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TITLE: Effect of Host Age on Progeny Production of *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae) Reared on *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae)

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THESIS

EFFECT OF HOST AGE ON PROGENY PRODUCTION OF *THEOCOLAX ELEGANS* (WESTWOOD) (HYMENOPTERA: PTEROMALIDAE) REARED ON *SITOPHILUS ZEAMAIS* (MOTSCHULSKY) (COLEOPTERA: CURCULIONIDAE)

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Bonginkhosi Edward Dlamini 2014: Effect of Host Age on Progeny Production of *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae) Reared on *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae). Master of Science (Tropical Agriculture), Major Field: Tropical Agriculture, Faculty of Agriculture. Thesis Advisor: Assistant Professor Weerawan Amornsark, Ph.D. 80 pages.

Five host ages of Maize weevil, *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) reared on brown rice were examined for progeny production of *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae). Brown rice kernels infested with *S. zeamais* were exposed to a mated female of *T. elegans* after 13, 15, 17, 19 and 21 days following *S. zeamais* introduction. Host stages were determined by measuring head capsule widths from all the host ages.

There was a significant difference ($P < 0.05$) in *T. elegans* progeny production among the different host ages. Total progeny, total female progeny and total male progeny produced by 19-day-old *S. zeamais* larvae were significantly higher ($P < 0.05$) compared to the other host ages. Progeny of *T. elegans* raised on 19-day-old *S. zeamais* larvae had a higher female: male ratio compared to the other host ages. *Sitophilus zeamais* larvae after 13, 15-17 and 19-21 days were found to be second, third and fourth instars, respectively.

I concluded that *T. elegans* can develop on second, third and fourth instar larvae of *S. zeamais*. However, 19-day-old (fourth instar) *S. zeamais* larvae produced more *T. elegans* progeny with a high female: male ratio.

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INTRODUCTION

Rice and maize are important food crops of many countries of the world. These crops are typically grown for grain. The grain is stored because it cannot be distributed or consumed immediately (Flinn and Hagstrum, 2002). Cereal grain is stored under maintained moisture conditions ranging from 13-14% (Ileleji *et al*., 2007). Stored products are susceptible to infestation by many species of stored-product insect pests at 14% or less moisture content (Flinn, 1998).

Stored-product insect pests attacking stored grains are significant pests because they feed and reduce the grain's weight, and cause high expenses for chemical treatment and sanitation (Phillips, 1997; Tefera *et al.*, 2010). About $8.5 billion is lost annually by farmers on chemical pesticides used to reduce losses caused by insect pests (Phillips *et al*., 2010). Storage insect pests feed on harvested grain and cause most economic damage due to spoilage and grain loss when they are not controlled (Jackai and Adalla, 1997; Phillips, 1997).

Storage insect pests can cause both quantitative and qualitative damage on stored grain (Adane *et al*., 1996; Moino *et al*., 1998). Quantitative grain loss is as a result of insect feeding; both immature and adults (Moino *et al*., 1998). Qualitative grain loss is as a result of product change; loss of grain nutritional value, loss of grain aesthetic value, increased grain rejects and reduction of industrial attributes (Moino *et al*., 1998). The damage on seed embryos by storage insect pests result in a reduced germination percentage (Adane *et al*., 1996; Moino *et al*., 1998). Grain loss can be reduced by controlling storage pests in storage facilities.

The over-reliance on chemicals has adverse effects on the consumer and the environment (Phillips, 1997; Charlet *et al*., 2002; Bale *et al*., 2007). Constant

synthetic chemical use can result in insecticide resistant insect pests (Adane *et al*., 1996; Moino *et al*., 1998). Resistance to Malathion was reported in 637 out of 1927 populations of storage insect pests tested (Moino *et al*., 1998). A further resistance to phosphine was reported in 82 out of 849 populations of storage insect pests examined (Moino *et al*., 1998). There is a need to control storage insect pests with alternative pest management methods to reduce pesticide resistance in the control of storage insect pests (Adane *et al*., 1996).

Synthetic chemicals have a relatively long residual effect on the environment (Flinn and Hagstrum, 2002; Weinzierl and Higgins, 2008)). Effective pest management and environmentally friendly approaches must be applied to prevent grain loss and spoilage while posing no threat to the environment and the consumer (Charlet *et al*., 2002; Ileke, 2007; Weinzierl and Higgins, 2008; Tefera *et al.*, 2010). However, the use of synthetic insecticides is coupled with adverse effects on the consumer and the environment (Charlet *et al*., 2002; Flinn and Hagstrum, 2002). Storage insect pests can be controlled to lower levels by using natural enemies or biological control agents.

A successful pest management program of storage insect pests can be achieved by good storage practices (Weinzierl and Higgins, 2008). The main aim of a sound pest management program is to maintain the grain free from storage insect pests while eliminating the use of insecticides (Weinzierl and Higgins, 2008). The use of biological control agents has no effect on the consumer nor the environment (Flinn, 1998; Tefera *et al.*, 2010).

Biological control agents live around the grain and are easy to remove from the grain by basic cleaning processes (Ahmed and Khatun, 1993; Flinn and Hagstrum, 2002). This means that losses due to spoilage and grain weight loss can be reduced (Brower *et al*., 1995; Flinn and Hagstrum, 2002; Tefera *et al*., 2010). *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae) is an efficient natural enemy of a number of storage insect pests including maize weevils, *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) (Flinn, 1998; Tefera *et al*., 2010).

Sitophilus zeamais is an important insect pest of stored maize and rice in tropical and sub-tropical regions of the world (Campbell *et al*., 1989; Flinn and Hagstrum, 2002; Tefera *et al*., 2010). High infestations of *S. zeamais* have been observed when cereal grains were stored without control of moisture content and chemical protectants (Bale *et al*., 2007; Tefera *et al*., 2010). *Sitophilus zeamais* infest stored grain by immigrating from outside to storage structures (Brower *et al*., 1995; Flinn and Hagstrum, 2002; Tefera *et al*., 2010). Large quantities of stored grain attract *S. zeamais* to infest the grain by getting through storage structure's openings (Weinzierl and Higgins, 2008).

Sitophilus zeamais can infest grain from other sources including infested residual grain in storage structures, grain spills and infested seeds (Weinzierl and Higgins, 2008). First infestation is usually initiated in the field and the weevil develops, and it's population grows while the crop is stored as grain (Flinn and Hagstrum, 2002; Tefera *et al*., 2010). Infestation may also occur in other cereals when the moisture content is conducive (moderate or high) for the storage insect pest to feed and lay eggs on the cereals (Campbell *et al*., 1989; Charlet *et al*., 2002).

There are 58 natural enemies of 98 storage insect pests reported to be inhibiting storage structures throughout the world (Schöller and Flinn, 2000). Several natural enemies and their hosts are distributed all over the world by grain shipments (Schöller and Flinn, 2000; Charlet *et al*., 2002). Widely reported natural enemies include parasitoids and predators (Schöller and Flinn, 2000). Parasitoids are biological control agents that feed on or in the tissue of other insects (hosts) and eventually kill them (Ahmed and Khatun, 1993; Ryan *et al*., 1993; Charlet *et al*., 2002).

Most parasitoids are assigned to two Orders: Hymenoptera and Diptera (Wang *et al*., 2003). Not all stages of a parasitoid's lifecycle are parasitic (Ryan *et al*., 1993). Only the larval stage is parasitic; adults are free-living, mostly feeding on nectar and honeydew (Ryan *et al*., 1993; Flint and Dreistadt, 1998; Bellows and Fisher, 1999). Parasitoids are categorised according to the host stage they attack: egg, larval, nymphal, pupal, and cocoon parasitoids (Bellows and Fisher, 1999; Charlet *et al*., 2002; Wang *et al*., 2003).

The impact of parasitic insects on stored grain insect pests can be substantial (Bellows and Fisher, 1999). For instance, 19 species of storage insect pests attacked by 13 species of parasitoids resulted in 163 of 212 estimates of pest mortality ranging from 70% to 100% (Flint and Dreistadt, 1998; Hagstrum and Subramanyam, 2006). In 87 of the estimates, insect pest mortality ranged from 90% to 100% (Hagstrum and Subramanyam, 2006). This means that natural enemies used in controlling storage insect pests can be very effective and used with success (Flint and Dreistadt, 1998; Flinn and Hagstrum, 2002; Bale *et al*., 2007).

Theocolax elegans studied on field experiments reduced populations of *S. zeamais* up to 50% (Flinn and Hagstrum, 2002). *Theocolax elegans* can control many storage insect pests (Herdman, 1921; Bale *et al*., 2007). Sharifi (1972) reported that *T. elegans* females parasitize pupae and 4th-instar larvae of *S. zeamais* but did not compare the impact of different host ages of *S. zeamais* on progeny production of *T. elegans*. My study compares the effect of different host ages of *S. zeamais* on progeny production by *T. elegans.*

OBJECTIVES

Overall objectives: My study will provide information on the use of *T. elegans* to control *S. zeamais* and determine optimal host rearing procedure for mass rearing *T. elegans* in an insectary.

Specific objectives: My study characterized the effect of *S. zeamais* age on progeny production by *T. elegans*.

LITERATURE REVIEW

1. Pest management

Grain loss caused by storage insect pests exceeds losses incurred while growing the crop in the field (Weaver and Petroff, 2004). Storage insect pests do not only consume the grain and reduce the grain weight, but also result in the accumulation of insect exuviae, frass and webbing on the grain (Gwinner *et al*., 1996; Weaver and Petroff, 2004). Accumulation of high levels of storage pest's detritus result in grain not fit for human consumption (Weaver and Petroff, 2004).

Storage environments change to warm and moist as a result of storage insect pest's infestation (Weaver and Petroff, 2004). Hotspots promote the development of fungi causing further losses (Weaver and Petroff, 2004; Tefera *et al*., 2010). Losses in storage facilities caused by insect pests are estimated to be between 5 and 10%. However, a 30% grain loss is incurred in the tropics (Weaver and Petroff, 2004; Tefera *et al*., 2010). Control of storage pests is the final stage of the struggle against insect pest's losses in agricultural production (Weaver and Petroff, 2004).

Early detection of *S. zeamais* developing in grain is important because the pest's larvae develop inside the grain and are difficult to detect (Akol *et al*., 2011; Gemu *et al*., 2013). Storage facilities need to be inspected regularly (Gwinner *et al*., 1996). This can be achieved by sampling the grain for insect pests, odor, hot spots and growth of fungi (Gwinner *et al*., 1996; Gemu *et al*., 2013). The grain should be sampled twice a month and once a month under warm and cool conditions, respectively (Gwinner *et al*., 1996).

Regular sampling of the grain reduces insect pest infestations because necessary control majors can reduce the establishment of storage insect pests (Emana, 1999; Weaver and Petroff, 2004; Gemu *et al*., 2013). Control strategies that can be used to control *S. zeamais* include cultural practices, physical control, inert materials, chemical control, Integrated Pest Management (IPM), Insect Growth Regulators (IGRs), insect pheromones, ionizing radiation and biological control (Gwinner *et al*., 1996; Gemu *et al*., 2013).

1.1 Cultural practices

Sanitation

Good sanitation reduces maize weevil infestation on grain (Gemu *et al*., 2013). This can be achieved by applying good storage hygiene techniques (Gwinner *et al*., 1996; Glenn *et al*., 2010). Good storage hygiene include cleaning storage facilities after every harvest, burning infested grain residues, storing pest free grain, and covering cracks and holes with cement, mud and cow dung (Gwinner *et al*., 1996; Tefera *et al.*, 2010; Upadhyay and Ahmad, 2011).

Cement storing facilities must be painted with coal-tar paint (repellent) to keep away stored-grain insect pests (Upadhyay and Ahmad, 2011). First infestation of *S. zeamais* is initiated in the field so early harvesting of the grain after maturity reduce infestation of grain by *S. zeamais* (Gwinner *et al*., 1996; Flinn and Hagstrum, 2002; Tefera *et al.*, 2010). The reduction in infestation is as a result of reduced time of exposure to insect pests in the field.

Agronomic practices

Practicing crop rotation and mixed cropping can reduce infestation from residual populations of insect pests (Gwinner *et al*., 1996). Different types of crops are affected by different insect pests (Tefera *et al*., 2010). Rotating crops control residual pest population by limiting the rate of reproduction of insect pests when an unpalatable crop is grown. Mixed cropping pull insect pests away from the cash crop and reduce infestations (Gwinner *et al*., 1996; Tefera *et al*., 2010; Gemu *et al*., 2013). Breeding for resistant cereal cultivars can reduce maize weevil infestation as *S. zeamais* would not feed on the resistant cultivars (Gwinner *et al*., 1996; Gemu *et al*., 2013).

Controlling the environment

Controlling the environment in storage structures can control storage insect pests (Gwinner *et al*., 1996; Tefera *et al.*, 2010). The environment can be controlled by reducing oxygen levels, enriching storage structures with carbon

dioxide, keeping humidity and moisture content below 15% (Gwinner *et al*., 1996; Gemu *et al*., 2013). Reduced oxygen levels eliminate oxygen required by insects and molds for growth (Gwinner *et al*., 1996; Tefera *et al*., 2010). Increased carbon dioxide levels limit respiration of storage insect pests (Gwinner *et al*., 1996). As a result *S. zeamais* cannot develop and reproduce hence controlling the pest.

1.2 Physical control

Removal of Insects from grain

Removing *S. zeamais* adults from stored grain using mechanical methods reduce the population of *S. zeamais* in the grain (Banks and Field, 1995; Gwinner *et al*., 1996). *Sitophilus zeamais* can be removed from the grain by sieving (Ahmed and Khatun, 1993; Flinn, 1998). Removing infested grain from grain to be stored eliminates storage pests and reduces storage insect pest's population (Gwinner *et al*., 1996; Flinn, 1998). The only limitation of using mechanical methods is that sieving and hand removal of infested grain requires many laborers and costly (Ahmed and Khatun, 1993; Gwinner *et al*., 1996). The removed insect pests should be removed from grain to be stored to prevent re-infestation (Gwinner *et al*., 1996; Flinn, 1998).

Temperature treatment

One of the effective ways of controlling storage pests is by using temperature treatment (Banks and Field, 1995; Upadhyay and Ahmad, 2011). Temperature affects reproduction, fecundity and survival of insects. Temperature treatment controls a number of insect pest's life stages in or on the grain (Upadhyay and Ahmad, 2011). Storage insect pests cannot grow and develop under extreme temperatures; heating and cooling (Zewar, 1993; Banks and Field, 1995; Gwinner *et al*., 1996; Upadhyay and Ahmad, 2011).

For effective control of storage insects, the extreme temperatures must be maintained for a long period (Upadhyay and Ahmad, 2011). However, the use of temperature treatments in storage facilities can lead to moisture on the grain

condensing as a result of the fluctuating temperature gradients in storage facilities (Zewar, 1993; Gwinner *et al*., 1996; Upadhyay and Ahmad, 2011).

Cooling stored grain reduce grain losses by reducing development and increasing mortality of storage insect pests and their immature stages, respectively (Upadhyay and Ahmad, 2011). Low temperatures make insect pests to be on diapause and usually result in death at temperatures below 12 °C (Upadhyay and Ahmad, 2011). Freezing the grain for a number of days and heating the grain for 24 hours is another way of controlling storage insect pests in grain kernels (Zewar, 1993; Gwinner *et al*., 1996). Insects rely on warm conditions for growth and development. Reducing the temperatures in storage facilities limits the growth and development of storage insect pests while maintaining the viability of seeds (Upadhyay and Ahmad, 2011).

Heating stored grain is effective in protecting grain for a long period without using insecticides (Upadhyay and Ahmad, 2011). An increase in temperature between 55-65 °C for 10 to 12 hours kills all storage pests (Gwinner *et al*., 1996; Upadhyay and Ahmad, 2011). Parboiling rice kernels kill any storage pest in the grain (Gwinner *et al*., 1996). Peasant farmers in developing countries can store their grain above fire in their kitchens (Flinn, 1998; Tefera *et al*., 2010). The heat and smoke produced by the fire inhibit storage insect pests from growing in the grain resulting to a pest free grain (Gwinner *et al*., 1996; Gemu *et al*., 2013). Further, the smoke increase carbon dioxide levels and limit respiration of storage insect pests (Gwinner *et al*., 1996). Furthermore, heating the grain reduce the moisture contest below 9% where insect pests cannot strive (Mbata and Phillips, 2001; Groot, 2004).

Moisture content control

Growth in storage insect pests is promoted by high grain moisture content before the grain is harvested and when stored in storage facilities (Upadhyay and Ahmad, 2011). Storage insect pests are adapted to moisture contents between 12 and 15% (Flinn, 1998; Tefera *et al*., 2010; Upadhyay and Ahmad, 2011). Moisture

contents lower than 11% are unconducive for storage insect pests (Upadhyay and Ahmad, 2011).

One way of limiting growth, development and reproduction in storage insect pests is reducing the grain moisture content to levels less than 11% (Flinn, 1998; Tefera *et al*., 2010; Upadhyay and Ahmad, 2011). However, reducing grain moisture content to minimum levels needed for growth in storage pests cannot be achieved in long-term storage facilities (Upadhyay and Ahmad, 2011). Survival of immature storage insect pests inside grain kernels is negatively affected by moisture levels below 9% (Upadhyay and Ahmad, 2011).

Low pressure

Low pressure is a nonchemical pest management method effective in the control of storage insect pests (Mbata *et al*., 2005; Upadhyay and Ahmad, 2011). The low pressure results in low oxygen levels in storage facilities which kill storage pests in the grain (Mbata *et al*., 2005; Upadhyay and Ahmad, 2011). The use of airtight storage facilities is more effective when storing grain for a long period of time (Gwinner *et al*., 1996). Airtight storage facilities are only applicable in warm and dry areas (Gwinner *et al*., 1996; Tefera *et al*., 2010).

In moist tropical parts of the world where relative humidity promotes the growth of molds, airtight storage facilities are not ideal (Gwinner *et al*., 1996; Tefera *et al*., 2010). Storing dried grain for a short period and reducing chances of condensation can reduce the growth of mold (Gwinner *et al*., 1996). Dry grain or atmosphere inhibits the development of fungi by preventing the fungal spores from germinating (Groot, 2004). Fungal spores are not killed by the dry conditions but remain on the grain for wet conditions that promote fungal growth (Groot, 2004).

1.3 Addition of materials on grain

Substances added on dried grain to control *S. zeamais* include minerals and plant materials (Gwinner *et al*., 1996; Gemu *et al*., 2013). Materials are usually added on the grain to reduce the activity of storage insect pests (Upadhyay and

Ahmad, 2011). Minerals used to control storage pests are wood ash, inert dusts and fine sand (Gwinner *et al*., 1996).

Wood ash

Ash from *Khaya senegalensis* and *Eucalyptus* are added on grain to control storage insect pests (Gwinner *et al*., 1996). Ash limits the movement of storage pests, inhibits insect development, cause wounds on insects resulting in desiccation and limiting respiration in storage pests (Gwinner *et al*., 1996). The only limitation of using ashes is that larger amounts are required (Gwinner *et al*., 1996; Gemu *et al*., 2013).

Inert dusts

Inert dusts include clay dust and quicklime which are added on top of grain as a protective top layer (Gwinner *et al*., 1996). Inert dusts inhibit insect development, cause wounds on insects resulting in desiccation and limiting respiration of storage insect pests (Gwinner *et al*., 1996). The use of inert dusts is limited by the large quantities required and because the grain normally require cleaning before consumption (Gwinner *et al*., 1996).

Fine sand is added on top of the grain as a protective top layer. Sand limits the movement of storage insect pests and results in increased mortality due to desiccation (Gwinner *et al*., 1996; Gemu *et al*., 2013). Fine sand stops storage pests from immigrating when put on top of grain. The use of fine sand is limited by the large quantities of sand required to make the top protective layer (Gwinner *et al*., 1996). Inert clay when added on grain resulted in 100% adult mortality within 24 hours and can be effective for 12 months (Upadhyay and Ahmad, 2011).

Plant Materials

Plant materials have insecticidal properties on different insect pest stages. Plant essential oils used to control storage insect pests include vegetable oils which are thoroughly mixed with the grain (Gwinner *et al*., 1996; Liu *et al*., 2006; Gemu *et al*., 2013). Plant essential oils inhibit the development and activities of

storage insect pests (Upadhyay and Ahmad, 2011). Small amounts of vegetable oils are required to stop female storage pests from laying eggs, and to control eggs and larvae of storage insect pests (Emana, 1999).

However, at the time of mixing vegetable oils and the grain, the grain should be free from infestations (Gwinner *et al*., 1996; Gemu *et al*., 2013). When vegetable oils are applied on infested grain, vegetable oils are not effective. Plant materials like *Solanum* spp. are toxic to humans and grain mixed with *Solanum* spp. cannot be used for human consumption (Gwinner *et al*., 1996). Plant materials that change the quality of grain are not conducive for grain designated for human consumption but are useful in seed protection (Gwinner *et al*., 1996; Emana, 1999).

1.4 Chemical control

More *S. zeamais* progeny are produced when the grain is stored without protection and inspection (Phillips, 1997; Charlet *et al*., 2002; Bale *et al*., 2007). Maize weevils must be controlled early before the population is increased. Regular sampling of the grain is required to detect infestations (Weaver and Petroff, 2004). Chemicals effective in controlling maize weevils include organophosphates such as fenitrothion and pirimiphos-methyl (Gwinner *et al*., 1996; Emana, 1999). Pyrethroids including permethrin and deltamethrin are of less importance in the control of maize weevils (Emana, 1999). Chemicals used for controlling storage insect pests are grouped into fumigants and contact pesticides (Weaver and Petroff, 2004).

Fumigants

Fumigants are toxic gasses used to control insect pests and other groups of living organisms (Emana, 1999; Wilkin, 2008). Fumigants require airtight storage structures to provide a sufficient concentration needed to control insect pests over a long period of time (Weaver and Petroff, 2004; Wilkin, 2008). Insects are controlled only when the fumigant is still contained in storage structures (Weaver and Petroff, 2004). Re-introduction of storage pests under low concentrations of fumigants result in the establishment of insect pests because fumigants have low toxic residues

(Wilkin, 2008). Fumigants are effective in controlling storage pests but are highly toxic to mammals so only qualified personnel can use them (Wilkin, 2008).

The use of methyl bromide in fumigation of stored grain is effective in controlling storage insect pests (Emana, 1999; Wilkin, 2008). Synthetic chemicals use in storage facilities has been reduced because of the detrimental effects associated with chemical use (Charlet *et al*., 2002; Flinn and Hagstrum, 2002). Chemicals are poisonous not only to the insect pest but even to the consumer so care must be taken when using them (Emana, 1999; Flinn and Hagstrum, 2002). Methyl bromide is a neurotoxin that affects cognitive function, muscular control and physical coordination (Wilkin, 2008). Constant use of chemicals leads to resistant insect populations making it difficult to control the resistant insect pests (Emana, 1999; Wilkin, 2008).

Carbon dioxide and nitrogen gases are used as fumigants to control storage insect pests (Wilkin, 2008). Carbon dioxide and nitrogen compounds are effective under high concentrations maintained for a long period in storage structures (Emana, 1999; Wilkin, 2008). Nitrogen is effective in reducing the concentration of oxygen to less than 1% in storage structures (Wilkin, 2008). The low oxygen levels limit the growth of insect pests and molds (Charlet *et al*., 2002; Flinn and Hagstrum, 2002). A concentration of carbon dioxide more than 40% is required to inhibit respiration of storage insect pests (Wilkin, 2008). Nevertheless, the high concentrations of carbon dioxide required make it impossible to use when treating bulky stored grain (Weaver and Petroff, 2004).

Contact pesticides

Contact pesticides are effective when the toxic chemical comes to contact with insect pests; through insect's cuticle, ingestion and respiration (Weaver and Petroff, 2004; Wilkin, 2008). Pesticides affect insect's metabolism by disrupting it (Emana, 1999). Contact pesticides are toxic to mites and insects compared to mammals (Emana, 1999; Wilkin, 2008). Contact pesticides are persistent and result in high residues in stored grain such that one treatment controls and protects against future infestations (Wilkin, 2008).

Contact insecticides commonly used in the control of storage insect pests include organophosphates, pyrethroids and synergized pyrethrins (Beckett *et al*., 2007). Organophosphates include malathion, dichlorvus, fenitrothion, pirimiphos-methyl, chlorpyrifos-methyl and chlorpyrifos-methyl with deltamethrin (Beckett *et al*., 2007). Pyrethriods used for controlling storage insect pests include biosmethrin, permethrin and deltamethrin (Beckett *et al*., 2007; Wilkin, 2008). However, insect resistance is a major problem associated with the use of chemicals adding to detrimental effects on the environment and the consumer (Beckett *et al*., 2007).

1.5 Integrated Pest Management (IPM)

Insect pests can be effectively controlled by not relying on one pest management method. The combination of pest management strategies and tactics is called Integrated Pest Management (IPM) (Subramanyam and Hagstrum, 1995; Weaver and Petroff, 2004; Weinzierl and Higgins, 2008). IPM involve a coordinated use of a number of pest management strategies simultaneously (Weinzierl and Higgins, 2008). Pest management strategies combined in IPM include cultural practices, addition of materials on grain, host resistance, biological control, physical control and chemical control (Weaver and Petroff, 2004).

Goals of an IPM program include the reduction of economic losses caused by insect pests, limiting the development of new insect pest biotypes that are resistant to pesticides, reduction of negative impacts of pest management strategies on the environment, reduction of pesticide residues in food and increasing farmer's income (Subramanyam and Hagstrum, 1995; Weaver and Petroff, 2004).

Insect pest populations that will cause economic loss are identified in an IPM program and environmentally friendly pest management strategies are used to control the insect pests (Weaver and Petroff, 2004; Weinzierl and Higgins, 2008). The pest management strategy used should blend with other pest management strategies (Weinzierl and Higgins, 2008; Khan *et al*., 2012).

1.6 Insect Growth Regulators

Insect growth regulators (IGRs) are effective in the control of insects by disrupting oviposition in insects. The disruption in oviposition behavior affects the reproduction system of insects (Tanaka and Takeda, 1993; Upadhyay and Ahmad, 2011). Insect growth regulators are more effective in the control of storage insect pests when released in closed environments (Upadhyay and Ahmad, 2011). Insect growth regulators used in the control of storage pests include methoprene and hydropene (Upadhyay and Ahmad, 2011). These IGRs can affect an insect in many ways; prevent emergence of both immature stages and adults, and reduce progeny production in adults (Tanaka and Takeda, 1993; Upadhyay and Ahmad, 2011).

1.7 Insect Pheromones

Insect pheromones are produced and used to control the behavior of insects associated with that pheromone (Upadhyay and Ahmad, 2011). Synthesized insect pheromones can be used with traps to capture and kill a large number of insects. This can be achieved by using sex pheromones and aggregation pheromone that attract opposite sex and both sex, respectively (Upadhyay and Ahmad, 2011).

Synthesized insect pheromones can be used to detect storage insect pests in storage facilities. This is achieved by trapping insects using insect attractants and baits (Tanaka and Takeda, 1993; Upadhyay and Ahmad, 2011). Small quantities are used when trapping insect with pheromones but can attract insects from a distance (Tanaka and Takeda, 1993; Upadhyay and Ahmad, 2011). Another way of controlling insects by pheromones includes the disruption of mating with pheromones (Upadhyay and Ahmad, 2011).

1.8 Ionizing Radiation

The use of ionizing radiation is effective in controlling all stages of storage insect pests in closed grain facilities while not affecting the nutritive value of the grain (Banks and Field, 1995; Upadhyay and Ahmad, 2011). The grain is exposed to β and γ radiation to kill storage insect pests (Upadhyay and Ahmad, 2011). Cobalt

60 and electrically are usually used to generate γ and β-radiation, respectively (Banks and Field, 1995; Upadhyay and Ahmad, 2011).

Doses of about 0.6 kGy radiation sterilize storage insect pests while low radiation kill storage insects when free radicals are produced (Banks and Field, 1995). Another way of controlling storage insect pests is by using colorized light which traps and kills a large number of flying insects (Banks and Field, 1995; Upadhyay and Ahmad, 2011). Exposing insects to 1MHz sound for 5 minutes kill all stages of storage insects in grain (Upadhyay and Ahmad, 2011).

1.9 Biological Control

Biological control is an important (once overlooked) aspect of Integrated Pest Management of storage insect pests (Press and Mullen. 1992; Schöller *et al*., 1997; Flinn, 1998). Biological control refers to the use of natural enemies to control insect pests to a lower pest density and damage than would occur in the absence of the natural enemies (Schöller *et al*., 1997; Charlet *et al*., 2002; Bale *et al*., 2007). There are three types of biological control including classical, augmentative and conservational biological control (Van Driesche and Bellows, 1996; Schöller *et al*., 1997).

Classical biological control

Classical biological control refers to the importation of natural enemies from the native range of the insect pest and establishment in a place where it has become a problem (Van Lenteren, 1993; Lee and Landis, 2001). Natural enemies are imported when the host insect (pest) is accidentally introduced into an exotic area while the natural enemies are left behind (Schöller *et al*., 1997; Flint and Dreistadt, 1998; Lee and Landis, 2001).

Augmentative biological control

Augmentative biological control involves artificially rearing natural enemies and releasing them into the environment to reduce a pest's population to a noneconomic level (Van Lenteren, 1993; Bellows and Fisher, 1999; Lee and Landis,

2001). Natural enemies can be introduced so they establish themselves in the environment, or large numbers of the natural enemies are released periodically to control the insect pests (Press and Mullen, 1992; Ryan *et al*., 1993).

Conservational biological control

Conservational biological control refers to manipulating the environment and the practices to protect the natural enemies already present in the environment (Bellows and Fisher, 1999; Lee and Landis, 2001; Charlet *et al*., 2002). Natural enemies manage the insect pest and prevent it from causing economic damage to crops (Lee and Landis, 2001; Charlet *et al*., 2002; Grieshop *et al*., 2007).

Natural enemies

Natural enemies are "safe" to use compared to synthetic chemicals (Schöller *et al*., 1997; Charlet *et al*., 2002). Methyl bromide has been used to control stored-product insect pests for many years, but has a negative effect on the ozone layer of the atmosphere (Flinn and Hagstrum, 2002; Sureshan, 2012). Natural enemies are important in regulating insect pest population in nature (Flinn, 1998). Biological control agents of storage insect pests have shown good efficiency in controlling stored-product insect pests (Williams and Floyd, 1971a; Flinn, 1998). Natural enemies have been used successfully worldwide as biological control agents of many insect pests and are grouped into three groups including parasitoids, predators and pathogens (Ryan *et al*., 1993; Schöller *et al*., 1997).

Parasitoids are very important in a biological control program. Biological control agent's immature stages feed on the haemolymph and tissue of their host insect (Lee and Landis, 2001). The host insect is eventually killed in the process (Lee and Landis, 2001; Charlet *et al*., 2002). Idiobiont parasitoids stop further development of the host insect after immobilizing it (Ryan *et al*., 1993). Koinobiont parasitoids allow further development of the host insect up to a certain stage while feeding on it (Ryan *et al*., 1993).

Parasitoids attack a specific stage and species of the host insect (Bellows and Fisher, 1999). Adults are free-living on nectar and can be predaceous by feeding on the fluid of the host insect pest (Flint and Dreistadt, 1998). Adult female parasitoids oviposit one or more eggs on or in the body of the host insect (Bellows and Fisher, 1999; Lee and Landis, 2001). Upon hatching, parasitoid larvae feed on the fluid of the host insect and pupate in or near the host's body (Press and Mullen. 1992; Van Driesche and Bellows, 1996).

Unlike parasitoids, predators are generalist feeders and are larger than their prey (Schöller *et al*., 1997; Charlet *et al*., 2002). Predators feed on more than one prey during their development and are predaceous as immatures and adults (Ryan *et al*., 1993). This means that predators are not host-specific compared to parasitoids (Arbogast and Mullen, 1990; Baker and Weaver, 1993). Eggs are laid near the prey and mobile immatures begin feeding on the prey insect after eclosion (Flint and Dreistadt, 1998; Grieshop *et al*., 2007).

Insect pathogens are important in biological control and include nematodes, fungi, viruses, bacteria and protozoans (Ryan *et al*., 1993; Van Lenteren, 2003; Throne and Lord, 2004). Insect pathogens control specific groups of pests and can cause rapid mortality in a short period of time (Charlet *et al*., 2002; Throne and Lord, 2004). Spore forming *Bacillus thuringiensis* (Bt) is commercially available to control insect pests. Bacteria and viruses affect insects in the insect gut.

Bacteria are applied on grain in a liquid or powdery form (Flinn *et al.*, 1996; Flinn *et al.*, 1997). *Bacillus thuringiensis* strains currently available are effective in controlling moths and do not have side effects on parasitoids (Flinn *et al.*, 1997; Flinn and Schöller, 2012). Viruses used in controlling storage insect pests are effective in regulating moths and beetles population. Viruses only control a certain species of storage insect pests (Vial *et al*., 1991; Flinn and Schöller, 2012).

Fungi infect all groups of storage insect pests; even sucking insects not controlled by bacteria and viruses (Khan *et al*., 2012). All insect groups are controlled because fungi penetrate the insect's body. Fungal growth is promoted by moist

conditions which are not acceptable in storage facilities (Lord, 2005). However, fungal spores overwinter as resting spores or sclerotia that maintain infection under dry conditions (Khan *et al*., 2012). Fungi can spread in an insect population quickly resulting in a collapse of the insect population (Lord, 2005; Khan *et al*., 2012). Fungi are effective in controlling storage insect pests. An example of fungi is *Beauveria bassiana* (Ferron and Robert) used for controlling *R. dominica* (Lord, 2001; Lord, 2005; Flinn and Schöller, 2012).

Protozoa normally affect insect development and insect fertility (Flinn and Schöller, 2012). A number of protozoa are found infecting stored-product insect pests (Lord, 2005). Protozoa are orally transmitted and are very effective in keeping the insect population growth to a minimum (Flinn and Schöller, 2012). Infections caused by protozoan species are seldom lethal but chronic; reduce fecundity and survivorship (Steidle and Schöller, 2001; Flinn and Schöller, 2012; Khan *et al*., 2012).

1.10 Advantages of Biological Control

Biological control agents used to control stored grain insect pests has many advantages over traditional chemical controls (Flinn and Matthias, 2012; Flinn and Schöller, 2012). Biological control agents leave no harmful residues on the grain as opposed to chemicals (Charlet *et al*., 2002; Flinn and Matthias, 2012). Brower *et al*. (1995) reported that biological control agents can be applied by unskilled labor and these agents are safe to humans.

Ideally, after biological control agents are released, they continue to reproduce and maintain the population of insect pests below the economic threshold (Brower *et al*., 1995; Bellows and Fisher, 1999; Charlet *et al*., 2002). Natural enemies can control insect pests for a long period when the hosts are available and the environmental conditions favour the development of the natural enemies (Brower *et al*., 1995; Lee and Landis, 2001).

Chemicals must be applied to a wide area and their application is expensive and labor intensive (Flinn and Matthias, 2012; Flinn and Schöller, 2012). In contrast, natural enemies can be released at a single location and spread to new

locations (Flinn and Matthias, 2012). Natural enemies control specific insect pests while broad spectrum chemicals can kill beneficial insects (Brower *et al*., 1995; Bale *et al*., 2007). Natural enemies spread, locate and attack insect pests deep within crevices and inside the grain (Bale *et al*., 2007; Flinn and Matthias, 2012).

Most pteromalids used as biological control agents to control storage insect pests are very small bodied (less than 10 mm including their ovipositor) (Noyes, 2003; Flinn and Matthias, 2012). Their life cycles are relatively short and females have high reproductive capacity (Charlet *et al*., 2002; Flinn and Matthias, 2012). Using normal cleaning procedures, biological control agents can be removed from the grain before milling (Press, 1992; Flinn and Hagstrum, 2002).

Storage structures prevent natural enemies from escaping and provide an optimum environment for deployment of biological control agents in controlling stored insect pests (Charlet *et al*., 2002; Flinn and Matthias, 2012). Resistance to biological control agents is unlikely to develop because natural enemies are coevolving with their hosts (Brower *et al*., 1995; Charlet *et al*., 2002; Flinn and Matthias, 2012). Biological control agents can be used with pathogens and pathogens can be spread when the parasitoids locate hosts within crevices and inside the grain (Brower *et al*., 1995; Flinn and Schöller, 2012).

1.11 Limitations of Biological Control

The main disadvantage of biological control is that it requires the handler to be more informed about the biology and host range of the biological control agents (Flinn and Matthias, 2012). Application of natural enemies requires careful timing compared to traditional chemical insecticides application (Charlet *et al*., 2002; Flinn and Matthias, 2012). To effectively control insect pests in storage grain, the handler must release the appropriate biological control agent (Bellows and Fisher, 1999; Bale *et al*., 2007). This can be a challenge because many parasitoids are host-specific rather than generalists (Brower *et al*., 1995; Flinn and Matthias, 2012). Brower *et al*. (1995) reported that to effectively control all storage insect pests

available in a stored product, different species of parasites must be mass reared and released to control the different pests.

Timing of release is critical for natural enemies to be successful (Lee and Landis, 2001). Biological control agents must be released early in the insect pest's growth cycle so that adult parasitoids can outnumber the insect pests (Flinn and Matthias, 2012). When the economic threshold has been reached, biological control agents cannot successfully manage insect pest population (Brower *et al*., 1995; Bale *et al*., 2007; Flinn and Schöller, 2012).

Typically, parasitoids require at least three years to become established because they are slow-acting compared to most chemicals (Brower *et al*., 1995; Charlet *et al*., 2002; Flinn and Schöller, 2012). Frequent release of the biological control agent is very important in order for the biological agents to be effective in controlling storage insect pests (Brower *et al*., 1995; Flinn and Schöller, 2012).

Mass rearing the biological control agents can provide a source of biological control agents for periodic release (Tefera *et al*., 2010; Flinn and Matthias, 2012; Flinn and Schöller, 2012). However, mass rearing and maintaining many parasitoids will result in higher maintenance costs (Ryan *et al*., 1993; Flinn and Matthias, 2012). Brower *et al*. (1995) and Tefera *et al.* (2010) reported that development of artificial diets and availability of commercial suppliers of artificial diets may reduce costs of mass rearing biological control agents.

Most biological control agents cannot be used simultaneously with chemical protectants (Brower *et al*., 1995). Nevertheless, pesticide resistant species of biological control agents are naturally present and can be mass reared (Brower *et al*., 1995; Lee and Landis, 2001). Releasing large numbers of biological control agents increase contamination of stored products by insect fragments particularly in manufactured food products that are not well packaged (Bellows and Fisher, 1999; Brower *et al*., 1995).

However, biological control agents can be removed from grain before milling using normal cleaning procedures (Ryan *et al*., 1993; Flinn and Hagstrum,

2002). Natural enemies, when used to control insect pests, should not eliminate the entire population of the insect pest (Brower *et al*., 1995; Lee and Landis, 2001; Charlet *et al*., 2002). A residual population of the pest is necessary for the natural enemies to remain in the environment (Charlet *et al*., 2002).

2. Stored grain insects

Storage insect pests attacking cereal products and grain in storage facilities are reported to be more than 70 (Table 1) (Upadhyay and Ahmad, 2011). Storage insect pests can result in an annual grain loss of 10-40% throughout the world (Weaver and Petroff, 2004; Upadhyay and Ahmad, 2011). The control of storage insect pest is, therefore, of paramount importance to continue feeding the increasing population of human beings throughout the world (Weaver and Petroff, 2004; Upadhyay and Ahmad, 2011).

Most storage insect pests found in storage structures are grouped in the Orders Coleoptera and Lepidoptera (Table 1) (Weaver and Petroff, 2004; Weinzierl and Higgins, 2008). Seven members of other insect Orders are found in grain storage structures but the Orders Coleoptera and Lepidoptera are the major storage insect pests (Table 1) (Weaver and Petroff, 2004). Beetles are highly diversified and result in high grain losses compared to moths found in storage facilities (Upadhyay and Ahmad, 2011).

Stored grain losses caused by Lepidoptera are as a result of lepidopteran larvae feeding and the silky secretions which spoil the grain (Miller, 1995; Sallam, 2012). Grain losses caused by Coleoptera are as a result of larvae and adults feeding on or in the grain (Miller, 1995; Sallam, 2012). The high grain losses caused by beetles compared to moths are as a result of the fact that both the immature stages and the adults of beetles feed on grain while only the immature stages feeds on grain in moths (Weaver and Petroff, 2004; Upadhyay and Ahmad, 2011).

Storage insect pests are grouped into two using their feeding habits: primary insect pests and secondary insect pests (Weaver and Petroff, 2004). Primary insect pests include insect pests that penetrate and feed on intact kernels of grain (Mason and

Obermeyer, 2010). Primary insect pests have immature stages that develop within grain's kernel. Secondary insect pests cannot infest intact grain (Weaver and Petroff, 2004; Weinzierl and Higgins, 2008). However, secondary pests feed on broken grain kernels, debris and grain kernels damaged by primary insect pests. Immature stages of secondary insect pests are found external to the grain (Weaver and Petroff, 2004).

Secondary insect pests can initiate an infestation because adequate quantities of broken grain kernels are available in storage facilities to promote an infestation by secondary insect pests (Weaver and Petroff, 2004). Further, secondary insect pests infestations promote grain spoilage. Grain quality is graded based on the number of insect-damaged-kernels, presence of live insects and other grain quality factors (Weaver and Petroff, 2004). More loss is caused by primary insect pests because they feed within grain kernels (Weinzierl and Higgins, 2008).

Primary insect pests commonly encountered in stored grain insects include the: Lesser grain borer, *Rhyzopertha dominica* (Fabricius) (Coleoptera: Bostrichidae), Larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae), Granary weevil, *Sitophilus granarius* (Linnaeus) (Coleoptera: Curculionidae), Rice weevil, *Sitophilus oryzae* (Linnaeus) (Coleoptera: Curculionidae) and *S. zeamais* (Weaver and Petroff, 2004).

Secondary insect pests found in stored grain include the: Rusty grain beetle, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Laemophloeidae), Indian meal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), Red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) and the Sawtoothed grain beetle, *Oryzaephilus surinamensis* (Linnaeus) (Coleoptera: Silvanidae) (Weaver and Petroff, 2004; Weinzierl and Higgins, 2008).

Other secondary insect pests found infesting grain include: the Hairy fungus beetle, *Typhaea stercorea* (Linnaeus) (Coleoptera: Mycetophagidae) and the Foreign grain beetle, *Ahasverus advena* (Waltl) (Coleoptera: Silvanidae) (Weaver and Petroff,

2004; Weinzierl and Higgins, 2008). *Typhaea stercorea* and *A. advena* feed on fungi found growing on high moisture grain kernels (Weaver and Petroff, 2004).

Other insect Orders often found infesting stored grains are the Psocoptera (booklice), Blattaria (cockroaches), Thysanura (silverfishes), Isoptera (termites) and Hymenoptera (ants and wasps) (Weinzierl and Higgins, 2008; Upadhyay and Ahmad, 2011). These insect Orders does not feed on stored grain but result in the accumulation of insect detritus and are a nuisance because they secrete noxious smell (Weinzierl and Higgins, 2008; Upadhyay and Ahmad, 2011).

Other Arthropods often found infesting stored grain include grain mites (Weinzierl and Higgins, 2008; Upadhyay and Ahmad, 2011). However, booklice and grain mites feed on fungi found in stored grain (Weaver and Petroff, 2004; Weinzierl and Higgins, 2008; Upadhyay and Ahmad, 2011). The presence of psocids and grain mites on stored grain indicates grain spoilage by fungi (Weinzierl and Higgins, 2008).

Adult beetles make holes on the grains and the females lay their eggs in small holes (Upadhyay and Ahmad, 2011). Beetles immature and adult stages feed on the grain and result in the accumulation of grain shells (Weaver and Petroff, 2004; Weinzierl and Higgins, 2008; Upadhyay and Ahmad, 2011). Storage insect pests can result in grain losses reaching 35% when the grain is improperly stored for 5-6 months while 60% grain losses can be incurred when stored for more than nine months (Odeyemi, 1993; Miller, 1995; Sallam, 2012). Losses incurred due to secondary insects pests can be minimised by storing undamaged grain; intact grain free from cracks (Sallam, 2012). The cracks on grain kernels promote infestation by storage insect pests and molds. Cracked or damaged grains are necessitated by threshing and drying the grain (Miller, 1995; Sallam, 2012).

Table 1 Major storage insect pests

Order	Family	Scientific name
Coleoptera	Anobiidae	*Lasioderma serricorne* (Fabr.)
		Stegobium paniceum (Lin.)
	Bostrichidae	*Rhizopertha dominica* (Fabr.)
		Prostephanus truncatus (Horn.)
	Bruchidae	*Pachymerus chinensis* (Lin.)
		Bruchus analis (Fabr.)
		Acanthoscelides obstectus (Latr.)
		Callosobruchus chinensis (Lin.)
		Callasobruchus maculatus (Fabr.)
	Cucujidae	*Cryptolestes ferrugineus* (Steph.)
	Curculionidae	*Sitophilous oryzae* (Lin.)
		Sitophilous granarius (Lin.)
		Sitophilus zeamais (Motsch.)
	Dermastidae	*Trogoderm granarium* (Li)
		Trogoderma glabrum (Herbst)
	Tenebrionidae	*Tribolium castaneum* (Herbst)
		Tribolium confusum (Jacq.)
	Scarabaeidae	*Holotrichia serrate* (Hope)
	Silvanidae	*Oryzaephilus surinamensis* (Lin.)
Lepidoptera	Galleriidae	*Corcyra cephalonica* (Staint.)
	Gelechiidae	*Sitotroga cerealella* (Oliver)
	Pyralidae	*Anagasta kuehniella* (Zeller)
		Ephestia cautella (Walker)
		Plodia interpunctella (Hubner)
Psocoptera	Liposcelididae	*Liposcelis bostrychophila* (Bad.)
		Liposcelis decotor (Pearman)

Source: Upadhyay and Ahmad (2011)

2.1 *Sitophilus zeamais* (Motschulsky)

Origin

Sitophilus zeamais is a cosmopolitan storage pest of cereal grain (Danho *et al*., 2002). *Sitophilus zeamais* is particularly a pest of maize in tropical and sub-tropical regions of the world. Maize weevil is native of India and has been distributed all over the world by shipments of grain (Campbell *et al*., 1989; Danho *et al*., 2002). All the three species grouped in the *Sitophilus* genus are native to the Oriental Region and were distributed throughout the world by wheat, maize and rice importation (Campbell *et al*., 1989; Akol *et al*., 2011).

Identification

Eggs of *S. zeamais* can be identified using their egg shape; opaque, ovoid to pear-shaped and shining white (Campbell *et al*., 1989; Peng *et al*., 2003). *Sitophilus zeamais* eggs are wide below the middle and the bottom is rounded, neck narrows gradually towards the top and flattened, and has a small rounded protruding structure keeping the egg in position (Campbell *et al*., 1989; Leelaja *et al*., 2007; Corrêal, 2013). *Sitophilus zeamais* eggs are very small; length 0.65 ± 0.04 mm and width 0.27 ± 0.02 mm (Nualvatna *et al.*, 2005).

Mature larvae are whitish, legless and are thick bodied (Campbell *et al*., 1989; Akol *et al*., 2011). The pupae of *S. zeamais* are white and gradually change to dark brown as they assume the adult structure (Khare, 1994). The length of the pupae is about 4.25 mm and width is about 1.75 mm (Campbell *et al*., 1989). The size of pupae and larvae are not constant but depends on the nutrient and type of rearing diet (O'Donnell, 1967; Campbell *et al*., 1989). When reared on nutritive diets, the size of the pupae and larvae will be larger compared to when mass reared on less nutritive diets. Adult beetles are small with their length about 4.5 mm long and their width about 2.45 mm (Campbell *et al*., 1989).

Sitophilus zeamais share a number of similarities with other species grouped in the same family (Baker and Weaver, 1993). Maize weevil's head projects

forward forming a snout (Ileleji *et al*., 2007; Tefera *et al*., 2010). The distal portion of the prolongation contains a pair of mandibles (Campbell *et al*., 1989). The adult beetle's colouration ranges from reddish brown to dark brown or almost black (O'Donnell, 1967). Newly emerged (teneral) adults of *S. zeamais* are pale brown to reddish brown in colour (Campbell *et al*., 1989; Khare, 1994). The long and narrow snout of *S. zeamais* also bears geniculate (elbowed), apically clubbed eight-segmented antennae (Tefera *et al*., 2010).

Sitophilus zeamais resembles *S. oryzae* but *S. zeamais* is longer in body length and displays four pale reddish-brown or yellowish pale oval spots on the elytra (Boudreaux, 1969; Khare, 1994). The thorax of *S. zeamais* is densely pitted with irregularly shaped punctures, except for the smooth narrow strip extending down the midline of the dorsum (Tefera *et al*., 2010). The abdominal tergites of *S. zeamais* are typically black (Campbell *et al*., 1989; Boudreaux, 1969).

The punctures on the pronotal dorsum of *S. zeamais* pronotum are nearly circular (Campbell *et al*., 1989). The pronotal punctures are equally spaced with no median puncture-free zone and more than 20 pronotal punctures occur along the midline from neck to the scutellum (Boudreaux, 1969). Also, the scutellar elevations are farther apart from their longitudinal length and extend longitudinally about halfway on the scutellum (Boudreaux, 1969).

The proepimera meets behind the fore coxae with a barely discernable notch at the meeting point along the posterior edge (Boudreaux, 1969). The male aedeagus has two dorsal longitudinal grooves (Boudreaux, 1969). The female sternum display lateral lobes that are apically acute (Boudreaux, 1969). Females can be distinguished from males by a long, narrow rostrum/snout with regular rows of punctures while males have a short and transverse rostrum/snout with large and irregular punctures and contact each other (Campbell, 2002).

Biology

This species requires three days following emergence before the females can begin oviposition; females lay eggs throughout their adult life (Fava and

Burlando, 1995; Tefera *et al*., 2010). *Sitophilus zeamais* fecundity increase and reach its maximum after 20 days while a decrease is expected after 30 days (Fava and Burlando, 1995; Akol *et al*., 2011). However, an increase in grain availability leads to an increase in female fecundity and grain infestation (Fava and Burlando, 1995; CABI, 2010). It is important to start controlling them early to reduce grain infestations (Akol *et al*., 2011).

Adults and larvae of *S. zeamais* can withstand cold winter conditions in storage structures (Campbell *et al*., 1989; Fava and Burlando, 1995). It is, therefore, important to clean storages structures before storing grain to reduce infestations (Campbell *et al*., 1989; Tefera *et al.*, 2010; Akol *et al*., 2011). The adults can withstand temperatures of -17.8 °C for several hours in temperate regions (Campbell *et al*., 1989). This means that *S. zeamais* can be a major storage pest in temperate regions of the world.

Adult females of *S. zeamais* make a slender hole on the seed coat into the endosperm using their mandibles before oviposition (Campbell *et al*., 1989). After oviposition, the ovipositor deposits a gelatinous secretion which covers the hole, presumably to protect and conceal the site of oviposition (Campbell *et al*., 1989). More eggs are laid on grain occupying lower part of a storage facility compared to grain occupying higher part of a storage facility (Danho *et al*., 2002; Gemu *et al*., 2013). Some female weevils can lay as many as 417 eggs during a period of 110 days (Campbell *et al*., 1989; Akol *et al*., 2011). However, most females in populations of *S. zeamais* lay more eggs during the first half of their five weeks life span (Campbell *et al*., 1989; Tefera *et al.*, 2010).

Nevertheless, a few females in populations of *S. zeamais* may lay more eggs after the first half of their five weeks life span (Campbell *et al*., 1989; Tefera *et al*., 2010). Females of *S. zeamais* can oviposit up to four eggs in one maize kernel and the sex ratio of the progeny is 1:1 (Campbell *et al*., 1989; Throne, 1994). As a result, in any population of *S. zeamais*, equal number of males and females is observed. Tefera *et al.* (2010) reported that *S. zeamais* adult females live longer compared to adult males.

Sitophilus zeamais has four larval instars (O'Donnell, 1967; Sharifi and Mills, 1971; Campbell *et al*., 1989). O'Donnell (1967) reported that the use of head capsule widths to determine larval instars of *S. zeamais* were more efficient compared to using the larval weights. *Sitophilus zeamais* larval weights are not constant but depend on the nutrient and type of rearing diet (O'Donnell, 1967; Campbell *et al*., 1989).

The head capsule widths for *S. zeamais* larvae reported by O'Donnell (1967) varied from 0.16-0.22, 0.25-0.29, 0.34-0.43 and 0.49-0.54 mm in the first, second, third and fourth instars, respectively. The larvae ages at first, second, third and fourth instars were found to be 8, 11, 15 and 21 days, respectively. In a laboratory experiment, Campbell *et al.* (1989) reported that the first, second, third, fourth instars and pre-pupal stages take 3, 5, 6, 3 and 3 days to complete the stage, respectively.

The short life cycle of *S. zeamais* results in high infestation within a short period of time (Akol *et al*., 2011). However, under extreme weather conditions (less than 10% moisture content and less than 40% RH) the first, second, third, fourth instars and pre-pupal stages can extend over 10, 7, 9, 11 and 5 or more days, respectively (Campbell *et al.*, 1989). Extreme weather conditions lengthen life cycle of *S. zeamais* resulting to low infestations (Campbell, 2002).

After enclosion, adults of *S. zeamais* inside the kernel chew the wall of the maize kernel, thereby forming a circular hole about 1.5 mm in diameter and working their way out (Campbell *et al*., 1989; Akol *et al*., 2011). Adults emerge and then feed on the outer layer of the grain (Kranz *et al*., 1997; Akol *et al*., 2011). Weevils use their elongated snouts with mandibles at the distal end for feeding (Kranz *et al*., 1997). As a result, *S. zeamais* feeding bore the grain and make holes on the grain (Campbell *et al*., 1989; Kranz *et al*., 1997; Akol *et al*., 2011).

Females also use their snout with mandibles for excavating a shallow depression on the grain's surface as an oviposition site (CABI, 2010; Tefera *et al*., 2010). The females have a high fecundity; when not controlled they can oviposit 300 and 400 eggs during an average life span of 4-5 months (Campbell *et al.*, 1989). This

makes the rate of increase of *S. zeamais* extremely high (200 females at 1:1 sex ratio x 400 progeny/female x 5 months = 400000 progeny/generation) (Tefera *et al*., 2010). Many offsprings can be produced which subsequently spoil the grain (Ileke, 2007; CABI, 2010).

The optimum temperature for mating and reproduction is 27-32 °C. At temperatures lower than 20 °C and above 32 °C these beetles do not reproduce (Campbell *et al*., 1989). The feed moisture content must be above 11% for adults to mate and reproduce (Tefera *et al*., 2010). Walgenbach *et al* (1987) reported that mating does not take place until the adults are three days old. At 30 °C on maize with 13% moisture content, *S. zeamais* require 31−64 days to complete development from egg to adult (Appert, 1987; Kranz *et al*., 1997). The type and quality of grain being infested influence the actual development period (Walgenbach *et al*., 1987). Appert (1987) and Kranz *et al.* (1997) reported that *S. zeamais* require 4-5 months to complete their life cycle.

Economic importance

About 80% of grain can be consumed by *S. zeamais* when the grain moisture content is above 11% and left undisturbed for a long period of time (Campbell *et al*., 1989; De Groote, 2002). *Sitophilus zeamais* infest grain in the field resulting to severe grain loss after the grain is harvested (Campbell *et al*., 1989). Campbell *et al.* (1989) reported that *S. zeamais* can literally reduce an ear of corn to powder. The infested grain is often damp and heats on the surface causing more grain damage (Campbell *et al*., 1989).

The damp conditions and the heating of the grain surface favour the growth of *Aspergillus flavus* (Link) (Eurotiales: Trichocomaceae) (Ileke, 2007; Tefera *et al*., 2010; Akol *et al*., 2011). Consuming the weevil-infested grain can result in consuming food contaminated with *Aspergillus flavus* mycotoxins (Tefera *et al*., 2010). The mycotoxins result to livestock and human poisoning, chronic health problems in humans, and loss of markets. Employees exposed to mycotoxins suffer from respiratory allergens resulting in a need to employ other grain handlers and

interruption of storage structure's operations (Ileke, 2007; Tefera *et al*., 2010; Akol *et al*., 2011).

The feeding behaviour of *S. zeamais* results in substantial loss of food by reducing the grain weight (Flinn, 1991; Boxall, 2002). *Sitophilus zeamais* left on cereal debris in traditional storage structures can reduce future grain yield up to 70% in all maize planted in eastern and southern Africa (Nawanich, 1996; Boxall, 2002). Boxall (2002) reported that 20% grain weight loss can occur under controlled environments while an 80% loss may occur when cereals are not treated. More grain loss (more than 80%) may occur when untreated cereal is stored in traditional structures used by many farmers in tropical and some sub-tropical countries (Nawanich, 1996).

Adult beetles feed on the seeds, pieces of seeds and cereal products (Campbell *et al*., 1989). *Sitophilus zeamais* adults can be seen feeding on the grain and removing the shells of kernels (Campbell *et al*., 1989). Larvae feed on the endosperm and complete their development inside the kernel (De Groote, 2002; Tefera *et al*., 2010). One larva develops in a kernel of rice but several larvae may develop in a kernel of corn (Campbell *et al*., 1989). More *S. zeamais* progeny is produced by each corn kernel than by one rice kernel. Campbell *et al.* (1989) reported that about 56% of the mass of rice kernels is consumed by the larvae, half of which is consumed by the fourth instar. Under heavy infestations, the kernels may be reduced to mere shells which explain the importance of controlling the beetles (Campbell *et al.*, 1989).

Food preferences

Maize Weevils are primary insect pests**;** when the grain is ground into powder or disturbed, they do not breed on it (De Groote, 2002). The beetles feed and reproduce within grains but maize is preferred than grain of other cereals (Nawanich, 1996). Maize Weevils cannot feed and reproduce on ground cereal food materials but they can feed and breed on products of cereals, examples are macaroni and noodles (Campbell *et al*., 1989; Tefera *et al*., 2010). Maize Weevils were reported attacking

Triticale; cross between wheat and rye (Campbell *et al*., 1989). Surveys conducted on silos showed that Maize Weevils were predominately found infesting rice, sorghum, maize, barley and wheat (Campbell *et al*., 1989; Tefera *et al*., 2010).

Natural enemies of *Sitophilus zeamais* (Motschulsky)

Sitophilus zeamais, like the other *Sitophilus* spp., are usually parasitized by a number of pteromalids (Table 2 and 3) (Campbell *et al.*, 1989; Kengkarnpanich, 2003). *Sitophilus zeamais* is occasionally parasitized by other Hymenoptera found in the Tropics (Campbell *et al.*, 1989; Kengkarnpanich, 2003; CABI, 2012).

Table 2 Natural enemies of *Sitophilus zeamais*

Family	Parasitoids
Pteromalidae	*Anisopteromalus calandrae* (Howard)
	Theocolax elegans (Westwood)
	Cerocephala donodiri (Graham)
	Dibrachys cavus (Walker)
	Lariophagus distinguendus (Forster)
Bethylidae	*Holepyris sylvanhnidis* (Bretes)

Source: Kengkarnpanich (2003)

Table 3 Natural enemies of *Sitophilus zeamais*

Family	Parasitoids
Pteromalidae	*Anisopteromalus calandrae* (Howard)
	Theocolax elegans (Westwood)
	Cerocephala donodiri (Graham)
	Dibrachys cavus (Walker)
	Lariophagus distinguendus (Forster)
	Cerocephala cornigero (Westwood)
	Lariophagus distinguendus (Forster)
	Pteromalus tritici (Goureau)
	Zatropis incertus (Ashmead)
Bethylidae	*Holepyris sylvanhnidis* (Bretes)
	Cephalonomia formiciformis (Westwood)
	Cephalonomia tarsalis (Ashmead)
	Cephalonomia waterstoni (Gahan)
Braconidae	*Chremylus rubiginosus* (Nees)

Source: Campbell *et al.* (1989)

Distribution of *Sitophilus zeamais* (Motschulsky)

Sitophilus zeamais is found in sub-tropical and tropical regions of the world (Table 4) (Longstaff, 1981). However, *S. zeamais* was reported in temperate regions (Table 4) (Campbell *et al.*, 1989). *Sitophilus zeamais* is spread throughout the world by grain shipments and can establish itself where there is grain with optimum moisture content (Longstaff, 1981; Campbell *et al.*, 1989; CABI, 2012).

Table 4 Distribution of *Sitophilus zeamais*

Continent	Country
Asia	Japan, Japan and Taiwan
	India, Bangladesh and Bhutan
	All countries of South East Asia
Africa	All countries of Africa
Europe	Greece, Spain, Turkey, Russia, and Yugoslavia
South America	Argentina, Brazil, Chile and Uruguay
North America	Mexico, USA and Canada
Australia	Northern Australia

Source: Longstaff (1981)

3. Natural enemies in storage structures

Parasitic wasps and predators are found in most tropical stores (Boxall, 2002). Hayashi *et al.* (2004) reported that 21 species of parasitoids (classified within seven families) occur in Thailand rice stores. The parasitic Hymenoptera families found were: Chalcididae, Eurytomidae, Pteromalidae, Eulophidae, Evaniidae, Braconidae and Bethylidae (Hayashi *et al*., 2004). These natural enemies naturally inhabit stored grain (Flinn *et al.*, 1996; Flinn *et al.*, 1997). When released, natural enemies continue to control storage insect pests for a prolonged period of time (Flinn, 1998; Flinn and Hagstrum, 2002; Flinn and Schöller, 2012).

Commercial release of natural enemies to control storage insect pests is gaining more support over the recent years (Schöller, 2010). The major use of natural enemies is focused mainly on controlling storage insect pests found infesting organic grain produced by small-scale farmers (Arthur and Rogers, 2003; Grieshop *et al*., 2006; Schöller, 2010).

Pteromalidae are among the numerically largest Families of Chalcidoidea (Hymenoptera) with species inhabiting all zoogeographical regions of the world (Sureshan, 2012). Entomophagous pteromalids typically are primary parasitoids and some species attack stored-product insect pests at different stages of development (egg, larva or pupa) (Williams and Floyd, 1971a; Flinn and Hagstrum, 2002). Some pteromalids are phytophagous and develop within seeds while other pteromalids induce gall formation on plants (Bare, 1942). Many adult pteromalids are metallic in colour and 1 – 48 mm long including the ovipositor (Sharifi, 1972; Noyes, 2003). Adults are free living and feed on nectar (Flint and Dreistadt, 1998; Sureshan, 2012).

Some Pteromalidae species are used as biological control agents of Coleoptera (Flinn and Hagstrum, 2002; Noyes, 2003). Pteromalids that attack stored product pests include: *T. elegans*, *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae), *Cerocephala dinoderi* (Gahan) (Hymenoptera: Pteromalidae), and *Lariophagus distinguendus* (Foerster) (Hymenoptera: Pteromalidae) (Hayashi *et al*., 2004). *Theocolax elegans* and *A. calandrae* are dominant parasitoids reported

attacking Coleopteran larvae in stored grains from Thailand (Hayashi *et al*., 2004; Sureshan, 2012).

Pteromalid wasps females including *L. distinguendus*, *A. calandrae* and *T. elegans* oviposit their eggs in host larvae and pupae found inside grain kernels (Schöller, 2010). The host larvae are usually paralyzed before the eggs are oviposited (Schöller and Flinn, 2000; Schöller, 2010). The parasitoid larva emerge from the eggs and feed outside of the host larva resulting to the host larva's death (Schöller and Flinn, 2000; Prozell and Schöller, 2003).

3.1 *Theocolax elegans* (Westwood)

Theocolax elegans is a cosmopolitan parasitic wasp that parasitizes some coleopteran species in stored grain (Herdman, 1921; Sedlacek *et al*., 1998). This wasp was described by Westwood in 1874 and Graham (1969) named it *Laesthia* Haliday as a synonym for *Theocolax* (Xiao and Huang, 2001). Taxonomic placement of this species has been problematic. This wasp has been assigned to the genera *Spalangiomorpha, Cercocephala, and Choetospila* by various authors (Herdman, 1921; Xiao and Huang, 2001). Most recently Boucek (1988) assigned it to the genus *Theocolax.*

Only eight species assigned to genus *Theocolax* are currently known (Xiao and Huang, 2001). The species assigned to genus *Theocolax* include: *T. elegans, Theocolax bakeri* (Crawford) (Hymenoptera: Pteromalidae), *Theocolax formiciformis* (Westwood) (Hymenoptera: Pteromalidae), *Theocolax frater* (Girault) (Hymenoptera: Pteromalidae), *Theocolax ingens* (Xiao and Huang) (Hymenoptera: Pteromalidae), *Theocolax oblonga* (Delucchi) (Hymenoptera: Pteromalidae), *Theocolax phloeosini* (Yang) (Hymenoptera: Pteromalidae) and *Theocolax radhakrishnani* (Sureshan and Narendran) (Hymenoptera: Pteromalidae). All species in this genus are natural enemies of storage beetles found in association with grain (Xiao and Huang, 2001).

Identification

Like other chalcidoid parasitoids, *T. elegans* is very small; ranging from 1.0-2.1 rnm in length (Ahmed and Khatun, 1993; Hayashi *et al*., 2004). The body of *T. elegans* is elongate (Figure 1) (Xiao and Huang, 2001; Hayashi *et al*., 2004). The head and thorax are dark brown and the abdomen is brown to black (Figure 1) (Noyes, 2003). The head is dorsally depressed, elongated and tapering towards the apex (Figure 1). The antennal insertions (toruli) are anterior of the posterior margin of the eyes (Figure 1) (Ahmed and Khatun, 1993; Xiao and Huang, 2001; Noyes, 2003). Females have eight-segmented antennae while males have nine-segmented antennae and the antennal scape varies from reddish to yellowish brown (Figure 1) (Xiao and Huang, 2001; Noyes, 2003). The following 3-4 segments of the antennae are dark reddish brown while the club is dark brown to black (Figure 1) (Noyes, 2003).

The thorax is smooth and shiny (Figure 1) (Noyes, 2003). *Theocolax elegans* seldom have shorter wings or are sometimes absent (Ahmed and Khatun, 1993). The forewings have distinguishing setae at the base of the marginal vein. The central portion of the forewing has fuscous setae while the margins have dense and fringed long setae (Noyes, 2003). The legs are yellowish brown with the fore and hind coxae pale whitish (Figure 1) (Noyes, 2003). The middle coxae are brown while the outer margins of femora of all the legs are brown (Figure 1) (Ahmed and Khatun, 1993; Noyes, 2003).

Figure 1 *Theocolax elegans* male and female (X20) (a) Lateral view of a male (b) Dorsal view of a male (c) Lateral view of a female (d) Dorsal view of a female

Biology

Theocolax elegans only parasitizes host larvae that are found feeding inside the grain kernel (Van den Assem and Kuenen, 1958). *Theocolax elegans* females parasitize 4th-instar larvae and pupae of *S. zeamais* (Sharifi, 1972; Smith, 1992). *Theocolax elegans* females oviposit one egg externally on each host and develop as an ectoparasite (Flinn, 1998). The wasp is a solitary parasitoid because only one progeny develops on each host (Ahmed and Khatun, 1993). Williams and Floyd (1971a) reported that *T. elegans* reproduction is arrhenotokous; male offspring are haploid and female offspring are diploid.

Following successful oviposition, *T. elegans* eggs require 10 days to hatch into larvae at 25 °C (Van den Assem and Kuenen, 1958). Larvae of *T. elegans* attach to the dorsal body wall of the host larvae and feed as an ectoparasite (Ahmed and Khatun, 1993). Larval development requires 8-11 days (Bare, 1942; Van den Assem and Kuenen, 1958). The pre-pupal stage lasts for 17.8-23.6 hours and the

pupal stage lasts for 4.6-5.4 days at 26 and 30 °C, respectively (Bare, 1942; Van den Assem and Kuenen, 1958).

The life cycle of the parasitoid is influenced mainly by environmental temperature (Bare, 1942). Sharifi (1972) reported that the life cycle of *T. elegans* is about 22 days at 27 °C. Females normally live 2-3 weeks provided that they find the host and food (Van den Assem and Kuenen, 1958). Flinn (1998) reported that one female *T. elegans* can parasitize up to 6 larvae per day. Adults do not feed on the grain and will normally die within 5-10 days if hosts and honey are not present in the grain (Ahmed and Khatun, 1993).

Host location

The hosts parasitized by *T. elegans* are found inside kernels of grain (Flinn, 1998). However, in rare cases, the host can be found outside the kernels of the grain (Van den Assem and Kuenen, 1958; Tang *et al*., 2009). Volatiles produced by cereals have a long-range attraction towards *T. elegans* and are significant in host habitat location (Germinara *et al*., 2004). Cereal kernels and hexane extracts from the kernels are attractive to both sexes of *T. elegans* (Germinara *et al*., 2004; Tang *et al*., 2009). *Theocolax elegans* adult females can distinguish grain kernels infested with host from those not infested by the host (Van den Assem and Kuenen, 1958).

Sitophilus zeamais adult faeces release odour that attract *T. elegans* females (Germinara *et al*., 2004; Tang *et al*., 2009). Artificially-damaged kernels of cereals do not emit sufficient amounts of volatiles to attract *T. elegans* females (Press, 1992; Germinara *et al*., 2004; Tang *et al*., 2009). However, cereal kernels damaged by the feeding of *S. zeamais* larvae and adults emit sufficient volatiles to attract both male and females of *T. elegans* (Press, 1992; Germinara *et al*., 2004; Tang *et al*., 2009).

Cereal grains extracts obtained from head and thorax of *S. zeamais* immatures and adults attract *T. elegans* (Tang *et al*., 2009). Sex pheromone signals emitted by *S. zeamais* to attract the opposite sex of *S. zeamais* allow *T. elegans* to find and attack the larvae and pupae of *S. zeamais* (Press, 1992; Germinara *et al*., 2004;

Tang *et al*., 2009). Aggregation pheromones produced by adult *S. zeamais* are useful signals for *T. elegans* females because the larvae of *S. zeamais* are always found in the kernels around the adults (Tang *et al*., 2009).

After finding the infested grain mass, the females begin vibrating their antennae on each kernel (Van den Assem and Kuenen, 1958). The vibration of the antennae results in *T. elegans* females locating the appropriate host which are the 3rd or 4th instar larvae. After the host has been located, antennal vibrations become intense (Van den Assem and Kuenen, 1958; Press, 1992). The intense vibration of the antennae after the females have located the host is called "drumming" (Van den Assem and Kuenen, 1958).

The use of olfactory cues by *T. elegans* is possible but drumming involves contact by mechanoreceptors and chemoreceptors which are critical for host location and oviposition (Van den Assem and Kuenen, 1958). The female then deposits eggs after successfully locating the host; 3rd or 4th instar larvae of the host insects (Flinn, 1998). When the host larvae are found outside the grain kernels, the female inspects the larva but does not oviposit on it (Flinn, 1998). Van den Assum and Kuenen (1958) reported that the oviposition stimulus of *T. elegans* females is only for larvae found within kernel grains.

Economic importance

Theocolax elegans was of little significance as a parasitoid of economically important insect pests (Birdwell, 1919; Goodrich, 1921). In contrast, *T. elegans* was recorded as a potential parasitoid of *R. dominica* (Herdman, 1921). *Theocolax elegans* parasitizes larvae and pupae of several insect pests of stored products (Bare, 1942; Williams and Floyd, 1971a; Sharifi, 1972). Stored insect pests that can be parasitized by *T. elegans* include *R. dominica*, *S. oryzae*, *S. granaries* and *S. zeamais*, to mention a few species (Bare, 1942; Williams and Floyd, 1971a; Sharifi, 1972).

Theocolax elegans could control up to 89% of *S. zeamais* in corn and was effective in reducing populations of *S. zeamais* by up to 50% in field experiments

(Williams and Floyd, 1971a; Flinn, 1998; Toews *et al*., 2001). *Theocolax elegans* also have parasitized larvae and pupae of other host insects on stored crops, including *R. dominica* in wheat (Wen and Brower, 1995; Flinn *et al*., 1996; Flinn, 1998; Toews *et al*., 2001; Flinn and Hagstrum, 2002). Flinn *et a1*. (1996) reported that *T. elegans* can control *R. dominica* populations up to 90% compared to control bins where *T. elegans* was not used. This shows that *T. elegans* can control many storage insect pests.

Augmentative releases of *T. elegans* to control *R. dominica* were more effective under cool temperatures (25-32 °C) (Flinn, 1998). *Theocolax elegans* adults die when exposed to subfreezing temperatures for a short period of time (few hours) (Williams and Floyd, 1971b; Flinn, 1991). However the larvae of *T. elegans* can withstand cold temperatures for up to 10 days of subfreezing conditions (Williams and Floyd, 1971b; Flinn, 1991). After 10 days, 90% increase in larval mortality can occur (Williams and Floyd, 1971b; Flinn, 1991). This shows that *T. elegans* can control many storage insect pests even under extreme weather conditions.

Hosts of *Theocolax elegans* (Westwood)

Theocolax elegans is a natural enemy of a number of storage insect pests grouped under the Order Coleoptera and Lepidoptera (Table 5). Parasitized larvae of storage insect pests feed inside the grain kernels (Noyes, 2003; Hayashi *et al*., 2004).

Table 5 Hosts of *Theocolax elegans*

Order	Family	Host
Coleoptera	Bruchidae	*Acanthoscelides obtectus*
		Callosobruchus analis
		Callosobruchus chinesis
		Callosobruchus maculatus
		Zabrotes subfasciatus
	Curculionidae	*Caulophilus oryzae*
		Sitophilus granarius
		Sitophilus linearis
		Sitophilus oryzae
		Sitophilus zeamais
	Cucujidae	*Cryptolestes ferrugineus*
	Anobiidae	*Lasioderma serricorne*
		Stegobium paniceum
	Bostrichidae	*Prostephanus truncatus*
		Rhizopertha dominica
Lapidoptera	Gelechiidae	*Sitotroga cerealella*

Source: Hayashi *et al*. (2004)

Distribution of *Theocolax elegans* (Westwood)

Theocolax elegans is a cosmopolitan parasitoid of storage insect pests (Boucek, 1988; Noyes, 2003). *Theocolax elegans* is found throughout the world with more reports in the Oriental and Australasian regions (Table 6) (Boucek, 1988).

Table 6 Distribution of *Theocolax elegans*

Continent	Country
Australia	Australia and New Zealand
Asia	Thailand, Malaysia and Myanmar
	Bangladesh, Pakistan and India
	Taiwan, Korea, China and Japan
Africa	Mauritius, Morocco and Egypt
	Malawi, Kenya, Nigeria and Tanzania
South America	Argentina, Bolivia, Brazil and Columbia
North America	Mexico and USA
Caribbean	Cuba and Jamaica
Europe	France, Greece, Italy, Czech Republic and United Kingdom

Source: Boucek (1988) and Noyes (2003)

MATERIALS AND METHODS

Experimental design

The experiment was completed at the National Biological Control Research Centre, Headquarters, Kasetsart University. The experiment was a Randomized Complete Block Design (RCBD). Mated female of *T. elegans* was released to 100 infested brown rice kernels at 13, 15, 17, 19 and 21 days after *S. zeamais* females were allowed to lay eggs on the brown rice. The treatments were replicated twenty-five times.

Materials

1. Insects and grain used in the experiment

Sitophilus zeamais used were obtained from a stock culture maintained at the NBCRC laboratory, Kasetsart University. *Sitophilus zeamais* was reared on brown rice, *Oryza sativa* L. (Poales: Poaceae) at 27 °C. The brown rice used in the experiment was frozen at -20±2 °C for at least 3 weeks to eliminate contamination (Tefera *et al*., 2010). Haines (1991) reported that the optimum grain moisture content for storage insects was 13–14%. The optimal moisture content (13–14%) was attained by measuring the moisture content using moisture meter and drying the grain when the moisture content was too high (Tefera *et al*., 2010). *Theocolax elegans* was sourced from a culture of the parasitoid mass-reared at the NBCRC laboratory, Kasetsart University. *Theocolax elegans* was mass-reared on fourth-instar larvae of *S. zeamais* at 30 °C in the same lab.

Methods

1. Effect of host age on progeny production of *Theocolax elegans* (Westwood)

A total of 125 glass jars, 5.5x15 cm, (one per treatment) containing 100 g of brown rice with an initial moisture content of 14% was infested with fifty unsexed adults of *S. zeamais* per treatment. The unsexed adults of *S. zeamais* were less than one month old. *Sitophilus zeamais* oviposit eggs that give a 1:1 progeny sex ratio so

the uncontrolled sex ratio will not affect progeny production in each treatment (Campbell *et al*., 1989). After 24 hours, all adult weevils from the different treatments were removed using a camel's hair brush. *Sitophilus zeamais* eggs were not destroyed when removing the adult weevils because the eggs were oviposited in a slender hole that was covered by a gelatinous secretion that protected and concealed the site of oviposition (Campbell *et al*., 1989). One hundred infested brown rice kernels were selected from each treatment, placed in glass jars (4 x 6.5 cm) and covered with a filter paper for ventilation.

Theocolax elagans wasps used in my experiment were 48 hours old. *Theocolax elagans* was aged by isolating the parasitized hosts into vials. Vials were inspected daily for any emerged *T. elagans*. After emergence, neonate *T. elagans* females were exposed to honey and males for 24 hours before the experiment. The hundred infested brown rice kernels per treatment/jar were exposed to mated female *T. elegans* at 13, 15, 17, 19 and 21 days after *S. zeamais* introduction. The hundred infested brown rice kernels provided 100 hosts per treatment per jar. *Theocolax elagans* females were removed from each treatment after 24 hours. Only one mated female of *T. elegans* was used per treatment per jar to minimize continuous fertilization of the females by males hence increasing the time for the female to continue ovipositing eggs on the hosts.

The life cycle of *T. elegans* is about 22 days at 27 °C (Sharifi, 1972; Ahmed and Khatun, 1993). Twenty days following release of *T. elegans*, I began daily records of the number of males and females of *T. elegans* produced from each treatment. The total number of males and females of *T. elegans* was used to calculate the total number of *T. elegans* progeny in each treatment and to calculate the sex ratio in each treatment. This provided information on the effect of the different host ages of *S. zeamais* (13, 15, 17, 19 and 21 days) to support progeny production of *T. elegans*.

2. Determination of larval instars

To determine the host stages, 100 *S. zeamais* adults were allowed to oviposit eggs on 200 g brown rice. I used a camel's hair brush to remove the 100 *S. zeamais*

after 12 hours. After 13, 15, 17, 19 and 21 days following oviposition, five infested brown rice kernels were randomly selected and dissected to obtain *S. zeamais* larvae. I measured head capsules widths of the larvae with a calibrated Olympus compound microscope (SZ-PT) from Japan by taking pictures of the dorsal aspect of the larvae head capsules. The largest capsule widths from the pictures were used to represent the capsule with for the *S. zeamais* larvae. The head capsule width of *S. zeamais* at each host age was an average of the five head capsule widths obtained after measuring the five *S. zeamais* larvae at 13, 15, 17, 19 and 21 days following oviposition.

3. Sanitation

Good sanitation measures are important to prevent contamination of the insect colonies by other insect species. Matured colony of *T. elegans* and *S. zeamais* was used to inoculate a new colony (Tefera *et al*., 2010). The old colony was removed from the rearing area because it was a source contamination. The old colony was cold-treated (frozen at -20±2 °C) for twenty-four hours to ensure that all the insects were killed. A plastic bag was used to contain the old colony and prevent live insects from escaping. The work area was kept free of spilled grain because grain are a source of unwanted insect populations and can infest the stock colony (Tefera *et al*., 2010). Equipment used to maintain the insect colony was washed using a detergent. The equipment was stored in a clean and uncontaminated area. The work surfaces was cleaned and disinfested before working with the insects (Tefera *et al*., 2010).

Data Analysis

Data on the effect of host age on total progeny production, total female progeny production, male progeny production and head capsule widths were analyzed using one way ANOVA. Means were separated using Least Significant Difference (LSD) at 95% confidence level. SPSS statistical package was used to analyze the data.

RESULTS AND DISCUSSION

Results

In this study, results were divided into 5 parts including the effect of host age on: total progeny production, total female progeny production, total male progeny production, sex ratio and the host stages at different host ages.

1. Effect of host age on total progeny production

Theocolax elegans progeny were collected for two weeks in each treatment. The first week had the largest number of *T. elegans* progeny collected (Figure 2). The number of progeny collected was high on the first day and decreased slowly. The total *T. elegans* progeny production was significantly different ($P < 0.05$) among the different host ages of *S. zeamais*. Total progeny produced ranged from 256 in *T. elegans* reared on 13-day-old *S. zeamais* larvae to 1335 in *T. elegans* reared on 19-day-old *S. zeamais* larvae (Figure 3). Total progeny produced by 19-day-old *S. zeamais* larvae was significantly higher ($P < 0.05$) than the other host ages (Figure 4). This result suggests that 19-day-old *S. zeamais* is the optimum host age for producing a high number of *T. elegans* progeny compared to the other host ages.

Progeny produced by 17-day-old *S. zeamais* larvae was the second highest and significantly different ($P < 0.05$) from 13-day-old, 15-day-old, 19-day-old and 21-day-old *S. zeamais* larvae (Figure 4). I found no significant difference between the total progeny production by 15-day-old and 21-day-old *S. zeamais* larvae. Progeny produced by 13-day-old *S. zeamais* larvae was the least and significantly different ($P < 0.05$) from progeny produced by 15-day-old, 17-day-old, 19-day-old and 21-day-old *S. zeamais* larvae (Figure 4).

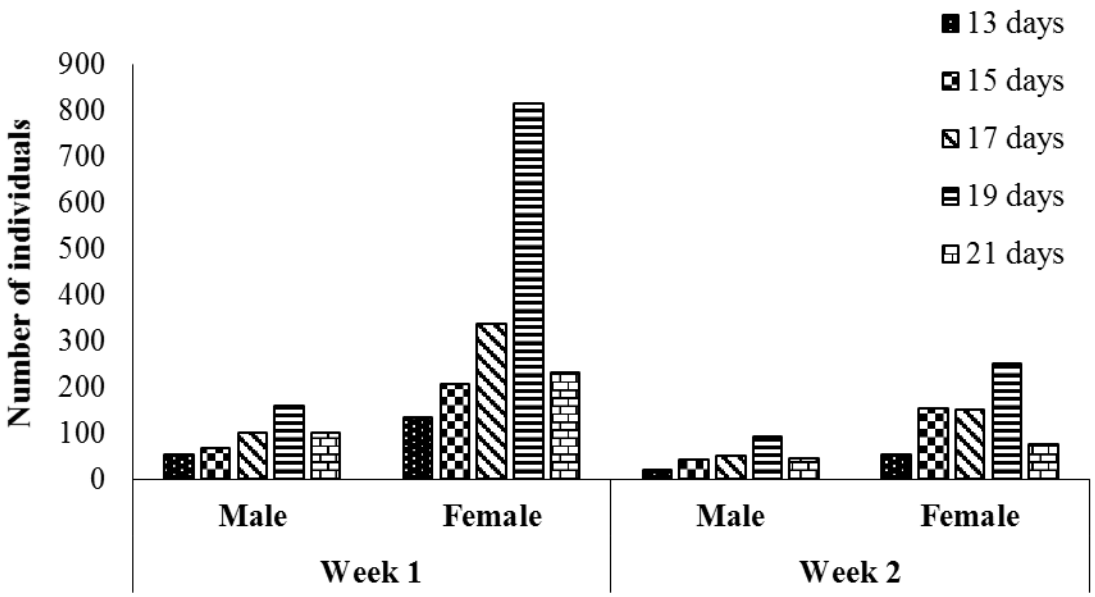

Figure 2 Total female and male *Theocolax elegans* progeny production for weeks 1 and 2

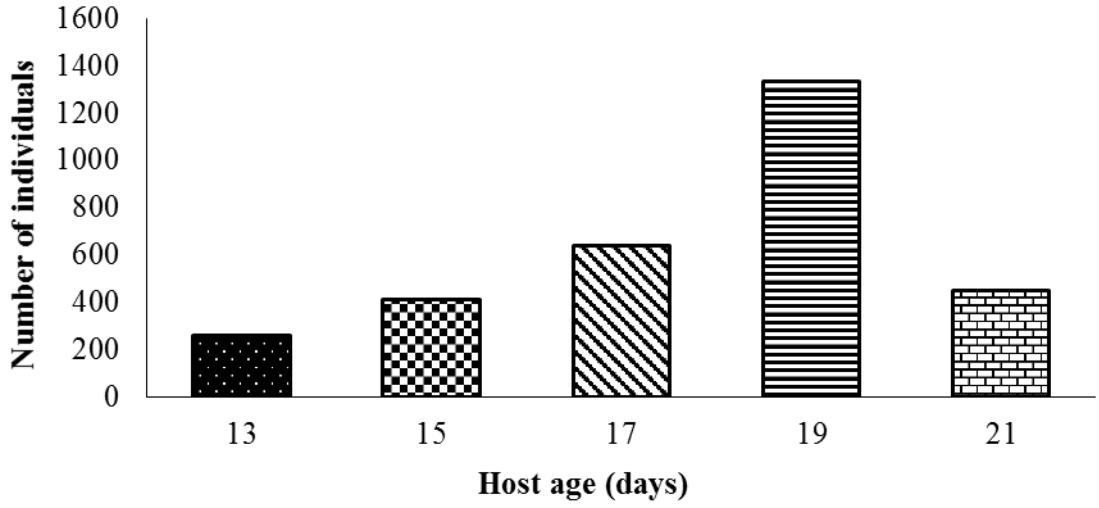

Figure 3 Total *Theocolax elegans* progeny production for different host ages

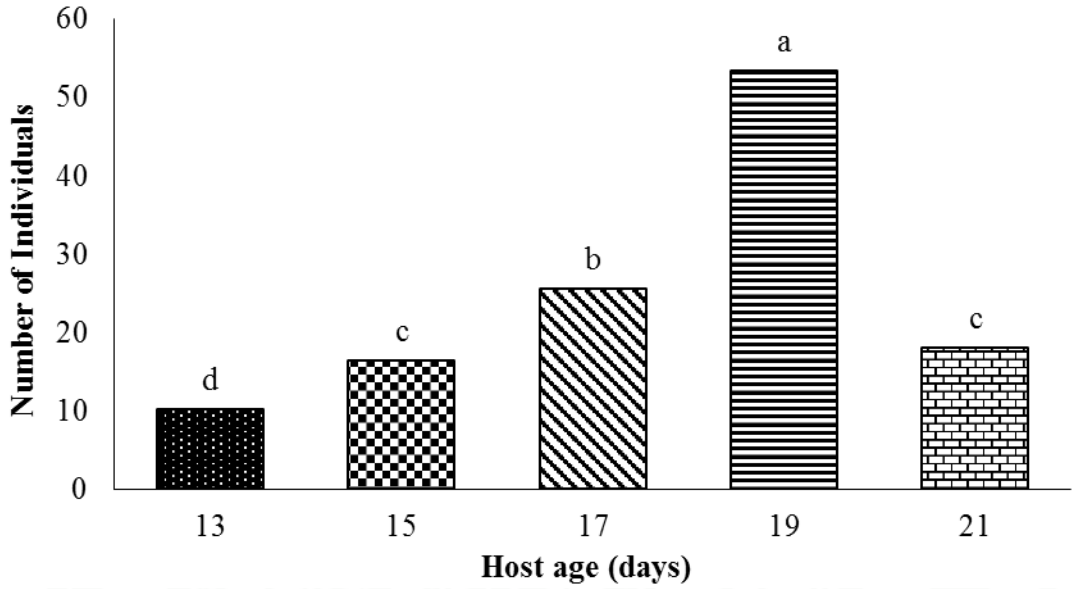

Figure 4 Average *Theocolax elegans* progeny production for different host ages. Means followed by same letter are not significantly different at $P < 0.05$

2. Effect of host age on female progeny production

Total female progeny produced ranged from 187 in *T. elegans* reared on 13-day-old *S. zeamais* larvae to 1084 in *T. elegans* reared on 19-day-old *S. zeamais* larvae (Figure 5). Total male progeny produced ranged from 69 in *T. elegans* reared on 13-day-old *S. zeamais* larvae to 251 in *T. elegans* reared on 19-day-old *S. zeamais* larvae (Figure 5).

The average female *T. elegans* progeny production was significantly different ($P < 0.05$) among the different host ages of *S. zeamais* (Figure 6). Average female progeny produced by 19-day-old *S. zeamais* larvae was significantly higher ($P < 0.05$) than average female progeny produced by the other host ages (Figure 6). Average female progeny produced by 17-day-old *S. zeamais* larvae was significantly different ($P < 0.05$) from average female progeny produced by the other host ages. Average female progeny produced by 15-day-old *S. zeamais* larvae was not significantly different from average female progeny produced by 21-day-old *S. zeamais* larvae but significantly ($P < 0.05$) different from average female progeny produced by 17-day-old and 19-day-old *S. zeamais* larvae (Figure 6). I found no significant difference

among average female progeny produced by 13-day-old and 15-day-old *S. zeamais* larvae (Figure 6). This suggests that 19-day-old *S. zeamais* larvae is the optimum host age compared to the other host ages in producing female *T. elegans* progeny.

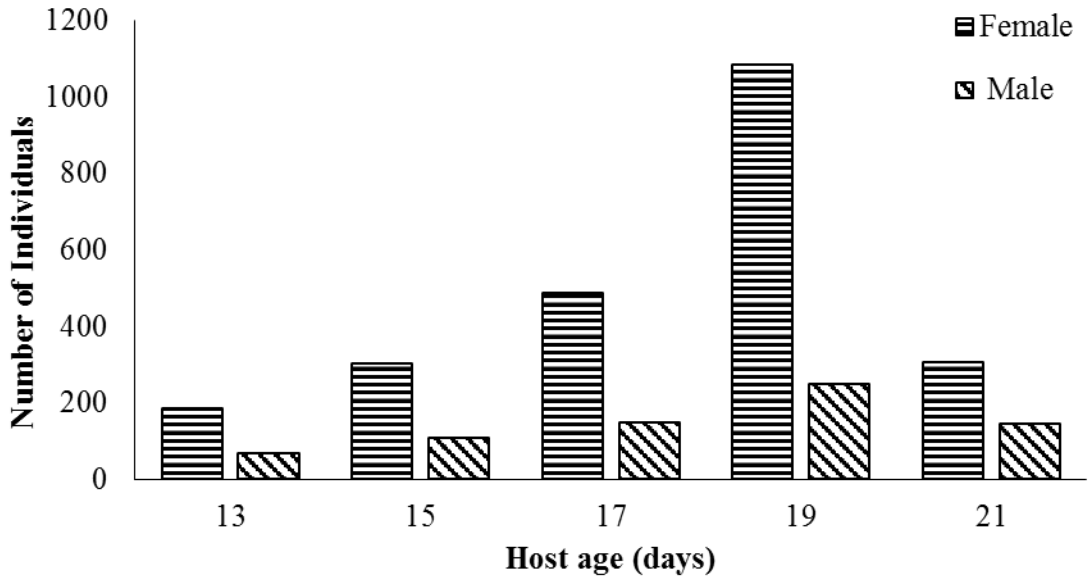

Figure 5 Total male and female *Theocolax elegans* progeny production for different host ages

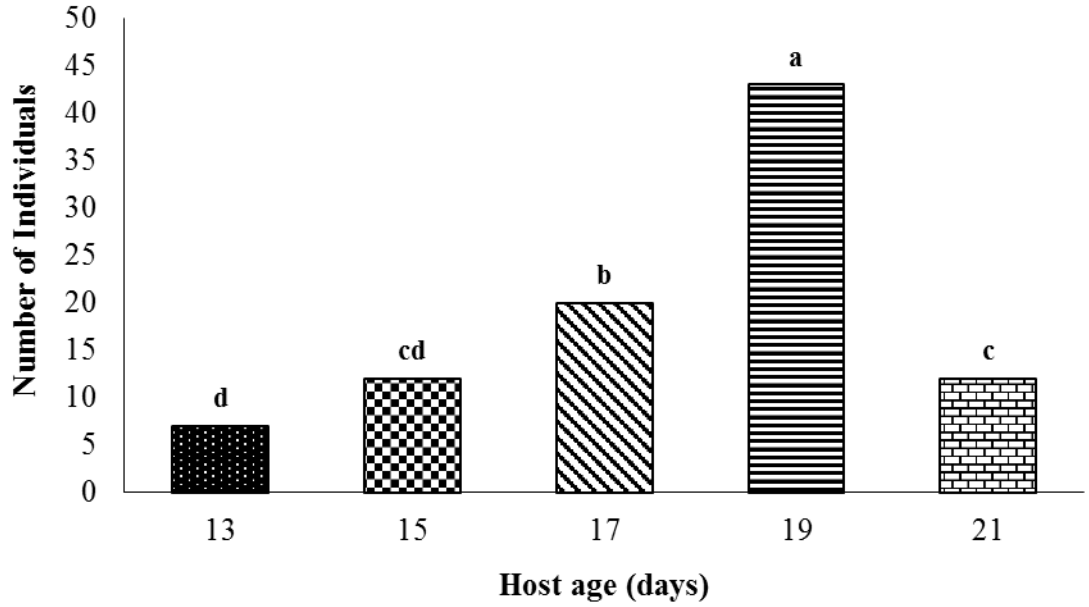

Figure 6 Average female *Theocolax elegans* progeny production for different host ages. Means followed by same letter are not significantly different at $P < 0.05$

3. Effect of host age on male progeny production

Total male progeny produced from the different host ages was lower than total female progeny produced from the different host ages. Average male *T. elegans* progeny production was significantly different ($P < 0.05$) among the different host ages of *S. zeamais* (Figure 7).

Average male progeny production by 19-day-old *S. zeamais* larvae was significantly different ($P < 0.05$) from average male progeny produced by all the other host ages (Figure 7). Average male *T. elegans* progeny produced by 15-day-old, 17-day-old and 21-day-old *S. zeamais* larvae were not significantly different from each other but significantly different ($P < 0.05$) from average male *T. elegans* progeny produced by 13-day-old and 19-day-old *S. zeamais* larvae (Figure 7). Average male progeny produced by 13-day-old *S. zeamais* larvae was not significantly different from average male progeny produced by 15-day-old old *S. zeamais* larvae but significantly different ($P < 0.05$) from average male progeny produced by 17-day-old, 19-day-old and 21-day-old *S. zeamais* larvae (Figure 7). This suggests that 19-day-

old *S. zeamais* larvae is the optimum host age compared to the other host ages in the production of male *T. elegans* progeny.

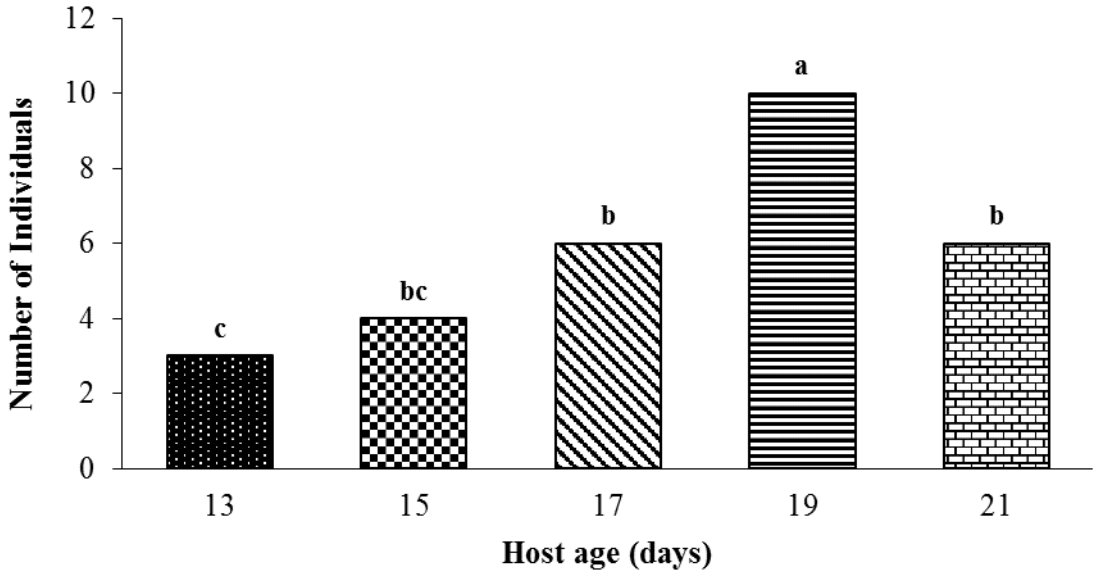

Figure 7 Average male *Theocolax elegans* progeny production for different host ages. Means followed by same letter are not significantly at $P < 0.05$

4. Sex ratio

Progeny of *T. elegans* when raised on 19-day-old *S. zeamais* larvae had higher female: male ratio. The female: male ratio was 2.7, 2.8, 3.3, 4.3 and 2.1 for 13-day-old, 15-day-old, 17-day-old, 19-day-old and 21-day-old *S. zeamais*, respectively (Table 7).

The high female: male ratio is important in host finding, parasitism of the host and in increasing the progeny of *T. elegans*. Only female parasitoids are involved in host finding, parasitism of the host and in oviposition of eggs on the host. Male parasitoids are important in mating. Nineteen days old *S. zeamais* larvae resulted to a total of 53.4 *T. elegans* progeny, higher than all the host ages (Table 7).

Table 7 Sex ratio of *Theocolax elegans* from different host ages n = 25

S. zeamais age (days)	Female	Male	Total	Sex ratio (♀ : ♂)
13	7.5	2.8	10.3	2.7
15	12.1	4.4	16.5	2.8
17	19.7	6.0	25.7	3.3
19	43.4	10.0	53.4	4.3
21	12.2	5.8	18.0	2.1

5. Host stage

Average head capsule widths of *S. zeamais* larvae were significantly different ($P < 0.05$) among the different host ages of *S. zeamais* (Figure 8). Average head capsule widths were 0.26, 0.41, 0.43, 0.50 and 0.54 mm after 13, 15, 17, 19 and 21 days, respectively (Table 8).

Average head capsule width of 13-day-old *S. zeamais* larvae was significantly different ($P < 0.05$) from the other host ages (Figure 8). Average head capsule widths of 15-day-old and 17-day-old *S. zeamais* larvae were not significantly different from each other but significantly different ($P < 0.05$) from average head capsule widths from the other host ages (Figure 8). Average head capsule widths of 19-day-old and 21-day-old *S. zeamais* larvae were not significantly different from each other but significantly different ($P < 0.05$) from average head capsule widths from the other host ages (Figure 8).

There were no results on the head capsule widths of the first instar larvae of *S. zeamais* because data was collected after 13, 15, 17, 19 and 21 days after oviposition. The results show that 13-day-old, 15-day-old to 17-day-old, and 19-day-old to 21-day-old *S. zeamais* larvae were second, third and fourth instars, respectively (Table 8).

Table 8 Stages of *Sitophilus zeamais* at different host ages

Host Age (days)	Head Capsule Width (mm)	Host stage
13	0.26	Second instar
15	0.41	Third instar
17	0.43	Third instar
19	0.50	Fourth instar
21	0.54	Fourth instar

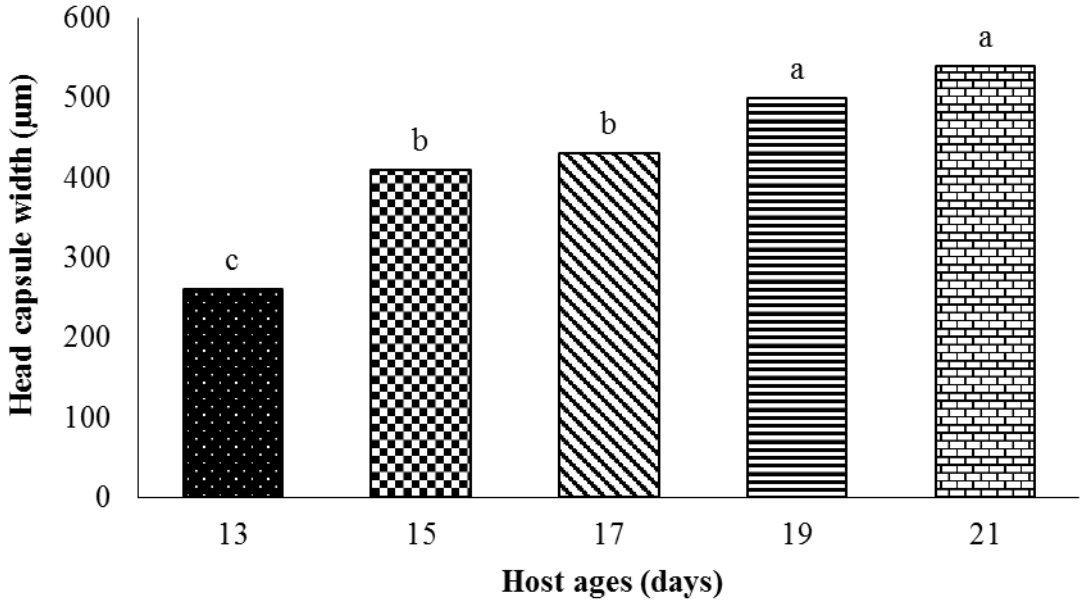

Figure 8 Average head capsule widths of *Sitophilus zeamais* larvae for different host ages. Means followed by same letter are not significantly different at $P < 0.05$

Discussion

Head capsule widths as an indicator of larval instar numbers in *S. zeamais* is more efficient compared to using larval weights (O'Donnell, 1967). O'Donnell (1967) reported that head capsule widths of *S. zeamais* varied from 0.16-0.22, 0.25-0.29, 0.34-0.43 and 0.49-0.54 mm for first, second, third and fourth instars, respectively. Results from my experiment showed that the second, third and fourth instar widths of *S. zeamais* larvae were consistent with the ranges reported by O'Donnell (1967). The first, second, third and fourth instars of *S. zeamais* took 3, 5, 6 and 3, respectively. The pre-pupal stage took 3 days (O'Donnell, 1967). *Sitophilus zeamais* larvae after 13, 15-17 and 19-21 days were found to be second, third and fourth instars, respectively.

Theocolax elegans females can parasitize fourth instar and pupae of *S. zeamais* (Sharifi, 1972). The experiment showed that *T. elegans* can develop on second, third and fourth instar larvae of *S. zeamais*. I observed a significantly high progeny production when *T. elegans* was reared on 19-day-old *S. zeamais* larvae. The results concurred with Sharifi (1972) who reported that *T. elegans* females parasitize fourth instar larvae of *S. zeamais.* After I studied the host stages, I found a high progeny production when *T. elegans* was reared on 19-day-old *S. zeamais* larvae. I later confirmed that 19-day-old *S. zeamais* larvae were in the fourth instar. The second and third can produce progeny but more progeny were obtained when fourth instar (19-day-old) larvae of *S. zeamais* were parasitized.

My experiment showed that *S. zeamais* larvae 21 days following oviposition were still in the fourth instar. At 21 days *S. zeamais* are expected to produce more progeny as the larvae are in the fourth instar. However, *T. elegans* reared on 21-day-old *S. zeamais* larvae produced total progeny not significantly different from *T. elegans* reared on 15-day-old *S. zeamais* larvae. I found that 15-day-old *S. zeamais* larvae were in the third instar. My findings did not concur with Sharifi (1972) but suggests that the resource quality (host larvae) at 21 days following oviposition is declining and thus affecting the quality of parasites emerging later. The number of progeny produced by 21-day-old *S. zeamais* larvae was significantly lower ($P < 0.05$)

than progeny produced by 19-day-old *S. zeamais* larvae. This implies that *T. elegans* parasitize more fourth instar larvae of *S. zeamais* at 19 days compared to 21 days. I concluded that timing of release of *T. elegans* to coincide with the same host stage and age is very important.

Parasitization of a host insect on stored grain at different host stages and ages is affected by host-finding, host stage and age, and the ability to sustain optimal parasitoid development (Burks *et al*., 1999). Optimal parasitoid development refers to high levels of parasitoid oviposition and parasitoid larval development. In heavily infested grain, host-finding is not of paramount importance since the parasitoids can easily locate infested host. In this experiment, host-finding was minimised by allocating equal infested rice kernels to a mated female of *T. elegans* for 24 hours. This means that the differences in progeny production of the different host ages are as a result of the ability of the host ages to sustain optimal growth of the parasitoids (*T. elegans*). *Theocolax elegans* reared on 19-day-old *S. zeamais* larvae had the highest progeny production compared to the other host ages. The high total progeny production when *T. elegans* was mass-reared on 19-day-old *S. zeamais* larvae was caused by the fact that 19-day-old *S. zeamais* larvae can sustain optimal development of *T. elegans* more compared to the other host ages.

After successfully finding the infested grain mass, females begin vibrating their antennae on each kernel (Van den Assem and Kuenen, 1958; Press, 1992). Vibration of the antennae results in *T. elegans* females locating the host larvae. More cycles per second of the antennal vibrations are observed when the female parasitoids locate their hosts in the grain (Van den Assem and Kuenen, 1958; Press, 1992). *Theocolax elegans* then oviposits on the specific place in the kernel where the drumming was accelerated (Press, 1992). This suggests that drumming determines the exact position of host larva inside the rice or maize kernels. The rapid antennal vibrations could be used to moderate another condition (chemical, heat, etc.). Apex of the antenna of *T. elegans* has a number of sensory receptors used to monitor the larva inside the grain.

The high progeny production by 19-day-old (fourth instar) *S. zeamais* larvae is as a result of the fact that grain kernels infested with 19-day-old *S. zeamais* produce a special texture. The special texture stimulates oviposition in the wasp and thus more progeny are produced. This implies that *T. elegans* females can differentiate the appropriate host size (within the same host stage) that stimulates oviposition in the wasp where more parasite progeny can be produced. The other host ages (13, 15, 17 and 21 days) could produce progeny because *T. elegans* was able to locate the host in the kernels but the texture perceived during drumming did not stimulate oviposition. When oviposition is not stimulated by the host age, the host is usually stung to reduce host immune defense (Press, 1992).

Flinn and Hagstrum (2001) reported that one female of *T. elegans* can parasitize up to six host per day. Results from my experiment were not consistent with Flinn and Hagstrum (2001) because a female of *T. elegans* produced an average of 10.24, 16.44, 25.56, 53.4 and 18 *T. elegans* progeny per day at 13, 15, 17, 19 and 21 days, respectively. The results were observed after one female was exposed to infested brown rice kernels for 24 hours. Females of *T. elegans* were exposed to males for 24 hours before the experiment to allow inseminaiton.

Theocolax elegans reproduction is arrhenotokous; male offsprings are haploid and female offsprings are diploid (Williams and Floyd, 1971a). This means that uninseminated females of *T. elegans* can produce male progeny parthenogenically. My results show that males were produced even though the females were inseminated. Insemination of female wasps does not ensure that all eggs are fertilized in parthenogenetic species. Inseminated females store sperms in spermathecal capsules. Females can choose sex of their progeny by releasing or not releasing sperms when an egg passes through the oviduct. When a female does not release sperms, the unfertilized egg will pass through the oviduct and develop to a male. When a female release sperms to fertilize an egg passing through the oviduct, the fertilized egg will develop to a female. Females can control their progeny sex ratio by controlling egg fertilization. Parasitic Hymenoptera typically have skewed sex ratios which explains why I observed a high number of females as compared to males.

Sitophilus zeamais is one of many agricultural pests which are hosts of parasitoid wasps (King, 1993). Release of parasitoid wasps to control agricultural insect pests is important in biological control programs. It is, therefore, important to produce a high number of females than males to release in a biological control program. Sex ratio is affected by environmental factors which are important when mass rearing parasitoids (King, 1993). Female parasitoids select their progeny sex ratio to pass their genes to future generations. The two environmental conditions that affect progeny sex ratio include resources that will be available to the progeny and the numbers of female parasitoids present (King, 1993).

Theocolax elegans is a pteromalid wasp known to manipulate its progeny sex ratio as a result of environmental conditions. Most pteromalids wasps produce a high proportion of males in smaller hosts (King, 1993). Results from my experiment show an increase in the sex ratio as the size or quality of the host increases (from 13-day-old to 19-day-old *S. zeamais* larvae). My results concurred with King (1993) because a high proportion of males (compared to the total progeny produced) were produced by smaller hosts and decreased as the size of the host increased resulting in a high proportion of females than males in bigger hosts.

However, when 21-day-old *S. zeamais* larvae were used to mass-rear *T. elegans*, the sex ratio decreased. Reduction of the sex ratio at 21 days following oviposition suggests that the number of males (compared to the total progeny produced) increased hence reducing the sex ratio. My findings did not concur with King (1993) but suggests that the resource quality (host larvae) at 21 days following oviposition is declining and thus affecting the sex of parasites emerging later. My data showed that 19-day-old *S. zeamais* larvae had a high female: male ratio. The high proportion of females compared to males when 19-day-old *S. zeamais* larvae were used to mass-rear *T. elegans* suggests that at 19 days following oviposition the host quality or size is conducive for producing a high number of females compared to males.

Female parasitoid wasps produce a high proportion of male progeny when other females are present than when alone (King, 1993). My experiment used only

one inseminated *T. elegans* female per treatment so I could not find the effect of other females on the sex ratio of *T. elegans* progeny produced.

CONCLUSION AND RECOMMENDATION

Conclusion

Host age played an important role in progeny production of *T. elegans* when reared on *S. zeamais* larvae. This was shown by the significantly high progeny production when *T. elegans* was reared on 19-day-old *S. zeamais* larvae compared to the other host ages.

I concluded that *T. elegans* can develop on second, third and fourth instar larvae of *S. zeamais* because *T. elegans* progeny were produced by these host stages. However, the highest progeny production was observed when 19-day-old (fourth instar) *S. zeamais* larvae were used to mass-rear *T. elegans.* The reason behind the high progeny production at 19 days following oviposition is the fact that 19-day-old *S. zeamais* larvae can sustain optimal development of *T. elegans* more than the other host ages.

I, also, concluded that timing the release of *T. elegans* within the same host stage is very important in optimizing parasite production in lab colonies. The importance of timing release of *T. elegans* within the same host stage is explained by the low progeny produced when *T. elegans* was mass-reared on 21-day-old *S. zeamais* larvae compared to progeny produced on 19-day-old *S. zeamais* larvae. The difference in progeny production was realized after both 19-day-old and 21-day-old *S. zeamais* larvae were found to be fourth instar. This explains the importance of the host age when timing the release of *T. elegans*.

Recommendation

Knowing the correct host stage and age for releasing *T. elegans* in an insectary can help in reducing colony maintenance costs and improve culture maintenance techniques. Knowing the right host age for releasing *T. elegans* assist in producing high progeny of *T. elegans* as results from my experiment showed that.

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APPENDIX

Appendix Table 1 Analysis of variance of effect of host age on female, male and total progeny production of *Theocolax elegans*

		Sum of Squares	df	Mean Square	F	Sig.
Female	Between Groups	20500.048	4	5125.012	71.474	0.000
	Within Groups	8604.560	120	71.705		
	Total	29104.608	124			
Male	Between Groups	733.328	4	183.332	15.649	0.000
	Within Groups	1405.840	120	11.715		
	Total	2139.168	124			
Total	Between Groups	28095.632	4	7023.908	70.036	0.000
	Within Groups	12034.880	120	100.291		
	Total	40130.512	124			

Appendix Table 2 Multiple mean separation of female *Theocolax elegans* progeny production

Treatment (I)	Treatment (J)	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
T1	T2	-4.60000	2.39507	0.057	-9.3421	0.1421
	T3	-12.08000*	2.39507	0.000	-16.8221	-7.3379
	T4	-35.88000*	2.39507	0.000	-40.6221	-31.1379
	T5	-4.76000*	2.39507	0.049	-9.5021	-0.0179
T2	T1	4.60000	2.39507	0.057	-0.1421	9.3421
	T3	-7.48000*	2.39507	0.002	-12.2221	-2.7379
	T4	-31.28000*	2.39507	0.000	-36.0221	-26.5379
	T5	-0.16000	2.39507	0.947	-4.9021	4.5821
T3	T1	12.08000*	2.39507	0.000	7.3379	16.8221
	T2	7.48000*	2.39507	0.002	2.7379	12.2221
	T4	-23.80000*	2.39507	0.000	-28.5421	-19.0579
	T5	7.32000*	2.39507	0.003	2.5779	12.0621
T4	T1	35.88000*	2.39507	0.000	31.1379	40.6221
	T2	31.28000*	2.39507	0.000	26.5379	36.0221
	T3	23.80000*	2.39507	0.000	19.0579	28.5421
	T5	31.12000*	2.39507	0.000	26.3779	35.8621
T5	T1	4.76000*	2.39507	0.049	0.0179	9.5021
	T2	0.16000	2.39507	0.947	-4.5821	4.9021
	T3	-7.32000*	2.39507	0.003	-12.0621	-2.5779
	T4	-31.12000*	2.39507	0.000	-35.8621	-26.3779

*. The mean difference is significant at the 0.05 level.

Appendix Table 3 Multiple mean separation of male *Theocolax elegans* progeny production

Treatment (I)	Treatment (J)	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
T1	T2	-1.60000	0.96810	0.101	-3.5168	0.3168
	T3	-3.24000*	0.96810	0.001	-5.1568	-1.3232
	T4	-7.28000*	0.96810	0.000	-9.1968	-5.3632
	T5	-3.00000*	0.96810	0.002	-4.9168	-1.0832
T2	T1	1.60000	0.96810	0.101	-0.3168	3.5168
	T3	-1.64000	0.96810	0.093	-3.5568	0.2768
	T4	-5.68000*	0.96810	0.000	-7.5968	-3.7632
	T5	-1.40000	0.96810	0.151	-3.3168	0.5168
T3	T1	3.24000*	0.96810	0.001	1.3232	5.1568
	T2	1.64000	0.96810	0.093	-0.2768	3.5568
	T4	-4.04000*	0.96810	0.000	-5.9568	-2.1232
	T5	0.24000	0.96810	0.805	-1.6768	2.1568
T4	T1	7.28000*	0.96810	0.000	5.3632	9.1968
	T2	5.68000*	0.96810	0.000	3.7632	7.5968
	T3	4.04000*	0.96810	0.000	2.1232	5.9568
	T5	4.28000*	0.96810	0.000	2.3632	6.1968
T5	T1	3.00000*	0.96810	0.002	1.0832	4.9168
	T2	1.40000	0.96810	0.151	-0.5168	3.3168
	T3	-0.24000	0.96810	0.805	-2.1568	1.6768
	T4	-4.28000*	0.96810	0.000	-6.1968	-2.3632

*. The mean difference is significant at the 0.05 level.

Appendix Table 4 Multiple mean separation of the total *Theocolax elegans* progeny production

Treatment (I)	Treatment (J)	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
T1	T2	-6.20000*	2.83253	0.031	-11.8082	-0.5918
	T3	-15.32000*	2.83253	0.000	-20.9282	-9.7118
	T4	-42.76000*	2.83253	0.000	-48.3682	-37.1518
	T5	-7.76000*	2.83253	0.007	-13.3682	-2.1518
T2	T1	6.20000*	2.83253	0.031	0.5918	11.8082
	T3	-9.12000*	2.83253	0.002	-14.7282	-3.5118
	T4	-36.56000*	2.83253	0.000	-42.1682	-30.9518
	T5	-1.56000	2.83253	0.583	-7.1682	4.0482
T3	T1	15.32000*	2.83253	0.000	9.7118	20.9282
	T2	9.12000*	2.83253	0.002	3.5118	14.7282
	T4	-27.44000*	2.83253	0.000	-33.0482	-21.8318
	T5	7.56000*	2.83253	0.009	1.9518	13.1682
T4	T1	42.76000*	2.83253	0.000	37.1518	48.3682
	T2	36.56000*	2.83253	0.000	30.9518	42.1682
	T3	27.44000*	2.83253	0.000	21.8318	33.0482
	T5	35.00000*	2.83253	0.000	29.3918	40.6082
T5	T1	7.76000*	2.83253	0.007	2.1518	13.3682
	T2	1.56000	2.83253	0.583	-4.0482	7.1682
	T3	-7.56000*	2.83253	0.009	-13.1682	-1.9518
	T4	-35.00000*	2.83253	0.000	-40.6082	-29.3918

*. The mean difference is significant at the 0.05 level.

Appendix Table 5 Analysis of variance of head capsule widths of *Sitophilus zeamais* larvae at different host ages

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	0.263	4	0.066	88.067	0.000
Within Groups	0.015	20	0.001		
Total	0.278	24			

Appendix Table 6 Multiple mean separation of head capsule widths of *Sitophilus zeamais* larvae at different host ages

Treatments (I)	Treatments (J)	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
T 1	T2	-0.14547*	0.01728	0.000	-0.1815	-0.1094
	T 3	-0.16917*	0.01728	0.000	-0.2052	-0.1331
	T4	-0.27810*	0.01728	0.000	-0.3141	-0.2421
	T 5	-0.27714*	0.01728	0.000	-0.3132	-0.2411
T2	T 1	0.14547*	0.01728	0.000	0.1094	0.1815
	T 3	-0.02369	0.01728	0.185	-0.0597	0.0123
	T4	-0.13262*	0.01728	0.000	-0.1687	-0.0966
	T 5	-0.13166*	0.01728	0.000	-0.1677	-0.0956
T 3	T 1	0.16917*	0.01728	0.000	0.1331	0.2052
	T2	0.02369	0.01728	0.185	-0.0123	0.0597
	T4	-0.10893*	0.01728	0.000	-0.1450	-0.0729
	T 5	-0.10797*	0.01728	0.000	-0.1440	-0.0719
T4	T 1	0.27810*	0.01728	0.000	0.2421	0.3141
	T2	0.13262*	0.01728	0.000	0.0966	0.1687
	T 3	0.10893*	0.01728	0.000	0.0729	0.1450
	T 5	0.00096	0.01728	0.956	-0.0351	0.0370
T 5	T 1	0.27714*	0.01728	0.000	0.2411	0.3132
	T2	0.13166*	0.01728	0.000	0.0956	0.1677
	T 3	0.10797*	0.01728	0.000	0.0719	0.1440
	T4	-0.00096	0.01728	0.956	-0.0370	0.0351

*. The mean difference is significant at the 0.05 level.

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