ECOPHYSIOLOGY OF MAIZE WEEVIL (*Sitophilus zeamais* Mots.)

by

MOHAMM ED QUARSHIE

(Under the Direction of Shayla Salzman)

ABSTRACT

The maize weevil, *Sitophilus zeamais*, is an economically important pest of stored grains causing significant losses. This study explored key ecological factors, including temperature and moisture that contribute to maize weevil survival. Thermal performance was assessed through critical thermal maximum (CT_{Max}) and thermal preference tests, which revealed no significant differences between sexes. Morphological analysis confirmed sexual dimorphism, with females having longer rostra and males having wider rostra, but no differences in weight. Moisture effects were evaluated through feeding and larval developmental trials under controlled conditions. Feeding was highest at 20% moisture content, with males exhibiting greater variability. Statistical analyses confirmed differences in feeding between 10% and 20% moisture content. Larval development showed the highest F1 progeny emergence at 20% moisture content, a smaller number of emergence at 10% moisture content, and no significant sex ratio difference. Grain damage was lowest at 10% moisture content. These findings provide insights into *S. zeamais* adaptability, emphasizing the impact of temperature and moisture on its population dynamics.

INDEX WORDS: *Sitophilus zeamais,* Thermal Tolerance, Ecophysiology, Critical Thermal Maximum (CT_{Max}), Oviposition, Thermal Preference.

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Mohammed Quarshie

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MOHAMMED QUARSHIE

Major Professor:	Shayla Salzman
Committee:	Michael Toews Patricia J. Moore

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
The University of Georgia
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DEDICATION

This thesis is dedicated to Dr. Brett Blaauw, who has always believed in me, supported me, and encouraged me. His advice has consistently given me hope and inspired me, and I am incredibly appreciative of the inspiration he has given me along the way.

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CHAPTER ONE

Biology and Economic Impact of the Maize Weevil (*Sitophilus zeamais*)

Introduction

Insects are grouped based on their feeding behavior, including herbivorous species, predators, fungivores, and scavengers. Coupled with weeds and diseases, insects are estimated to account for 40% of the world's food production being lost during the preharvest stage, and another 20% during storage (Pimentel & Peshin, 2014;Huey & Stevenson, 1979;Throne & Cline, 1991). There are new findings that prove the reverse of this common assertion and argue that, possibly, Hymenoptera outnumbers Coleoptera in diversity of species (Forbes et al., 2018). Indeed, Coleoptera remains very highly diversified, and estimates done to date vary between 350,000 to 1.5 million species globally, (Beutel & Leschen, 2005; Stork et al., 2015). Coleoptera are the most varied group of animals on the planet, with about 380,000-400,000 described species to date (Baca et al., 2021; Smith & Marcot, 2015). They have been around for at least 285 million years, as evidenced by fossil records, with the oldest North American fossil dating back to the Permian period (Lubkin & Engel, 2005). Recent phylogenomic studies have provided insights into beetle evolution, estimating the origin of modern beetles around 317 Ma in the mid-Carboniferous and the divergence between Archostemata and Adephaga around 296 Ma in the early Permian (Baca et al., 2021).

Of the 32 insect orders, species from the orders Coleoptera (beetles), Lepidoptera (moths) and Psocoptera (psocids) are major stored commodities pests. In contrast, species from Hemiptera (bugs) and Hymenoptera (wasps) are mainly predators or parasites of these pests (Rees, 2004). Stored product pests are opportunistic and diverse. Many beetles were originally found under the bark of trees, moths came from dead and ripening fruits, and psocids from leaf litter (Rees, 2004). However, some pests are specially adapted to storage environments, such as the granary weevil, *Sitophilus granarius*, which has never been found outside of storage (Plarre, 2013). The recording of pests of stored products dates to ancient Egypt, where, at that time, *Tribolium confusum*, *Oryzaephilus surinamensis*, and *S. granarius* were mentioned (Rees, 2004). Pests in stored products can cause serious physical and economic damage to grains, pulses, seeds, and other plant and animal materials that are stored (Hill, 2002). Significant financial losses can result from pest damage, which can range from physical destruction and quality degradation to decreased marketability. Insects are one of the main causes of the estimated 10-50% of stored grain losses worldwide that result from pests (Demis & Yenewa, 2022).

The pests of stored grains and their products can be broadly categorized into primary and secondary pests. Primary pests attack whole grains, penetrate undamaged seed coats, and feed on embryos, endosperms, or cotyledons. Secondary pests feed on already processed grains or grains that are already damaged either by the primary pest infestation or during handling and transportation of grains (Daglish & Nayak, 2018). Primary pests generally have narrow food preferences, while secondary pests have a wider range of hosts, which include processed food items. The genus *Sitophilus* (Coleoptera: Curculionidae), includes species of economic importance as both primary and secondary stored product pests (Arthur & Throne, 2003; Danho et al., 2002; Plarre, 2013). *Sitophilus* species are considered primary pests of stored grains, as they can infest whole kernels (Copatti et al., 2013; Trematerra et al., 2004). However, they also contribute to secondary pest infestations by creating frass and excavated kernels, which support the development of externally feeding beetles (Vendl et al., 2022). First described by Linnaeus in 1758 as *Curculio*, the genus has undergone several reclassifications until it was finalized by Schoenherr as *Sitophilus* in 1838 (Riley & Melville, 1959).

Sitophilus zeamais is a polyphagous pest that causes significant damage to a variety of processed foods and stored grains. It mainly attacks maize, causing 18-40% yield losses (Sebayang et al., 2023). In addition, it infests processed foods like pasta and biscuits as well as other cereals like sorghum, rice, and wheat (Sebayang et al., 2023; Trematerra, 2009). Food source preferences have been recorded for *S. zeamais* showing that superfino and parboiled rice were more attractive to the weevils than other rice types. Similarly, among pasta types, corn pasta was the most preferred (Trematerra, 2009).

Economic Importance of *Sitophilus zeamais*

The increasing demand for food for a growing global population has led to the increase of global cereal production over the past 40 years (Tilman et al., 2002). Primary pests of cereals include species such as various *Sitophilus* species (rice weevil, maize weevil, granary weevil), lesser grain borer (*Rhyzopertha dominica*), larger grain borer (*Prostephanus truncatus*), and the Angoumois grain moth (*Sitotroga cerealella*). Similarly, primary pests of legumes include bruchids such as the bean weevil (*Acanthoscelides obtectus*) and cowpea weevils (*Callosobruchus spp.*) (Daglish & Nayak, 2018). Secondary pests include *Tribolium* species (rust red flour beetle and confused flour beetle), *Cryptolestes* species (rusty grain beetle and flat grain beetle), *Trogoderma* species (Khapra beetle and warehouse beetle), saw-toothed grain beetle (*Oryzaephilus surinamensis*), warehouse moth (*Cadra cautella*), and others (Daglish & Nayak, 2018). Of the stored grain pests, only three species of *Sitophilus* (*S. granarius*, *S. oryzae*, and *S. zeamais*) are considered globally significant. These species are among the most damaging pests of stored cereals, causing substantial losses in both quality and quantity (Levinson & Levinson, 1994; Longstaff, 1981; Plarre, 2013; Throne & Cline, 1989).

Damage Caused by *Sitophilus zeamais*

The feeding behavior of adult *S. zeamais* includes both shallow and deep feeding on stored grains, with deep feeding closely linked to oviposition (Tipping et al., 1986). The insect's specialized mouthparts, including mandibles, maxillae, and a labium with various sensilla, play a vital role in its feeding mechanism (Chen et al., 2016). Its ability to damage grains is linked to its alimentary canal morphology, including the crop for storage and the proventriculus for grinding food (Sousa et al., 2013). Both adults and larvae feed on grains, causing severe post-harvest losses. Females chew deep holes into grains, lay eggs, and seal them, allowing larvae to develop inside the grains (Longstaff, 1981). The resulting damage reduces grain quality, weight, and commercial value, while also producing grain dust that attracts secondary pests like *Oryzaephilus surinamensis*, *Tribolium castaneum*, and mites (Hill, 2002; Longstaff, 1981).

Sitophilus. zeamais infestation increases the temperature and humidity of stored grains, thereby creating conditions favorable for secondary pests and pathogens to attack (Hardman, 1977; Longstaff, 1981). High temperatures significantly accelerate *S. zeamais* reproduction and damage (Copatti et al., 2013; Khan, 2023). Activity of S. *zeamais* degrades grain quality, as it affects the protein composition, reducing wet and dry gluten content, gluten index, and changing protein fractions and secondary structures (Wu et al., 2022). Additionally, the activity of *S. zeamais* reduces the protein, starch, and moisture content of maize grains, with the extent of damage directly correlating to the insect population size (Osipitan et al., 2012).

Sitophilus zeamais infestation significantly affects the quality of pasta and wheat products, leading to both quantitative losses and alterations in nutritional composition. Susceptibility varies among different pasta types (Babarinde et al., 2013). Infestation of maize leads to reduced germination rates, tryptophan content, and commercial quality (Caneppele et al., 2003; Usman et al., 2016). Beyond stored grains, *S. zeamais* has been reported to damage other crops, including vineyards in Brazil, Botton et al., (2005) observed up to 80% of Cabernet Sauvignon grapes damaged by *S. zeamais* in February 2003. The pest has also affected peaches, apples, and grapes in various regions of Brazil causing both direct damage through perforation and indirect damage by promoting bacterial growth (Botton et al., 2005). *Sitophilus zeamais* damages corn kernels by grinding through the inside of the seed, leaving behind an attack trail marked by pitted and powdery seeds among the infested material. These insects can damage corn cobs and seeds from the time they are planted in the field until the seeds are stored in warehouses. Pest attacks on seeds leave drill marks characterized by holes, with many adult weevils found on the surface of the seeds (Hasnah & Suryanti, 2014).

Economic Losses

Sitophilus. zeamais results in severe economic losses owing to its infestation, since damage to stored materials, often ready for consumption, can mean major financial losses related to quality degradation, weight loss, nutritional value, marketability, and contamination from feces or aflatoxins (Herlina & Istiaji, 2013; Manueke et al., 2015; Napoleão et al., 2013). Weight losses due to infestation in maize have been shown to range from 12.65 to 21.54%, while in rice, it is comparatively milder (Arrahman et al., 2022). The damage level has reached as high as 85% in South Sulawesi, with up to 17% shrinkage in the stored materials (Hasnah & Suryanti, 2014). Infestations of *S. zeamais* can cause 30-40% damage when the product being stored has a high moisture content (Bergvinson & García-Lara, 2004; García-Lara & Serna-Saldivar, 2019).

Taxonomy

The genus *Sitophilus* has had several taxonomic changes: Originally described as *Curculio* by Linnaeus, 1758. Re-named to *Calandra* by Clairville & Schellenberg, 1798. Then described as *Sitophilus* by Schoenherr, 1838 (O'Brien & Wibmer, 1982). This naming was subsequently ratified by the International Commission on Zoological Nomenclature in 1959 (Riley & Melville, 1959).

The classification of *S. zeamais* is as follows:

- Kingdom: Animalia
- Phylum: Arthropoda
- Subphylum: Atelocerata
- Class: Hexapoda (including Insecta)
- Subclass: Pterygota
- Order: Coleoptera
- Superfamily: Curculionoidea
- Family: Curculionidae
- Subfamily: Dryophthorinae
- Genus: *Sitophilus*
- Species: *zeamais*

Species Distinctions

According to (Plarre, (2013), there are 14 species of these weevil pests, including one fossil taxon.

These include:

- *Sitophilus erosa*
- *Sitophilus glandium*
- *Sitophilus conicollis*
- *Sitophilus cribrosus*
- *Sitophilus oryzae* (rice weevil)
- *Sitophilus quadrinotatus*
- *Sitophilus granarius* (wheat or granary weevil)

- *Sitophilus linearis* (tamarind weevil)
- *Sitophilus zeamais* (maize weevil)
- *Sitophilus vateriae*
- *Sitophilus rugicollis*
- *Sitophilus punctatissimus* (fossil taxon)
- *Sitophilus sculpturatus*
- *Sitophilus rugosus*

Key Differences Among Grain Weevils

S. granarius is easily distinguished from *S. zeamais* and *S. oryzae* by the lack of four reddish-yellow spots on its elytra and its flightless nature as well (Srivastava & Subramanian, 2016). The granary weevil is larger and darker, lacks coloration but has more prominent longitudinal rows on elytra. Of the three species, *S. granarius*, *S. oryzae*, and *S. zeamais*, several differences can be outlined. The granary weevil is fully synanthropic, adapted to artificial grain storage, and is generally found in temperate climates. It is often reported from archaeological contexts but is absent from the natural reservoirs (Plarre, 2013; Solomon, 1965). Grain weevils are not strictly host-specific, although strong preferences are seen for instance, the larger grain size is preferred by *S. zeamais*, while wheat and rye are better substrates for *S. oryzae* and *S. granarius* (Corrêa et al., 2013; Haines, 1981; Throne & Cline, 1991).

Sitophilus zeamais and *S. oryzae* have conventionally been regarded as two races of a single species (Kiritani, 1956; Richards, 1945). Historically, *S. zeamais* Motschulsky and *S. oryzae* Linnaeus were jointly known as *Calandra oryzae*. The two species have a very similar morphology and ecology and are often misidentified. (Rees, 2004). Some researchers consider *S. oryzae* and *S. zeamais* as variants of the same species because of similarities in their internal and external anatomy. However, these two species differ in habitat and size: *S. oryzae* is smaller and more associated with rice, while *S. zeamais* is larger and primarily infests maize.

Sexual Diagnostic Features

Correct identification of *S. zeamais* and *S. oryzae* is based on the following morphological characteristics: Male *S. zeamais*: Presence of three longitudinal ridges on the outer surface of the aedeagus. Male *S. oryzae*: Outer surface convex (Floyd & Newsom, 1959; Halstead,1963; Kuschel, 1961).

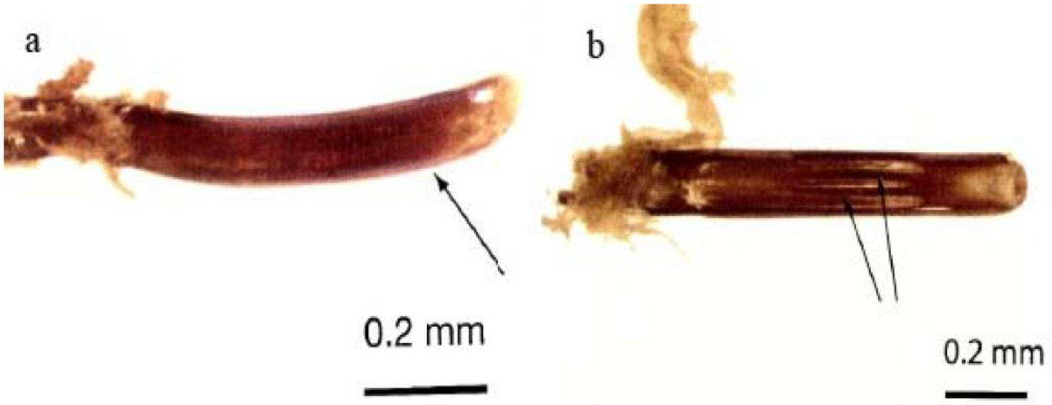


Figure 1.1: Aedeagus of (a) *Sitophilus oryzae* and (b) *Sitophilus zeamais*, adapted from Rees (2004). Note the ridges present on *S. zeamais*.

Ecological Preferences

Sitophilus oryzae is a poor flier, is rarely encountered in field infestations of cereals, and prefers subtropical climates (Corrêa et al., 2013; Throne & Cline, 1991), while the stronger flier *S. zeamais* often infests maize before harvest in the field and prefers warmer climates (Corrêa et al., 2013; Longstaff, 1981). *Sitophilus zeamais* is widely distributed across multiple continents. In China, *S. zeamais* is prevalent nationwide, whereas *S. oryzae* is primarily found in the southern and central regions (Wu & Yan, 2018). Similarly, in Brazil, *S. zeamais* dominates across the country, likely due to its preference for maize and adaptation to tropical climates (Corrêa et al., 2013). Its presence has also been documented throughout mainland Greece and the island of Crete (Athanassiou & Buchelos, 2001). In Benin, West Africa, *S. zeamais* is commonly found in maize storage facilities, with its incidence fluctuating by season (Meikle et al., 1998). Danho et al, (2002) stated, thus, *S. zeamais* prefers thermal and slightly humid conditions.

Life Cycle

The life cycle and reproductive characteristics of *S. zeamais* vary depending on the study and host grain. The total development period from egg to adult ranges from 33.5 to 34.7 days, depending on the cereal host (Ojo & Omoloye, 2016). However, other studies report an egg-to-adult development period ranging from 33.5 to 49.13 days (Manueke et al., 2015; Ojo & Omoloye, 2016b). The larval stage consists of four instars and lasts between 21.6 and 23.1 days, depending on the host grain (Ojo & Omoloye, 2016). After 25 days, the pupa becomes darker and yellow in which legs and antenna are separated from body (Figure 1.4). Fecundity varies widely, with a single female laying between 38.67 and 400 eggs during her lifetime. Peak egg-laying occurs within the first 7-8 weeks (Ojo & Omoloye, 2016; Van Dzuong & Long, 2019).

The development and reproduction of *S. zeamais* are shaped by environmental factors like temperature, humidity, and host grain type (Ojo & Omoloye, 2016; Visarathanonth et al., 2010). Its egg-to-adult developmental period varies between 33.5 and 34.7 days, depending on the host grain and temperature (Ojo & Omoloye, 2016). Van Dzuong & Long (2019) reported that on long-grain rice, egg-laying begins 10 days after eclosion and can last up to 145 days, peaking between days 55 and 95.

Eggs

Adult *S. zeamais* burrows into cereal grains using its strong rostrum, creating a cavity into which it lays a single egg. Females deposit each egg individually in the hole she creates in grains and seals it with a waxy plug (Danho et al., 2002). The eggs are oval, whitish in color, and rounded at the bottom (Ojo & Omoloye, 2016b). The average dimensions of the egg are 0.2 ± 0.01 mm wide and 0.5 ± 0.01 mm long (Ojo & Omoloye, 2016). After hatching, the larva emerges as a creamy white, apodous grub with a light brown sclerotized head (Ojo & Omoloye, 2016). Interestingly, females prefer to lay eggs on grains already infested with conspecific eggs, resulting in a contagious distribution pattern (Danho et al., 2002; Mathias et al., 2015).

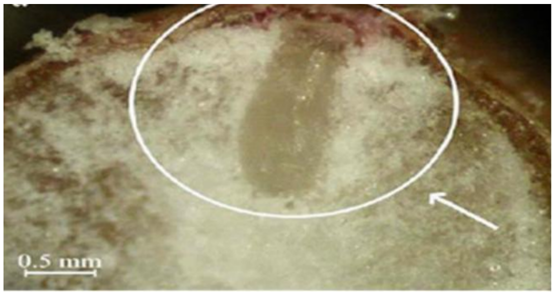


Figure 1.2: Egg of *S.zeamais* Motsch (egg enlarged) (from Flay 2010)

Larvae

The number of larval instars in Coleoptera varies among species, with four instars commonly observed. *S. zeamais* undergoes four instars, with head capsule widths ranging from 0.225–0.775 mm (Nguyen et al., 2023). Larval body size increases with each instar, and head capsule width is consistent within each stage (Le et al., 2018). They are white, legless, and have dark brown heads. The larval stage lasts 22–23 days (Ojo & Omoloye, 2016; Subramanyam, 1995), during which larvae consume seed contents, increasing the size of burrows. They excrete fluids into the burrow walls, creating a smooth, strong texture for cocoon formation (Pracaya, 2007). Larval development is faster when feeding at the endosperm-germ interface, with resistant maize varieties showing shorter fourth instar periods (Urrelo & Wright, 1989).

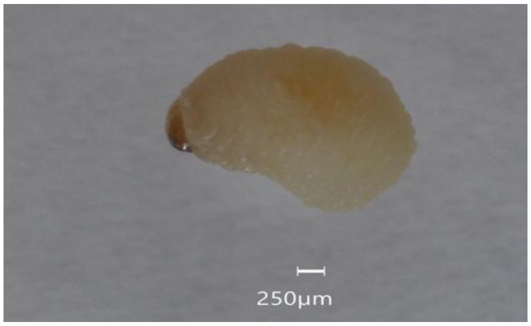


Figure 1.3: *Sitphilus zeamais* Motsch (larvae). This picture was taken in the present study.

Pupa

Pupae are white, 3–4 mm long, and similar in size and shape to adults. The pupal stage takes place inside the seed's larval feeding tunnel and lasts for approximately six days, with a range of three to nine days (Subramanyam, 1995). The adult imago spends a few days inside the seed after pupation before coming out. Pupation takes place within the seed burrow made by the larva. When the adult (imago) emerges, it remains inside the seed for several days before leaving. Food host also influenced the body measurement of maize weevil pupa, with longest body length and width being recorded on maize (3.8 ± 0.04 mm and 1.1 ± 0.02 mm) and the shortest being observed on millet (3.1 ± 0.06 mm and 1.0 ± 0.06 mm) (Ojo & Omoloye, 2016b).

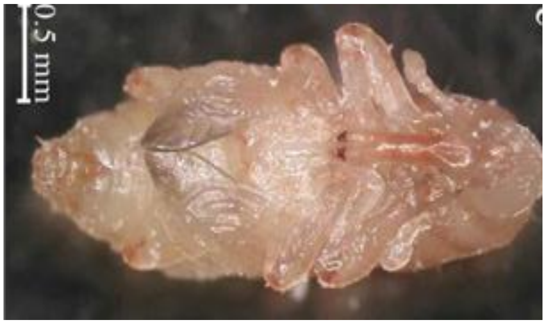


Figure 1.4: Pupa of *Sitophilus zeamais* Motsch (enlarged) (from Flay, C. D. 2010)

Adult

Adult *Sitophilus zeamais* can live for several months and range in length from 2.5 to 4.5 mm (Le et al., 2018; Ojo & Omoloye, 2016) with size influenced by larval diet-corn-fed adults measure 3.9-4.9 mm, while rice-fed adults are smaller (Maceljski & Korunić, 1973). Adults have mandibulate mouthparts at the tip of their rostrum, with sclerotized mandibles and specialized sensory structures on maxillary and labial palps (Chen et al., 2016). High seed moisture content (above 15%) facilitates rapid population growth (Teetes et al., 1983). Adults younger than 36 days cause the most damage to stored grains (Nwosu, 2018)**.**

Figure 1.5: Adult *S. zeamais* Motsch. This picture was taken in the present study.

Morphology

Sitophilus zeamais, is reddish-brown to black, with a long, snout-like rostrum and four orange or red spots at the corners of the elytra that fade inward toward the middle (Rees, 2004) (Figure 1.6). The prothorax is strongly pitted, and the elytra have rows of pits arranged within longitudinal grooves (Rees, 2004). Each wing (elytron) also has two pale patches. The pronotum carries rounded depressions that are fairly close together. The antennae are elbowed and have eight segments, and the head is unmistakably snout shaped. They are approximately 3–4 mm in length, with the reddish or yellowish markings appearing on the ventral part of the wings (Borror & DeLong, 1954; Halstead, 1963; Kartasapoetra, 1991).

Sexual Dimorphism

Males and females are similar in general appearance but differ in rostral morphology. Males possess shorter, wider rostra with more irregular and larger indentations, while females have longer thinner rostra with shallower indentations running consistently along the rostrum (Halstead, 1963) (Figure 1.6). Dorsally, male rostra appear larger, dull, and rough while female rostra are smooth and mottled. From a side view, the female rostrum is narrower, longer, and slightly curved downward, while the male rostrum is shorter and wider (Flay, 2010).

Figure 1.6: Male and female *S. zeamais* adapted from (Flay, 2010).

Mouthpart Morphology

The elongated rostrum is a distinctive feature of weevils (Curculionoidea), particularly in females, serving as a tool for egg deposition in plant tissues (Wilhelm et al., 2011). This sexual dimorphism extends beyond length to include material properties and morphological features that enhance buckling resistance and flexibility (Matsumura et al., 2021). The mouthparts of Coleoptera exhibit remarkable adaptations while retaining a largely conservative structure (Beutel & Yavorskaya, 2019). Ancestral feeding apparatuses in Myxophaga and basal Polyphaga are characterized by large mandibular molae and epi- and hypopharyngeal bulges with microtrichia, suitable for processing soft plant tissues (Beutel & Yavorskaya, 2019). The mouthparts of many insects have evolved into highly specialized structures and sensilla for feeding and sensory functions. In *S. zeamais*, mandibulate mouthparts are situated at the tip of the rostrum, consisting of sclerotized mandibles, maxillae with four-segmented palps, and a three-segmented labium (Chen et al., 2016). Sensilla basiconica on maxillary and labial palps function as chemo- or gustatory receptors in many insects (Chen et al., 2016; Gaino & Rebora, 2003; Yan et al., 1987). The number and the position of these sensilla vary in different species, which correspond to different modes of life and feeding. In addition to the chemoreceptors, there are mechanoreceptors on the mouthparts: sensilla campaniformia and sensilla chaetica habits (Gaino & Rebora, 2003; Giglio et al., 2003). The maxillary palps are essential for the processes of food exploration and selection, whereas the labial palps facilitate the mechanical examination of substrates (Gaino & Rebora, 2003).

Flight Capabilities

The maize weevil has poor flying skills with a flight range of about a quarter mile (Giles, 1969). Flight activity is independent of gender and dependent on temperature (Cui et al., 2016; Williams & Floyd, 1970). According to a study by Williams & Floyd (1970), *Sitophilus zeamais* exhibits peak dispersal around July 7, with maximum flight activity occurring between 4–6 PM, coinciding with the warmer temperatures in Baton Rouge, Louisiana. High temperatures (34°C) impede flight in females, though flying speed is optimal for both sexes at 28°C (Cui et al., 2016). *Sitophilus zeamais* exhibit seasonal flight activity, typically from late March to early November in South Carolina, with flight occurring when temperatures exceed 20-23°C (Throne & Cline, 1989; Williams & Floyd, 1970).

General Mating Behavior

Sitophilus zeamais exhibits a structured pattern of precopulatory, copulatory, and postcopulatory phases in its mating behavior (Walgenbach & Burkholder, 1987). Males use rostral probing or antennation to make contact, frequently mounting the female backward before shifting positions. While the male clings and occasionally rubs his hind legs against her abdominal sternites, the female moves actively. With an average time of 20.2 minutes from first contact to successful mounting, the male persistently remounts if dislodged (Walgenbach & Burkholder, 1987). Abdominal flexing occurs rhythmically every 28.3 seconds during copulation, which lasts for about 4.8 hours and has an unknown purpose. This behavior has been seen in other beetles (Hatfield et al., 1982; Lew & Ball, 1979). Although there isn't any solid proof, it might be connected to sperm activation (Khan & Musgrave, 1969). Males extrude their aedeagus within 3.8 minutes of dismounting, and they frequently repeat this behavior (Walgenbach & Burkholder, 1987). Virgin females mate more easily than previously mated ones, and mating does not take place before three days of age. Males with more experience are more successful, and females who have already mated have longer precopulatory periods (Walgenbach & Burkholder, 1987). Although mating takes place all day, copulation is considerably sped up and shortened by starvation. Compared to *Sitophilus granarius* (30-72 minutes) and other curculionids, *S. zeamais* has a longer copulation period (4.8 hours) (Wojcik, 1969). According to (Walgenbach & Burkholder, 1987a) *S. zeamais* generally displays a stereotypical mating sequence with protracted copulation and persistent male mounting behavior.

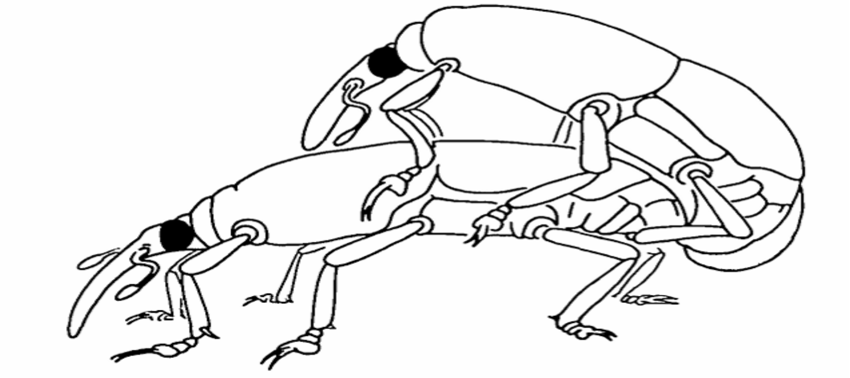


Figure 1.7: Abdominal flexing by male maize weevils during copulation Adapted from (Walgenbach & Burkholder, 1987b).

Divergence and Fossil Evidence - Evolutionary

The first Japanese description of *S. zeamais* appears in historical records from ca. 1000 BP (Yasue, 1959, 1976). Genetic and fossil evidence indicates that *S. zeamais* and *S. oryzae* diverged approximately 8.7 million years ago, long before agriculture (Corrêa et al., 2016). Obata et al. (2011) results suggest that eastern Asian grain pests, including the *S. zeamais* and probably the *S. oryzae*, evolved differently from the granary weevil in Europe (Obata et al., 2011). Obata et al. (2011) discovered the world's oldest *S. zeamais* impressions, dating back ~10,500 BP, in Jomon pottery from the Sanbonmatsu site, Tanegashima Island, Japan, predating European records (~7000 BP) (Plarre, 2013). DNA analysis suggests *S. zeamais*, *S. oryzae*, and *S. granarius* share a common Asian ancestor (Conord et al., 2008; Lefevre et al., 2004), challenging the belief that grain pests originated solely in Southwest Asia. Instead, *S. zeamais* likely infested stored acorns, chestnuts, or bamboo seeds in Jomon-era settlements (Delobel & Grenier, 1993; Obata et al., 2011) before transitioning to grains. Unlike flightless *S. granarius*, *S. zeamais* can disperse naturally (Yoshida et al., 1956). X-ray computed tomography and scanning electron microscopy have been used to find impressions and cavities in pottery, revealing evidence of plant seeds and maize weevils *S. zeamais* (Obata et al., 2020; Obata et al., 2011). Recent studies have revealed new insights into the genetic structure of *S. zeamais* populations. While earlier studies showed a globally low level of genetic differentiation among worldwide *S. zeamais* populations (Corrêa et al., 2016), more recent genome-wide analysis has shown fine-scale genetic structure in Mexican populations, possibly due to human-mediated maize movement and geographical barriers (Baltzegar et al., 2022). In West and Central Africa, high genetic diversity and evidence of population growth since the Pleistocene have been observed (Mama Racky et al., 2017). Comparative analysis of wet and dry regions in these areas indicated that wet regions possess stable populations with low genetic diversity, whereas dry regions have expanding populations with greater genetic diversity (Sarra et al., 2022). The Senegalese and Central African populations differed genetically, yet there was vast genetic variation between countries but minimal variation within subpopulations (Bambou et al., 2014). The origin of cereals in Asia, and subsequently other continents, likely enabled grain weevils' initial spread throughout Asia, then to Europe, Africa, and the Americas (Obata et al., 2011; Plarre, 2013). These findings challenge the notion that stored-product pests spread solely via agriculture and suggest they first adapted to wild plant storage before cereal domestication (Plarre, 2013).

There have been many studies on the biology and life of *S. zeamais*, but critical questions remain about how factors like temperature and corn moisture affect their behavior and physiological processes. This study aims to fill these gaps in our knowledge by examining the reaction of *S. zeamais* to thermal and moisture and hopefully providing us with a better insight into how it may be able to alter its behavior and physiology based on changing environmental conditions.

CHAPTER TWO

2.1. Thermal Tolerance of *Sitophilus zeamais*

Introduction

Temperature is one of the most important abiotic factors regulating ecological community organization and influencing survival of organisms (Angilletta Jr, 2009; Chown & Nicolson, 2004; Sibly et al., 2012). Most natural environments, ranging from tundra to deserts, experience >60°C temperature fluctuation over a year, and they exhibit high spatial and temporal thermal heterogeneity (Ghalambor et al., 2006; New et al., 1999; Overgaard et al., 2014). Insects regulate their physiological processes using environmental temperatures; hence they are highly sensitive to temperature fluctuations. Their thermotolerance is closely linked to biogeography, with the lowest tolerated temperatures corresponding to the minimum temperatures of their natural habitats (Hazell et al., 2010; Kellermann, Loeschcke, et al., 2012; Kimura, 2004). Further, researchers have proposed that the geographic distribution of insects closely ties with their physiological heat stress response (Bozinovic et al., 2011). The climatic variability hypothesis of Addo-Bediako et al. (2000), hypothesizes that variation in range size is associated with thermal tolerance. In their study of 250 species, Addo-Bediako et al. (2000) observed that broader thermal tolerance exists among higher latitude species than in lower latitudes.

The subject of arthropod thermal tolerance has been of increased interest in recent years, and an enormous research effort has been directed towards many insect species, including bees, beetles, flies, termites, and true bugs (Hoffmann et al., 2013; Janowiecki et al., 2020; Just & Frank, 2020; Kellermann, Overgaard, et al., 2012; Klockmann et al., 2017; Klok et al., 2004; Oyen et al., 2016;

Polato et al., 2018; Sheldon & Tewksbury, 2014; Slatyer et al., 2016). Arthropod thermal tolerance can be defined by several internal and external reasons (Sinclair et al., 2012). Internal factors contributing to variation in thermal tolerance include developmental stage (Kingsolver et al., 2011), age (Bowler & Terblanche, 2008), gender (Blanckenhorn et al., 2014), physical traits such as size and color (Baudier et al., 2015; Rajpurohit et al., 2008), and overall health (Terblanche et al., 2011).

External factors, including diet (Krebs & Loeschcke, 1994), light cycles, (Rodgers et al., 2006) oxygen availability (Bozinovic & Pörtner, 2015; Verberk et al., 2016, and parental temperature fluctuations (Abram et al., 2017) also play crucial roles in the development of thermal tolerance. In addition, different arthropods exhibit different thermal threshold values: Acari and Diptera generally have the lowest thresholds, while Coleoptera and Blattodea tend to have the highest (Stejskal et al., 2019). The thermal tolerance threshold also differs throughout the lifespan of insects. Species with complete life cycles are exposed to different temperature extremes in their microhabitats, resulting in physiological trade-offs that reflect common mechanisms across life stages (Angilletta Jr, 2009; Huey & Kingsolver, 1993). Survival in warming environments depends on thermal tolerance, which involves complex physiological and biochemical mechanisms including stress responses, thermoregulation, and metabolic regulation (Dillon et al., 2010; Verberk et al., 2016).

The thermal stress effect is directly connected with its persistence, frequency, and intensity (Cheng et al., 2017; Chiu MingChih et al., 2015). Duration beyond CT_{Max} causes permanent damage, illustrated in amphibians with a +4°C temperature rise lowering thermal safety margins (TSMs) from 11.69°C to 9.41°C in terrestrial environments (Jørgensen et al., 2021). Prolonged exposure enhances damage, with recovery only possible below specific thresholds, depending on the balance between injury and repair processes (Faber et al., 2024; Jørgensen et al., 2021). Furthermore, repeated thermal stress depletes energy reserve and limits recovery, especially in species with limited thermal ranges, such as Mediterranean beetles and Drosophila from stable climates, which show restricted plasticity in their optimal temperature range (MacLean et al., 2019).

Most insect physiologies are significantly under threat by temperatures at the extremes, which tends to cause harm to biomolecules such as proteins and DNA, leading to denaturation and cellular dysfunction (Abram et al., 2017). The critical thermal maximum (CT_{Max}), the temperature beyond which survival becomes impossible, fluctuates together with the thermal optimum and serves thus as a good estimator of climatic susceptibility for a particular species (Angilletta Jr, 2009; Cowles & Bogert, 1944; Deutsch et al., 2008). As body temperature approaches CT_{Max}, the metabolic rates are increased and enzymatic failure probabilities, protein denaturation, and cell membrane disruption are enhanced (Hochachka & Somero, 2002; Schulte, 2015). Behavioral adaptations are crucial in mitigating these stresses.

Small ectothermic creatures, such as insects, can obtain body temperatures that vary substantially from ambient air temperature via behavioral thermoregulation (Fey et al., 2019; Hunt et al., 2016; Kleckova & Klecka, 2016). Some recent research works have shown that gradual exposure of insects to high temperature leads to a decreased level of tolerance (Sunday et al., 2014). Heat stress can also trigger dispersal, which compels the insects to shift to sites with suitable temperatures to find appropriate microhabitats. For example, aphids exhibit heat-avoidance behaviors to cope with high temperatures, which are becoming more frequent due to climate warming. These behaviors include dropping off host plants and seeking cooler microhabitats (Ma et al., 2018). Most insects cope with high temperatures by choosing different microhabitats since they rarely change their geographical range (Hughes et al., 2003). Thus, heat-stress in the microhabitat directly influences insects to displace into areas with cooler temperatures. For example, *Rhopalosiphum padi* avoids deleterious heat stress by seeking cooler microhabitats, such as below the soil (Wiktelius, 1987).

High temperatures are dealt with using a variety of physiological mechanisms developed by insects. These include sensory systems that possess neurons and neurotransmitters and that initiate metabolic regulation and anaerobic metabolism (Gillooly et al., 2001; Verberk et al., 2016). Although insects are ectothermic, they can regulate their body temperature to a certain degree through physiological and behavioral adaptations and hence be capable of optimizing performance under high temperatures (Chapman, 1998). Primary protection mechanisms involve the production of heat shock proteins (HSPs) that shield cells from thermal damage (Feder & Hofmann, 1999). Hormones also regulate physiological responses and behavioral adaptations to heat stress, further aiding survival (Emerson et al., 2009). Combined, these mechanisms enable insects to successfully react to environmental changes, rendering them resilient yet vulnerable under rapidly changing climate conditions.

Climate change is compelling insects to shift their ranges, decrease their abundance, and experience increased rates of extinction at an increased rate than other taxonomic groups (Parmesan, 2006; Sánchez-Guillén et al., 2016; Thomas et al., 2004). Habitat loss compounds these problems by lowering the availability of thermal refuges and increasing dependence on physiological and behavioral adaptations (Denlinger & Yocum, 2019). Phenotypic plasticity in such traits is likely of importance in the maintenance of fitness under thermal variation and climate change (Gunderson & Stillman, 2015; Sgrò et al., 2016). Survival of *S. zeamais* is dependent on mechanisms of physiological thermotolerance, thermoregulation, and refuge of microclimatic character, with population thermal acclimation of considerable importance in heat stress alleviation (Gunderson et al., 2017; Gunderson & Stillman, 2015; Sunday et al., 2014). Knowledge of the thermal tolerance of *S. zeamais* populations is critical in order to predict its survival, ecological distribution, and function in stored grain ecosystems under conditions of a changing climate.

Temperature is of paramount significance to the physiological process, survival, and reproduction of *S. zeamais*. Optimum development occurs within the temperature range of 25-30°C; both higher and lower temperatures from this optimum impede growth or, in extreme cases, result in population collapse (Fields, 1992; Strang, 1992). Environmental temperature also influences flight ability, which is vital for dispersal (Cui et al., 2016). Thus, the flight capabilities of *S. zeamais* are influenced by temperature, with both male and female indicating peak flight velocity at 28°C. Temperature impacts not only *S. zeamais* flying ability but also their willingness to take flight (Cui et al., 2016). As temperatures increased from 22°C to 31°C, both sexes showed a greater inclination and ability to fly; however, this tendency decreased at higher temperatures. While temperature did not significantly affect male flight performance, females exhibited reduced flight distance and duration at 34°C compared to lower temperatures, suggesting that females are more sensitive to temperature changes in terms of their flying capacity (Cui et al., 2016). These temperature limits correspond closely to the highest microclimate temperatures usually reached in their natural environments (Ceruti et al., 2008; Throne, 1994a; Van der Merwe et al., 1997). Temperature not only impacts *S. zeamais* physiology but also its interactions with other species in stored grain ecosystems. Above 25°C, *Prostephanus truncatus* reproduces more and damages grain more than *S. zeamais*, which has a competitive advantage at warmer temperatures (Baliota et al., 2022; Quellhorst et al., 2019).

Most of the studies on the thermal tolerance of stored-product insects have been directed towards establishing lethal temperatures for various species and life stages (Beckett & Morton, 2003;

Evans, 1987; Johnson et al., 2003; Mahroof et al., 2003; Mbata & Phillips, 2001). For instance, a solar heating experiment on *Sitophilus oryzae* recorded 100% mortality at 45°C after three hours (Abdelsamea et al., 2023). Similarly, *S. zeamais* adults exposed to 36°C for 1-5 hours showed improved survival when later exposed to temperatures that were lethal (43–55°C), with longer durations increasing tolerance (Lü & Zhang, 2016). Related results in *Tribolium castaneum* show that exposure to 36°C and 42°C decreased mortality, with 42°C having a more pronounced effect (Lü & Liu, 2017).

However, gender-specific differences in *S. zeamais'* heat tolerance remain largely unexplored. This is a fundamental knowledge gap for the formulation of effective thermal treatment strategies for understanding species' responses to thermal tolerance and climate change adaptation. Variations in CT_{Max} between male and female adults could significantly impact population dynamics yet have been minimally investigated. Here, the objective was to fill these gaps by examining the critical thermal maximum (CT_{Max}) of male and female *S. zeamais* of a Georgia, USA population. Specifically, there were two primary questions: (1) What are the highest thermal tolerances of *S. zeamais* populations commonly encountered in Georgia? and (2) Are there differences in thermal tolerances between males and females? Grasping these distinctions is vital for enhancing pest control methods and forecasting the species' adaptability under shifting climate conditions.

Materials and Methods

Sitophilus zeamais were collected from infested field corn weevils on 8/21/2024 from a wagon in Tift County, GA in Spring 2024 containing 150 bushels (3, 810 kg) of shelled corn. The weevils were subsequently reared under controlled conditions at 24-25°C with 60-70% relative humidity, and a 12:12 (L:D) photophase for several generations. This environment ensured consistent conditions for the weevil populations used in the experiments.

For the thermal tolerance assays, the *S. zeamais* had continuous access to maize grain ensuring they were well fed prior to the experiment. To account for potential CT_{Max}, the first experiment utilized a large sample size of 180 unsexed weevils. The second experiment, aimed at determining sex-specific differences in thermal tolerance, involved 30 males and 30 females. These experiments sought to describe the critical thermal maximum of the Tift County Georgia population and to determine whether thermal tolerance varies between the sexes.

Maize weevil CT_{Max} was measured using a custom-built temperature control unit. Ten weevils (5 males, 5 females) were assayed simultaneously per trial, with their behavior closely monitored until the onset of muscle spasms (Terblanche et al. 2006) and subsequent loss of righting response (LRR) occurred (Shah et al., 2017). Each weevil was placed in a 1.5 mL Eppendorf tube, which was closed tightly with its lid to prevent *S. zeamais* escape and water penetration. The tubes were submerged in a 3L water bath affixed to a magnetic bar. The initial average water temperature ranged from 22.2 to 23°C, with an initial hold of 2 minutes. The CT_{Max} Temperature Controller (CTC) was set to increase at 0.3°C per minute until the temperature was at CT_{Max} of 60°C to ensure the experiment continued until all weevils had reached their CT_{Max}. The CTC included several key components: a controller unit (SOLO Temperature SL 9696 Controller, Taiwan) set to the temperate ramp protocol, a RTD (resistance temperature detector)-probe that measured the water bath temperature in a feedback to the controller unit, Finnex 500W titanium heating rod (Edinburgh, Indiana, USA) that was controlled by the control unit, and a 120V (Intertek, Mexico) submersible water pump to mix the water and maintain an even temperature. The RTD probe was positioned carefully to avoid interference from the titanium heating rod. To account for any variation between water temperature and the temperature that the insects were experiencing, a

Elitech Hobo thermal probe attached to a HOBO 4-Channel Thermocouple Data Logger (onset, USA), was placed within an empty Eppendorf tube that was placed in the water next to trial tubes. The ramp time was calculated as follows:

Ramp Time$= \frac{Target\ Temp - Initial\ Temp}{Ramp\ rate} = \frac{60°C - 22°C}{0.3°C/min} = 126.7\ minutes$

Thus, the system was programmed to run for approximately 2 hours and 6 minutes, with a final temperature set at 25°C. This was to prevent the controller from trying to heat the bath after the experiment is over upon cooling.

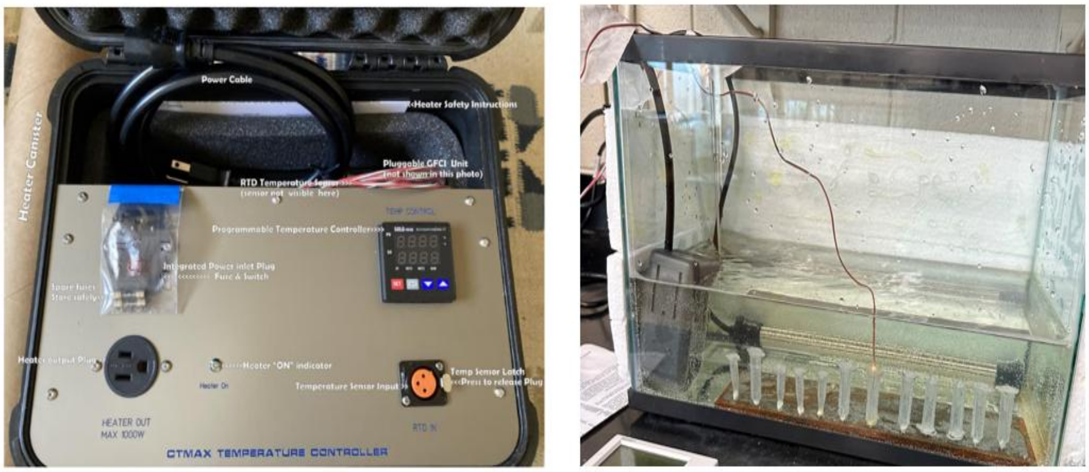


Figure 2.1. Experimental set up for thermal tolerance assays

A total of 30 males and 30 females were tested to assess potential sex-based differences in thermal tolerance. Once CT_{Max} was reached, weevils were immediately removed from the water bath, and the corresponding temperature was recorded. Following removal, weevils were allowed to recover and only those that recovered to full activity were employed for the ultimate analysis. To avoid variability and minimize observer bias, all experiments were performed by a single observer under controlled laboratory conditions at temperatures ranging from 20 to 25°C.

Statistical Analysis

All data were analyzed using the R statistical software (Core Team, 2021). Descriptive statistics, including mean, standard deviation (SD), median, minimum, and maximum values, were calculated for CT_{Max} in both male and female *S. zeamais*. Normality of the data was tested using the Shapiro-Wilk test. A standard two-sample *t*-test was used to compare CT_{Max} between males and females when equal variances were assumed. However, three male *S. zeamais* failed to recover and were excluded from the analysis. To account for this heteroscedasticity, Welch's *t*-test was applied. For the analysis, statistical significance was set at $p < 0.05$. Data visualization was done using the 'ggplot2' package to generate box plots and scatter plots for illustrating thermal tolerance distributions. The 'dplyr' package was used to make summary statistics tables.

Results

The critical thermal maximum (CT_{Max}) values for male and female *S. zeamais* were similar, with males exhibiting an average ± standard deviation of 47.21 ± 0.26°C and females 47.17 ± 0.29°C (Table 2.1). The Shapiro-Wilk test indicated that CT_{Max} values were approximately normally distributed for both males ($W = 0.927$, $p = 0.06$) and females ($W = 0.931$, $p = 0.053$). Statistical comparisons revealed no significant difference in CT_{Max} between males and females. Given that both sexes satisfied the assumption of normalcy, an F-test was used to compare the equality of variances. The mean differences between the groups were thus compared using Welch's T-test. A t-statistic of 0.55 and a p-value of 0.584 were obtained from the test, indicating that there was no statistically significant difference in the average CT Max between male and female *S. zeamais*.

Table 2.1: Summary statistics of CTMax (°C) for male and female *S. zeamais*

Gender/ CT Max	**Mean ± SD**	**Median**	**Maximum**	**Minimum**
Female	47.17± 0.29	47.21	47.66	46.7746.54
Male	47.21± 0.26	47.21	47.66	46.5446.77

Table 2.2: Statistical test results comparing CT Max values between male and female *S. zeamais*

Test	Statistic	P values
Shapiro (Female)	0.931	0.053
Shapiro-Wilk (Male)	0.927	0.06
F-test for Equal Variance	0.844	0.664
Welch's T-Test	0.550	0.584
Wilcoxon Test	423.5	0.772

The box plot (Fig. 2.2) visually represents the distribution of CT_{Max} values for both sexes, demonstrating overlapping interquartile ranges and nearly identical medians. However, two low outliers were observed in the female group, with CT_{Max} values falling below 46.7°C.

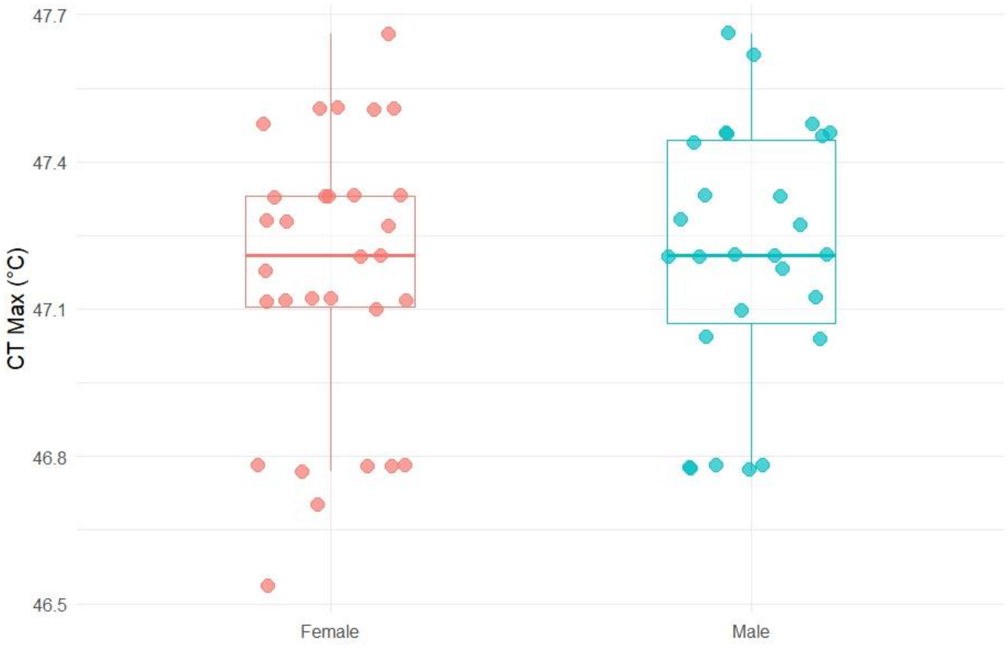


Figure 2.2: A box plot showing the distribution of CT_{Max} values for male and female *S. zeamais*, with raw data points overlaid as a scatter plot using jitter to prevent overlap

Discussion

Here the authors report a thermal tolerance of ~47°C for a Tift County Georgia population of *Sitophilus zeamais* and find no significant difference between the males and females. These findings agree with the study on other Coleoptera, tenebrionid beetles included, that exhibit no significant sexual dimorphism of thermal tolerance (Klok et al., 2004). Nevertheless, there was a difference indicated in the standard deviation between the females (0.29°C) and the males (0.26°C). There were two low outliers also in the females, temperatures lower than 46.7°C. The ratio of variances 0.84366 ($p = 0.665$) indicates a probable sex-specific thermal tolerance mechanism. These differences may be ecological (ex. due to physiological adaptation, body size, or ecological role) or experimental (ex. the physiological state of the individuals tested or the sensitivity of the thermocouples. The presence or absence of sexual dimorphism in thermal tolerance varies across taxa. For instance, in butterflies of *Thymelicus lineola*, males are more resistant to heat because they have lower wing loading and longer activity times (Pivnick & McNeil, 1986). In contrast, the absence of significant differences in *S. zeamais* ($p = 0.586$) may be caused by rearing conditions being highly similar to the thermal optimum of *S. zeamais*, which might have minimized sex-specific differences.

Body mass is usually also associated with thermal tolerance because larger individuals would have lower plasticity, particularly in wild populations (Pottier et al., 2021). Body mass is directly related to CT_{Max} in *Xenoglossa pruinosa* bees, particularly for males (Jones et al., 2024). Some females in Diptera have demonstrated greater CT_{Max} plasticity than males (Weaving et al., 2023). In contrast, studies on *Melanoplus differentialis* (Orthoptera) revealed a slight increase in CT_{Max} values for heavier males, but no apparent correlation between thermal tolerance and body size (Preston & Johnson, 2020).

Thermal history of insects is an important determinant of their thermal tolerance. Insects cultured at high temperatures tend to have a higher survival rate when subjected to acute heat stress due to physiological acclimation, whereas those with colder environments preferentially tolerate chronic mild heat stress better (Cooper & Shaffer, 2021; Sejerkilde et al., 2003). In this study, *S. zeamais* were reared at 23-24°C and 60-70% RH-conditions, likely close to their thermal optimum (Throne, 1994). This may have minimized thermal stress and, as a result, impacted their thermal tolerance. Developmental temperature has a large effect on thermal plasticity as adults, with warmer rearing temperatures potentially suppressing variance at CT_{Max} (Healy et al., 2019; Kellermann & Sgrò, 2018). The moderate rearing conditions used here may have limited the strength of adaptive responses, contributing to the relative narrow range in females (46.54°C to 47.66°C) This could reflect a general adaptive strategy which enhances survival and reproduction by adjusting environmental variation, with no sex-specific differential in thermal resistance.

For instance, warmer environment flies exhibit higher survival for acute heat stress due to reduced cell size, and cooler environment flies exhibit improved performance with longer duration of mild heat stress due to increased cell sizes (Verspagen et al., 2019). Such findings suggest that developmental conditions have lasting effects on physiological traits that impact thermal performance. Additionally, cold-reared flies demonstrate enhanced cold survival and cold-shock tolerance compared to warm-reared ones, accompanied by changes in membrane phospholipid composition (Overgaard et al., 2008) and enlarged wing areas that improve flight performance at lower temperatures (Frazier et al., 2008). These insights highlight the complex interplay between developmental history and thermal resilience in insects.

The absence of significant CT_{Max} differences between male and female *S. zeamais*, p-value of 0.586 indicates shared physiological adaptations to high temperatures, likely a reflection of their tropical and subtropical origins (Throne, 1994). However, this lack of differentiation may also indicate a potential vulnerability to environmental changes that push *S. zeamais* populations closer to their thermal limits. Estimating sex-specific thermal tolerances is essential in predicting population responses to climate change. Both sexes of *S. zeamais* demonstrated high heat-tolerance, with CT_{Max} values exceeding 46.8°C, an indication of their adaptive traits that enhance survival in warming environments. By maintaining cellular function in the face of heat stress, heat shock proteins (HSPs) are essential for thermal tolerance. Numerous insects, including pests of stored products, have been shown to upregulate HSPs in response to temperature changes. Reiterating the function of HSPs in reducing heat-induced cellular stress, Mahroof et al. (2005) showed that *Tribolium castaneum* displays high *hsp70* expression upon exposure to high temperatures. Likewise, *S. zeamais* upregulates several heat shock protein genes, such as *Szhsp70*, *Szhsc70*, and *Szhsp90*, in response to temperature stress (Tungjitwitayakul et al., 2015). The most upregulated of these was *Szhsp70*, suggesting that it plays a major part in the response to heat stress. In addition to temperature stress, other environmental stressors can cause *S. zeamais* to express HSP. Studies by Tungjitwitayakul et al. (2016) revealed that exposure to UV-C and microwave radiation dramatically raised the expression of these genes, especially *Szhsp70*, indicating that HSPs offer protection against more than just temperature extremes. Beyond temperature, thermal tolerance interacts with other environmental factors such as humidity and food availability, shaping *S. zeamais* ecology. Khan (2009) highlighted that *S. zeamais* thrives in high humidity, with optimal survival occurring near 100% relative humidity, reinforcing the importance of microclimate conditions in defining its ecological niche. Among stored-product insects, thermal tolerance varies with environmental conditions. For example, *Sitophilus oryzae* thrives in cool, wet environments, while *Cryptolestes ferrugineus* prefers warmer, humid conditions, and *Tribolium castaneum* favors warmer, drier environments (Beckett, 2011). Thermal stress responses also exhibit variability among beetles. For instance, the dung beetle *Allogymnopleurus thalassinus* has a CT_{Max} exceeding 50°C but displays limited thermal plasticity (Machekano et al., 2021). This diversity indicates the complexity of thermal adaptation and highlights how both intrinsic physiological traits and extrinsic environmental factors shape insect responses to their surroundings. Understanding these interactions is crucial for assessing how insect populations will respond to future climatic shifts. Climate change has added complexity to the thermal ecology of *S. zeamais*. The Intergovernmental Panel on Climate Change (IPCC, 2001) projected global temperature increases ranging from 1.1°C to 5.4°C, and empirical data indicate an average rise of 0.74°C (Meehl et al., 2007). As temperatures increase, so does heat stress, which can disrupt insect behavior, reproductive success, and overall population viability (Bale et al., 2002; Parmesan & Yohe, 2003). Understanding how *S. zeamais* copes with these changes is essential for predicting its future distribution and ecological impact.

Future research on gender-specific differences in thermal tolerance should focus on the physiological mechanisms underlying these differences, such as metabolic rates, hormonal regulation, and enzymatic activity, to determine their adaptive significance (Terblanche et al., 2010). For instance, Terblanche et al. (2010) demonstrated that thermal acclimatization enhances performance in natural environments in *Ceratitis capitata*, suggesting that similar investigations in *S. zeamais* may provide valuable insight into their thermal tolerance. Moreover, Sasaki et al. (2019) showed that reduced thermal tolerance in marine copepods increases their vulnerability to climate change, emphasizing the need for similar research in terrestrial species such as *S. zeamais.* Investigating the relationship between CT_{Max} values and field performance in *S. zeamais* will be crucial for forecasting how this species may adapt to changing climatic conditions. Moreover, future research should explore the consequences of thermal tolerance for other fitness-related traits, such as reproductive success, foraging ability, and survival in natural ecosystems. Understanding how rearing *S. zeamais* under elevated or fluctuating temperatures influences thermal tolerance may reveal important links between developmental environments, CT_{Max}

variability, and the adaptive potential of both sexes. These findings could offer valuable insights into the ecological resilience of *S. zeamais* in response to climate change.

Finally, examining thermal tolerance variation across different populations may show patterns related to local adaptation and phenotypic plasticity. Under climate change scenarios, populations may exhibit differential responses, which could be critical for management and conservation efforts. For instance, Shah et al. (2017) demonstrated that tropical lowland aquatic insects exhibit more limited thermal breadths compared to temperate populations, which signifies limited acclimatory plasticity in stable environments, which signifies limited acclimatory plasticity in constant environments, and that terrestrial insects like *S. zeamais* can display equivalent adaptive tendencies. Future research also needs to study thermal tolerance diversity across development stages, populations, and phylogenetically conserved species. Since developmental stages exert significant influences on survival and reproduction (Pincebourde & Casas, 2015), examining fluctuations in thermal resistance for both larvae and adults of *S. zeamais* may provide better insights into its adaptability.

Conclusion

Both male and female *S. zeamais* from Tifton Georgia with larger than average CT_{Max} values of 46.5°C showed equal thermal tolerance, indicating that their heat adaptations at a physiological level are similar. These findings suggest the species' resistance to heat stress and potential susceptibility to climate change. In a warming climate, conservation efforts and pest management plans can benefit from an understanding of thermal tolerance mechanisms and how they interact with human-induced and environmental factors.

2.2. Thermal Preference

Introduction

Insects regulate their exposure to thermal extremes behaviorally by choosing warmer or cooler microhabitats, a strategy that works to optimize their physiological performance despite individual thermal preferences (Coggan et al., 2011; Killen, 2014; Shinner et al., 2020). However, due to their small body size, insects are extremely sensitive to temperature change (Digby, 1955). Although ectotherms are able to behaviorally regulate body temperature to avoid excessive heat, global warming temperatures could still interfere with important processes like nutrient uptake, social communication, and reproduction, which are vital for population viability (Basson et al., 2017; Huey & Kingsolver, 2019). In some ectotherm species, changed temperatures could impact one sex over the other, leading to potential population dynamic asymmetries (Darnell et al., 2013; Huey & Pianka, 2007; Lailvaux, 2007). There exists a variety of optimum temperature for survival and reproduction for every weevil species. For instance, *Metamasius callizona*, a bromeliad-feeding weevil, develops optimally at 25-30°C, with egg-laying occurring between 22–33°C (Cooper & Cave, 2016). Similarly, pepper weevil, *Anthonomus eugenii*, achieves optimal development at 30°C whereas the alfalfa weevil, *Hypera postica*, achieves the highest number of progenies at comparatively low 20°C and the highest growth rate at 24°C (Levi-Mourao et al., 2022; Toapanta et al., 2005).

Temperature extremes, either low or high, have a severe impact on insect survival, reproduction, and population increase, generally causing increased mortality and geographic range limitations (Hallman & Denlinger, 2019; Hoy, 2019). To cope with such thermal stress, including behavioral adaptations, dormancy, and seeking thermally appropriate refuges (Hoy, 2019). There is also a genetic basis to temperature preference and host-plant resistance to insect pests. Such interactions are significant to predict the responses of insects to climate change and to apply effective pest management strategies.

Temperature plays a significant role in the regulation of all stages of *S. zeamais* development, and every stage responds uniquely to thermal levels. Pupation is optimal at around 25°C, while lower temperatures retard the emergence of adults (Pitan & Jallow, 2021). The minimum development temperature is around 15.6°C (Arthur et al., 2001), while optimal development for *S. zeamais* and maximum fecundity and progeny production is attained at 30°C and 75% relative humidity (Throne, 1994).

Behavioral thermoregulation allows insects to select optimal thermal habitats that enhance survival and fitness (Duffy et al., 2015; Pincebourde & Suppo, 2016; Sunday et al., 2014). Stored-product insects such as *S. zeamais* are highly sensitive to temperature fluctuations since they possess limited thermal ranges for development and reproduction (Sinha & Watters, 1985). High pupal-stage temperatures can inhibit emergence of the adult, and low temperatures retard development, affecting population dynamics by desynchronization with the availability of food (Huma et al., 2019). Comparative studies indicate that *S. zeamais* is more tolerant to lower temperatures than *Prostephanus truncatus*, which is tolerant to higher temperatures (Copatti et al., 2013). When they occur together in mixed colonies, there are competitive interactions, but the two species can coexist in the range 25-30°C (Quellhorst et al., 2019). Besides, lower temperatures reduce grain damage from *S. zeamais* as well as by other insects including *Oryzaephilus surinamensis* and *Laemophloeus minutus* (Copatti et al., 2013).

Temperature exerts significant influence on metabolic processes within insects and affects the way energy stores are converted and utilized (Clarke & Fraser, 2004; Rho & Lee, 2017). Thus, sex-specific reproductive investment should be balanced in relation to thermal optima that maximize temperature-dependent metabolisms (Forsman, 2018; Rogowitz & Chappell, 2000; Shillington, 2005). Females may favor temperatures for maximizing nutrient intake to optimize reproduction, while males can favor thermals to maximize mating success. Sexual dimorphism often results in distinct thermal optima and energetic demands. Thermal preference can be determined by intrinsic conditions like developmental stage, age, and sex, and extrinsic conditions like humidity and prior thermal experience (Fischer & Karl, 2010; Hoffmann et al., 2005). For instance, females of *Callosobruchus maculatus* prefer warmer temperatures, likely for reproductive reasons, and male Mediterranean fruit flies (*Ceratitis capitata*) prefer more superior temperatures to promote sexual performance (Weldon et al., 2022). Similarly, male katydids and crickets also undergo thermoregulation to accommodate the metabolic demands necessary for acoustic signaling used in mate attraction (Erregger et al., 2017) while male *Eucalyptus*-boring beetles exhibit higher rates of metabolism during mate searching (Rogowitz & Chappell, 2000).

Thermoregulatory conditions also influence nutrient assimilation efficiency and energy stores. In *Drosophila melanogaster*, reserves of lipids and glycogen are lower at temperatures greater than 27°C due to increased metabolic needs and lower assimilation efficiency (Klepsatel et al., 2019). Thermoregulatory differences between sexes may influence nutrient intake, viability, and population growth (Huey & Berrigan, 2001; Huey & Kingsolver, 2019). Understanding thermal limits and preferences is important for predicting the distribution of insects and responses to climate change (Bonebrake & Deutsch, 2012; Deutsch et al., 2008; Dillon et al., 2010). Insects regulate their body temperature with morphological, physiological, and behavioral mechanisms that avoid unfavorable temperatures (Bursell, 1974; Casey & Hegel, 1981; Clench, 1966; Kreuger & Potter, 2001; Schmitz, 1994; Willmer, 1982). Moreover, exposure to pesticides can change thermal choice-prey locusts treated with pyrethroids choose higher temperatures, whereas those that receive oxadiazine pesticides choose lower temperatures (Tegowska et al., 2001).

Sitophilus zeamais populations in South Carolina have a year-round activity, but most activity occurs at temperatures greater than 20°C (Throne & Cline, 1991). Infestation level varies by climatic regions in Georgia, suggesting that the species is highly climatic-sensitive (Dix & All, 1986). Though optimal temperature for survival and reproduction has been documented (25-30°C) (25-30°C) (Ceruti et al., 2008; Throne, 1994), thermal preference, specifically in reference to potential variation between the sexes, has been inadequately explored. The objective of this study was to investigate the existence or non-existence of sex-specific thermal preference in *S. zeamais* under laboratory conditions. That is, we aim to determine whether males and females prefer to be at different temperatures, potentially reflecting differences between their reproductive and physiological strategies. We hypothesize that males of *S. zeamais* will prefer low temperatures to enhance mating success and that females will prefer high temperatures to optimize reproductive activities such as egg maturation and oviposition.

Materials and Methods

Maize weevils were collected from infested field corn in Tift County, Georgia, and maintained in the controlled laboratory environment of 24-25°C, 60-70% relative humidity, and 12:12 light/dark cycle for a number of generations. For consistency, only adult weevils of the same age, size, and physiological condition were employed for experiments. A temperature gradient apparatus was employed in this experiment to identify the thermal preferences of *S. zeamais*. The apparatus allowed individual weevils to move freely along an experimenter-controlled temperature gradient so that direct measurement and observation of their optimal temperature ranges could be made.

Sitphilus zeamais thermal preference was measured with a temperature-regulated, altered setup constructed from (Antoł et al., 2019) originally used to study the heat reaction of woodlice. The set-up included a 6 × 24-inch plain aluminum sheet metal plate (Everbilt, Atlanta, USA) with six aluminum tracks for concurrent testing of a maximum of six weevils. A layer of thermally conductive grease (CRC Industries. Inc, Pennsylvania, USA) was applied to the bottom of these tracks to ensure optimal thermal contact with the metal plate. Insects are placed in arenas made of thin plastic tubes sealed with parafilm on each end that are set within the aluminum tracks and surrounded with water. This set up allows thermal conductivity from the metal plate to the tracks and the surrounding water and creates a behavioral arena completely within the manipulated thermal range. To create a thermal gradient, a hot plate (Fisher Scientific, Durbuque, Iowa, USA) was positioned at one side of the metal plate and an ice bath at the other ensuring a stable temperature gradient. Both ends of every corridor were observed with a 1 mm diameter thermocouple to within the nearest 0.01°C, ensuring a consistent gradient of between 15°C and 45°C along the sheet metal. These temperatures were selected according to *S. zeamais'* previously established physiological tolerances to have an appropriate range within which to observe thermal preference.

Experimental Procedure

For every trial, six adult weevils were randomly picked from laboratory-maintained stock, with attempts to balance sex ratio where feasible (Figure 2.3). To reduce positional bias, three weevils were placed at the cold end and three at the warm end of apparatus. Every weevil was confined in a single plastic tube, sealed on both ends using parafilm to avoid escape. The experiment was conducted within a light and sound free room at 24°C to reduce any potential environmental biases. Weevils were provided with free movement within the tubes for 30 minutes as initial trials indicated that this was sufficient time for the weevils to acclimatize in desired temperature ranges.

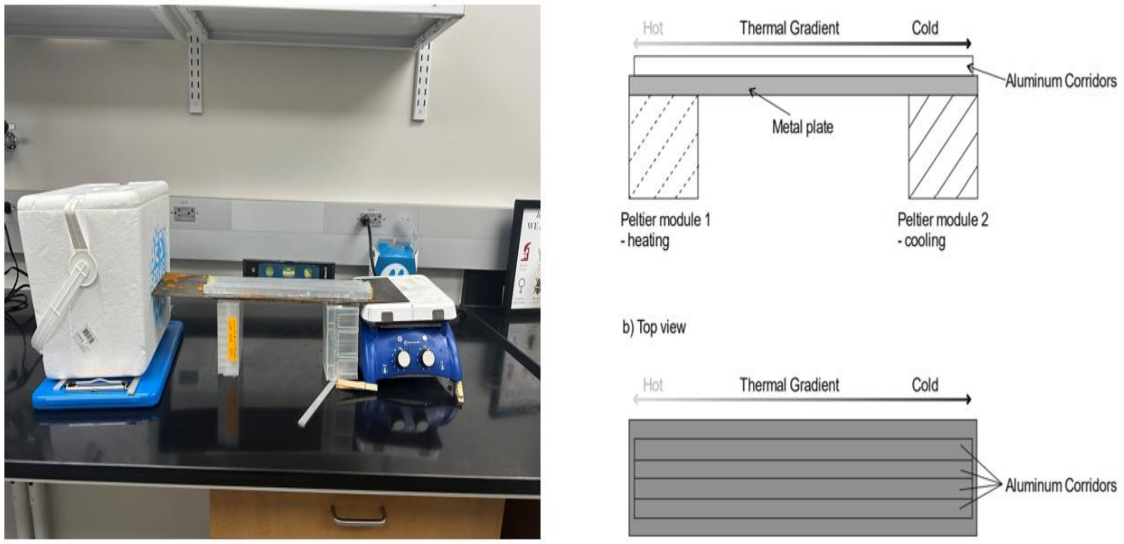


Figure 2.3: Experimental Set-up Showing Thermal Preference Assay

Data Collection

Surface temperatures within the tubes were recorded at two points: the cold and hot ends of each corridor, at both the beginning and end of each trial. At the conclusion of each trial, the position of each weevil was marked, and the corresponding temperature was recorded. Weevils were then carefully removed, and their sex was determined using morphological characteristics of the rostrum and abdominal sternites under a microscope (Halstead, 1963). Prior to digitalization for statistical analysis, all data were first entered onto prepared data sheets. To minimize potential pheromone contamination due to *S. zeamais* already tested, tubes were aerated before reuse (Coster & Vité, 1972).

Statistical Analysis

Normality tests using the Shapiro-Wilk test showed that female temperature data were not normally distributed (W = 0.764, $p < 0.001$), whereas male data followed a normal distribution (W = 0.962, p = 0.247). Due to this deviation, both parametric (independent t-test) and non-parametric (Wilcoxon rank-sum test) approaches were used for comparison. An independent t-test comparing male and female mean temperatures yielded a t-statistic of 0.307 (df = 68, p = 0.759), with a 95% confidence interval ranging from -1.45°C to 1.98°C, indicating no significant difference between the sexes. Similarly, the Wilcoxon rank-sum test produced a W-statistic of 622 and a p-value of 0.911, further confirming the absence of significant differences in median thermal preference. Both Levene's test (p = 0.836) and the F-test (p = 0.336, variance ratio = 1.3929) show that there is no significant difference in variance between males and females. Descriptive statistics indicated that female weevils (n = 34) exhibited a mean preferred temperature of 24.31°C (SD = 3.89°C), with a median of 23.8°C and an interquartile range (IQR) of 3.23°C. The male weevils (n = 36) showed a mean preferred temperature of 24.05°C (SD = 3.30°C), with a median of 23.5°C and an IQR of 3.68°C (Table 2.3).

Results

Parametric and non-parametric tests were employed to compare male and female weevils' thermal preference. Temperature data were plotted in a box plot with overlaid points. Analysis was conducted in R version 4.1.0 (R Core Team, 2021), and data visualization was achieved with ggplot2 package (Wickham & Wickham, 2016). The results indicated no significant difference in thermal preference between male and female weevils (Figure 2.4). There was no difference in thermal preference between male and female weevils (Figure 2.4). The independent t-test showed no difference (p = 0.759), and the Wilcoxon rank-sum test also showed a non-significant difference (p = 0.911). Temperature ranges between trials remained within the same limits, with the temperature gradient being preserved. Levene's test shows a p-value of 0.836, indicating no difference between the sexes in the variability of temperature, and this is also supported by the outcome of the F-test (p = 0.336). Initial temperatures at the cold and warm ends of the apparatus were 19.13°C and 34.13°C, respectively, with final recorded temperatures averaging 22.02°C (cold end) and 39.51°C (warm end).

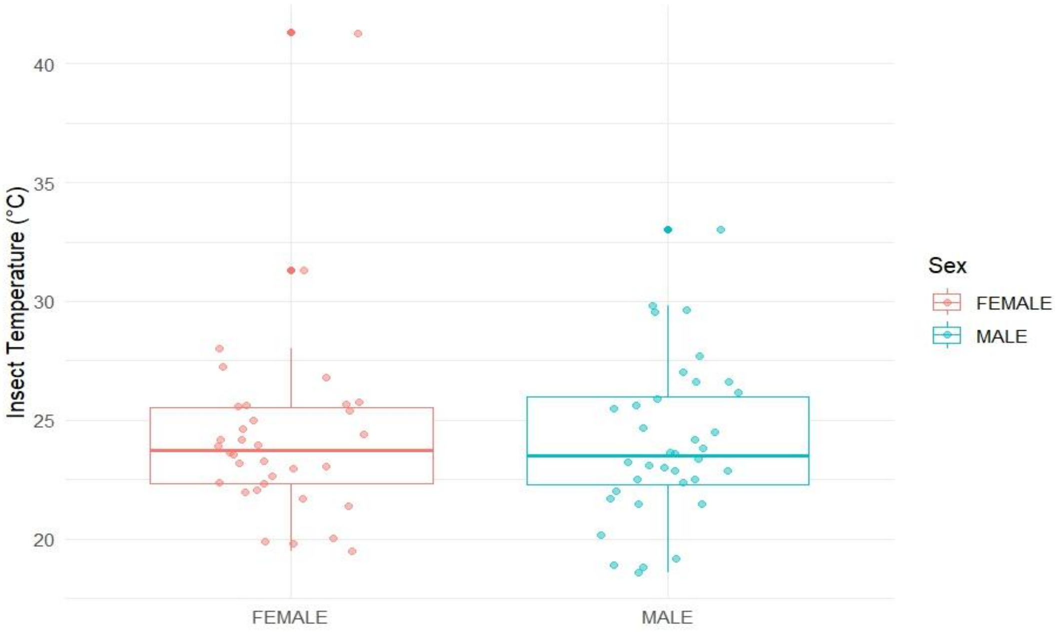


Figure 2.4: Box plot with overlaying raw data points illustrating the distribution of thermal preference values for male and female *S. zeamais*. Note that outliers will be represented twice on this graph, once from the boxplot and once from the scatter plot.

Table 2.3: Summary of Statistical Results

Summary Statistics	Mean	Median	Standard Deviation
Female	24.31	23.80	3.89
Male	24.05	23.50	3.30

Discussion

This study examined the temperature preferences of *Sitophilus zeamais* across an average temperature gradient of 22.02°C to 39.51°C. Results indicated the mean temperature that female *S. zeamais* preferred was 24.31°C (±0.72°C SE), whereas males preferred a slightly lower but statistically insignificantly different 24.05°C (±0.56°C SE). Notably, females appear to exhibit a broader temperature range (19.9°C–41.8°C) compared to males (18.7°C–33.3°C), suggesting greater thermal breath in female thermal selection. The variance test further revealed no significant difference in temperature variability between males (p = 0.336) and females (p = 0.836), possibly reflecting similar physiological or behavioral traits Levene's test for homogeneity of variance on weight for both males and females was 0.41, indicating no difference in variability in weight between the two sexes. This suggests that the variability in weight is the same for both males and females

The thermal preferences observed in this population of *S. zeamais* suggest an adaptation to moderate thermal conditions with females *S. zeamais* preferring 24.31°C while male preferred 24.05 °C. Previous research has documented optimal growth conditions for *S. zeamais* at 30°C with 75% relative humidity (Throne, 1994), while others have reported a developmental optimum around 27°C (Dari et al., 2010; Pitan & Jallow, 2021). The lower preferred temperature observed in this study may represent a behavioral adaptation to limit intraspecific competition and mortality and to facilitate reproductive success under fluctuating environmental regimes. However, choosing temperatures within the mid-range, *S. zeamais* may facilitate survival and reproductive robustness, particularly in response to thermal variability.

Temperature is of primary significance in the regulation of metabolic rates in ectothermic organisms, directly influencing growth, reproduction, and survival (Bowler & Terblanche, 2008). The ~24°C preference recorded here must be a balance between energy conservation and metabolic demands, a trend also observed in other insect orders. For instance, in the case of *Hypera postica* (alfalfa weevil), studies report that it has the highest generation of offspring when maintained at 20°C and grows the most rapidly at 24°C (Levi-Mourao et al., 2022; Toapanta et al., 2005), Similarly, pine weevils (*Hylobius abietis*) also exhibit temperature-dependent oviposition and feeding behavior, with a preference for thermal regimes of 19°C to 28°C (Son & Lewis, 2005).

Similarly, pine weevils (*Hylobius abietis*) exhibit temperature-dependent feeding and oviposition behavior, favoring thermal ranges of 19°C to 28°C (Christiansen & Bakke, 2009). These findings support the hypothesis that temperate conditions are essential for the growth and reproduction of *S. zeamais*. Although maize weevils are extremely tolerant of a wide range of temperatures (Tungjitwitayakul et al., 2015), their reproductive efficiency appears to be within a more limited range of 22°C-28°C. This study discovers ~24°C to be a thermal optimum, an equilibrium point between fitness and preventing the cost of fitness in suboptimal temperatures.

Most insects actively maintain body temperature to avoid costs in fitness during suboptimal conditions (Martin & Huey, 2008). These findings show that thermal preference in females remains measurable by reproductive condition and metabolic requirements, a trend consistent with other taxonomic observations. For instance, *Colias* butterflies adjust body orientation to regulate temperature for optimal flight function (Kingsolver & Watt, 1983). Similarly, *S. zeamais* females may adjust their thermal preferences to maximize fitness under varying environmental conditions. Interestingly, there were no significant differences ($p = 0.911$) in female and male *S. zeamais* thermal preferences as observed, meaning shared ecological strategy in conditions of storage. This contrasts with many insect species, where sexual dimorphism in thermal preference is common due to divergent reproductive roles (Hallsson & Björklund, 2012; Weldon et al., 2022). Lack of appreciable sexual dimorphism in *S. zeamais* indicates that the two sexes are equally suited to storage conditions. The noted preference for ~24°C can be involved in controlling weevil activity and reproduction, possibly providing insights into pest management practices that manipulate storage temperatures to minimize infestation risks.

Statistical analysis found no statistical differences in thermal preference between males and females. However, the relatively small sample size limits the statistical power of this study, and future research using larger population samples is required to confirm these results. In addition, age, reproductive stage, and hormonal fluctuations may influence thermal preference, since this too is shown to vary with metabolic and physiological demands and may have been the cause of the outlier, as observed in other organisms (Bowler & Terblanche, 2008; Huey & Pianka, 2007). Follow-up studies incorporating these factors, as well as mating status, may result in an even more refined understanding of *S. zeamais* thermal preference. Research on other insects, such as Enchenopa treehoppers, has demonstrated temperature-dependent mating across a narrow temperature range (Macchiano et al., 2019), illustrating the complex role of temperature in insect reproduction.

Conclusion

This study provides new insights into the temperature preference in *S. zeamais* for moderate temperatures (~24°C), with a minimal sexual dimorphism. The findings suggest that behavioral thermoregulation has the potential to buffer this *S. zeamais* against environmental variation. However, with the intensification of climate change, thermal niche shifts can influence their physiology, distribution, and survival. An understanding of these thermal preferences is necessary to predict how *S. zeamais* and other ectotherms will respond to rising global temperatures.

2.3. Measurement Analysis of *Sitophilus zeamais*

Introduction

Morphological features in insects are crucial in identifying their ecological roles and adaptive strategies. The body shape and size in ground beetles relate to environmental factors and sexual dimorphism (Sukhodolskaya, 2014). For instance, dung beetles require standardized body size to get accurate functional diversity estimates, and dry weight is the best method (Gómez & Tonelli, 2022). Pronotum shape in pygmy grasshoppers reflects macrohabitat adaptation (Rebrina et al., 2024), while in ants, body size, eye position, and scape length correlate with trophic level (Drager et al., 2023). These studies highlight the need to employ standardized morphometric techniques to enhance interspecific comparisons of insects. The morphology of *S. zeamais* significantly influences its feeding behavior, reproductive success, and ecological function. The morphological architecture of *S. zeamais* directly influences its feeding activity, reproductive efficiency, and ecological function. The species possesses a clear rostrum, thorax, and pronotum that are required in the utilization of resources. The size and shape of the body influence feeding efficiency, movement, and reproductive fitness, and the greater specimens exhibit higher survival under stress (Greenberg et al., 2005; Wade French & Hammack, 2010). Rostrum length and body size are key to species identification within *Sitophilus*, as morphological determination through pronotal punctures is not dependable (Hidayat et al., 1996). Molecular markers and hyperspectral imaging are some of the new technologies that improve classification (Cao et al., 2015; Suhriani et al., 2023). With these technologies, sexual dimorphism of *S. zeamais* is still yet to be investigated but can contribute to ecological differentiation.

Female *S. zeamais* would presumably possess longer rostra and larger body sizes, facilitating deeper grain penetration during oviposition (Ojo & Omoloye, 2016), while males may possess stronger thoracic structures for mating competition. Studies on related weevils suggest rostrum length correlates with host seed size, optimizing reproductive efficiency (Hughes & Vogler, 2004). Such allometric relationships influence feeding efficiency, mobility, and reproductive success, although no quantitative studies exist for *S. zeamais*. Morphological traits, particularly rostrum and mouthpart structure, directly impact feeding behavior, because well-developed rostrum assists grain kernel penetration (Cordeiro et al., 2017). Conversely, smaller individuals may navigate stored grains more efficiently (Ngom et al., 2021). More fecund and longer-lived females would be the larger ones in order to lay more eggs (Wade French & Hammack, 2010). Similarly, larger males will also possess longer copulation durations, enhancing reproductive success (Greenberg et al., 2005). Weight, particularly dry weight, is a reflection of energy reserve and nutritional state, and heavier ants exhibit greater survival capability upon starvation (Richards, 1945; Tan et al., 2010). In weevils, body weight is linked to flight ability, reproductive success, and mortality, which are established by larval diet, metabolic reserves, and genetics (Greenberg et al., 2005; Šešlija & Tucić, 2003).

Sexual size dimorphism in *S. zeamais* may have significant ecological and physiological implications. Larger size females tend to have higher reproductive potential, as seen in boll weevils (Greenberg et al., 2005), while male body mass will most likely influences mating competition and flight capability. In bean weevils, trade-offs between body mass, reproductive output, and lifespan suggest that size variation is a key life-history trait (Šešlija & Tucić, 2003). Body size also determines tolerance to environmental stressors, including desiccation and temperature extremes. Dry body mass serves as an index of energy reserves, with heavier individuals demonstrating better survival and reproductive fitness (Bolívar-Silva et al., 2018; Richards, 1948). Advanced resolution examination and digital imaging techniques can be used to connect morphology variation with functional traits such as reproductive success and feeding efficacy. Regional studies in Nigeria have documented morphometric divergence between *Sitophilus* populations (Oyewale et al., 2022), though their ecological adaptive significance and relevance to sex-related traits remain uncertain.

The objective of the study was to fill knowledge gaps by analyzing sex-specific morphological traits in *S. zeamais*, with a focus on their ecological and physiological significance. By measuring rostrum length, thoracic dimensions, and body weight in 30 males and 30 females, this research seeks to establish the presence of sexual dimorphism and its functional implications. The authors hypothesized that females would have larger body sizes and longer rostra, reflecting their roles in oviposition and resource allocation, whereas males will display adaptations related to reproductive competition and mobility. These findings will increase the understanding of morphological diversity within *S. zeamais*.

Materials and Methods

The weevils used in this study were initially used to conduct behavioral assays before being used for morphological measurements. A total of 30 specimens, comprising both males and females, were examined. Prior to measurement, the weevils were soaked in 70 % ethanol for six hours to ensure euthanasia and remove remaining corn dust that may interfere with accurate measurements. Morphometric measurements were conducted using a VHX-7000 Digital Microscope (Osaka, Japan) at 30x magnification, with a 250 µm calibration scale applied for all measurements. The morphological measurements such as dry weight, pronotum length, rostrum length, and rostrum width were obtained. Specimens were handled carefully to avoid breakage, and each was allocated to a well within one multi-well plastic container after measurement to avoid misidentification or cross-contamination. During measurement intervals, weevils were kept chilled to preserve specimen integrity. Following morphometric measurement, all the weevils were air-dried to be measured for dry weight. Specimens were dried in a Thermo Scientific Heratherm OGS180 oven (Langenselbold, Germany) at 56°C for 24 hours to eliminate variations due to water content. Once dried, the weevils were weighed using a Toledo Model TS-U-2 microbalance scale (Swedesboro, NJ, USA) to ensure high accuracy in dry weight measurements.

Statistical Analysis

All statistical analyses were performed in R (version 4.4.2) using the ggplot2, dplyr, patchwork, effsize, and MASS packages. The Shapiro-Wilk test was used to assess the normality of each morphological variable. Welch's t-test was applied to compare normally distributed parameters between male and female weevils ($p > 0.05$), while a Wilcoxon rank-sum test was used for non-normally distributed parameters ($p < 0.05$) to ensure robust comparisons. Levene's test for homogeneity of variance on weight between males and females yielded a p-value of 0.41

Results

The Shapiro-Wilk normality test indicated that rostrum length, rostrum width, and weight followed a normal distribution ($p > 0.05$) in both sexes. However, pronotum length was not normally distributed in females ($p = 0.005$) but conformed to normality in males ($p = 0.606$). Based on these results, Welch's t-tests were conducted for normally distributed variables, while a Wilcoxon rank-sum test was applied for pronotum length due to its deviation from normality in females. Significant differences were observed in several morphological traits between sexes. Females showed significantly longer rostra (1172 ± 80.1 µm) than males (1112 ± 80.9 µm) ($t = 2.885$, $df = 57.995$, $p = 0.005$. Conversely, males had significantly wider rostra (192 ± 17.3 µm) compared to females (180 ± 16.5 µm) ($t = -2.721$, $df = 57.863$, $p = 0.009$). Pronotum length also differed significantly between sexes, females showed longer pronotums on average (1384± 95.5 µm) than males (1320 ± 84.6 µm), as confirmed by the Wilcoxon rank-sum test ($W = 603.5$, $p = 0.024$). However, no statistical difference was detected in weight between males and females ($t = 1.955$, $df = 55.813$, $p = 0.056$). Levene's test for homogeneity of variance on weight between males and females yielded a p-value of 0.41, indicating no significant difference in weight variability between the sexes. This suggests that the distribution of weight is similar for both males and females in the sample. The mean weight for females was 0.00145 g, while for males was 0.00130 g. The standard deviations (SD) for females and males were 0.000333 g and 0.000272 g, respectively. The p-value for the comparison between males and females was 0.056. Antenna width measurements were not feasible for all 30 individuals per sex during data collection. The antennae were often hidden, nestled between the limbs of the weevils. They were not forced to be adjusted for measurement to avoid damaging the specimens. This limitation highlights the need for improved methodologies in future studies to enhance the completeness of morphometric data collection.

Table 2.4: Summary of Morphometric Measurements in Male and Female *S. zeamais*

Mean	Female	Male	SD Female	SD Male	p- value
Weight (g)	0.00145	0.00130	0.000333	0.000272	0.056
Length of Rostrum (µm)	1172	1112	80.1	80.9	0.005
Width of rostrum (µm)	180	192	16.5	17.3	0.009
Pronotum length (µm)	1384	1320	95.5	84.6	0.008

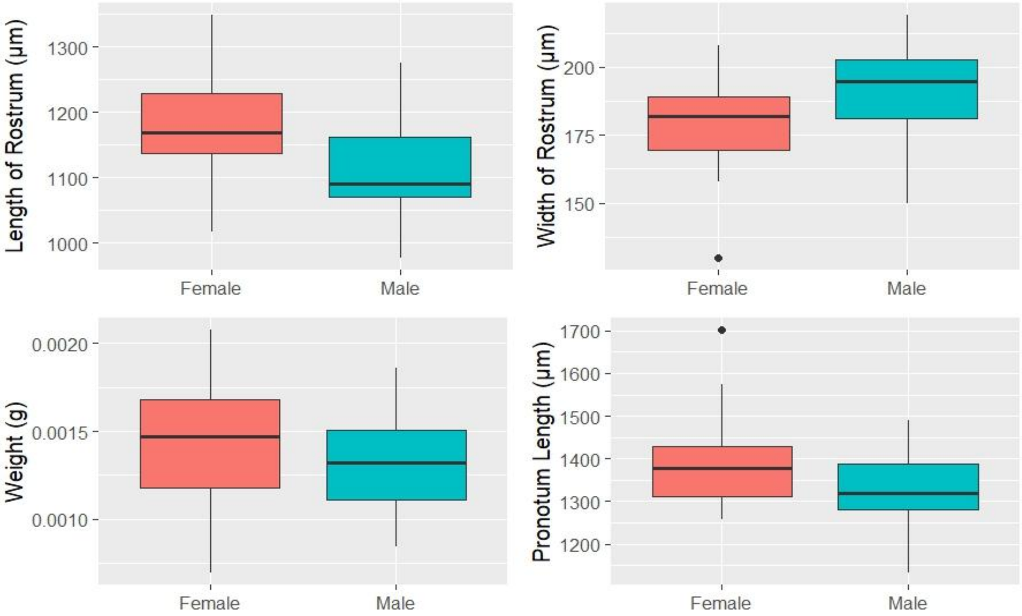


Figure 2.5: Boxplots of Rostrum Length, Rostrum Width, Weight, and Pronotum Length in Male and Female *S. zeamais*.

Discussion

This study highlights notable sexual dimorphism in the morphological features of *Sitophilus zeamais*, contributing to a deeper understanding of their reproductive biology and ecological adaptations. In insects, body weight is frequently used as a stand-in for body size, indicating that females may typically be larger. This result is consistent with the known pattern of sexual size dimorphism (SSD) in insects, where females tend to be larger because of the higher energy expenditure needed for reproduction, especially the production of eggs (Hayward & Gillooly, 2011; Teder & Tammaru, 2005). The "fecundity advantage" hypothesis (Darwin, 1871) proposes that larger female size enhances reproductive output; however, further studies with expanded sample sizes are needed to determine whether this hypothesis applies to *S. zeamais*. SSD is frequently attributed to fecundity selection, as larger females tend to produce more offspring (Afaq, 2013). Empirical studies indicate that SSD often increases with body size across insect species and that female size is more responsive to environmental factors (Teder & Tammaru, 2005). For instance, a selection experiment in *Drosophila* demonstrated that artificial selection for increased fecundity resulted in larger female body size compared to males (Reeve & Fairbairn, 1999). The degree of SSD is also strongly associated with sex-specific differences in larval developmental time, with the larger sex generally requiring a longer developmental period (Teder, 2014). Collectively, these findings show the role of fecundity-related factors in shaping SSD patterns among insect populations.

The most pronounced sexual dimorphism in *S. zeamais* was observed in rostrum dimensions. Female weevils exhibited significantly longer rostra (1172 ± 80.1 µm) than males (1112 ± 80.9 µm, $p = 0.0055$), which is consistent with their oviposition role requiring penetration into hard plant tissues for egg deposition (Manivannan & Ezhilvendan, 2017; Zhang, 2021). Conversely, males had significantly wider rostra (192 ± 17.3 µm) compared to females (180 ± 16.5 µm, p =

0.009), potentially enhancing feeding efficiency or serving other ecological functions (Shine, 1988). These differences reflect evolutionary adaptations that optimize reproductive and survival strategies in each sex. Additionally, females exhibited significantly longer pronota than males (p = 0.008), possibly as an adaptation for reproductive efficiency and oviposition. Pronotum size has been linked to increased fecundity in other insects, including mantids and beetles, and may provide structural support during egg-laying (Kingsolver & Norris, 1977; Maxwell & Frinchaboy, 2014). In contrast, male pronotal traits may be influenced by selective pressures related to mating competition or mobility.

The observed sexual dimorphism in *S. zeamais* supports the hypothesis that morphological differences between males and females reflect adaptations to their respective reproductive and ecological roles. The elongated rostrum in females aligns with oviposition demands, while the broader rostrum in males may provide functional advantages such as increased feeding efficiency. These patterns are consistent with findings in other weevil species, where rostrum size and shape correlate with host plant selection and reproductive strategies (Hughes & Vogler, 2004; Zhang, 2021). Future research should investigate potential geographic or environmental influences on morphological traits, as well as the relationship between body size, sexual dimorphism, and reproductive success in *S. zeamais*.

Conclusion

This study demonstrates clear sexual dimorphism in *S. zeamais*, particularly in rostrum dimensions and pronotum length. While females exhibited traits that facilitate reproductive efficiency, such as longer rostra and pronota, males displayed adaptations such as wider rostra that may enhance feeding and survival. These findings contribute to understanding the evolutionary pressures shaping sexual dimorphism in insects and provide valuable insights into the ecological roles of *S.*

zeamais. Future studies should expand sample sizes and examine additional morphological traits to refine understanding of the selective forces driving dimorphic patterns in *S. zeamais*.

CHAPTER THREE

3. 1. Amount of food eaten

Introduction

Moisture content is one of the most important environmental parameters that impact the growth and behavior of insects, particularly in near-optimal conditions (Hagstrum & Milliken, 1988). Moisture is an essential parameter that affects the feeding habits of stored-product insects, grain palatability, insect survival, and efficiency of feeding. Studies indicate that grains with optimal moisture content are more susceptible to infestation due to softened kernel texture, which leads to increased feeding activity and greater damage (Phokwe & Manganyi, 2023). *Sitophilus zeamais* exhibits two primary feeding behaviors in maize kernels: shallow feeding on the endosperm surface and deep feeding into the kernel (Tipping et al., 1986). Insects get moisture primarily from food and atmospheric humidity, and excessive grain moisture has been found to enhance weevil feeding efficiency and population development (Arlian, 1979). Further, previous work has established that insect feeding is able to alter grain moisture content in response. For instance, in wheat, increased weevil activity increases moisture levels in the kernel, stimulating fungal growth, which in turn influences grain quality (Agrawal et al., 1958; Christensen & Hodson, 1960). In stored maize, *S. zeamais* feeding facilitates easy entry by fungi such as *Aspergillus flavus*, which produce aflatoxins (Beti et al., 1995).

Sexual dimorphism in insect feeding behavior has been observed in many species and is often linked to reproductive investment. In *S. zeamais*, females possess a longer rostrum than males, enabling them to penetrate deeper into kernels (Wilhelm et al., 2015, also see chapter 2). While this morphological advantage is hypothesized to facilitate greater food consumption, no study has directly tested whether rostrum length correlates with feeding quantity in *S. zeamais*. However, similar patterns have been observed in other stored-product pests; for instance, in *Sitophilus granarius,* wheat extracts influence both feeding and oviposition, with water acting as a key stimulant (Levinson & Kanaujia, 1982). Feeding activity is also influenced by environmental factors such as darkness, which has been shown to increase food intake in stored-product insects (Barnes & Ratcliffe, 1967; Koehler & Gyrisco, 1963). Although there has been intensive research on *S. zeamais* feeding damage, there is limited information on the effect of moisture content on food consumption over short time intervals, especially by sex. Previous studies have concentrated on grain quality deterioration and infestation levels, with no information on how moisture content affects immediate feeding behavior. The research explores the effects of varying maize kernel moisture content (10%, 20%, and 30%) on food consumption by male and female *S. zeamais* in a 24-hour time frame. A 24-hour time frame provides a perspective of short-term feeding preference, which has the potential to influence early infestation dynamics and, subsequently, population growth. By quantifying weight loss due to feeding, the authors aim to provide estimates of food intake and ascertain whether moisture differentially affects feeding rates for the sexes.

Given the improved palatability and softer kernel that makes ingestion easier, the authors predict that food consumption will increase with higher grain moisture. Furthermore, because of their higher nutritional needs for reproduction and the benefit of having a longer rostrum for more effective deep feeding, the authors hypothesize that females will consume more than males. To understand the wider ecological significance of *S. zeamais* feeding behavior and its association with moisture content, it is important to explore these interactions between varying moisture content and food consumption. The study will provide insights into pest dynamics for enhancing the development of pest risk assessment and forecasting patterns of infestation under varying conditions of the environment. It can also support predictive models of grain susceptibility by identifying moisture levels influencing feeding activity.

Materials and methods

The maize cultivar, P1870YHR used for all the experiments in this study as it is a popular cultivar in Georgia. The samples were manually cleaned to remove all foreign materials such dust, dirt, small broken and immature kernels and was sieved over a U.S. standard number 6 sieve (sieve openings 3.35 mm) before use. The moisture content of all grain samples used in the experiment was initially 13%, as measured with an AMTAST Grain Moisture Meter (AMTAST Inc., Florida, USA). Maize weevils were collected from infested field corn in Tift County, Georgia, and reared under controlled conditions at 24-25°C with 60-70% relative humidity and a 12:12 light/dark cycle for several generations (Revco Scientific, Inc., North Carolina, USA). Only adult weevils of uniform age, size, and were selected for the experiments to ensure consistency.

Maize samples used for the experiment were first conditioned to obtain different moisture contents. The samples of the desired moisture level, thus 20% and 30% wet base (w.b.) were prepared using the common rewetting technique (Brusewitz, 1975; Nimkar & Chattopadhyay, 2001; Shepherd & Bhardwaj, 1986) by adding the amount of distilled water as calculated from the following equation, (Balasubramanian, 2001)

$$Q = \frac{Wi(Mf - Mi)}{100 - Mf}$$

Where: Q is the mass of added water (kg), Wi is the initial mass of the sample (kg), Mi is the initial moisture content of the sample in % w.b. and Mf is the final desired moisture content of the sample in % d.b.

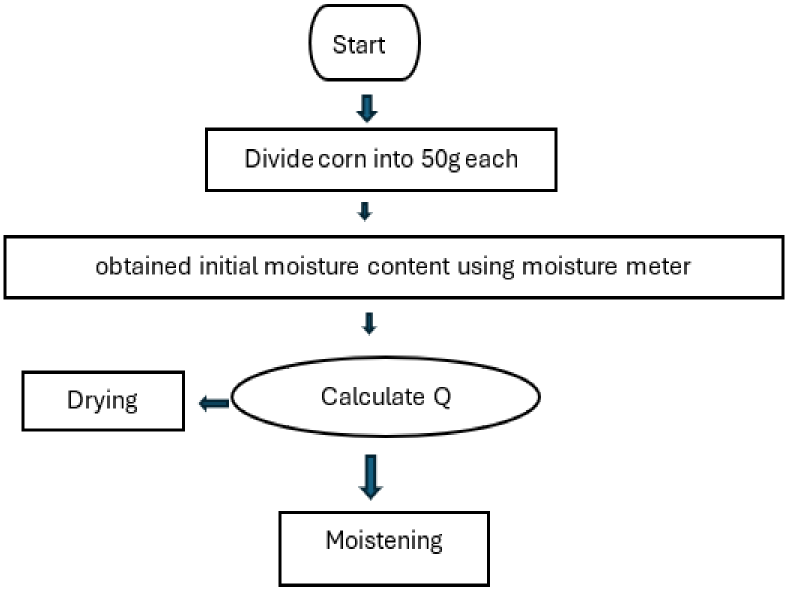
The samples along with the calculated necessary additional water were placed in high-density thick polyethylene bags, and the bags were sealed separately tightly using Metronic Impulse Sealer

(Jiaro International, Texas, USA) and kept in an incubator at 5°C for a week to ensure uniform distribution of moisture throughout the sample. The mass of distilled water needed to achieve the target moisture level was measured using a pipette**.** About 0.5ml extra distilled water was added to compensate for the loss of water adhering to the wall of the polyethylene bags.

To achieve a moisture content of 10%, corn kernels were placed in a tared moisture dish and dried in an oven dried using the 30GC analog lab oven (Quincy Lab, Inc, Illinois, USA) at 103ºC for 72 h (Gupta & Das, 2000) at a consistent temperature. The drying process was carefully monitored to ensure that the kernels reached the 10% moisture level. After the drying period, the samples were allowed to cool in a desiccator. When the grain's moisture content was extremely low, the moisture meter was unable to measure moisture levels accurately, the formula given by Hellevang (1995) and Shrink (1991) was used to verify that the kernels had attained the desired moisture content of 10%. This method was required:

$$Moisture\ Shrink\ (\%) = \frac{Initial\ Moisture\ (\%) - Final\ Moisture\ (\%)}{100 - Final\ Moisture\ (\%)} \times 100$$

Figure 3.1a: Flowchart of Experimental Test



To measure food consumption by *S. zeamais*, we adapted the method described by Simon et al., 2023, which accounts for natural weight loss due to desiccation. The experiment was conducted at three grain moisture levels (10%, 20%, and 30%), with 30 replicates for each condition. Weevils were separated by sex according to Halstead's (1963) method, with separate groups for males and females, each consisting of 30 replicates per moisture level. Experimental groups consisted of individual weevils placed with a single maize kernel in separate 2 oz plastic containers, while control groups contained only maize kernels without weevils. Initial kernel weights of both the experimental and control groups were measured using a Toledo Model TS-U-2 balance (Swedesboro, NJ, USA). All experiments were incubated at 24°C (±0.5°C) and 60%-70% relative humidity for 24 hours to ensure consistent environmental conditions. After 24 hours, both experimental and control groups were weighed again. The food consumption by the weevils was calculated by subtracting the average weight change observed in the corresponding control group (which accounts for environmental desiccation or hydration) from the total measured weight change. This adjustment ensured that the weight change attributable to desiccation or hydration was not considered in the calculation of food consumption.

Results

The analysis revealed significant differences in feeding behavior when grouped by gender and moisture content. The mean feeding rate values ranged from -0.00768g for males at 10% moisture to 0.00159g for males at 20% moisture (Figure 3.1b). Males exhibited greater variability at 10% moisture (SD = 0.0746, VAR = 0.00557) compared to females, who had lower variability (SD = 0.00317, VAR = 0.0000100). Across all treatments, female's kernels exhibited slightly higher mean weight gain (-0.00388g) than male's kernels (-0.00446g), but males showed greater variability (SD = 0.0456, VAR = 0.00208). When data from both male and female weevils were combined, the average change in feeding remained close to zero at all moisture levels: -0.00651 g (10%), -0.000463 g (20%), and -0.00555 g (30%). These near-zero values suggest that weevils either consumed very little kernels or any feeding was offset by weight loss, possibly due to moisture stress. The highest variability in responses occurred at 10% moisture, especially among males, indicating inconsistent feeding behavior. This inconsistency may be due to stress from the dry conditions or differences in individual feeding motivation.

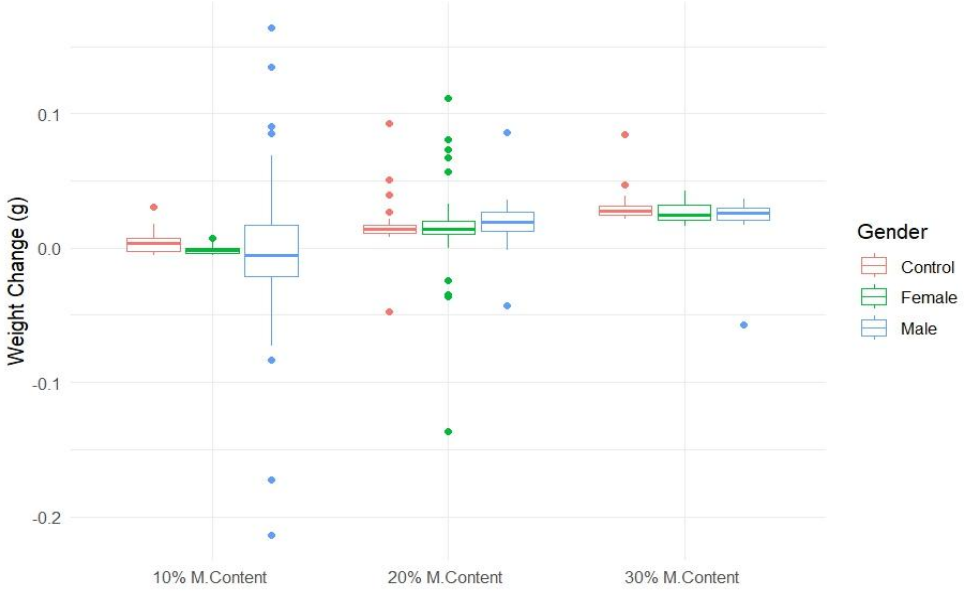


Figure 3.1b: Raw Values Depicting the Change in Weight of all Experimental Groups

Interestingly some kernels appeared to gain weight even when accounting for the control samples which resulted in negative feeding rate values. This unexpected outcome suggests greater moisture absorption by the kernels or condensation effects than feeding effects. Due to this, a reduced dataset was generated where only measurable observed feeding values were analyzed in (Figure 3.1c). These are cases where the change in weight of the experimental kernel was greater than the average change in weight of the control samples. This filtered dataset showed the highest mean feeding rate for males at 10% moisture (0.0555g, SD = 0.0546) and females at 20% moisture (0.0326g, SD = 0.0326). The sample sizes, however, varied across treatments, with females at 10%

moisture content having only three samples with measurable feeding, while males at 20% moisture had the highest count (n = 16). A bar plot (Figure 3.1e) illustrated the variation in sample sizes across moisture levels.

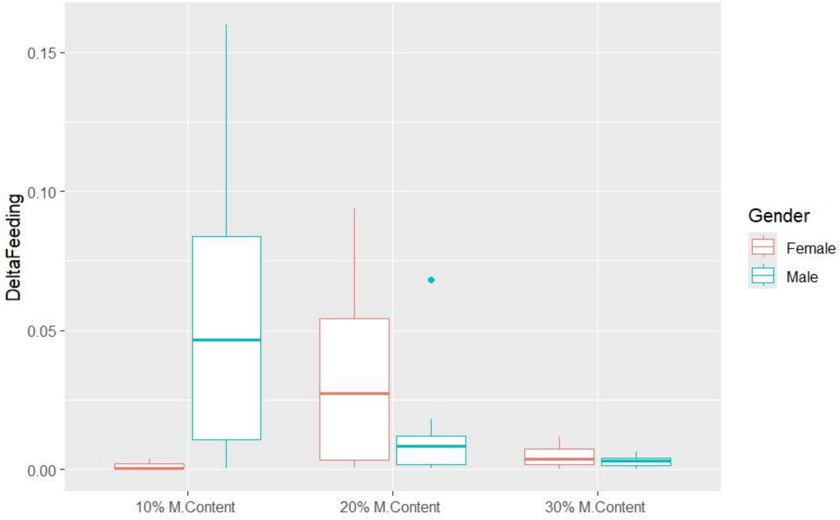


Figure 3.1c: Box Plot Showing Feeding Mass Consumed by Maize Weevils Above Zero Delta Feeding at Different Moisture Contents.

The three-sample test for equality of proportion of number of experimental weevils with measurable feeding revealed a marginally significant result ($\chi^2 = 5.95$, df = 2, p = 0.051), suggesting potential differences across moisture levels. Pairwise comparisons indicated a significant difference between 10% and 20% moisture (p = 0.032), but no significant differences between 10% and 30% (p = 0.635) or 20% and 30% (p = 0.143). Confidence intervals for feeding proportions were estimated, with the highest feeding occurrence at 20% moisture (proportion = 0.441, 95% CI = [0.314, 0.575]). A final visualization of feeding proportions (Figure 3.1d and Figure 3.1e) highlighted these differences across moisture levels and sex.

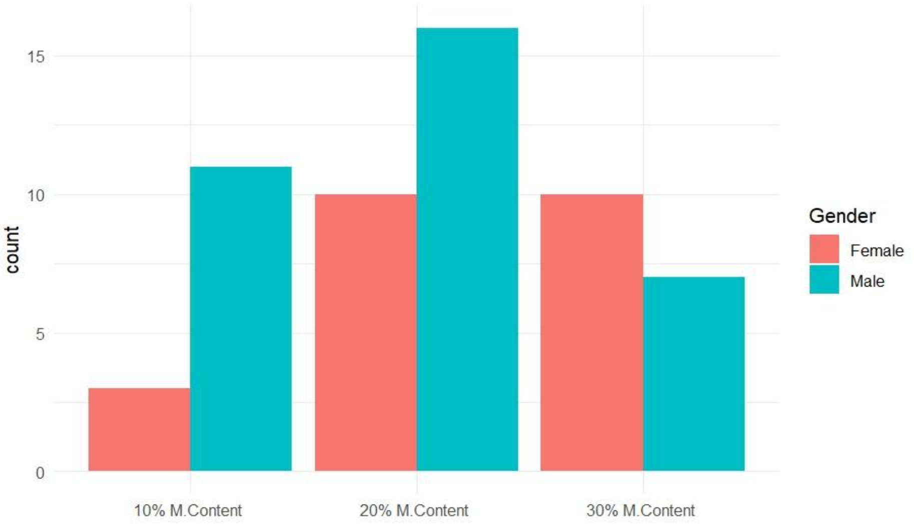


Figure 3.1d: Sex Distribution of *S. zeamais* with Measurable Feeding Across Treatment

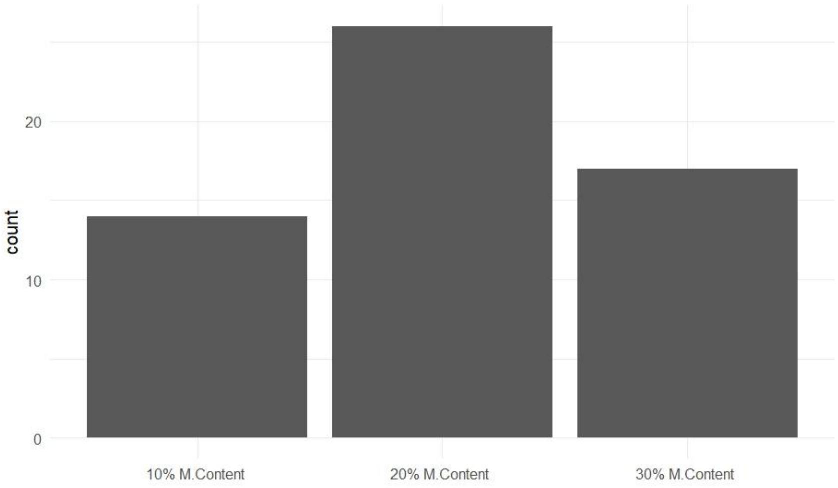


Figure 3.1e. Box Plot Showing Raw Values of Total Number of Measurable Feeding Across Treatment

Discussion

The study examined the effect of moisture content on *S. zeamais* feeding activity. The maximum number of weevils with observable feeding was at 20% moisture, indicating that moderate moisture enhances feeding by offsetting kernel softness and energy expenditure. In contrast, the minimum observable feeding was at 10% moisture, perhaps due to kernel hardness preventing feeding. A proportion test suggested a potential difference in feeding across moisture levels (p = 0.051), with a significant pairwise difference between 10% and 20% moisture (p = 0.032). This marginally significant result suggests that there is a trend for a moisture effect on feeding that a larger sample size may detect as significant. This agrees with previous findings that weevil infestation and feeding behavior are influenced by moisture content of grain in storage. The grains more prone to infestation by the weevil have higher moisture content (Babarinde & Kolawole, 2012; Mandizvidza et al., 2015). Similarly, with varying moisture levels, feeding as well as oviposition activities differ in the rice water weevil *Lissorhoptrus oryzophilus* (Stout et al., 2002). These findings further support this relationship, as we observed that *S. zeamais* responded differently to grains with varying moisture contents, reinforcing the role of moisture in shaping infestation dynamics. At 10% moisture, the average feeding rate was -0.00530 g for females and -0.00768 g for males, suggesting minimal or no feeding, and possibly weight loss. At 20% moisture, males showed a slight positive mean (0.00159 g), indicating some feeding, while females still had a negative mean (-0.00245 g). only measurable observed feeding values were analyzed in (Figure 3.1c). These are cases where the change in weight of the experimental kernel was greater than the average change in weight of the control samples. Measurable observed feeding dataset showed the highest mean feeding rate for males at 10% moisture (0.0555g, SD = 0.0546) and females at 20% moisture (0.0326g, SD = 0.0326). The sample sizes, however, varied across treatments, with females at 10% moisture content having only three samples with measurable feeding, while males at 20% moisture had the highest count (n = 16), which contrasts with previous research that suggests females, with higher energy demands for reproduction, feed more consistently (Van Dzuong & Long, 2019). The slight positive mean (0.00159g) in male feeding behavior at lower moisture levels may reflect an opportunistic strategy in response to resource scarcity. Additionally, the small number of measurable feeding females at 10% moisture (n = 3) may have introduced variability, complicating sex-based comparisons. Similar patterns have been observed in *Rhyzopertha dominica*, where females exhibit more foraging behavior under resource-limited conditions (Cordeiro et al., 2016), further supporting the idea that environmental constraints influence feeding strategies differently cross sexes.

Contrary to the initial hypothesis, males showed slight positive mean feeding particularly at 10% moisture, while females, despite elevated reproductive energy demands, fed less under low-moisture conditions. This suggests that females require stable conditions for consistent feeding, whereas males may adopt an opportunistic approach, driven by competition and dispersal pressures (Carval et al., 2015; Li & Kokko, 2019). Although no visible mold was found during the 24-hour experiment, male feeding rate remained even at 30% moisture. If this was the case, feeding behavior would be shaped differently for each sex, implying a trade-off between diet quality and moisture availability. This possible relationship between moisture, fungal growth, and feeding behavior is consistent with earlier studies that demonstrated the species- and life-stage-specific effects of volatile organic compounds (VOCs) generated by fungi on insect feeding preferences. For instance, *Sitophilus oryzae* interacts more with grain that has been infected by *Aspergillus flavus's* in the sexual growth stage compared to the asexual growth stage (Ponce et al., 2022). Similarly, larvae of *Tenebrio molitor* exhibit species-specific behavior, avoiding *Fusarium avenaceum* but preferring kernels infested by *F. proliferatum* and *F. poae* (Guo et al., 2014).

Both the males and the females *S. zeamais* exhibited their minimal feeding rate at 10% moisture with no difference between sexes. This suggests a similar physiological response to moisture stress, potentially driven by metabolic or genetic factors. While *S. zeamais* populations are typically female-biased, early colonizing groups tend to have a higher proportion of males, which may influence feeding dynamics (Dix & All, 1986). Notwithstanding these results, sample size differences between treatments could have influenced statistical power, especially for females at 10% moisture. Environmental conditions, with temperature maintained at 24°C (± 0.5°C) and relative humidity at 60%–70%, were controlled ensuring that variations in feeding were primarily influenced by moisture content rather than broader abiotic factors. Temperature fluctuation in subsequent research should explore its effect on *S. zeamais* feeding, weight loss, and reproduction. Observational study may assist in establishing whether and how males respond with exploratory feeding behavior when under moisture stress. Further research should also explore how *S. zeamais* survival and reproduction are influenced by fungal metabolites and feeding activity. Understanding the microbial associations between weevil feeding and moisture-rich kernels could provide valuable insights into postharvest pest dynamics.

Conclusion

With ideal feeding taking place at 20% moisture content, this study emphasizes the important influence of moisture content on *Sitophilus zeamais* feeding behavior. Feeding activity at lower moisture rate was higher among males than females, which may be a reflection of sex-dependent responses to resource abundance, even though females were expected to have higher food requirements due to greater energy demands. These results demonstrate the intricate connections among weevil consumption, food quality, and moisture.

3.2 Larval development

Introduction

Environmental conditions, particularly during early developmental stages, play a crucial role in influencing growth, reproduction, and long-term fitness in insects, including stored-product pests such as *Sitophilus zeamais* (Bateson et al., 2014; Bradshaw, 1965; Eyck et al., 2019). Maternal oviposition choices directly influence offspring performance, including larval development and survival (Agrawal et al., 2002; Ballabeni et al., 2001; Craig et al., 1989). Factors like food quality, moisture availability, and predation risk shape reproductive success and adult traits (Craig et al., 1989; Mainali et al., 2015; Rajapakse & Walter, 2007). Variation in resource quality during development affects adult body condition, reproductive performance, and fitness (Dmitriew & Rowe, 2011).

Grain moisture content is a critical factor that significantly influences the biology and behavior of *S. zeamais*, affecting egg viability, larval survival, and adult emergence (Powell & Floyd, 1960; Sedlacek et al., 1991). While related species such as *S. granarius* and *S. oryzae* have been extensively studied in this context (Longstaff, 1981b; Richards, 1948; Segrove, 1951), research on *S. zeamais* remains limited. Grain moisture content includes one of the most essential factors that have a very decisive effect on the biology and behavior of *S. zeamais*. Optimal moisture levels promote larval survival and adult emergence, while both excessively low and high moisture content hinder developmental processes and reduce reproductive success (Sedlacek et al., 1991; Strong & Sbur, 1964).

Despite the importance of moisture content, the quantitative relationship between moisture levels and the biology of *S. zeamais* has not been thoroughly investigated. The oviposition behavior of *S. zeamais* is highly adaptive, with females modifying egg-laying strategies based on host grain moisture content, which in turn affects offspring viability and reproductive success (Honěk, 1993; Smith, 1987). This adjustment influences egg distribution, adult emergence rates, and progeny viability (Danho et al., 2002; Stejskal & Kučerová, 1996). However, while studies have shown that high grain moisture contents reduce the efficacy of protectants against *S. zeamais* (Mutambuki, 2013; Superfine, 2012) much remains unknown about the moisture-related effects on life-history traits such as body weight, sex ratio, and progeny emergence.

Sitphilus zeamais can lay 38.67 eggs on average in 145 days, and the highest egg production is in days 55-95 (Van Dzuong & Long, 2019). Maize has been found to be a preferred host for *S. zeamais*, which is more fecund (290.30 eggs/female) than other cereals (Salim et al., 2023). Moisture content can be one of the most significant parameters that determine egg viability and larval survival; at optimal levels, moisture ensures proper development. Moisture content influences developmental traits and reproductive capacity as seen in the carob moth, where lower moisture content in fruit increased larval mortality, extended developmental times, and reduced egg production (Nay & Perring, 2006).

Environmental factors, including moisture and temperature, are known to affect sex determination in various species. In some reptiles, wetter and cooler conditions produce more males, while drier and warmer conditions favor females (Lolavar & Wyneken, 2017; Sifuentes-Romero et al., 2018). Similarly, in insects, abiotic stresses such as temperature, nutritional condition and humidity could affect hormonal and genetic signals governing sex determination and create sex ratio bias (Verma et al., 2024). The impact of moisture on sex ratio has been studied in various organisms, but its influence on *Sitophilus zeamais* remains unexplored. Understanding how moisture affects sex ratio in *S. zeamais* is important, as it could shed light on population dynamics and the ecophysiology of *S. zeamais* in varying moisture condition. In addition, grain weight loss and damage following *S. zeamais* infestation may be dependent on moisture levels. For instance, earlier research showed that *S. zeamais* causes grain weight losses of up to 21.54% in wet conditions (Arrahman, et al., 2022) and 35.8% in open stored conditions (Likhayo et al., 2018).

The objective of this study was to compare the effect of different moisture levels in maize grains of *S. zeamais.* It explores, particularly, the effect of moisture content on number of emerged offspring (F1 progeny emergence and weight), grain damage, developmental time, and sex ratio (male:female). Understanding these factors is crucial to predicting how populations of *S. zeamais* may evolve in storage environments, improve the pest management procedures and provide new insight into grain moisture influences on growth and reproduction of *S. zeamais* that are relevant to a wider set of knowledge on stored-product insects' ecology and biology.

Materials and Methods

Sitophilus zeamais were originally sampled from field corn infested in Tift County, Georgia, and cultured over several generations in the Salzman Lab under standard conditions (24-25°C, 60-70% relative humidity, and a 12:12 light/dark photoperiod, cite incubator here). To ensure uniformity, adult weevils of similar age and size were chosen. Maize grains were stored at -20°C for one week to kill any potential contaminants and then equilibrated for 36 hours and conditioned to three moisture levels: 10% (low), 18% (medium), and 20% (high). The study examined the effect of grain moisture content on *S. zeamais* F1 offspring emergence, adult weight at emergence, sex ratio, and grain damage. For each moisture treatment, 10 kernels were placed in 2 oz plastic containers with 3 tiny perforations in the lids to allow air circulation. Three males and three females of the adult *S. zeamais,* were sexed based on rostrum and abdominal sternite morphology under a microscope (Halstead, 1963) and introduced into each container to ensure balanced mating and oviposition. The experiment had 30 replicates per treatment. Adult weevils were removed via sieving after a week of mating and oviposition, and infested kernels were kept in their respective containers for development of larvae.

Containers were monitored daily for the emergence of adults. Data collected included temperature and relative humidity, number of adults emerged, each adult's date of emergence and weight, emergent offspring total per treatment, and kernel damage. To minimize potential spatial effects, treatments were set randomly within the incubator. Grain damage was taken at the end of the experimental period. All kernels were inspected with a hand-held magnifying glass and categorized as undamaged, insect-damaged (existent feeding holes), broken (mechanical damage or damage not caused by existing holes), or insect-damaged and broken. Developmental time was calculated as the number of days between parent adult removal and F1 progeny emergence determined.

$$\text{Percentage insect damaged grain } = \frac{Nd}{(Nd + Nu)}\ x\ 100$$

with Nd representing the number of insect damaged grains, and Nu representing the number of undamaged or non-insect damaged grains (Boxall, 1986).

Statistical Analysis

All statistical analyses were performed with R (version 4.4.1). Generalized linear mixed models with negative binomial distribution were used to estimate emergence success with treatment and sex as fixed and replicate as a random factor. Model fit was tested with residual diagnostics (DHARMa package), and the significance was tested with Type II Wald chi-square tests. Estimated marginal means (EMMs) were back-transformed for inference. For F1 emergence weight, a one-way ANOVA was conducted to test treatment effects, and Tukey's HSD to make pair-wise comparisons. Shapiro-Wilk and Kolmogorov-Smirnov tests were utilized to test normality; where there was violated normality, non-parametric tests such as Kruskal-Wallis and Wilcoxon rank-sum were conducted. Chi-square tests were used to test differences in sex ratios between treatments. Development time was fitted with a linear model, and comparisons between male and female weevils were made with Mann-Whitney U tests. The Shapiro-Wilk test revealed that the percentage damage data was not normally distributed (W = 0.9042, $p < 0.001$).

Results

A total of 165 F1 emergence events were assessed in the three-moisture treatments: 10% (n = 9), 18% (n = 69), and 20% (n = 87). The sex ratio showed that at 10% t females66.7%; males 33.3% at 18%, females: 43.5%; males 56.5% at 20%, females: and 49.4%; males 50.6 at moisture content (Figure 3.2a). Chi-square tests revealed no statistical difference in sex ratios between treatments (p = 0.317, p = 0.279, p = 0.915), which implies that the relative number of males and females was not affected by the moisture content.

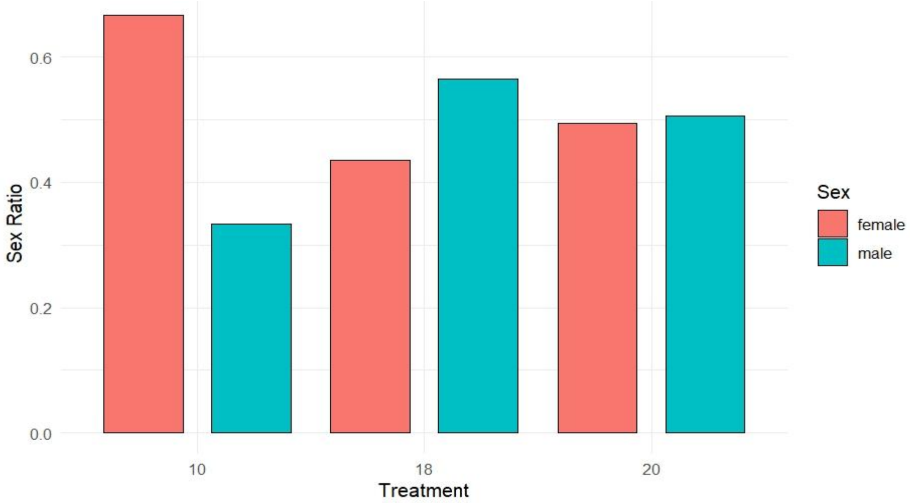


Figure 3.2a: Impact of Moisture Content on Sex Ratio in *Sitophilus zeamais* F1 Progeny Emergence

The highest emergence occurred at 20% moisture, but it was more consistent at 18%, with more pronounced peaks at 20% (Figure 3.2b and 3.2c). A generalized linear mixed model (GLMM) demonstrated a significant impact of moisture on emergence ($\chi^2 = 12.45$, df = 2, p = 0.002), while sex ($\chi^2 = 0.78$, df = 1, p = 0.377) and the interaction between treatment and sex ($\chi^2 = 1.12$, df = 2, p = 0.571) showed no significant effects. The most consistent emergence was observed at 18% moisture (mean = 42.7, SE = 3.2), followed by 20% (mean = 36.5, SE = 2.8), and lastly at

10% (mean = 21.3, SE = 2.1). Overall, emergence was faster and higher in the highest moisture content grain (Figure 3.2c).

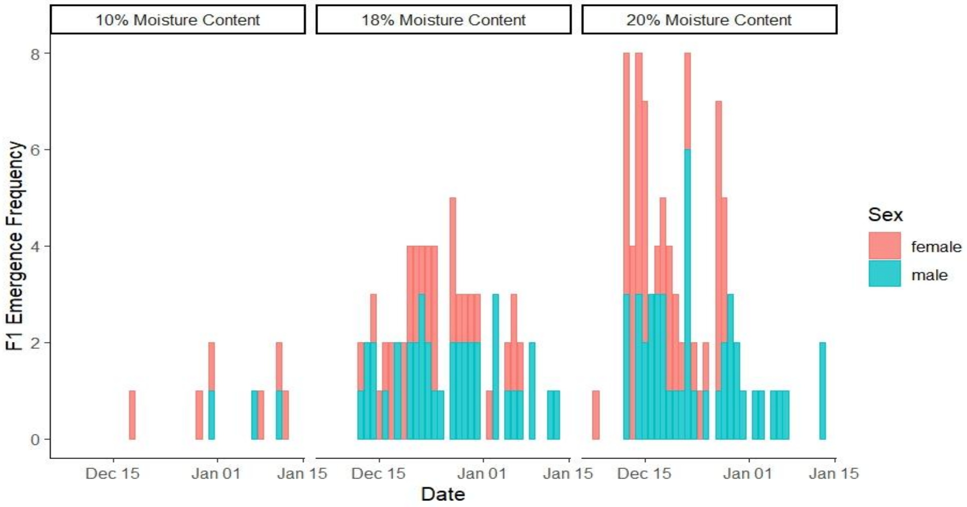


Figure 3.2b: Effect of Moisture Content on *Sitophilus zeamais* F1 Emergence Patterns

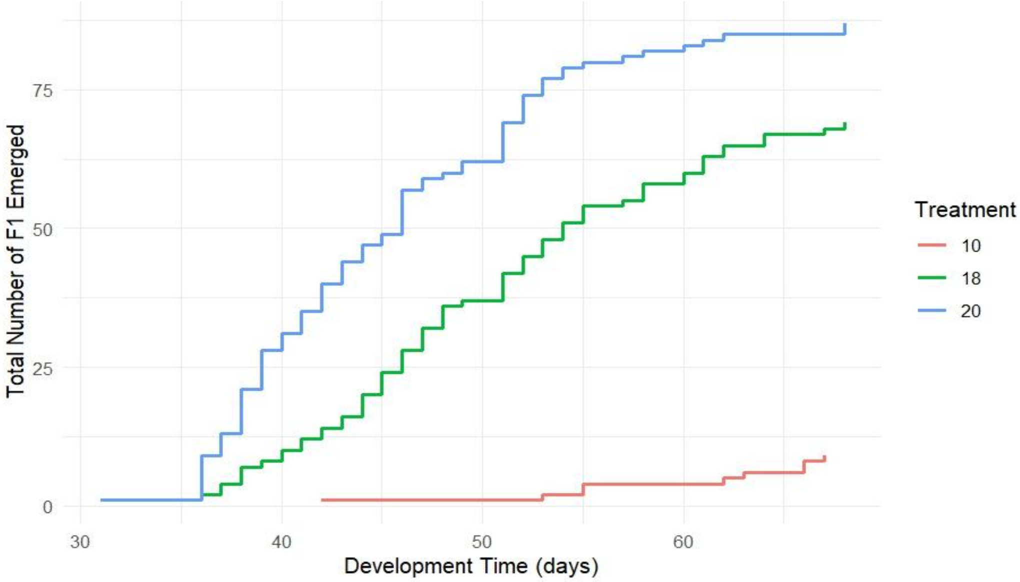


Figure 3.2c: Cumulative *Sitophilus zeamais* F1 Emergence Over Time Across Moisture Treatments

F1 emergence weight varied among treatments (Figure 3.2d). F1 progeny at 10% moisture averaged 0.00323 g (SD = 0.000408), at 18% moisture averaged 0.00318 g (SD = 0.000428), and at 20% moisture averaged 0.00336 g (SD = 0.000358). ANOVA showed a significant effect of moisture on larval weight (F(2,162) = 4.457, p = 0.0131), with post-hoc Tukey's HSD showing F1 at 20% moisture was significantly heavier than those at 18% moisture (p = 0.00998), but no significant difference was found between 10% and 18% or 10% and 20%.

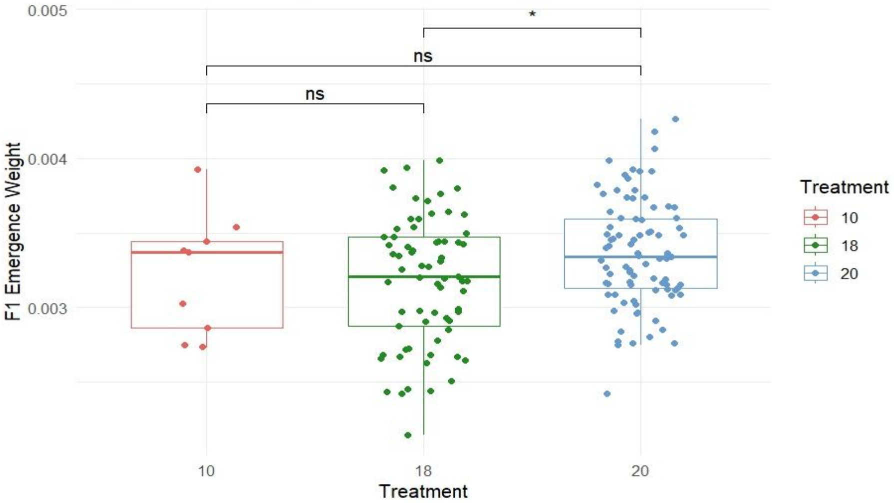


Figure 3.2d: Distribution of *Sitophilus zeamais* F1 Emergent Body Weight Across Treatments.

Development time significantly differed with moisture treatments (χ^2 = 9.83, df = 2, p = 0.007), with larvae at 18% (mean = 32.5 days, SE = 1.8) and 20% moisture content (mean = 34.1 days, SE = 2.0) developing faster than those at 10% (mean = 39.8 days, SE = 2.4) (Figure 3.2c). When male and female development time was compared within each treatment, there were no statistical differences (χ^2 = 0.56, df = 1, p = 0.452). However, females appeared to develop slightly faster than males across all treatments (Figure 3.2e). At 10% moisture, males took 62.1 days on average to develop, while females took 57.7 days. Similarly, at 18% moisture, males developed in 51.7 days, while females developed in 47.3 days. The trend was repeated at 20% moisture, with males requiring 46.9 days and females 42.5 days. Despite these differences, the sex-based variation in developmental time was not statistically significant.

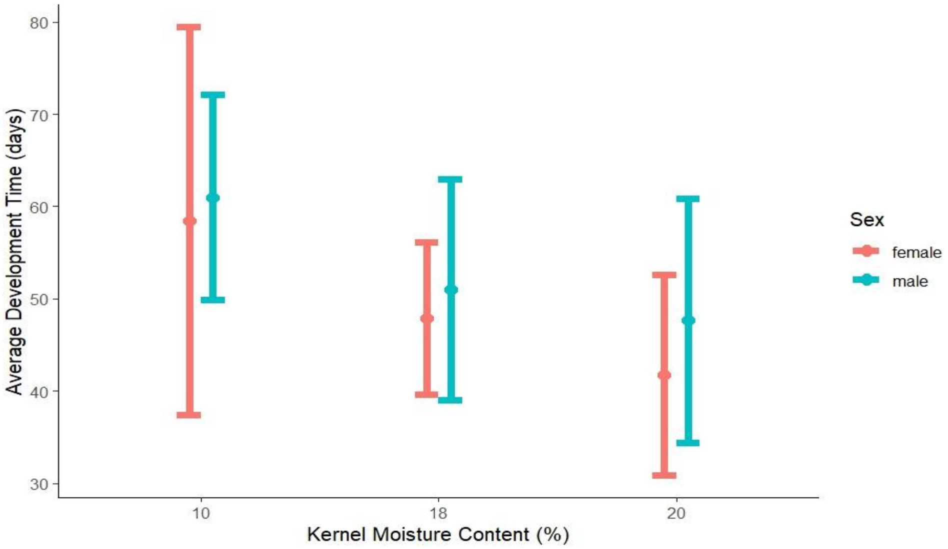


Figure 3.2e: Developmental Time Across Treatment

For percentage damage, the Kruskal-Wallis test revealed differences between treatments (χ^2 = 19.72, $p < 0.001$). Post-hoc Dunn test revealed statistically significant differences between treatments 10 and 18 ($p = 0.00598$) and between treatments 10 and 20 ($p < 0.0001$) in percentage damage but no difference was found between treatments 18 and 20 ($p = 0.6725$). Corn kernel damage varied with moisture. The 10% moisture content treatment had the lowest mean damage (17.7% ± 8.62%), while treatments 18% moisture content (31.0% ± 16.0) and 20% moisture content (37.3% ± 19.6) showed significantly higher damage levels. Boxplots (Figure 3.2f) confirmed these trends, with treatment 10% moisture content consistently exhibiting lower damage.

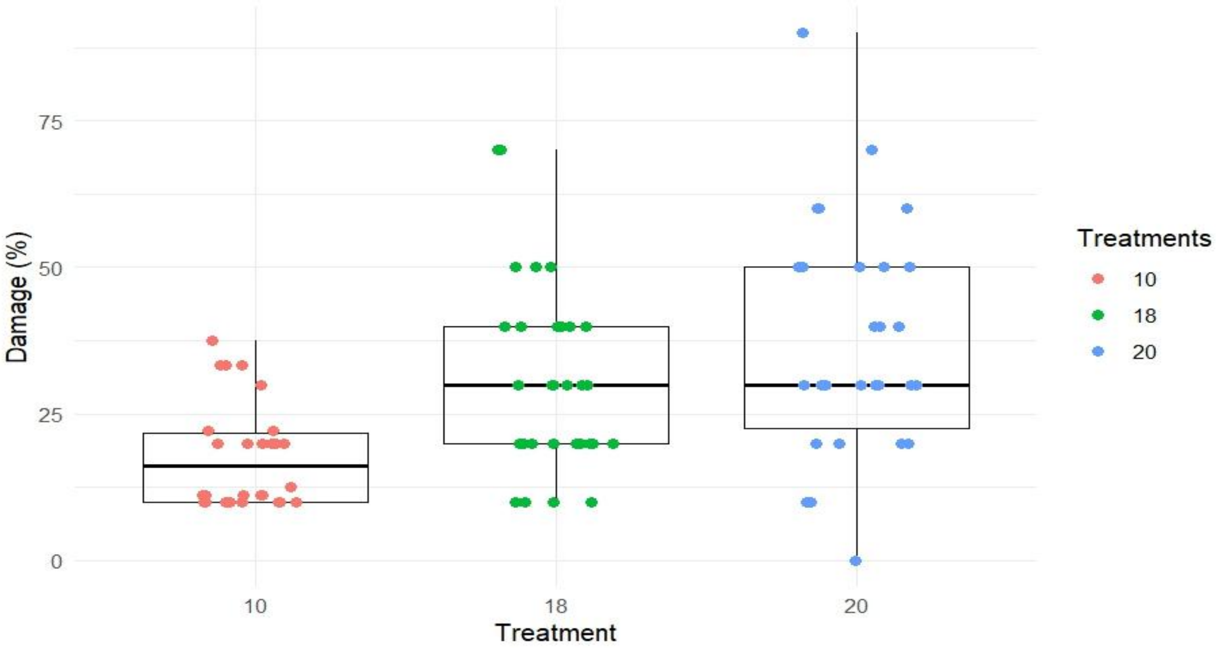


Figure 3.2f: Boxplot showing Percentage Damage by Treatment

Discussion

This study identifies moisture content as a key factor in *S. zeamais* F1 emergence and development. Emergence was fastest and highest at 20% moisture content, followed by 18%, and was lowest at 10% indicating that higher moisture supports larval development and adult emergence (Powell & Floyd, 1960). While emergence at 18% was evenly distributed, 20% showed more peaks. Moisture had minimal effect on the sex ratio, with females comprising 66.7% at 10%, 43.5% at 18%, and 49.4% at 20%, supporting previous findings that environmental factors influence insect growth but not sex determination (Pittendrigh et al., 1997; Throne, 1994). As *S. zeamais* sex ratios vary between generations (Dix & All, 1986), These results suggest moisture alone does not drive sex allocation. Further research is needed to explore potential physiological or behavioral influences.

Moisture content significantly impacted *S. zeamais* F1 emergence success (p = 0.002), with maximum emergence being observed at 18% and 20%, and minimum at 10%. This finding affirms the requirement of moisture for larval feeding, metabolism, and pupation, while desiccation stress induced by low moisture content (10%) suppresses development (Hagstrum & Milliken, 1988; Punzo & Mutchmor, 1980). Moisture acts in combination with temperature to influence insect growth, tending to act more at temperatures near optimum (Hagstrum & Milliken, 1988). The most stable rate of emergence was 18%, followed by 20% and 10% moisture content. The emergence at 18% moisture content was more uniformly distributed over time, but the overall emergence peaked at 20% moisture content. This could be because a more gradual emergence pattern is supported by a stable balance between moisture loss and availability. The more intense emergence at 20% moisture content, on the other hand, might be explained by rapid development brought on by high moisture levels at first, followed by decreased moisture availability. This supports the important role of moisture in the population biology of stored-product insects (Powell & Floyd, 1960). Similar trends in thrips and beetles link emergence to moisture content (Holland et al., 2007; Juncá-Morales et al., 2025). *Sitophilus zeamais* progeny emerged at higher rates from corn with 12.3% moisture compared to 9.7%, particularly at 22°C and 29°C (Sedlacek et al., 1991), suggesting optimal development occurs within a moisture range. Moisture influences larval development to a greater degree than temperature, particularly at species' thermal optima (Hagstrum & Milliken, 1988), highlighting the need for further research on moisture variations in stored environments.

Moisture content significantly impacted F1 progeny emergence weight with the highest mean weight observed at 20% moisture content, significantly higher than 18% ($p = 0.01$). No significant differences were found between 10% and 18% moisture content ($p = 0.938$) or between 10% and 20% moisture content ($p = 0.568$). Greater moisture content likely supports growth by enhancing nutrient access utilization (Cammack & Tomberlin, 2017; Kröncke & Benning, 2022). On the other hand, to make up for water loss by generating metabolic water, insects typically consume more food in drier environments. Nevertheless, this increased consumption of food frequently results in slower development and smaller body size rather than faster growth (Fraenkel & Blewett, 1944). The greater F1 weight observed at 20% moisture content confirms the role of moisture in optimizing digestion and growth, yet the absence of significant differences between 10% and 20% suggests other factors, such as texture of the grain or microbial interaction may also influence growth. Moisture influenced developmental time (p = 0.007) with 18% and 20% moisture content treatments developing faster than 10% treatments. Development was slowest at 10% moisture content, likely due to difficulties in maintaining water balance, which could have influenced enzymatic activity and metabolism. For instance, insects display developmental plasticity in response to moisture changes (Barnes, 2021), with diet moisture influencing larval development, weight, and adult emergence, as seen in flies breeding on carrion (Bauer et al., 2020). This study showed moisture content to have significant effects on insect growth, with the level of moisture decreasing progressively across the experiment. Initial moisture content (20% and18%) declined to approximately 12% moisture content towards the end of the experiment, except for the 10% moisture content treatment, which slightly increased to 11.5%. This decline likely caused desiccation stress, impacting growth and modifying emergence patterns. Future research should employ using desiccators with saturated salt solutions to ensure equilibrium grain moisture content stays stable ((Ellis & Hong, 2007). Low moisture enhances mortality and delays development, whereas ideal moisture enhances rapid growth (Hagstrum & Milliken, 1988; Nay & Perring, 2006). Although faster development and emergence were made possible by higher initial moisture, variation in emergence peaks was influenced by the decrease in kernel moisture. Although hygroscopic absorption is indicated by the slight increase in moisture at 10% treatment, the initial moisture deficit was not sufficiently addressed because development was still delayed. Future research should determine the ideal peak moisture levels for insect development and examine how insects adjust to future moisture reductions.

Males generally took longer to develop, consistent with findings that developmental time is often female-skewed due to reproductive effort (Jarošík & Honek, 2007). Despite sexual size dimorphism (SSD) tending to associate with developmental time variation in the larva (Teder, 2014), no interacting effect was apparent between sex and moisture content, suggesting that both sexes responded in like manner to change in moisture. Larger sample sizes and future studies are needed to substantiate these patterns. In turtles, *Trachemys scripta elegans* moisture during embryogenesis influences developmental rates, with cold and damp conditions delaying development (Sifuentes-Romero et al., 2018) and wetter substrates produced more males (Sifuentes-Romero et al., 2018). Similarly, a meta-analysis determined that substrate dampness significantly affects turtle sex ratios, but not for other squamates (Bell et al., 2025).

While weight change of the corn was not explicitly tested for, we did observe that the 10% moisture content treatment, while having lower emergence, resulted in higher weight loss (0.462%) compared to the 20% (0.165%). This was likely due to longer developmental time (mean = 39.8 days) which lengthened the feeding period and consequently the weight loss despite fewer numbers of emerging F1 progeny. Similar outcomes were observed for *Bactrocera minax* larvae, where low moisture extended development and feeding duration (Li et al., 2019). In contrast, 18% and 20% moisture treatments had higher F1 emergence rates but also higher damage (31.0% and 37.3%, respectively), consistent with studies relating higher emergence to increased kernel damage (Hamby & Zalom, 2013). The lower moisture content in the 10% treatment may have induced more intensified feeding activity, as observed in *Manduca sexta* (Van’t Hof & Martin, 1989).

These results show how significant a role moisture plays in insect development and damage, and that further research on environmental conditions such as temperature and humidity, as well as with other stored product insects, may optimize pest management in storage systems. Investigating the physiological mechanisms of weight loss and damage, particularly in relation to feeding and development, would offer valuable insights into *S. zeamais* ecophysiology.

Conclusion

Moisture content had a significant effect on *S. zeamais* emergence, weight, and development time, with optimal emergence and development at 18–20% moisture. Sex ratio was not influenced, however, which implies that moisture alone does not influence sex allocation. Low moisture content (10%) extended development time, perhaps due to physiological stress, with possible consequences for overall survival and pest dynamics. These findings stress the overriding role of moisture in the regulation of the behavior of storage-product pests, particularly for growth, emergence, and survival.

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