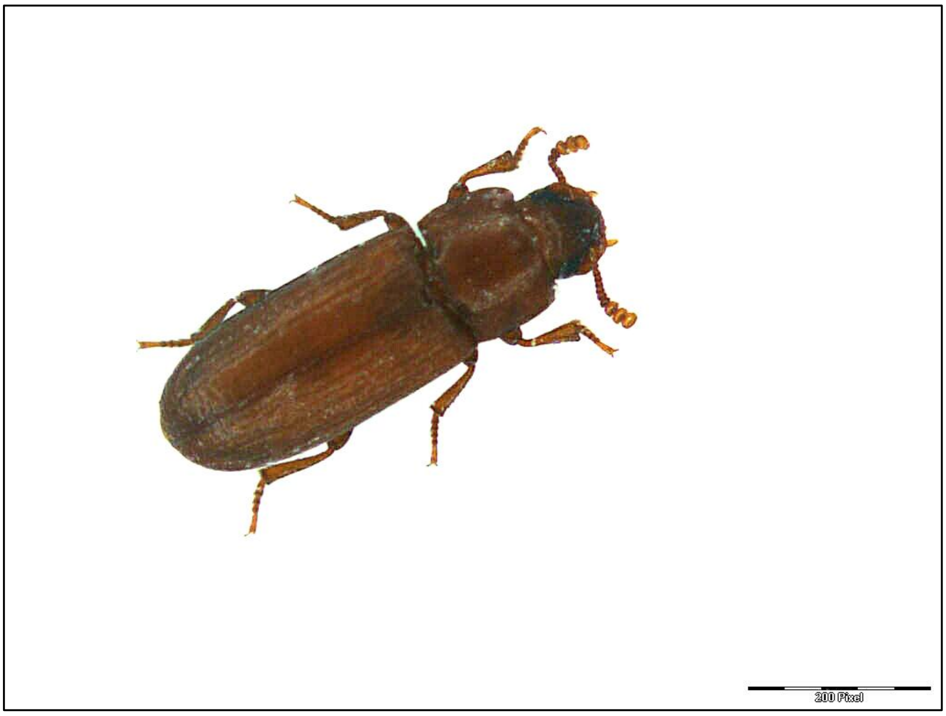


Plate 2.5: Adult *Tribolium castaneum*.

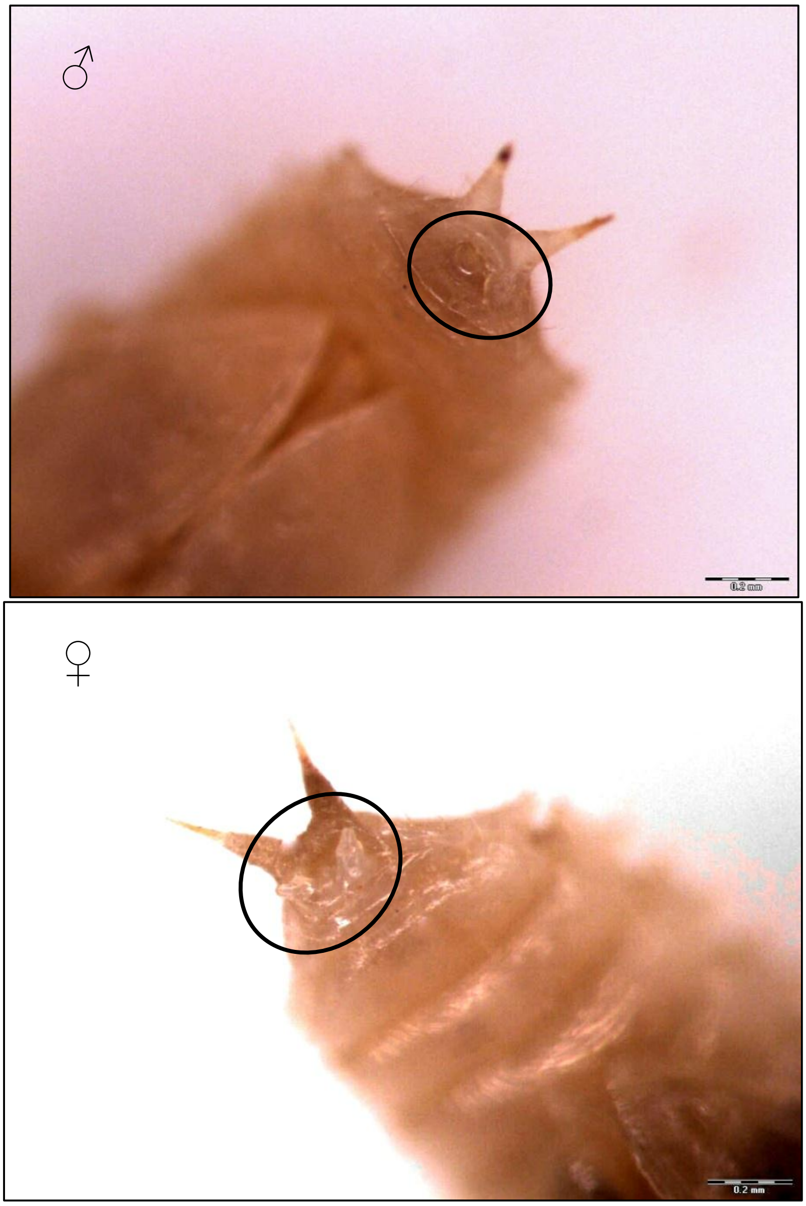


Plate 2.6: The genital papillae of male are small and shrunken (♂). Female has larger pair of papillae (♀).

influenced by the ambient temperature and humidity (Park and Frank, 1948; Howe, 1962b) and the type of food they consumed (Sokoloff et al., 1966; Wong and Lee, 2011). There are also studies which reported that *T. castaneum* preyed on eggs and immature stages other species have markedly higher reproduction and developmental rate (LeCato, 1975c; LeCato, 1978; Arbogast and Mullen, 1988; Weston and Rattlinggourd, 2000).

An adult female lays about 150 to 600 eggs in its lifetime. Eggs are laid at random in between the stored food products. The eggs take 2 to 3 days to hatch under favourable conditions. Larva has 7 to 8 instars and then 13 days later it will undergo pupation. The larval stage takes up most of the developmental period; only less than 40% of the time is spent as egg and pupa stages. Larva consumes commodities and other tiny insects. The development of the pupal stage requires 4 to 5 days to complete (Hill, 1990; Rees, 2004). Cannibalism among larvae and adults is very common. This is one important way to regulate their population size, especially in a nutritionally poor or overcrowded environment (Rich, 1956; Sonleitner, 1961; Park et al., 1965). Studies have shown that male adults prefer to cannibalize pupae, whereas female adults tend to cannibalized eggs (Via, 1999; Longstaff, 1995).

2.5.3 Feeding Behaviour

Tribolium castaneum is distributed worldwide and it thrives very well in tropical regions. The larval and adult stages are secondary pests of cereals and cereal products and are major pests of mills. They prefer to feed on damaged grains but they do attack whole and intact grains. They usually consume the germinal part of whole grains (Rees, 2004). *Tribolium castaneum* secretes benzoquinones from abdominal and thoracic defence glands which can cause pungent and unpleasant odours in the stored food products, especially in serious infestation (Hodges et al., 1995).

2.6 Factors Regulating Insect Population

2.6.1 Temperature and Relative Humidity

There are many abiotic factors that regulate insect population, such as temperature, humidity, light intensity, rainfall, soil, seasonality, food, topography, etc (Schowalter, 2006). However, in the case of stored product insects, temperature and relative humidity (RH) play the most important role, because they are often confined within a closed environment with abundant food resource. Insects do not have the ability to maintain a constant body temperature like mammals and birds. Their survival and population growth are highly dependent on surrounding temperatures (Gullan and Cranston, 2005). Stored product insects in particular are very sensitive to surrounding temperatures and RHs. When conditions are favourable, they are able to multiply rapidly and achieve pest status (Howe, 1965).

Insects take longer time to develop when the surrounding temperature is below optimum temperature. The growth rate is decreased as well. Physiology, behaviour, ecology and other biological aspect can also be affected by surrounding temperature (Neven, 2000). Studies have shown that temperature has considerable influence on the developmental period, reproduction and survival, and subsequently affects the population dynamics (Hagstrum and Milliken, 1988). Different species have different tolerance limits towards temperature (Sönmez and Gülel, 2008). Stored product insects usually breed within temperature of 15-42°C and the rate of population growth increases with temperature when the temperature is above the minimum until it reaches optimum condition (usually in the range of 25-33°C). Beyond this point, the rate of population growth declines drastically due to heat stress (Rees, 2004).

When insects live in environment with higher temperature in a long-term period, it can cause a few implications. Most insects tend to increase in energy levels when the ambient temperatures are in the range of 15 to 35°C. Higher energy levels modify physiological processes of insects. Insects may produce more eggs at higher temperature (Child, 2007). In the experiment conducted by Giga and Smith (1987), regardless of the food they were being provided, egg production of *Callosobruchus rhodesianus* and *C. maculatus* was significantly affected by temperatures. These two species shown significantly higher number of eggs laid at 30°C when compared to 20°C. Egg hatchability of both species was also reported to be higher at 30°C.

RH influences the population growth and development of insects, including stored product insects, as water is a limiting resource for most insects. Stored product insects inhabit in environment where not only free liquid water is sparse, surrounding water vapour activity and the water content in food are also limited. Therefore, to gain enough water to sustain their physiological processes, these insects absorb water from their food, from the oxidation carbohydrates and fats in the form of metabolic water, and also from the surrounding environment (Arlian, 1979). Stored product insects obtain water from the moisture content in the food (i.e. grains, pulses, etc.) they consumed, and the water vapour that is trapped in the spaces among the grains is proportionate to the water content in the grain (Weston and Hoffman, 1991). Water content in the food changes directly with the ambient RH (Menusan, 1936). Higher moisture content may increase fertility. Egg production is increased and the reproductive period is shortened. Moist grain also promotes longer generation time, higher emergence rate and longer life span (Evans, 1982).

For example, Ali et al. (2011) demonstrated that RH had significant influence on carpet beetle *Attagenus fasciatus*. At 30°C, the pupal duration was shortened with increasing RH. Percentage of adult emergence was also affected by the different RHs (40, 60 and 80%) tested. They have also shown that egg duration was positively correlated to RH. Besides that, adult longevity was longer with higher RH. Therefore, it is evident that RH plays a significant role in regulating the abundance of stored product insects.

Some species of stored product insects thrive better in some range of humidity; while some might tend to avoid those conditions and those conditions might even be detrimental to them. Stored product insects have different tolerance towards RH range, depending on species (Howe, 1965). High RH increases the grain moisture content, which provides a favourable condition for fungal growth. Many fungi are able to produce toxic metabolites which are detrimental to insect reproduction and development (Weston and Hoffman, 1991). Insects also tend to exhibit different response when exposed to different RH (Arbogast, 1974; Arbogast, 2003). Water balance is a crucial factor in determining the response of many insect species towards humidity (Arbogast and Carthon, 1972).

The effect of temperature on regulating the abundance of all organisms is correlated with the water exists in the atmosphere. Water is an essential component for the survival and reproduction of all organisms. The exact amount of water in the atmosphere (absolute moisture content) influences the biological and physiological activity of an organism. When the ambient temperature rises, the RH, i.e. the capacity of water the air is able to carry, will also follow suit (Sinha and Watters, 1985).

Based on regression equations on the developmental times of nine species stored product beetles, Hagstrum and Miliken (1988) concluded that temperature generally plays more important role in determining the developmental time than moisture, and diet is the least important among these three factors. However, their studies also reported that larval developmental time was affected more by moisture and diet than temperature when the larvae was reared close to the optimum development temperature for each species. These finding shows that these abiotic factors are important in regulating insect pest populations, especially temperature and moisture.

Since insects have sensitive response towards ambient temperature, and also due to the increasing demand in the market for chemical-free commodities storage and with the insecticide resistance problems getting more and more serious, many have opted to manipulate storage temperature as a means to protect commodities from pest attacks and also to disinfest (Beckett, 2011). Many studies have proven that elevated temperature and also cooling of the commodities are effective ways in managing pest problems in stored commodities (Nakakita and Ikenaga, 1997; Beckett, 2011; Loganathan et al., 2011). Fields (1992) have reviewed and summarised a list of over 50 research papers on the use of extreme temperatures in controlling stored product insects. He reported that the optimum temperature range for population growth and reproduction of most stored product insects is around 25-33°C. They are capable of completing development and reproduce at the temperature range of 13-25 or at 33-35°C. However, beyond this range (<13 or > 35°C) is detrimental to the insects. Different species have different tolerance towards extreme temperatures. The tolerance level is also dependant on the developmental stage, acclimatization, and also RH. Thus, species identification and the understanding of their biology under temperature and RH influence are crucial in achieving sufficient level of pest prevention and disinfestation.

Knowing these facts, close monitoring and managing of temperature and RH in food storage facilities is also essential in tackling stored product insect pest problems. Dry or low RH conditions are able to provide protection against stored product pests to a certain extent. Low RH helps keeping the insect pest numbers at low level and may even help preventing the establishment of the insect pests (Beckett, 2011). The manipulation of the temperature and RH of the storage is able to enhance the efficacy of many different types of pest control treatments, such as ethyl formate fumigation (Damcevski and Annis, 2006), inert dust treatment (Arthur, 2000; Arthur, 2001; Stadler et al., 2011).

2.6.2 Interspecific Competition

Competition is a phenomenon whereby two or more organisms vie for a common and limited resource. It is an important biotic factor that regulates insect numbers. Space and food are the major competition resources. Competition can occur among members from the same species (intraspecific competition), and also between the individuals that come from different species (interspecific competition) (Klomp, 1964; Varley, 1973; Townsend et al., 2003; Begon et al., 2006).

In interspecific competition, there will always be individuals from a single species sustaining decrement in reproductivity, development or survivorship.