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School of Life Sciences

Department of Biological Sciences and Biotechnology

PHYSIOLOGICAL AND ECOLOGICAL RESPONSES OF THE LARGER GRAIN BORER, *PROSTEPHANUS TRUNCATUS* (HORN) TO CHANGING ENVIRONMENTS: IMPLICATIONS FOR POPULATION DYNAMICS AND MANAGEMENT

By

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DECLARATION AND COPYRIGHT

I, Shaw Mlambo, declare that this dissertation is my own original work and that it has not been presented anywhere and will not be presented to any other University for a similar or any other degree award.

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CERTIFICATION

The undersigned certify that they have read and hereby recommend for acceptance by the School of Life Sciences a dissertation titled: **Physiological and ecological responses of the larger grain borer, *Prostephanus truncatus* (Horn) to changing environments: implications for population dynamics and management**, in fulfilment of the requirements for the degree of Doctor of Philosophy in Biological Sciences at BIUST.

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Date: 20 August 2025	Date: 20 August 2025	Date: 20 August 2025

DEDICATION

I dedicate the success of this work to my wife Anitah Tavenhave Mhindu and our daughter Ginelle Mlambo.

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ABSTRACT

The rapid change in environments owing to anthropogenic activities and climate change has reshaped the geographical range and status of different insect pests of economic importance. Further, the mechanisms by which conspecific and allospecific species phenotypes vary and how that influences species adaptation in novel environments are poorly understood. The larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), is one of the quarantine pests which poses serious threats to stored maize and dried cassava tubers and has continued to expand its ranges in Africa. However, physiological and ecological data required to map the dispersal pathways and factors limiting geographical distribution of such pests in diverse environments are largely understudied. A combination of literature reviews, field (questionnaire survey and pest monitoring through pheromone baited traps) and laboratory studies were conducted to determine (i) the presence and geographical range of *P. truncatus* in Botswana (Chapter 2), (ii) local farmers' knowledge, practices and perceptions on cereal postharvest management including the efficacy of current storage technologies against *P. truncatus* (Chapter 3), (iii) the drivers and implications of *P. truncatus* and *Spodoptera frugiperda* biological invasions in Africa (Chapter 4), (iv) effects of increasing temperatures on the transgenerational (Chapter 5) and intergenerational (Chapter 6) responses of *P. truncatus*, (v) feeding rates and effects of maternal host preferences on progeny fitness (Chapter 7) and (vi) effects of intra- an interspecific competition on *P. truncatus'* physiological and ecological performance (Chapter 8). Standardised physiological (critical thermal maxima [CT_{max}], critical thermal minima [CT_{min}], heat knockdown time [HKDT], upper lethal temperatures [ULTs]) and ecological performance (% maize grain damage, % grain weight loss, progeny production, % insect feeding dust) traits were measured under controlled temperature and relative humidity conditions in climate chambers. Results confirmed, for the first time, the presence of *P. truncatus* in Botswana, but its distribution is still patchy. Although the pest seems not yet well-established inland, the current farmer practices dominated by use of botanical pesticides makes them vulnerable if *P. truncatus* was to become dominant. Lack of information and awareness of the dangers that *P. truncatus* pose and lack of improved grain storage facilities further expose local smallholder farmers to this threat. Laboratory assays showed behaviourally plastic responses to increased temperatures and varying hosts. First, trait-dependent thermal plasticity responses are passed on to offspring through transgenerational and intergenerational plastic physiological responses which mediate *P. truncatus* progeny fitness. Alongside, maternal experiences or decisions by offspring through transgenerational plasticity act as signals for adaptation to a host. Ecological performance of *P. truncatus* was high at 25 and 30°C in response to temperature suggesting high pest activity under elevated temperature conditions. This may mean that *P. truncatus* poses serious threats to food security with increasing temperatures under climate change. However, damage was highly suppressed at higher suboptimal temperatures of 35°C. *Prostephanus truncatus* failed to survive on mopane wood suggesting that the wood may not be a suitable host for the pest. The study shows *P. truncatus* physiological adaptative responses to changes in the environment and climate and calls for concerted efforts to monitor the pest inland, forewarn farmers of the dangers of the pest and train them on appropriate efficacious grain storage technologies to manage the pest. This work contributes insights into the ecology and physiology of *P. truncatus*, which are important in developing models for early warning and control, as well as integrated national and regional pest management strategies against the pest.

CHAPTER 1

General introduction

1.1. Background

The human population is expected to reach 10.4 billion by 2080 (Gerland et al. 2014; UN 2022). This increase exerts pressure on ecosystems, their integrity, the provision of ecosystem services, food security, and in part, contributes to the spread and successful establishment of invasive species (Millennium Ecosystem Assessment, 2005; Liebhold et al. 2017; Skočajić andNešić, 2021). Various overarching trends e.g., climate change, globalisation, anthropogenic activities and agricultural intensification have contributed to the dispersal of these invasives to sub-Saharan Africa (SSA), and indeed globally (Crowl et al. 2008; Hulme, 2009; Arthur et al. 2019; Skendžić et al. 2021; Harman et al. 2024). Recent decades have seen the African continent invaded by many different insect pest species that have caused significant impacts to the agricultural sector through damage and loss on crops of economic importance (Szita and Gyo, 2021). Some of the major invasive species that have been reported include the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Goergen et al. 2016); the tomato leaf miner, *Tuta absoluta* (Meyrick) (Garzia et al. 2012); the spotted stem borer, *Chilo partellus* (Swinhoe) (Diagne et al. 2021a); the larger grain borer (LGB), *Prostephanus truncatus* (Horn) (Farrell and Schulten, 2002; Quellhorst et al. 2020); and other pest invaders (Sileshi et al. 2019; Tarusikirwa et al. 2020; Timilsena et al. 2022; Nyamukondiwa et al. 2022); that have brought significant biosecurity threats to the agricultural industry in SSA (Mlambo et al. 2024a) and globally (Nyamukondiwa et al. 2022). Notably, most of the invasive species and research conducted on invasive species have focused on field crop pests like *S. frugiperda*, *C. partellus* and *T. absoluta* and few studies have focussed on invasive pests of stored products, particularly those of quarantine importance. The current study focuses on *P. truncatus*, a postharvest invasive pest of maize grain and dried cassava. The activity of these invasive species is exacerbated by various biotic and abiotic factors with increasing temperatures due to climate change and associated changes in environments.

1.2. Climate change and pest invasions

Changes in global climatic conditions, e.g., increased temperatures, and increased anthropogenic activities through international trade and agricultural intensification (Clusella-Trullas et al. 2016) have created enormous insect pest pressure on agricultural production systems (Singano et al.

2020; Szita and Gyo, 2021). Increasing temperatures, for example, have significant effects on insect physiological and ecological performance (Musolin, 2007; Sinclair et al. 2012; González-Tokman et al. 2020), including stored product insects (Gerken and Morrison, 2022). Invasive insect pests are reproducing and colonising new territories at faster rates than the local pests (Seebens et al. 2017; 2018) and becoming more difficult to control (Nyamukondiwa et al. 2022). For example, synthesis reports suggest that, globally, the costs of invasive species including invasive insects, exceed US$423 billion annually (IPBES, 2023), a figure expected to double every six years (Diagne et al. 2021b). Estimates for the period between 1980 and 2019 suggest that these costs by invasive species were of a similar magnitude (US$ 1,2 trillion) to those of natural hazards (US$ 1,9 trillion for storms and US$ 1,1 trillion for earthquakes), but the costs of invasive species are increasing at a faster rate (Turbelin et al. 2023). Warming climatic conditions also characteristically alter insect physiology (e.g., poikilothermic responses) in terms of metabolism and population growth rates (Deutsch et al. 2018; Skendžić et al. 2021). High temperatures increase insect metabolic rates and thus functional responses (feeding and damage to crops and harvests) (Irlich et al. 2009). Furthermore, rising temperatures are expected to affect insect pest fecundity and survival leading to increased or decreased populations depending on species (Schneider et al. 2022; Tonnang et al. 2022). Crop losses will, therefore, increase substantially in cases where rising temperatures increase both metabolic rates and population growth rates due to more generations per year. Winter, on the other hand, is a critical period for tropical insects where increased mortalities are observed due to low temperatures. Increased mean average temperatures will result in warmer winter temperatures, facilitating increased overwintering survival of insect pests (Skendžić et al. 2021). This also quickens the onset of insect attack and increases population densities resulting in increased pest pressure and crop damage in the next growing season (Skendžić et al. 2021; Tonnang et al. 2022). As postulated by the ambient energy hypothesis; growth and reproduction are greater at high temperatures. Thus, increased temperatures will favour growth and shorter life cycle durations, causing insects to produce more generations per year; all contributing to increased crop damage and losses under climate change (Deutsch et al. 2018; Skendžić et al. 2021). Generally, a 2 °C rise in temperatures potentially increases the number of insect generations five-fold increasing crop losses by 10–25 % (World Economic Forum, 2021; Bale et al. 2002). Climate change has also driven the geographical range expansion of insect pests with observed shifts towards new ecological niches created by climate anomalies (Skendžić et al. 2021; Schneider et al. 2022; Gerken and Morrison III, 2022; Harman et al. 2024). Furthermore, increased temperatures can de-synchronize insects and their natural enemies causing uncontrolled natural insect population growth, pest resurgence and/or outbreaks (Skendžić et al. 2021; Harman et al. 2025).

1.3. Anthropogenic activities

Besides climate change, various human activities such as international trade, smuggling and modification of habitats facilitate the movement of insect pests and their establishment in new environments (Turner et al. 2021). The invasion of new territories by insect pests is also facilitated by the movement of commodities through international trade in different forms of transportation (Blackburn et al. 2011; Mlambo et al. 2024). Over 8 billion tonnes of agricultural goods are transported internationally every year (McKirdy et al. 2014). This movement of goods in regional and international trade has acted as routes for hitch-hike by insects, facilitating their spread into new environments (Diagne et al. 2021a; Turner et al. 2021). Furthermore, smuggling of goods through illegal entry points along country borders also results in introduction of insect pests, which create undesirable impacts on agriculture, ecosystems and biodiversity (McKirdy et al. 2014; Tshikhudo et al. 2021). In SSA for example, farmers along border villages can traverse across countries to mitigate food shortages and alleviate price fluctuations and other socio-economic issues (Smart and Smart, 2012; Tshikhudo et al. 2021). In so doing, they may unintentionally bring new pests through unsanctioned 'importation' of agricultural commodities (Golub, 2015). Furthermore, in-country informal trade in grains, for example, inevitably facilitates the distribution of insects following introduction (Nyagwaya et al. 2010). In response, the International Plant Protection Convention (IPPC) was formed to develop international phytosanitary measures and to promote their application thereby ensuring safe trade and environmental protection (IPPC, 2025). However, some travellers evade phytosanitary regulations through non-compliance at border posts, while sometimes the lack of infrastructure and human resources to detect illegal material also results in weak enforcement (Whattam et al. 2013).

The introduction of *P. truncatus* to Africa is linked to grain trade with meso-America (Muatinte et al. 2019; Arthur et al. 2019; Quellhorst et al. 2021). The pest originated from central America where it is known to occasionally infest and cause serious losses in stored maize. The first record and outbreak of *P. truncatus* in Africa was in Tanzania in 1981 in the Tabora region (Hodges et al. 1983). Its first appearance in Africa and the level of damage and losses reported thereafter, were unprecedented, leading to multi-donor funded control programmes in the East African region (Golob, 1988). In Southern Africa, the pest was first reported in Malawi (1991), then Zambia (1993), South Africa (1999), Zimbabwe (2005) (Nyagwaya et al. 2010). The latest reports of detection of *P. truncatus* in Africa include in Mozambique (Muatinte and Cugala, 2015) and Ethiopia in 2023 (Dako and Abebe, 2024). Modelling suggests that the pest is likely to continue expanding into new geographical areas (Arthur et al. 2019; Quellhorst et al. 2021; Harman et al. 2024). *Prostephanus truncatus* is a member of the Bostrichidae family known as wood borers although it has adapted and become a serious pest of stored maize and dried cassava chips (Quellhorst et al. 2021). There are five described species in the genus *Prostephanus* (Table 1.1) (Borowski and Węgrzynowicz, 2011). Members of the Bostrichidae family are commonly known as wood-boring pests. However, *P. truncatus* and a closely related species *Rhyzopertha dominica* (Fabricius, 1792) have evolved from wood-boring diets and have become adapted to feeding on stored grains; maize and wheat/sorghum respectively, with the former also feeding on cassava tubers.

Table 1. 1: A list of members of the Bostrichidae (wood-boring beetles) family. Of these, *Prostephanus truncatus* and *Rhyzopertha dominica* (see Fig. 1.1) have evolved from wood-boring to become serious pests of stored maize and wheat/sorghum respectively.

Order	**Family**	**Genus**	**Species**
Coleoptera	Bostrichidae	*Prostephanus*	*truncatus* (Horn, 1878)
			punctatus (Say, 1826)
			arizonicus (Fisher, 1950)
			apax (Lesne, 1930)
			sulcicollis (Fairmaire and Germain, 1861)
		Rhyzopertha	*dominica* (Fabricius, 1792)

Besides *P. truncatus,* which is an alien invader, SSA is host to various other cosmopolitan insect pests in the value chain of cereal grains. These insect pests include *Sitophilus zeamais*

(Motschulsky), *Sitophilus oryzae* (L.), *Sitotroga cerealella* (Olivier), *Rhyzopertha dominica* (F.), *Tribolium castaneum* (Herbst) among others (Fig. 1.1, Obeng-Ofori, 2011; Zhu et al. 2022).

Figure 1. 1: A list of major insect pests of stored cereal crops common in most parts of sub-Saharan Africa. Images adopted from Zhu et al. (2022).

The insects (both larvae and adult stages) feed on the grain kernels causing damage on grains and reduce grain weight. This also consequently reduces grain nutrition, seed germination quality and market value (Suleiman et al. 2015; Ahmad et al. 2021). The introduction of *P. truncatus* as an alien invader has resulted in two- to three-fold more grain losses than previous recorded across different African countries (Mutambuki and Ngatia, 2012; Quellhorst et al. 2021). Estimates suggest as high as 10–20 % cereal losses are incurred during storage (World Bank et al. 2011). Given the wide range of other storage pests (Fig 1.1), their interactions with *P. truncatus* could also be complementary, further compounding storage losses in grains (Mukundi et al. 2010; Baliota et al. 2022). Furthermore, given that SSA has reported other devastating invasive pests affecting cereals in the field, e.g., *Spodoptera frugiperda* (Lepidoptera: Noctuidae), the impacts of *P. truncatus* can increasingly be felt by farmers owing to potential synergistic effects of the field and postharvest pests. For example, when *S. frugiperda* and *P. truncatus* occupy the same ecological niche, their interactive effects cause a continuum of food losses in the maize value chain (Mlambo et al. 2024a), resulting in high crop loss impact on already vulnerable smallholder farmers.

1.4. Attributes that favour *P. truncatus* thriving in SSA

Prostephanus truncatus has various species attributes including its biology that potentially facilitates its invasiveness. Further, event attributes and traditional practises in invaded regions in SSA favours the establishment of the pest. For example, smallholder traditional storage practises may facilitate infestation including cases where maize cobs are stored on raised platforms exposed to the external environment for drying or shelled maize grains either bagged or in bulk in the house or traditional granary for storage (Hodges et al. 1983; Nyagwaya et al. 2010; Mutungi et al. 2019). In the first report of *P. truncatus* in Tanzania, it was observed that the pest infested maize cobs at physiological maturity whilst still in the fields; laying eggs that would serve as inoculum in storage. It was also observed that losses were higher on unshelled than shelled maize (grain) and that feeding dust produced was correleted to the number of insects in a sample (Hodges et al. 1983). Besides maize grains, *P. truncatus* adult and larval stages were also confirmed to feed on dried cassava and various other wild grass and tree species that act as alternate hosts (Nang'ayo et al. 2002; Muatinte and Van den Berg, 2019). Furthermore, factors such as the lack of an adapted natural enemy in Africa, the ability of the pest to initiate long-distance flight, aggressive aggregation pheromone (Quellhorst et al. 2021), the wide range of suitable domesticated and wild hosts (Muatinte and Van den Berg, 2019) and its ability to attack different other materials such as dried wood, plastic and soap (Nyagwaya et al. 2010; Nwankwo et al. 2016) and its high thermal tolerance (Machekano et al. 2020; Mutamiswa et al. 2021) increases the likelihood of its continued range expansion under global change and particularly in the warming tropical southern Africa (Davis-Reddy andVincent, 2017). This will likely increase the pest status and biosecurity threat as it is already a pest of quarantine importance. *Prostephanus truncatus* has thus, been able to invade new territories (Arthur et al. 2019) and become a seriously damaging pest of especially stored maize and cassava globally (Quellhorst et al. 2021), including SSA (Muatinte and Van den Berg, 2019; Muatinte et al. 2019). Research shows that *P. truncatus* can also attack and cause significant damage to other staple food crops in Africa, including sorghum, millets, wheat, cowpeas and cocoa beans (Shires, 1977) and can also affect their products e.g., grain flour (Hodges, 1986) even though it is not able to breed successfully on these commodities (Athanassiou et al. 2017). Most of these crops e.g., sorghum and millets are increasingly being recommended because of their climate change resilience in

SSA climate hotspots. Thus, the ability of *P. truncatus* to colonise these climate smart crops acts as an adversity multiplier, adding an additional food security/biosecurity threat.

Smallholder farming in SSA is generally characterized by mixed cropping systems where cereals (maize, sorghum, millets), legumes (soya beans, cowpeas, sugar beans and related) and root and tuber crops (cassava, sweet potato) are grown in the same fields within each growing season (Franke et al. 2018). For polyphagous insects, this mixed cropping system provides opportunities for host switching for different reasons, either as preference, alternative food or as refuge. *Prostephanus truncatus* is known to switch between grain and cassava stores in mixed farming communities. Furthermore, adult beetles flee into nearby forests to survive on dead wood when stores are treated with pesticides (Nang'ayo et al. 2002; Nansen et al. 2014; Quellhorst et al. 2021). However, for *P. truncatus*, it is not known how this host switching can affect its fitness traits and environmental adaptation. In many invertebrates, females determine mate choice, propagule size and their spatio-temporal dispersal as well as protection of offspring from biotic or abiotic stress. For example, in oviparous insects, females lay eggs which hatch into progeny on maternally chosen hosts. Such maternal decisions influence progeny knowledge and choices of suitable and alternate hosts as well as oviposition sites in the environment (Slater et al. 2019; Lampasona et al. 2022). Polyphagous insects would be well adapted when there is good synchronization between the pests and the host plant (suitability and availability) and environmental conditions (Singer and Parmesan, 2010; Skendžić et al. 2021). A mismatch of host and environmental conditions manifest as maladaptation with a trade-off in fecundity and mortality (Singer and Parmesan, 2010; Gerken and Morrison III, 2022). It is therefore hypothesised that *Prostephanus truncatus* inflicts significant damage in SSA due to the combination of favorable high tropical temperatures and the availability of a diversity of optimal and alternative hosts.

The biology of *P. truncatus* is one of the key drivers to its dispersal and establishment across heterogeneous environments. *Prostephanus truncatus* thrives at high temperatures and high relative humidity (RH) – having an optimal developmental temperature and RH at 32°C and 80% respectively. Under these optimal conditions, *P. truncatus* completes one life cycle in 27 days (Quellhorst et al. 2021). The adult beetles tunnel into grain and feed from inside the grain tunnels. Further, female beetles make short, perpendicular tunnels for egg laying (Morey, 2023). When eggs hatch, the larvae feed from inside grain until pupation and adult stages. This characteristic of developing inside grain helps the pest evade contact pesticide when applied on grains (Mlambo et al. 2018). Furthermore, the tunneling creates large quantities of feeding dust that can ‘dilute’ the pesticide (Chigoverah and Mvumi, 2016; Mlambo et al. 2017; 2018). The pest is also highly competitive at high temperatures at 25 and 30°C where it has been shown to outcompete native species in introduced environments (Quellhorst et al. 2020). Based on this, it is hypothesised that prevailing favorably high tropical temperatures experienced in SSA therefore favor proliferation of the pest in terms of range expansion and damage caused (Arthur et al. 2019).

The seasonal patterns in SSA are such that a single rainfall season ranging from 4–6 months and a dry season of 6–8 months characterise a calendar year (Nukenine, 2010). Consequently, cereal grain crops such as maize, sorghum and millets are produced during the rainy season, dried and stored for gradual food supply and buffering against price volatility during the dry period (Mvumi and Stathers, 2003; Mlambo et al. 2017; Glantz, 2019). Moreso, farmers store their grain for later sale as market grain prices rise during the dry off-season owing to increased demand (Glantz, 2019). It is during this storage period that farmers suffer losses due to storage insect pests. The length of the dry season and the type of facilities that farmers use to store their grain therefore, become key factors that determine how much losses farmers incur due to storage insect pests. Some reports indicate that farmers can store grain for more than 2 years for fear of or in anticipation of droughts (Nukenine, 2010). The recent changes in global stability with the war in Ukraine (Europe’s breadbasket) and pandemics (e.g., Covid-19) which restricted grain supply even in good seasons further emphasized the need for and importance of prolonged grain storage (Tushar et al. 2023). The vulnerability of smallholder farmers in SSA may therefore be partly due to poor storage technologies that predispose the stored grain to high pest pressure owing to favourable climates.

Smallholder farmers further rely on untested traditional storage methods which predispose their grains to storage insect pests attack. Naturally occurring plant materials (e.g., pyrethrum daisy, *Tanacetum cinerariaefolium*; neem tree, *Azadirachta indica*, and other related botanicals) have often been used in their crude form for insect pest control (Isman, 2006; Bezabih et al. 2022). Whilst botanicals are a cheaper option for grain storage, major concerns on their use include lack of consistency in efficacy due to lack of standardization in their preparation and application, production of unpleasant flavors or discolouration of grain by some botanicals and health safety concerns because of unknown toxicity (Isman, 2006; Stevenson at al. 2014; Sola et al. 2014). It is commonly assumed that botanical pesticides are relatively safer than synthetic pesticides although this may not entirely be true (Phillips and Throne, 2010). Furthermore, commercial application of most botanical pesticides only shows moderate level of grain protection and hence does not guarantee protection of stored grain crops (Phillips and Throne, 2010).

Smallholder farmers in SSA also regularly use synthetic grain protectant pesticidal dusts, and few use improved non-chemical storage facilities (Stathers et al. 2020). The efficacy of synthetic pesticides can be affected under high temperatures. Climate change, particularly increased temperature, has an effect on the efficacy and residual activity of grain protectant dusts (Singano et al. 2019). For example, high temperatures are associated with faster degradation of synthetic pesticides (Delcour et al. 2015). Further, high temperatures shorten insect life cycles and facilitate quicker evolution to pesticides' tolerance and/or resistance (Velázquez-Fernández et al. 2012; Mubayiwa et al. 2018). Further, unregulated use of synthetic pesticides has selected for pesticide' resistance, leading to poor efficacy (Isman, 2006; Phillips and Throne, 2010) including grain protectants (see e.g., Mlambo et al. 2018; Mubayiwa et al. 2018). These factors therefore increase the vulnerability of farmers to postharvest losses. On the other hand, the use of hermetic storage techniques e.g., hermetic bags, cocoons and metal silos, which have improved efficacy due to their airtight properties, is still low in SSA (Moussa et al. 2014; Okori et al. 2024). Hermetic techniques prevent oxygen entry and circulation in the unit causing insect asphyxiation, as the metabolic activity of insects themselves depletes their oxygen supply.

As noted by Ngwenyama et al. (2023), training in grain storage management is crucial to the protection of stored grains. Across many African counties, extension has been biased towards crop field production with little or no emphasis on issues related to postharvest grain management (Muroyiwa et al. 2020), despite the potential negative synergistic effects of combined field and postharvest pests (Mlambo et al. 2024a). Lack of training for both extension officers and farmers on postharvest management of grains including efficacious grain storage technologies have thus been described as the major determinant of losses under smallholder management (Tefera et al. 2011; Midega et al. 2016; Stathers et al. 2020).

1.5. Projected *P. truncatus* trends in Africa

A model 'developed using occurrence and background location from *P. truncatus'* native range in Mexico and Central America', predicted Southern African climate as being 20–40% suitable for *P. truncatus* range expansion (Arthur et al. 2019). This prediction, based on temperature and RH placed Botswana and neighbouring countries: Zimbabwe, South Africa, Namibia and Zambia in the same geographical suitability category for *P. truncatus* range expansion. This is mainly because the pest favours high temperatures and a wide range of RH conditions; 32°C and 65–80% respectively (see Quellhorst et al. 2021). Daytime temperatures in Botswana can reach 40°C while the typical average monthly temperature range is between 15 to 27 °C (Akinyemi and Abiodun, 2019). The temperature range also represents climatic conditions responsible for the successful establishment of *P. truncatus* in many of the confirmed areas (Arthur et al. 2019; Quellhorst et al. 2021; Harman et al. 2024), highlighting the importance of temperature tolerance studies to comprehend the pest's climate responses that are crucial to its management.

A full understanding of the responses of the pest to abiotic stress factors and how that shapes its life history traits currently and in future, both within and across generations is therefore paramount for designing effective early warning systems and pest management strategies (Arthur et al. 2019; Nyabako et al. 2020). For this, critical thermal limits to activity (critical thermal maxima [CT_{max}], critical thermal minima [CT_{min}]), heat knockdown time (HKDT) and upper lethal temperature limits (ULTs) are used as standard metrics to measure insect physiological thermal responses (Angilletta et al. 2002; Chown and Nicolson, 2004; Terblanche et al. 2011). These metrics are reasonable proxies for estimating species ecological niches (Chown and Nicolson, 2004) and are important measures of insect thermal tolerance as they are measured using ecologically relevant static and dynamic standard protocols synonymous with pest experiences under natural environments (Gunderson and Stillman, 2015). A recent meta-analysis showed that information on the relationship between the biology of *P. truncatus* and climate factors, especially how changing climatic conditions affect its transgenerational life history traits, behaviour and functional responses is limited (Quellhorst et al. 2021). This limits the effectiveness of models used to predict its potential spatio-temporal distribution required in proactive quarantine pest management programmes.

Furthermore, farmers are trapped in a conventional synthetic pesticide vicious cycle, where they use chemical grain protectant dusts without guaranteed protection due to lack of effective alternative options (Mlambo et al. 2018; Machekano et al. 2019). There is also dearth of information regarding postharvest management practises by smallholder farmers in Botswana and this requires a wider survey to document cereal postharvest management practises of smallholder farmers in the country. According to Motsumi et al. (2012), smallholder farmers continue to rely on traditional granaries made of reeds smeared with cow-dung purportedly, to repel insects. These systems are, however, vulnerable to *P. truncatus* which can attack most plant materials and whose continued range expansion is climate mediated (Arthur et al. 2019; Nyabako et al. 2020). Further, apart from droughts, the increasing incidences of global instability limiting grain movement and recent COVID-19-induced “lockdowns” and associated travel restrictions have made food supplies temporarily inaccessible. These restrictions have also brought to light the significance of household grain storage as a buffer against man-made or natural biotic shocks (Milgroom and Giller, 2013). On the other hand, the efficiency of agricultural systems - a metric that accounts for postharvest losses across agricultural value chains has grown increasingly important (African Union, 2018; Viana et al. 2022).

The current study was reinforced through field and laboratory experiments. Field studies aimed at establishing baseline information on the occurrence and distribution of *P. truncatus* in Botswana and the challenges faced by smallholder farmers on their existing grain storage systems, with special reference to *P. truncatus* vulnerability within the context of other key pests of economic importance in stored grains. Laboratory experiments aimed to determine the physiological and ecological responses of *P. truncatus* to variations in environmental conditions (biotic and abiotic) to ascertain its potential survival and spread risks under prevailing and projected climate change. The findings will open the door to other numerous points of scientific investigations and interventions to contribute to sustainable development goals (SDGs) 2 (Zero hunger), 3 (Good health and well-being), 12 (Responsible consumption and production) and 13

(Climate action) (United Nations, 2020) through reduction of stored grain losses in SSA, and improved stored product pest management techniques. Information and expertise can be a protracted link between food loss and food security (Bekele, 2021).

1.6. Problem statement and justification

Prostephanus truncatus is a quarantine pest which poses a serious threat to farm-stored maize across many countries in SSA. Apart from high basal heat tolerance (Machekano et al. 2020), plasticity and cross tolerance (Mutamiswa et al. 2020), the dangers of *P. truncatus* spread are exacerbated by the lack of locally adapted natural enemies, ability of the pest to initiate long distance flight, wide host range (Muatinte and Van den Berg, 2019), and high resource colonisation capacity (Boxall, 2002). Evidence of the occurrence of *P. truncatus* in Botswana is anecdotal, suggesting the need for a proper scientific study to provide empirical evidence of its presence or absence, and if present, establish local spatio-temporal distribution. On the other hand, farmers' knowledge, and level of awareness and experiences with *P. truncatus* damage and management, are unknown. The vulnerability of existing farmers' storage systems to this pest has not been determined. If the pest is widely distributed in Botswana, the physiological and ecological factors behind *P. truncatus* adaptation to arid, high temperature tropical Botswana needs investigation, including forecasts on population dynamics and management based on this information. Furthermore, temperature increase with climate change may affect insect feeding rates, mating, general activity and metabolism, but how that translates to behavioural and or functional responses modifications and overall effects on the pest status of the *P. truncatus* is currently unknown. The current study therefore aimed to determine the occurrence of *P. truncatus* in Botswana and its physiological and ecological responses to changing environments.

1.7. Objectives

1.7.1. Broad objective

The broad objective of this work was to determine the occurrence in Botswana and abiotic stress response mechanisms of *P. truncatus* under changing environments and their implications to population dynamics and pest management.

1.7.2. Specific objectives

The specific objectives were to:

1. Determine the occurrence and distribution of *P. truncatus* in Botswana
2. Assess knowledge, practices and perceptions (KPP) on cereal postharvest management in smallholder farmers in Botswana with particular reference to *P. truncatus*.
3. Determine the effect of temperature and relative humidity (abiotic stress) on the transgenerational and intergenerational responses of *P. truncatus*.
4. Determine the functional responses and maternal fitness of *P. truncatus* to different hosts and temperature regimes.
5. Evaluate *P. truncatus* and *S. zeamais* inter-specific competition in stored maize under varying environmental conditions.
6. Determine the thermal plasticity through thermal tracking fluctuation in critical limits under multifactorial *in situ* environments

1.7.3. Hypotheses

The study will be guided by the following hypotheses:

1. *Prostephanus truncatus* is likely to be present and widely distributed in Botswana.
2. Climate change and increasing insect pressure from invasive pests are affecting smallholder postharvest management practices in Botswana.
3. Transgenerational and intergenerational effects have behavioural and/or life history costs and benefits for *P. truncatus*.
4. Rising temperatures, different relative humidity levels and host type affect *P. truncatus* functional responses and offspring fitness.
5. Interspecific competition between *P. truncatus* and *S. zeamais* increases maize grain damage due to synergistic pest interaction.
6. Climate change-related temperature variations affect the development (life cycle and population growth) of *P. truncatus*

1.8. References

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CHAPTER 2

First record of the occurrence of the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) in Botswana[1]

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2.1. Introduction

Climate change and variability as well as increased international trade have broken biogeographical constraints of many insect pests, facilitating their spread from native ranges and subsequent introduction and establishment in novel environments (Hill, 1987; Hulme, 2009; Skendžić et al. 2021). This has increased biosecurity threats in vulnerable regions, especially tropical environments that offer conducive biological and physical environments for biodiversity (Li et al. 2016; Nyamukondiwa et al. 2022). For example, the past two decades have seen sub-Saharan Africa being invaded by an unprecedented number of alien pests (see discussions in Seebens et al. 2017; Singano et al. 2020) including the fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) (Goergen et al. 2016) and the tomato leafminer, *Phthorimaea absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Mansour et al. 2018).

The larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) is a wood boring insect native to Central America. The pest was accidentally introduced in Africa in the 1970s and continues to spread across the continent (Hodges et al. 1983; Nyabako et al. 2020; Quellhorst et al. 2021) and the world (Arthur et al. 2019) where it has turned into a serious pest of stored maize and dried cassava roots in postharvest ecosystems causing up to 50% commodity losses (Cugala et al. 2007). As a wood borer (Jia et al. 2008; Oppert et al. 2022), *P. truncatus* has negative effects on natural and managed forests and their ecosystem functions. The pest has also been reported to damage other miscellaneous household commodities through its boring activities including plastic, rubber, leather, firewood, furniture and others (Hodges, 1986; Nyagwaya et al. 2010; Muatinte and Van den Berg, 2019), increasing the magnitude and diversity of its socioeconomic and ecological impacts. *Prostephanus truncatus* can also survive on non-agricultural host plants found in the savanna forest of sub-Saharan Africa (Nang'ayo et al. 1993; Borgemeister et al. 1998; Nansen et al. 2004; Muatinte and Van den Berg, 2019; Quellhorst et al. 2021) that act as permanent reservoirs for population inoculum for its known typical sporadic re-introductions, hence complicating the management efforts.

While maize grain and dried cassava roots are the preferred hosts (Hodges et al. 1983; Arthur et al. 2019), the beetle can also damage other staple food crops in Africa including sorghum, millets, wheat, cowpeas and cocoa beans (Shires, 1977; Mailafiya et al. 2007; Muatinte and Van den Berg, 2019; Quellhorst et al. 2021). However, literature supporting the attack, damage and reproduction thereof of *P. truncatus* on small cereal grains especially sorghum and millets have been highly ambivalent (Boxall, 2002), especially outside the laboratory, although anecdotal evidence suggests so (*pers. obs.*). Available reports suggest that *P. truncatus* breeding on small grain crops may be affected by grain size, starch content, grain moisture content and commodity stability for effective boring (Bell and Watters 1982; Boxall, 2002).

Prostephanus truncatus continues to have devastating effects even after over 40 years of research since its first introduction in Africa (Quellhorst et al. 2021). The major reasons for its continued spread and damage relate to increasingly favourable environments in Southern Africa due to climate change and anthropogenic activities (Arthur et al. 2019; Nyabako et al. 2020), short life cycle, high basal thermal limits (Machekano et al. 2020), considerable plasticity (Mutamiswa et al. 2021) and high reproductive capacity under high tropical temperatures (Boxall, 2002; Quellhorst et al. 2021) as well as tolerance to organophosphate and pyrethroid based insecticides (Rumbos et al. 2013; Mlambo et al. 2017, 2018). Furthermore, wide host range and the alternation between cultivated and wild hosts favour its establishment across diverse habitats (Muatinte and Van den Berg, 2019). For example, beetles can thrive in dry wood and thatch grass used to construct grain stores under smallholder farmer settings, effectively providing refuge sites for the pest when stores and grains are treated and/or unavailable. This makes *P. truncatus* management especially difficult under smallholder grain storage systems (Kossou, 1992; Addo et al. 2002; Nang'ayo et al. 2002; Muatinte and Van den Berg, 2019). Favourable conditions for development of *P. truncatus* are 32°C and 80% relative humidity (RH) (Quellhorst et al. 2021). At these optimum conditions, the pest can complete its life cycle in 27 days, supporting multiple generations per year. These multiple generations can thus be highly damaging under high temperature tropical environments. Adult beetles tunnel into grain, producing copious amounts of grain dust on which the larvae feeds (Hodges, 1986; Quellhorst et al. 2021). Commodity damage and losses vary with commodity type and length of storage period, but as much as 50% weight losses in stored maize have been reported within 6–8 months storage periods (Cugala et al. 2007).

Prostephanus truncatus was first reported in Southern Africa in 1991 in Malawi, Zambia in 1993, Namibia in 1998 and South Africa in 1999 (Quellhorst et al. 2021). Since then, the pest has been reported in Zimbabwe in 2005 (Nyagwaya et al. 2010; Quellhorst et al. 2021; Morey 2023) and Mozambique in 2007 (Muatinte and Cugala, 2015) among others (see e.g., Gueye et al. 2008). This shows that in the last two decades or so, the pest is rapidly spreading across Africa (see distribution map in Figure 2.1) where maize and cassava are the staple crops.

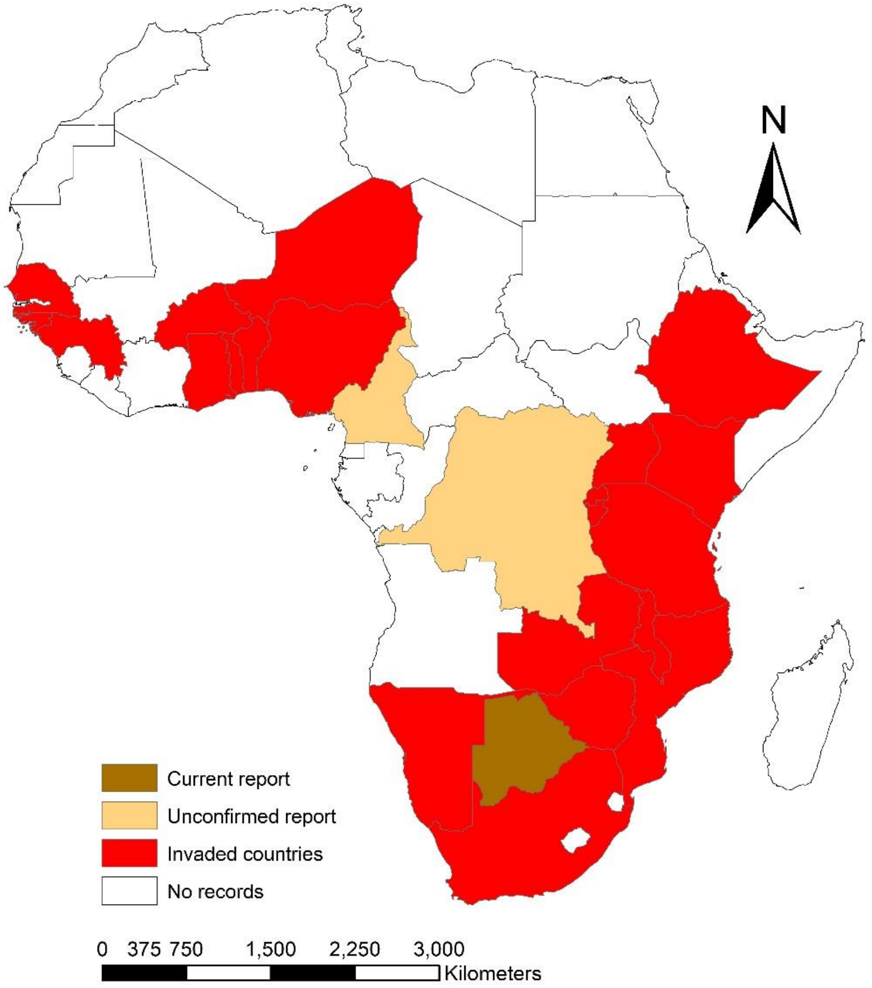

Figure 2. 1: Distribution map of *Prostephanus truncatus* as of December 2024 in Africa (red-shaded); unconfirmed reports (yellow-shaded); and Botswana (brown-shaded) (current study).

The most recent record of *P. truncatus* is from Ethiopia (Dako and Abebe, 2024). However, anecdotal evidence suggest that the pest might be present in more countries in Africa e.g., in Cameroon and Democratic Republic of Congo (unconfirmed reports in Hodges, 1994). More specific studies or official reports are required to confirm presence of the pest in such countries. Since *P. truncatus* has already been reported in neighbouring countries bordering Botswana, it is logical therefore that the Botswana Ministry of Agricultural Development and Food Security has been monitoring the pest around national borders and inland. Based on their findings and further trapping and confirmation, herein, the first occurrence of *P. truncatus* in the Southern district of Botswana is thus reported and further recommending for: (i) coordinated and concerted monitoring efforts of the pest to update the extent of its geographical distribution, (ii) scoping of host plants (crop and non-crop, including its food bio-security threats), (iii) determining the socio-economic impacts, and (iv) development of policy-based strategies for managing the invasive pest.

The first report of such alien, invasive economic pest species is significant not only for stakeholder awareness, but also for safeguarding the national and regional biosecurity and enable concerted, harmonised designing and implementation of farm level and area wide management strategies (Perrings et al. 2005; Li et al. 2016), including related policy adjustments and re-alignments. This first report of the larger grain borer in Botswana is an early warning notification to the relevant stakeholders including policy-makers on the dangers that the pest poses to national food security and the broader economy and outline possible measures to control it.

2.2. Methods

2.2.1. Study site and sampling

Three white delta traps with sticky pads, baited with ProTru (NovAgrica, Hellas, South Africa), a pheromone dispenser for the larger grain borer (active ingredients: 1-Methylethyl (E)-2-pentenoate and 1-Methylethyl (E,E)-2,4-dimethyl-2,4-heptadienoate) were set up in Ramotswa (24°52´18´´S; 25°51´47´´E), a village in the South-Eastern district of Botswana bordering South Africa. Ramotswa is an arid region largely dominated by mopane trees, *Colophospermum mopane* (J.Kirk ex Benth.) J.Kirk ex J.Léonard that make up the greater part of the savannah ecosystem. The traps, set and monitored monthly from April to August 2022, were hung about

1.5 m above ground (Hodges et al. 2004). Similar traps were also set up in the area surrounding Plant Protection Research Institute of the Ministry of Agricultural Development and Food Security offices (24°35′01″S; 25°56′49″E) in Gaborone, Botswana and monitored on a daily basis. Live beetles trapped daily were carefully removed from the sticky pads and maintained on dried sterilised yellow maize grain (SeedCo 608 variety) in Memmert climate chambers (HPP 260, Memmert GmbH + Co.KG, Germany) at 32 °C, 70% RH and 12L: 12D photoperiod. F_1 adults from the parent colony raised in the laboratory from these trap populations was used for morphological identification and molecular confirmation.

2.2.2. Morphological identification

Morphological identification was done by a team from the Plant Protection Research Institute (Gaborone) and entomologists from the Department of Biological Sciences and Biotechnology, Botswana International University of Science and Technology. Two major morphological features were used to confirm the identity of *P. truncatus viz.* (i) a head curving downwards and (ii) the square-cut (truncated) posterior end of the beetles (Figure 2.2) as described in Farrell and Haines (2002) and Spilman (1983) respectively. Other features such as the beetle size (~4 mm), mouthparts, clavate antennae and shape of the convex elytra complemented morphological features confirming positive identification (Spilman 1983; Farrell and Haines 2002; Suma and Russo 2005). Beetles were sexed using gross morphology under a stereo microscope, following methods by Shires and McCarthy (1976). Females were observed to have more pronounced and spaced clypeal tubercles than males consistent with descriptions given by Shires and McCarthy (1976).

Figure 2. 2: Key morphological characteristics identifying and confirming the collected *Prostephanus truncatus*: **A**: 3-dimensional specimen images; **B**: mouthparts and clavate antennae and **C**: head curving downwards and a truncated posterior end of the beetle.

2.2.3. Production of specimen images

Images were acquired on a Leica M165Fc stereoscope equipped with a 1x front lens, dome illumination and a FlexacemC1 color camera (Leica Microsystems, Wetzlar, Germany). 2x/4x zoom was used for full beetle/ head images. In total, 6 images with different Z-focus were acquired spanning the entire depth of the specimen and computed into a single sharp image using the "Extended Depth of Field" algorithm integrated into the Leica application Suite software (LASX 3.8.2.27713).

2.2.4. Micro-computer tomography

Specimens were fixated in 99.9% ethanol (Enterprise Ethanol, South Africa) and subsequently kept for one day in 100% acetone (Carl-Roth, Germany) and air dried for 4 hours before the micro-computer tomographic scan on a SkyScan 1272 equipped with a Hamamatsu XIMEA xiRAY 16 camera (Bruker, Germany). Scans were recorded with a resolution of 2452 × 1640 pixel, a 360° scan with 1° rotation steps, three frame averaging and an isotropic resolution of 2.500387 µm pixel size, source voltage of 35 kV and 150 µA current. Cross sections were reconstructed with the NRecon software (V 2.0.0.5 Bruker, Germany) with post alignment adjustment correction of 33.50, 10% beam hardening correction and smoothing setting of 2. Files were further processed in the Dragonfly Workstation (V 2020.1 Build 1259). First, the pipette tips used for scaffolding were removed manually. The beetle was segmented with an Otsu based threshold recognition, filling of the interior space with three iterative repetitions in all individual planes. Particulate scanning artefacts were eliminated by keeping only the largest connected structure. A contour mesh was calculated with 2 or 3-fold subsampling.

2.2.5. DNA extraction and sequencing

Two specimens preserved in absolute ethanol (99.9% alcohol) were used for DNA extraction and sequencing. Genomic DNA was extracted at Inqaba Biotechnical Industries (Pty) Ltd, South Africa from the whole tissue specimen (identified as specimen G05 and H05) using the Quick-DNA™ Miniprep Plus Kit (Zymo Research, Catalogue No. D4068) and following the protocol of Zymo Research, USA. Sequencing of the COI gene (mitochondrial cytochrome c oxidase I) was done. The universal COI primers (LCO1490 and HCO2198) were used to amplify a fragment of the 5' end of the COI gene, which is highly informative for species identification across different taxonomic categories (Folmer et al. 1994; Hebert et al. 2003). The COI target region was amplified as presented in Table 2.1.

Table 2. 1: COI Primer sequences used for larger grain borer species identification

Name of primer	Target	Sequence 5' to 3'
LCO1490	**COI**	GGTCAACAAATCATAAAGATATTGG
HCO2198	**COI**	TAAACTTCAGGGTGACCAAAAAATCA

2.2.5.1. Polymerase Chain Reaction (PCR)

The general PCR protocol followed was denaturation at 94°C for 5 minutes followed by 35 cycles of 94°C for 30 seconds, 50°C for 30 seconds, 68°C for 1 minute and a final extension at 68°C for 10 minutes, holding at 4°C. The integrity of the PCR amplicons was visualized on a 1% agarose gel (CSL-AG500, Cleaver Scientific Ltd) stained with EZ-vision® Bluelight DNA Dye. The NEB Fast Ladder was used on all gels (N3238) as size standard. Fragments were enzymatically purified using the ExoSAP procedure (NEB M0293L; NEB M0371). The amplicons were then purified for sequencing (Zymo Research, ZR-96 DNA Sequencing Clean-up Kit™, Catalogue No. D4050), and sequenced in the forward and reverse direction (Nimagen, BrilliantDye™ Terminator Cycle Sequencing Kit V3.1, BRD3-100/1000) using the ABI 3730xl Genetic Analyzer (Applied Biosystems, Thermo Fisher Scientific).

2.2.5.2. Sequence assembly

FinchTV version 1.4 was used to view the raw chromatogram files (.abi). CLC Bio Main Workbench was used to assemble the forward and reverse sequencing reads to form a consensus sequence for each sample. The Basic Local Alignment Search Tool (BLASTN) analysis with default parameters (Altschul et al. 1997) was performed on the National Centre for Biotechnology Information (NCBI) website (https://www.ncbi.nlm.nih.gov/) to determine if a sequence in the database matched the query sequences. The nucleotide sequences of the two specimens G05 and H05 were deposited in the GenBank.

2.2.6. Evolutionary relationship of the taxa

Phylogenetic relatedness of the Botswana specimens to those in the GenBank (Accession number: JN097721.1, JN097722.1, KP410257.1, and KP410257.1) was investigated using three different methods. First evolutionary history was inferred using the Neighbor Joining method based on the Kimura 2-parameter model (Kimura, 1980) in Molecular Evolutionary Genetics Analysis software (MEGA 11) (Tamura et al. 2021). The ends of the sequences were trimmed to eliminate sequence size differences, removing primers (if any) and come up with consensus sequences (Cabras and Cruz, 2016). Support was estimated with a setting of 1000 bootstrap replicates (Felsenstein 1985; Tamura et al. 2021). The analysis involved 7 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All ambiguous positions were removed for each sequence pair by pairwise deletion option (Kumar et al. 2008). There were a total of 609 positions in the final dataset. *Anthrenus oberthueri* (Accession number MN182947.1) (see Bell and Philips, 2012; Sire et al. 2019) was used as an outgroup to produce the phylogenetic tree.

Second, a Bayesian phylogenetic tree was reconstructed using Bayesian Evolutionary Analysis by Sampling Trees (BEAST2) software v.2.7.5 (Bouckaert et al. 2019). The BEAST2 v.2.5 built-in package, bModelTest (Teske and Beheregaray 2009), was used to estimate the best nucleotide substitution model. The advantage of this method is that it averages over all models and takes this uncertainty into consideration during the phylogenetic tree-building step. BEAST2 was run for five chains, each 500 million iterations with 150 million initial burn-in steps. The convergence of the multiple runs was visually investigated in Tracer v.1.7 (Jin et al. 2020), and a consensus phylogenetic tree was reconstructed in TreeAnnotator (Drummond and Rambaut, 2007) and subsequently visualised in Figtree v.1.4 (https://github.com/rambaut/figtree). Finally, a Maximum Likelihood tree was constructed in IQ-TREE2 v.2.2 (Stiller et al. 2022) using the program's default setting, including using the server's built-in automatic model selection tool for the selection of the best nucleotide substitution model and 1000 bootstraps for the consensus tree.

2.3. Results

2.3.1. Pheromone trapping and morphological identification

Pheromone-baited species-specific trap catches showed that both male and female larger grain borer beetles were attracted to the pheromones and positively identified. Morphological features consistent with *P. truncatus* were observed, including: (i) a head curving downwards and (ii) the square-cut (truncated) posterior end of the body of the beetles as described in Farrell and Haines (2002) and Spilman (1983), respectively. Other features; (i) ventrally directed mouthparts; (ii) a hard, dark brown exoskeleton at adult stage, (iii) three-segmented clavate antennae and (iv) convex elytra were all consistent with the morphological features typical of *P. truncatus* taxonomy as described by Spilman (1983) and Farrell and Haines (2002). The specimens therefore conformed 100% to the morphological features of *P. truncatus* as described by Shires and McCarthy (1976); Spilman (1983) and Farrell and Haines (2002).

2.3.2. Molecular identification

Molecular analysis results matched the Botswana specimens G05 and H05 to sequences in the GenBank, confirming the specimens as *P. truncatus* with 95.83% and 96.02% identity respectively (Table 2.2). The nucleotide sequences of the two specimens were assigned accession numbers PP731513.1 and PP731512.1 respectively.

Table 2. 2: Summarised results of a BLASTN showing percentage identity of Botswana specimens to those in the GenBank under accession number JN097721.1

Specimen ID	**Nearest species identity**	**Query cover (%)**	**Percentage identity (%)**	**Accession number**	**Date**
G05	*Prostephanus truncatus*	100	95.83	JN097721.1	23 January 2024
H05	*Prostephanus truncatus*	100	96.02	JN097721.1	23 January 2024

2.3.3. Evolutionary relationship of the taxa

The COI gene sequences of the two specimens were matched with existing COI sequences of *P. truncatus* in the GenBank forming different topologies. The visual inspection of the Bayesian analysis trace files confirmed that convergence has been achieved. The specimen G05 and H05 are very similar to each other, and they cluster well with JN097721.1 (Figure 2.3). Similarly, the Maximum Likelihood method receives the same identical topology.

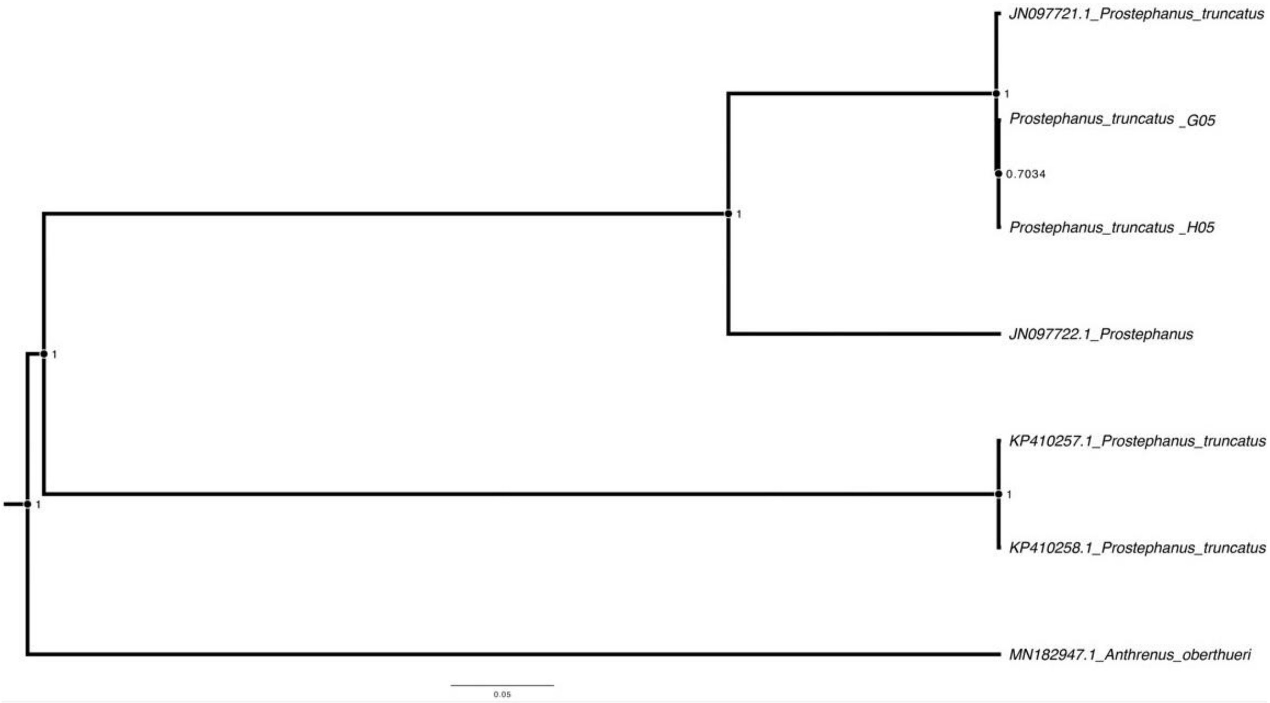

Figure 2. 3: An ultrametric Bayesian phylogenetic tree generated in BEAST2 showing the placement of two sequences generated in this study compared to other closely related species with publicly available records in the NCBI database. The scale-bar is proportional to the number of nucleotide substitutions, and the numbers next to each node shows the corresponding posterior support for the split. The figure confirms that generated sequences are almost identical to JN097721.1 with a posterior probability of 1.

2.4. Discussion

Trapping results showed the presence of *P. truncatus* in Botswana. Use of pheromones at two sites indicated the attraction of both sexes of the adult beetle to 1-Methylethyl (E)-2-pentenoate and 1-Methylethyl (E,E)-2,4-dimethyl-2,4-heptadienoate, a pheromone specific to *P. truncatus* which confirmed the specimens' identity. Both sexes of the *P. truncatus* are attracted by the same aggregation pheromone (Cork et al. 1991), a contributory indicator to the positive identity of the species. Furthermore, morphological identification confirmed the specimens as *P. truncatus*, consistent with the taxonomic keys for the species (see Farrell and Haines, 2002; Spilman, 1983). Follow-up molecular analysis of the samples through mitochondrial COI (cytochrome c oxidase subunit I) sequencing linked the Botswana *P. truncatus* samples to Accession number JN097721.1, with similarity of BLAST (~ 96%). The specimens G05 and

H05 were therefore positively identified as *Prostephanus truncatus* (Horn, 1878), a wood-boring invasive, alien Bostrichidae, that has become a serious pest of stored maize and dried cassava roots globally (Hodges et al. 1983; Golob 1988; Boxall 2002; Arthur et al. 2019). The results of the current study, however, show relatively lower (95.83% and 96.02%) BLASTN similarity to other *P. truncatus* species identified (100%) (e.g., accession number JN097721.1 see Bell and Philips, 2012) although the highly supported posterior probabilities show a lot of consistency in sequences alignment (Bouckaert et al. 2019). The low BLASTN similarity may indicate within species variations (Lin et al. 2015; Afizah et al. 2019) which maybe a result of mixture of populations from different areas (multiple introduction) during the years of spread since the beetle's arrival. It is therefore possible that with multiple introductions of *P. truncatus* from different geographical regions (Arthur et al. 2019), this could have brought about genetic diversity and facilitated hybridisation (see discussions in Guntrip et al. 1996) in the beetle populations in Africa. In most cases therefore, to improve the robustness of DNA sequence results, as in this study, morphological identifications are used to supplement molecular technologies such as DNA barcoding (Afizah et al. 2019). Using the complementary morphological identification, it is therefore positively confirmed the specimens as *P. truncatus* and herewith report the first report of this invasive pest species in Botswana.

Prostephanus truncatus became established in Africa following multiple accidental introductions; the first of which was in Tanzania and then in Togo (Nang'ayo et al. 2002). Thereafter similar introductions may have occurred, and the pest continued to spread across Africa due to favourable bio-physical conditions (Bellard et al. 2013; Seebens et al. 2015; Arthur et al. 2019). Following introduction, the beetles can spread by adult flight, and adults reportedly fly distances of 0.25 to 1 km in successive flights (Fadamiro et al. 1998). Furthermore, given its wide host range, propagules can also easily spread with transport and trade in wood, thatching grass, fodder trade and related materials (Nang'ayo et al. 1993, 2002; Muatinte and Van den Berg, 2019). In line with this, the trap catches show the presence of *P. truncatus* at Ramotswa border post which is part of the regional grain trade routes connecting South Africa (which is linked to numerous Cape ports both in the South Atlantic and Indian Oceans), and also Botswana and the rest of the southern African region by land (rail and road) and air routes. The latest report on the occurrence of *P. truncatus* in Botswana follows similar reports in neighbouring countries

Zambia, Namibia, South Africa and Zimbabwe in 1993, 1998, 1999 and 2005 respectively (Quellhorst et al. 2021).

The beetle has been reported to cause maize grain damage as high as 50–100% and grain weight losses of 15–50% over 6–8 months storage periods (Mutambuki and Ngatia, 2006; Njoroge et al. 2014; Mlambo et al. 2018; Mutambuki et al. 2019). The damage causes massive weight loss and renders grain unfit for human consumption (Bechoff et al. 2022) while seed grain loses viability. Scattered evidence suggests that the beetle also breeds on stored sorghum grain (Verma and Lal, 1987; Mailafiya et al. 2007; Osipitan et al. 2012; Machekano et al. 2020; Morey, 2023). Occurrence of *P. truncatus* on sorghum is of significance because sorghum is the world's fifth most important cereal grain (Akinseye et al. 2017; Mundia et al. 2019) and Africa's second most important cereal crop after maize (Mundia et al. 2019). It is also the staple crop in Botswana (Mpofu et al. 2022). Sorghum is receiving increasing attention as the anchor for resilient cropping systems owing to its drought tolerance (Rurinda et al. 2014; Nezomba et al. 2018). Thus, its suitability as a host for *P. truncatus* can negate the resilience of tropical African climate change adaptation strategies and food security systems.

Apart from cultivated hosts, the larger grain borer also breeds on wild host tree species such as *Colophospermum mopane* (J. Kirk ex Benth.) (Muatinte and Van den Berg, 2019), a common tree species in Botswana and the savanna ecosystem (Makhado et al. 2014). The prevalence of host tree species such as mopane will therefore increase the potential invasion areas across Botswana's savanna woodlands; simultaneously presenting a challenge in controlling the pest as then it would alternate between stored grain and wild hosts. Furthermore, the beetle is reported to breed on *Hyparrhenia* grass species (Muatinte and Van den Berg, 2019), which is a common grass species in Botswana and one that is commonly used as thatch grass (Kabelo and Mofakate, 2004). The ability of *P. truncatus* to alternate between cultivated and non-cultivated wild hosts therefore poses a challenge in its control as the forest can act as a reservoir for wild propagules that sporadically attack stored grains. *Prostephanus truncatus* can also facilitate spreading of fungal spores, predisposing stored maize grain to fungal infection leading to mycotoxin contamination thus posing major threats to human health (Danso et al. 2017).

As with most invasions, the detection of *P. truncatus* in Botswana calls for suitable quarantine measures and monitoring systems, the training of extension staff and farmers to be able to recognise and identify the pest, awareness campaigns and availing of efficacious pesticides to enable farmers to manage the pest during grain storage (Hodges et al. 1983; Addo et al. 2002). The efficacy of these control measures may need to be complemented by the development of an integrated management strategy for the control of this invasive pest. Furthermore, there is need to confirm its presence at various other land border trade route areas and then tighten import inspection at ports of entry (Addo et al. 2002) as well as the trade and exports of host commodities (see discussions in Perrings et al. 2005). At farm level, the use of improved storage structures including brick and concrete made granaries (Stathers et al. 2002, 2020; Nyagwaya et al. 2010), modern airtight hermetic technologies (De Groote et al. 2013; Ndegwa et al. 2016; Mutambuki et al. 2019; Baributsa et al. 2020; Ngwenyama et al. 2022) and metal silos (Tefera et al. 2011; Chigoverah and Mvumi, 2016) is also encouraged, as part of an integrated management strategy.

2.5. Conclusion

The current study therefore confirm the positive identification of *P. truncatus* in Botswana using a combination of gross morphology based on standard taxonomic keys and molecular confirmation. Furthermore, complementary positive sex specific pheromone lure trapping for the species, and molecular techniques were used to further confirm the specimens as *P. truncatus.* In conclusion, it is confirmed and hereby presented the first report of *P. truncatus* in Botswana. Further, it is recommended that suitable phytosanitary, quarantine and monitoring systems be harmonised with appropriate policy-based control methods to minimise spread and impact of this invasive pest on local farmers and the entire grain industry and postharvest ecosystem at large.

2.6. References

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CHAPTER 3

Farmers' knowledge, practices, perceptions and determinants of postharvest management options in Botswana with special reference to the larger grain borer[2].

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3.1 Introduction

Farmers are the land holders and primary producers of agricultural commodities either for family subsistence in which only surplus can be sold or they can produce solely for sale to generate household income (Rees et al. 2000). Under unimodal rainfall seasons as experienced in sub-Saharan Africa (SSA), or due to climate induced droughts and food shortages, staple cereal grain crops such as maize and sorghum are harvested, dried and stored for eventual consumption until the next harvest (Stathers et al. 2013; Midega et al. 2016; Hossain et al. 2022). The growing population in SSA necessitates more food production, however, food production in the region is on a declining trajectory due to the impacts of climate change on crop production and increased insect pests causing high losses to stored grains (Bosekeng et al. 2010; Tesfaye et al. 2015). Studies indicate that 20–30% cereal postharvest losses are incurred annually in SSA resulting in losses valued at US $ 4 billion (World Bank et al. 2011; Midega et al. 2016). While losses occur at different stages of the postharvest value chain and handling processes, which include grain drying, storage, processing and marketing (Prusky, 2011), most losses are recorded during grain storage (10–20%) due to storage insect pests that cause deterioration in quality and quantity of the stored grain crops (Hodges et al. 2011; World Bank et al. 2011). This underscores the importance of improved grain storage to guarantee protection of stored grains. The major insect pests of stored maize and sorghum grain in SSA include the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) and Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelichiidae) and the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) (Midega et al. 2016; Mlambo et al. 2017; Quellhorst et al. 2021; Mlambo et al. 2024). Unlike other insect pests, *P. truncatus* is an invasive quarantine pest of stored maize whose increasing geographical range is climate mediated (Arthur et al. 2019; Quellhorst et al. 2021; Harman et al. 2024; Mlambo et al. 2024).

According to Stathers et al. (2020), many of the cereal postharvest losses incurred are preventable through training of farmers in grain handling and storage, adoption and use of efficacious grain storage technologies backed by good governmental and regional policies aligned to the United Nations Sustainable Development Goals e.g., reducing food losses along production and supply chains (SDG 12.3) (United Nations, 2015). At a regional level, the Southern Africa Development Community (SADC) states have agreed under the Malabo Declaration on reducing the current postharvest losses by half by 2025 (ReSAKSS and IFPRI, 2014). While these policies are in place, decisions on pest management for example the type of control method to use often depends on several factors e.g., farmer perceptions, beliefs, resources available and objectives (Hashemi et al. 2009; Davis et al. 2010; Midega et al. 2016; Sugri et al. 2021). This underscores the importance of farmer engagement and training so that they acquire knowledge and information to make informed decisions on the choice of pest control (Hashemi et al. 2009). Training is especially important in the case of new insect pests invading an area for example with the case of *P. truncatus* which has invaded many countries in SSA including recently in Botswana (Mlambo et al. 2024; Chapter 2). Invasive insect pests cause significant "surprise damage" because they establish in an area without the local farmers' knowledge or awareness. According to Li et al. (2021), training improves farmer perceptions, awareness and management of invasive insects. Furthermore, with the advance of climate change, farmers' perceptions and awareness of the role that climate change plays in altering insect species dominance is important (Sharma, 2014). When alien invasive insect pests invade new environments, extension awareness becomes important in updating the public with knowledge on recognising the pests, advising on the best practices and efficacious options to manage the pests (Eryanto et al. 2023; Chen et al. 2024).

Studies show that farmers in SSA use an arsenal of methods to control storage insect pests and these include botanical pesticides, synthetic pesticides, fumigants as well as metal silos and hermetic bags among other methods to guard against storage pests (Tefera et al. 2011; Murdock et al. 2012; Njoroge et al. 2014; Mlambo et al. 2017; Singano et al. 2019; Mubayiwa et al. 2021). These technologies vary in their effectiveness as determined by the type of insect pests involved, pest pressure and storage conditions such as hygiene and environmental conditions (Stathers et al. 2020). For example, botanical and synthetic pesticides have been reported to be less effective against *P. truncatus* (Mutambuki et al. 2012; Mlambo et al. 2017, 2018; Singano et al. 2019) while other storage options like metal silos and hermetic bags have been reported to be effective (Mlambo et al. 2017; Mutambuki et al. 2019; Singano et al. 2020; Ngwenyama et al. 2022). This further underscores the importance of farmer training which can influence their adoption of improved storage options.

Agricultural extension is well-acknowledged in SSA and Botswana agriculture (Kingshotte, 1980; Gboku and Modise, 2008; Aina, 2012). However, with the recent record of *P. truncatus* in Botswana, there is no documentation or clear understanding of farmers' postharvest practices and their coping strategies especially under threats from quarantine or invasive pests which have become more frequent under climate change. The current study assessed knowledge, practices, perceptions and determinants of smallholder farmers' behaviour on cereal postharvest management in Botswana with particular reference to *P. truncatus*. It was hypothesised that: (i) farmers' knowledge and current practices are detached from recent advances in postharvest technologies, (ii) climate change could have potentially increased insect pressure and affected smallholder postharvest management practices and perceptions leading to self-initiated innovations, (iii) there are limited sources of information specifically focused on postharvest management for both farmers and (vi) different factors affect farmers' choice of storage options. The findings of this study can give government and other stakeholders insight into the vulnerability of communities to *P. truncatus* and climate change and provide possible interventions that government can take to guarantee protection of farmers' stored grains and stabilise food security in Botswana.

3.2. Materials and methods

3.2.1. Study sites

Consultative meetings with the Department of Plant Health of the Ministry of Lands and Agriculture, Botswana established that *P. truncatus* had been detected from pheromone baited traps in Ramotswa (South-east district; 25°0′ S, 25°45′ E) and Kasane (Chobe district; 18°39' S, 24°24' E) that had been set up for surveillance since the *P. truncatus* had been reported in neighboring countries (Chapter 2). The detection of the pest in the two districts plus the farming history of the communities formed the basis of selecting the two as study sites in the current study. Ramotswa, is a savannah ecosystem village with a population of 33 271 (Statistics Botswana, 2024) and is located in the South-Eastern district bordering South Africa (McGill et al. 2019). The region is semi-arid; characterized by 450 mm summer annual rainfall between October and March (McGill et al. 2019) and is largely dominated by mopane woodlands, *Colophospermum mopane* (J.Kirk ex Benth.) J.Kirk ex J.Léonard (a reported host of *P. truncatus*, see Muatinte and Van den Berg, 2019). Kasane, on the other hand, is located in the Chobe district, north of Botswana, bordering Namibia, Zambia, and Zimbabwe, and is largely designated as a wildlife area. As of 2022, the population of Kasane stands at 9 095 (Statistics Botswana, 2024). Kasane, along with Maun, is located in Botswana's hottest region, with summer temperatures reaching up to 45°C (Jain et al. 2006). Kasane has an average annual rainfall of 580 mm, which falls between December and April (Gökçekuş et al. 2021).

3.2.2. Data collection

Data were collected using a household questionnaire designed to, respectively, gather information from farming households on their knowledge, practices and perceptions on cereal postharvest management so as to determine the resilience of current storage technologies against, in particular *P. truncatus* which had recently been reported in the country. The questionnaire had open-ended and closed questions depending on whether a question needed an explanation or not. Questionnaires were loaded onto Kobo Toolbox (Poloju et al. 2022 in reference to Kobo Toolbox) in Samsung Galaxy (64bit Quad Core Processor) tablet devices. A pilot survey was then conducted with a team of three enumerators in May and September 2023 in Palapye Central district of Botswana to test the household questionnaire and adapt the questions and responses to local farming practices. The actual survey was then conducted in June 2024 with the same team of enumerators. A total of 130 households were interviewed (74 from Ramotswa and 56 from Kasane). Farmers gave their consent by signing a consent form allowing the information given to be used for research purposes only.

3.2.3. Data analysis

Data collected from household questionnaires was exported from Kobo Toolbox to Microsoft excel before being exported to STATA 17 (Gould et al. 2006) for analysis. In excel, frequency tables were generated for descriptive purposes. Multinomial logistic regression analysis by maximum likelihood estimator (Chan, 2005; Makana and Thebulo, 2018) were performed in STATA 17 to determine categorical factors (age, sex, level of education, marital status, household size, district) that influence farmers' choice of grain treatment methods. The multinomial logistic regression model describes the behavior of consumers when they are faced with a variety of goods with a common objective (Makana and Thebulo, 2018). Since multinomial logistic regression model estimates only give direction of effects of the independent variables on the dependent variable; marginal effects were computed to explain the magnitude of change (Greene, 2001; Makana and Thebulo, 2018).

3.3. Results

3.3.1. Socio-economic characteristics of respondents

Survey participants were drawn from three villages in Chobe district and seven villages from the South-Eastern district (Table 3.1). Participants from Chobe district represented 47% of the survey population while the South-eastern district had 53% respondents. Male participants constituted 28% of the population while females constituted 72% across the two districts.

Table 3. 1: Demographic characteristics of participants from Chobe and South-Eastern districts of Botswana.

District	**Village**	**Respondents' gender**		**Grand totals**
		Male (%)	**Female (%)**	
Chobe	Mabele	4.62	16.92	
	Kachikau	1.54	6.15	
	Kavimba	4.62	13.08	**46.92**
South-East	Ramotswa	3.08	3.08	
	Moshupa	3.08	11.54	
	Tlhareseleele	2.31	2.31	
	Dinatshana	3.08	7.69	
	Pitsani	0.77	1.54	
	Rakhuna	3.08	5.38	

	Ramatlhabama	2.31	3.85	**53.08**
Grand totals		**28.46**	**71.54**	**100.00**

Amongst the households, 43% were married, 27% widowed, 27% single and never married and 3% were divorced. A sizable number of farmers (18%) had no formal education, whilst the majority (40%) attained primary education, 19% attained ordinary level (form 1–4), 7% attained vocational training, 8% attained advanced level education (form 5–6) and another 8 % had attained tertiary level education. Majority of households constituted 1-5 family members (73%), 22% constituted 6-10 members whilst 5% of the households had eleven or more family members staying together. Across the two districts, 45% of the respondents take farming on a fulltime basis whilst 55% were part-time farmers.

3.3.2. Crop production and livelihood sources

Most farmers grow maize (89%), cowpeas (57%), sorghum (51%) and watermelons (41%). A few households grow sugar beans (5%), vegetables (4%) groundnuts (2%) and other crops, especially sweet reeds (15%) (Figure 3.1). However, the majority of farmers (31%) cited employment as their main source of household income, however, 22% rely on staple crop sales and 20% rely on government support in the form of community tenders. A few farmers rely on remittances (5%), horticultural crop sales (3%), livestock sales (3%), rental collections (2%) and 14% rely on other numerous income sources. Among the respondents, 28% indicated they harvested enough maize, cowpeas (15%), sorghum (11%) and groundnuts (1%) for household use in the 2022/23 season.

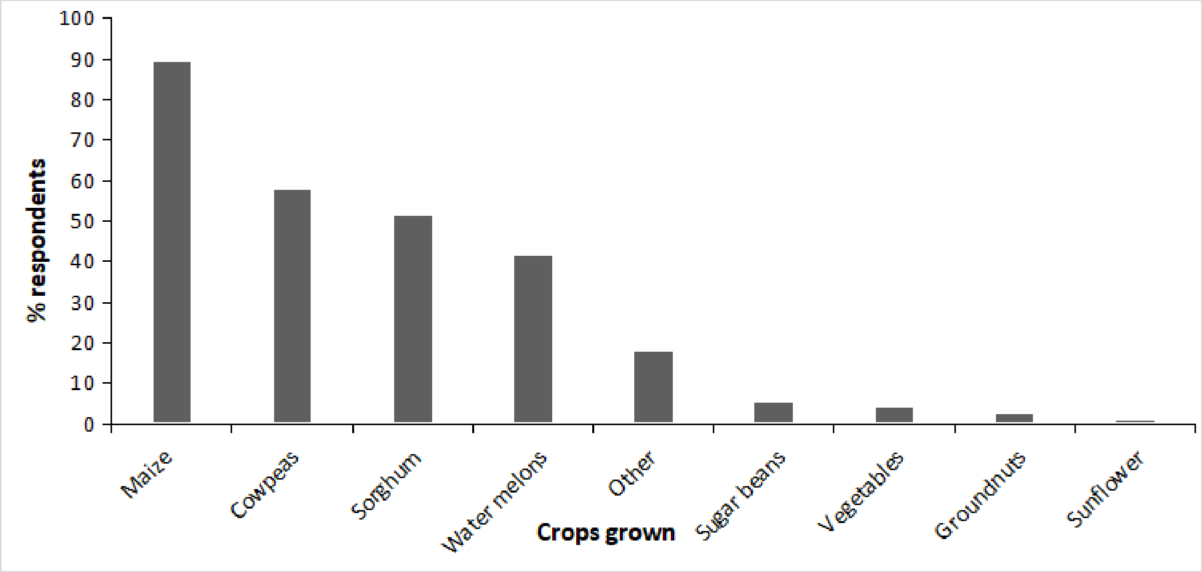

Figure 3. 1: Major crops grown by farmers in Chobe and South-eastern district of Botswana.

3.3.3. Grain postharvest handling practices

Cereal postharvest handling practices of most farmers start in April and May and these include cutting, stooking, dehusking, drying, transportation, shelling, winnowing, grain treatment and storage (Table 3.2). Most of the work regarding production, harvesting and storage on the farm is done by family members. Farmers in the two districts store grain for three major reasons; (i) family consumption during the dry season (95%), (ii) livestock feed (42%) and (iii) for use as seed (32%).

Table 3. 2: Cereal postharvest handlings practiced by most farmers in Chobe and South-east district of Botswana.

Postharvest practices	**How**	**Who**	**When**	**Where**
1. Cutting	Bare hands	Whole family	April-May	Field
2. Stooking	Pyramid	Whole family	April-June	Field
3. Dehusking	Bare hands	Whole family	April-July	Field
4. Drying	Field	Whole family	April-July	Field
5. Transportation	Self	Whole family	July-August	From field to homestead
6. Shelling	Bare hands	Whole family	April-July	Homestead
7. Winnowing	Manual	Whole family	July-August	Homestead
8. Grain treatment	Admixing with grain	Whole family	July-August	Homestead
9. Admixing with pesticide	Bare hands	Whole family	July-August	Bulk grain in container
10. Storage method	Bags on timber	Whole family	July-August	Ordinary room

Grain is usually packed in polypropylene bags following treatment and the bags are stored in ordinary rooms as indicated by 75% of respondents (Figure 3.2). Storage facilities and granaries are used by 12% and 7% of farmers respectively while 5% store grain in drums and containers. Botanical ashes prepared using Motswere (*Combretum imberbe*) wood ash dominated grain treatments as practiced by 68% of the farmers. Some farmers treated grain with phosphine (15%) and grain guard (active ingredients: Mercaptothion 10g/kg; Permethrin 1.5g/kg) (8%) while 16% do not treat their grains at all. In terms of rationale, farmers prefer the above-mentioned storage methods for reasons of cost/affordability (37%), local availability (20%), efficacious (17%), lack of knowledge on other methods (11%), experience (2%), easy of application (2%) and other reasons e.g., small quantities of grain harvested etc. (4%).

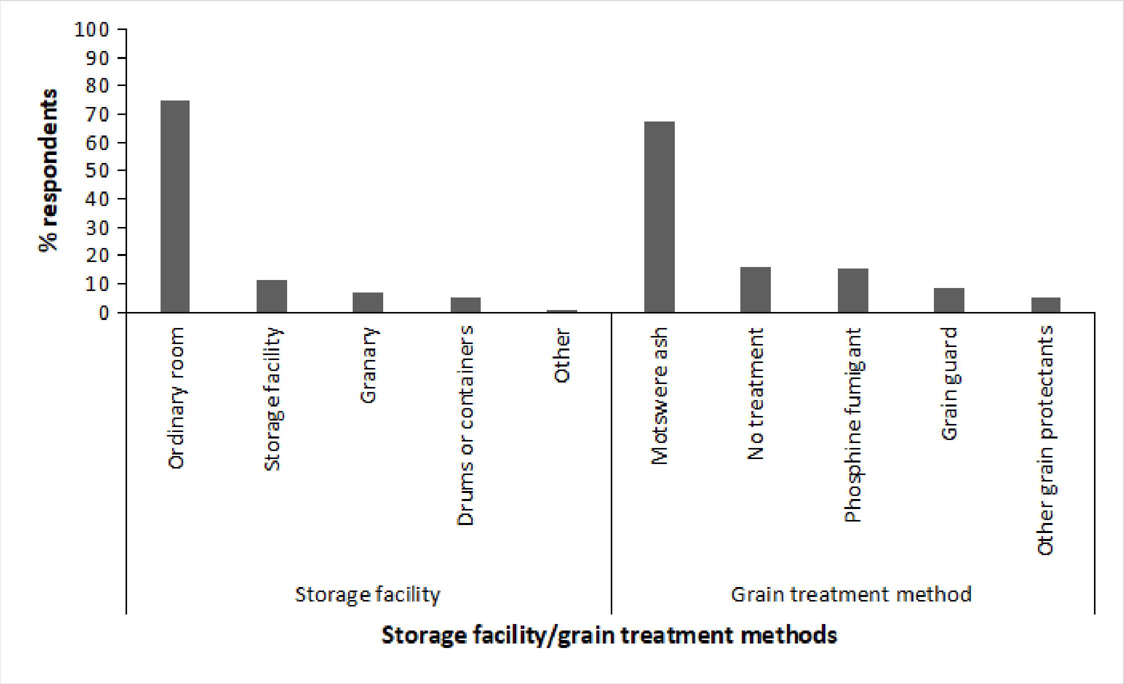

Figure 3. 2: Grain storage facilities and grain treatment methods used by farmers in Chobe and South-east district of Botswana.

3.3.4. Causes of poor harvests and grain storage losses.

Climate change related issues were cited as the major cause of poor crop production (48%) in Chobe and South-eastern districts with other (14%) farmers even opting not to grow crops in the 2022/23 season as they anticipated a poor harvest (Figure 3.3). A few farmers cited shortage of labour (8%) and Covid-19 related issues (5%) as factors that had affected their production. On the other hand, storage insect pests was reported as a major cause of losses by most farmers (90%), followed by rodents (59%), theft of grain (7%) and spoilage due to rain and moisture (5%) (Fig. 3.3).

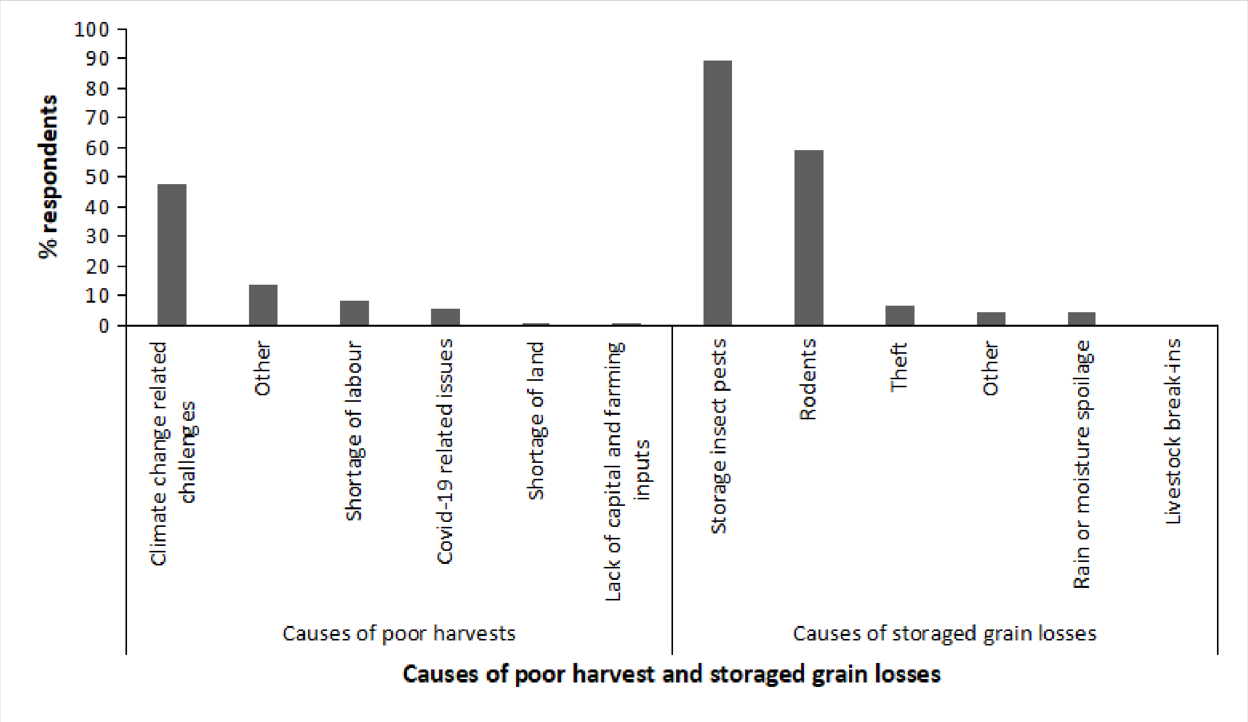

Figure 3. 3: Causes of poor harvests and grain storage losses among farmers in Chobe and South-east district of Botswana.

3.3.5. Pests of importance in stored maize, sorghum and cowpeas

The majority of farmers (57%) agree that cowpea is the most damaged crop during storage followed by maize (28%), beans (8%) and sorghum (5%). The most important pests of cowpeas are *Callosobruchus* species, *T. castaneum* and rodents, *Rattus* species while *S. zeamais* and *S. oryzae*, *S. cerealella* and *Rattus* species are the most problematic pests for maize and sorghum (Table 3.3). Notably, *P. truncatus*, a quarantine pest recently reported in Botswana (Chapter 2) has not been reported as a major problem by farmers.

Table 3. 3: Order of importance for pests of stored crops in Chobe and South-eastern districts of Botswana according to farmers' responses

Crop	**Order of important crop pests**		
	1st	**2nd**	**3rd**
Maize	*Sitophilus zeamais* (48%)	*Sitotroga cerealella* (24%)	*Rattus* species (37%)
Sorghum	*Sitophilus oryzae* (28%)	*Sitotroga cerealella* (28%)	*Rattus* species (38%)
Cowpeas	*Callosobruchus* species (70%)	*Tribolium castaneum* (25%)	*Rattus* species (45%)

Most farmers (49%) perceive climate change to have caused changes in pest dynamics over the years. The highest insect pest pressure is noted between September and December according to 53% of the respondents. Major changes in pest dynamics include increased pest pressure as indicated by 28% of respondents, early onset of insect pest infestations (4%) and that insect pests no longer respond to synthetic pesticides (6%). On the other hand, 2% of the farmers reported a decrease in insect pest infestations with the advance of climate change.

Knowledge of *P. truncatus* among farmers in Chobe and South-east districts was very low. Only 11% of farmers knew *P. truncatus*; the majority (70%) did not know the pest and 18% were not sure if they know the pest making 88% of farmers who were unaware or unsure about the new quarantine pest (Table 3.4).

Table 3. 4: Knowledge of *Prostephanus truncatus* among respondents

Knowledge category	**Respondents gender**		**Totals**
	Male	**Female**	
YES	3%	8%	11%
Not sure	5%	13%	18%
NO	20%	50%	70%

3.3.6. Use of modern grain storage facilities

The use of modern efficacious, pesticide free storage technologies such as air-tight metal silos and hermetic bags is low amongst respondent farmers. As highlighted in Figure 3.4, only 9% of respondents use sealed plastic bins, 2% use metal silos and 1.5% use sealed drums for grain storage. Less than 1% of the farmers use hermetic bags or cocoons.

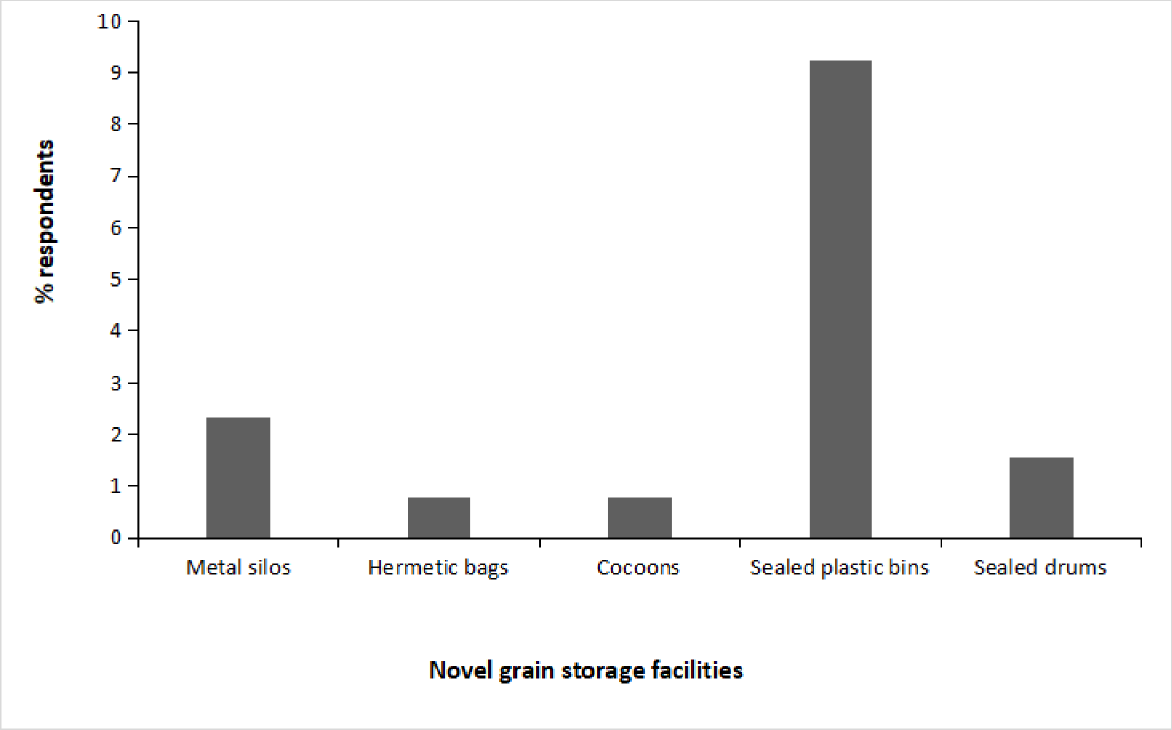

Figure 3. 4: Use of modern grain storage technologies amongst respondent farmers in Chobe and South-eastern districts, Botswana.

3.3.7. Determinants of farmer postharvest practices

Marital status, district, sex and level of education were significant determinants of the choice of grain treatment method used by farmers (Table 3.5). Divorced household heads ($\chi 2 = 17$, df = 36, $p < 0.001$) were negatively affected and less likely to use grain guard for grain treatment. District ($\chi 2 = 17$, df = 36, $p = 0.026$) also significantly influenced farmers' choice of using grain guard as the practice was more common in the South-east district compared to Chobe district. As the age of household heads increased, the likelihood of using synthetic pesticides (grain guard) decreased ($\chi 2 = 17$, df = 36, $p = 0.033$). Level of education ($\chi 2 = 17$, df = 36, $p < 0.001$) was a significant determinant of using grain guard as the likelihood of use positively increased with level of education. Household size ($\chi 2 = 17$, df = 36, $p = 0.029$) further significantly affected the choice of grain treatment method with increased household sizes increasing the likelihood of using grain guard dust. Divorced household heads ($\chi 2 = 17$, df = 36, $p < 0.001$) were less likely to use phosphine fumigants. The likelihood of using phosphine fumigants was also influenced by district ($\chi 2 = 17$, df = 36, $p = 0.061$) as the practice was more common in Chobe than the South-east district.

Table 3. 5: Determinants of farmers' likelihood of using a certain grain treatment method when Motswere ash is used as a base outcome in Chobe and South-eastern districts of Botswana. Multinomial logistic regression: Number of observations = 130; Wald $\chi 2$ (36) = 17.

Categorical variable	**Dependent variable: grain treatment method**	**coefficient**	**std. error**	**z**	**P>IzI**
	Grain guard				
Marital status	Divorced	14.461	1.423	-10.110	0.000***
	Single (never married)	-0.071	0.845	0.080	0.933
	Widowed	0.262	0.923	0.280	0.777
	District	1.643	0.739	2.220	0.026**
	sex	0.394	0.764	0.520	0.605
	Age	-1.414	0.663	-2.130	0.033**
Highest level of education	Secondary	14.788	1.027	14.390	0.000***
	Primary	15.125	-0.788	21.360	0.000***
	Tertiary	13.583	1.249	10.870	0.000***
	Household size	2.400	1.096	2.190	0.029**
	logY_1	0.727	-0.823	0.880	0.376
	log_area	-0.379	1.295	-0.290	0.769
	_cons	-18.888	2.988	-6.320	0.000***
	Phosphine fumigant				
Marital status	Divorced	14.220	1.340	-10.610	0.000***
	Single (never married)	0.051	0.796	0.060	0.949
	Widowed	-0.178	0.898	-0.200	0.843
	District	2.248	1.213	1.870	0.061*
	sex	-0.212	0.805	-0.260	0.792
	Age	-0.186	0.537	-0.350	0.729
Highest level of education	Secondary	-0.275	1.071	-0.260	0.798
	Primary	0.119	0.988	0.120	0.904
	Tertiary	-0.101	1.312	-0.080	0.939
	Household size	0.262	0.847	0.310	0.757
	logY_1	0.875	0.631	1.390	0.166
	log_area	1.147	1.064	1.080	0.281
	_cons	-6.648	2.977	-2.230	0.026**
	Other traditional plants				
Marital status	Divorced	1.381	1.276	1.080	0.279
	Single (never married)	-0.549	0.732	-0.750	0.453
	Widowed	0.529	0.572	0.930	0.354
	District	-0.414	0.500	-0.830	0.409
	sex	-0.008	0.551	-0.010	0.988
	Age	-0.554	0.497	-1.120	0.264
Highest level of education	Secondary	1.097	0.799	1.370	0.170
	Primary	-0.105	0.716	-0.150	0.883
	Tertiary	0.494	0.859	0.570	0.566
	Household size	0.654	0.546	1.200	0.231
	logY_1	0.087	0.515	0.170	0.865
	log_area	0.443	0.7287	0.610	0.544
	_cons	0.183	1.633	0.110	0.911

*Significant at *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.*

3.3.8. Agricultural extension services

Farmers accessed agricultural information through agricultural extension officers as indicated by 77% of respondents and audio and visual media (70%). This information covers seasonal climate updates, prices of agricultural commodities, new technologies, pests and insects affecting crops and their control and where farmers can access services like soil tests and nutritional analyses of their crops. In terms of specific postharvest information, 49% indicated having access whereas 51% did not have access to postharvest information. The majority of farmers in the study were satisfied with extension delivery in terms of the adequacy, availability, relevancy, ease of use and recency of information they receive from extension services (Table 3.6).

Table 3. 6: Farmers' rating of postharvest extension services received from extension staff in Chobe and South-eastern districts, Botswana.

Satisfaction indicator	**% Rating of information**				
	Poor	**Satisfactory**	**Good**	**Very good**	**Excellent**
a. Adequacy	8.46	3.08	50.00	33. 85	3.85
b. Availability	10.77	4.62	48.46	32. 31	3.08
c. Relevancy	6.15	5.38	46.92	35. 38	5.38
d. Ease of use	6.15	3.08	53.08	33.08	3.85
e. Currency/modernity	6.15	4.62	50.00	33.85	4.62

Although there is a general feeling of satisfaction amongst farmers on the postharvest extension services delivered by extension staff, the majority of farmers indicated they still need training on (i) insect and pest management practices (74%), (ii) insect identification (29%), (iii) general postharvest handling (21%), (iv) grain storage hygiene (20%) and (v) modern hermetic storage technologies (14%). Farmers enumerated (i) training in postharvest management (69%), subsidizing synthetic pesticides for grain storage (48%), (iii) buying of grain from farmers before it is damaged (27%), (iv) use of improved granaries (14%) and use of the warehouse receipt system (5%) as suitable government interventions to improve grain storage in Botswana.

3.4. Discussion

The demographic statistics of the survey show that women dominated the farming households. The result follows the current population trends in Botswana where women slightly constitute the majority (see O'Neill, 2024). Furthermore, it is a common trend in SSA and developing regions where women constitute the majority and are relied on to provide the larger share of agricultural labour force (Raney et al. 2011; Midega et al. 2016). It was also observed that most of the farming duties are performed by family members that constitute the household. According to Moyo (2016), farming in SSA is a family business primarily aimed at sustaining the family and earning income through sale of surplus produce. Under this socio-economic orientation, the family farming members usually reside together in the rural areas and in times of need (e.g., drought year), other members move to the city to look for part-time employment to sustain the family (Moyo, 2016). Household size and composition are important features of farming communities under smallholder systems as they can be used to predict household food availability and overall food security of the household using food availability ratio. Frelat et al. (2016) found that on small farms, food availability decreased with increasing household sizes thus, large families are a constraint to household food security *ceteris paribus*. Less than 50% of the farmers in the two districts take farming on a fulltime basis, this may indicate the unsustainability of relying on rain-fed cropping in Botswana especially under the current climate change scenarios characterized by rain shortfalls and high temperatures that increase the vulnerability of crop production (Chapanshi et al. 2003; Batisani and Yarnal, 2010; Juana et al. 2013; Nkemelang et al. 2018). Common across systems in SSA therefore, farmers often have to supplement crop production with livestock sales and/or off-farm income e.g., temporal formal or informal employment commonly referred to as “piece jobs” to feed their families (Moyo, 2006; Frelat et al. 2016).

Farmers in the two districts followed common grain handling practices including harvesting, homestead or field drying, winnowing and storage among others. Of these stages, grain storage is the most critical where storage insect pests need to be guarded against to prevent storage losses. In the current study, most farmers rely on the use of botanical ashes from Motswere wood as compared to grain guard synthetic pesticidal dust or other methods. Most studies done in SSA indicated synthetic grain protectant dusts as the major option used for grain protection (Kamanula et al. 2010; Sola et al. 2014; Midega et al. 2016; Nyabako et al. 2021; Ngwenyama et al. 2023). On the other hand, the use of phosphine fumigants (Aluminum phosphide), though not recommended at smallholder level, is increasing in SSA as also seen in the current study. This practice may be driven by observed and reports of poor efficacy of synthetic pesticides by farmers (Mlambo et al. 2017; 2018). The observed high usage of botanical pesticides for grain treatment in this study can be explained by their local availability, unaffordability of other options and lack of knowledge and access to improved grain storage options as enumerated by respondents. While botanicals are a cheaper option for grain storage, major concerns on their use include lack of consistency in efficacy due to lack of standardisation in their preparation and application and production of unpleasant flavors or discoloration of grain by some botanicals and the health safety concerns because their toxicity has never been tested (Isman, 2006). The use of modern grain storage technologies is very low in both districts. According to local extension, there are no local suppliers of hermetic bags therefore access to the technology is a problem, in addition, in Botswana to import the bags will increase costs for farmers, making the technology unaffordable. Lack of technology delivery systems thus hinders adoption of otherwise good technologies (see Shiferaw et al. 2015). Elsewhere in neighboring Zimbabwe, adoption of hermetic storage technologies is reported to be still low as well; some farmers who have hermetic technologies only got them mainly as part of promotional activities by development partners such as Food and Agriculture Organization and World Food Programme (Mvumi and Chigoverah, 2018).

Farmers enumerated *S. zeamais*, *S. oryzae*, *T. castaneum*, *S. cerealella*, *Callosobruchus* species and *Rattus* species as the key pests of stored cereal and legume grains in their farming areas. Knowledge of *P. truncatus* is lacking among the farmers as 70% did not know the pest and only 11% had knowledge of the pest. This lack of knowledge on new insect pests is one of the major causes of their reluctancy to improve and adopt new efficacious storage technologies (Midega et al. 2016). Furthermore, as explained by Mendesil et al. (2007), current farmer perceptions which are built on the history and performance of their current storage options against native insect pests cannot easily change without new knowledge being acquired. This therefore emphasises the role and need for extension to bring in new knowledge on efficacious grain storage options, invasive quarantine insect pests e.g. *P. truncatus* and the impacts of climate change which synergistically expose them to grain storage losses. The other reported storage pests are cosmopolitan pests of stored cereals in SSA (Hodges and Stathers, 2012; Hiruy and Getu, 2018). In legume grains, bruchids are the major insect pests including cowpea weevils, *Callosobruchus* species and been weevils, *Acanthoscelides obtectus* (Hodges and Stathers, 2012). Besides insects, rodents (rats and mice) pose a big challenge in storage as they feed on grain either starting in the field or in storage. Rodents also attack bagged grains resulting in the need to replace damaged bags. Furthermore, rodent droppings and urine affect food quality (Hodges and Stathers, 2012). Insects and pests start in the field when grains reach physiological maturity. Insects feed and lay their eggs on grain and the eggs hatch in storage and the cycle continues (Mason and McDonough, 2012). Furthermore, mixing grains from different seasons and poor storage hygiene can result in carryover of insects (Hodges and Stathers, 2012). Insects and rodents can also invade storage areas from nearby bushes. The perception around climate change and insect pests among the farmers was that pest pressure has increased with climate change. Elsewhere also, similar surveys done in Congo highlighted that 90% of the farmers reported proliferation of pests as one of the major impacts that has come with climate change (Balasha et al. 2023). This concurs with various research that concluded on similar findings across SSA (Chijioke et al. 2011; Stathers et al. 2013; Kaminski and Christiaensen, 2014; Van Ittersum et al. 2016; Singano et al. 2020; Baptista et al. 2022).

Multinomial logistic regression showed effects of different categorical variables in influencing the likelihood of a household to use a certain grain storage method. Factors such as age, level of education, marital status affected the use of grain guard (active ingredients: Mercaptothion 10g/kg; Permethrin 1.5g/kg), a synthetic grain protectant dust. Less educated, divorced and old aged farmers were less likely to use grain guard than their counterparts. Similar factors such as age have been reported to negatively influence the choice of storage technology adoption by farmers (Basappa et. al. 2007; Maonga et al. 2013). Middle aged household heads are more likely to adopt new or improved storage technologies compared to older farmers who become laggard in making decisions (Makana and Thebulo, 2018).

Most farmers access agricultural information through local extension services. The role of agricultural extension services has become integral to improved food security in SSA as weak extension services can exacerbate postharvest food losses (Amadu et al. 2024). The system started in the United States of America and was designed to improve the livelihoods of rural citizens through provision of crop and livestock extension services to farmers by government employed agricultural personnel (Mukembo and Edwards, 2015; Sennuga et al. 2020). The extension system has become common across many countries in SSA and is one of the major determinants of farmers' adaptive capacity (Balasha et al. 2023). As their role include recommending climate smart technologies and provision of information on weather and climate, lack of farmer access to extension therefore forestalls farmers from being able to understand, anticipate, prepare and manage climate risks as well as integrating their perceptions and indigenous knowledge with scientific knowledge (Juana et al. 2013; Balasha et al. 2023). With recent technological advancements, the use of mobile phones by farmers to access agricultural information is also expanding (Kabbiri et al. 2018).

Knowledge, practices and perceptions of farmers are important factors that help farmers decide on storage technologies to use. The study found that: (i) farmers in Chobe and South-east districts, do not know about the larger grain borer, *Prostephanus truncatus* that has invaded their country, (ii) farmers in Chobe and South-east districts rely on Motswere ash for grain treatment as opposed to recent improved storage options, (iii) farmers perceived that climate change has increased the onset and pressure of insect pests, (iv) high cost and lack of local suppliers/manufacturers or distributors affect adoption of improved (hermetic) storage technologies and (v) age, marital status, household size, level of education and district were significant determinants of farmers' choice of grain storage method used. These findings are important as they outline the knowledge, practices, perceptions and determinants of farmer behaviour on postharvest management in Botswana. This relevant information is vital in assessing the information, training and technological needs of local farmers to improve postharvest management in changing climates.

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CHAPTER 4

The fall armyworm and larger grain borer pest invasions in Africa: drivers, impacts and implications for food systems[3]

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4.1. Introduction

Biological invasion is the introduction, establishment, spread and proliferation of biological organisms outside their native range (Renault et al. 2018). This introduction and establishment often lead to reorganisation of ecosystem structures to new ecological equilibria which often affects local biodiversity and ecosystem function (Perrings et al. 2002; Ehrenfeld, 2010; Simberloff et al. 2013). The United Nations Sustainable Development Goals (SDG) 2 ("*zero hunger*") and 12 (*"responsible consumption and production"*) emphasise attainment of resilient food systems through sustainable production and consumption (United Nations, 2022). However, the maintenance of these vulnerable food systems in Africa has been retarded by climate change, anthropogenic effects (Lodge, 1993; Vitousek et al. 1996) and associated consequences such as increased biosecurity threats posed by biological invasions (Bjornlund et al. 2022). Invasive insect pests have extensive economic, social and environmental consequences, thus disproportionally threaten food and livelihood systems particularly in low- and medium-income countries in Africa (Paini et al. 2016, Pratt et al. 2017; Durocher-Granger et al. 2021). Increased global connectivity, anthropogenic climate change and a surge in human population size has accelerated the rate of biological invasions with no indications of imminent saturation (Renault et al. 2018; Pyšek et al. 2020; Diagne et al. 2021; Nyamukondiwa et al. 2022). The SDG 12 emphasises improved and sustainable production (improved yields) reinforced by sustainable consumption and even sets specific targets related to the reduction of food loss and waste including postharvest management (FAO, 2019; Bekele, 2021; Bechoff et al. 2022; Totobesola et al. 2022).

Pests can cost billions of dollars in agricultural losses and control programs and have lasting effects on human populations (Goodell et al. 2000; Diagne et al. 2020; Diagne et al. 2021). Insect pests in particular are also major contributors to loss of business, export markets and product value and quality (Paini et al. 2016). On a global scale, it is estimated that invasive alien species have caused economic losses of at least US$1.288 trillion (for the period 1970-2017) (Diagne et al. 2021; Zenni et al. 2021). Global losses incurred from crop damage and efforts directed at pest management is estimated to be US$76 billion annually (Diagne et al. 2020), whereas those from Africa cumulatively ranged between US$18.2 billion and US$78.9 billion between 1970 and

2020 (Diagne et al. 2021). In recent decades, agricultural production in Africa has been severely hampered by invasive insect pests (Sileshi et al. 2019) with significant food losses of up to 30% being reported (World Bank et al. 2011; Tefera, 2012; Totobesola et al. 2022). In order to meet the food requirements of the exponentially growing human population in Africa, projections suggest that agricultural production must double by the year 2050 (FAO, 2009; Skendžić et al. 2021). However, this doubling of production may compromise sustainability, ecosystems and ecosystem services (Tilman et al. 2002). For example, invasion by alien insects with a high pest status has had devastating effects on the production of staple cereal crops such as maize and sorghum in Africa (Sileshi et al. 2019). The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is one of the major pests affecting maize and sorghum field production in Africa (Diagne et al. 2021). On the other hand, the larger grain borer (LGB), *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), is a notorious alien insect pest of stored maize and dried cassava roots rapidly spreading in Africa (Hodges, 1986; Richter et al. 1997; Quellhorst et al. 2021). The arrival of *P. truncatus* in Africa has doubled maize grain losses in affected areas (Muatinte et al. 2019).

Reported maize field losses from *S. frugiperda* range from 9-54% in Africa (De Groote et al. 2020; Abro et al. 2021) while those of *P. truncatus* range from 20-50% on weight basis reported within 6-9 months of storage (Boxall, 2002; Mutambuki and Ngatia, 2012; Muatinte and Cugala, 2015; Mlambo et al. 2018). Combined therefore, *S. frugiperda* and *P. truncatus* may account for between 30-100% in food losses where they successively attack the same crop(s) along the different stages of the production chain under the same farmer. *Spodoptera frugiperda* larvae damages maize at all stages of growth, including cobs, though it is most devastating during early crop growth phases. Field losses are thus higher during early maize growth phases and decrease during late growth and physiological maturity stages (Fig. 4.1). *Prostephanus truncatus*, on the other hand, infests maize cobs at physiological maturity and persists during grain drying to storage phases (Mlambo et al. 2018). Grain and seed losses due to both larvae and adult stages increase with increasing storage duration (Fig. 4.1). When the two insect pests occur successively in the same niche, the cumulative field losses due to *S. frugiperda* in the field plus drying and storage losses due to *P. truncatus* are thus higher, resulting in excessive loss impact per farmer.

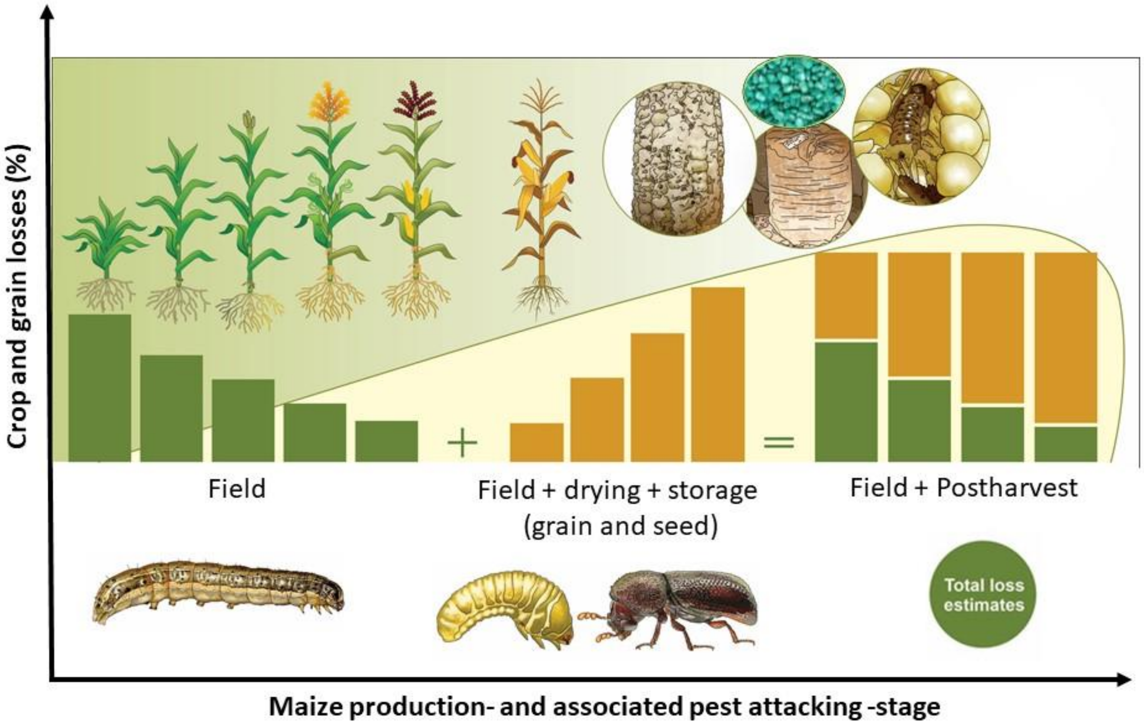

Figure 4. 1: Conceptual hypothetical framework showing cumulative losses associated with *S. frugiperda* damage on field maize and *P. truncatus* damage to stored maize (not drawn to scale; source: Author). Crop damage from *S. frugiperda* is usually higher during initial crop growth stages and declines as the crop approaches physiological maturity at which stage *P. truncatus* takes over up to postharvest storage thus inflicting cumulative synergistic losses that can be monetarily quantified. However no scientific data are available to validate the hypotheses as yet.

In less than 10 years since its first detection in West and Central Africa in 2016, *S. frugiperda* had spread to 47 out of 54 African countries (Fig. 4.2), causing significant food and nutrition threats (Wan et al. 2021; Timilsena et al. 2022). The pest prefers maize and sorghum, although it can feed and complete its life cycle on >350 plant species including several food crops (Montezano et al. 2018; Wan et al. 2021). This polyphagous characteristic enables the pest to survive across diverse host environments. *Spodoptera frugiperda* larvae defoliate crops during vegetative growth reducing crop growth and reproductive capacity (Pratt et al. 2017; Day et al. 2017; Kassie et al. 2020; Rwomushana et al. 2018; FAO, 2022; Nyamutukwa et al. 2022; Kenis et al. 2022). In maize, the pest attacks the crop up to soft dough stage, increasing the crop vulnerability to additive losses through storage insects and mycotoxins contamination (FAO, 2022). *Spodoptera frugiperda* is multivoltine, facilitating high and quick population build-up. Adult females can lay ~300 eggs on the underside of leaf sheaths (McLeod et al. 2003). The first and second instars can disperse by suspending themselves on silk threads and are swinged by wind to reach other host plants (Timilsena et al. 2022).

On the other hand, *P. truncatus* has increased the magnitude of postharvest losses incurred in stored maize and dried cassava roots in Africa due to its characteristic extensive tunnelling and feeding that reduces whole kernel grains and cassava chips into powder (Scholz et al. 1997; Hodges et al. 2003; Tefera et al. 2011). The pest was first reported in Tanzania in 1981 (Dunstan and Magazini, 1981; Hodges et al. 1983) and has since spread to at least 21 African countries in the last four decades (Fig. 2) in sub-Saharan Africa (Muatinte et al. 2019; Quellhorst et al. 2021; Morey, 2023). *Prostephanus truncatus* can also survive on wild hosts in the forest (Nang'ayo, et al. 1993; Borgemeister et al. 1998a) and exhibits a sporadic attack, making it difficult to manage (Fadamiro and Wyatt, 1995; Scholtz et al. 1997; Borgemeister et al. 1998b; Hodges et al. 2003). Increased feeding behaviour has been observed at higher temperatures (Fadamiro and Wyatt, 1996). The adult beetles can disperse through flight in search of food and suitable oviposition sites (Fadamiro and Wyatt, 1996; Scholtz et al. 1997). Males release an aggregation pheromone attractive to both sexes when they encounter a favourable host, and this allows the beetles to quickly colonise and exploit host resources (Scholtz et al. 1997). The beetle can burrow through hard material and prefers the bottom of bagged or bulk grain for leverage (Nansen and Meikle, 2002; Tefera et al. 2016).

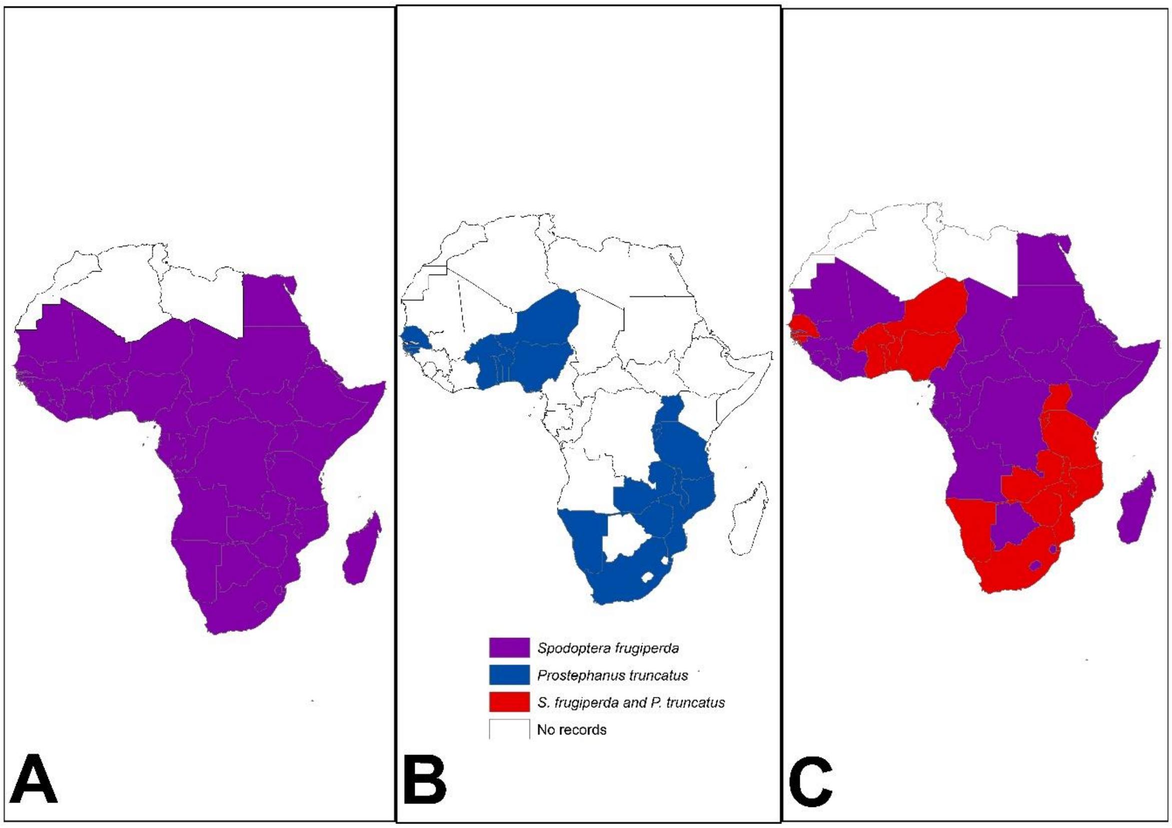

Figure 4. 2: Distribution of (A) *Spodoptera frugiperda* (Wan et al. (2021) for distribution time scale) and (B) *Prostephanus truncatus* in Africa (Quellhorst et al. (2021) for distribution time scale) as of July 2023. Insert (C) shows countries where both pests have been reported (Source: Author's compilations from various sources).

Regardless of overwhelming evidence that *S. frugiperda* and *P. truncatus* are the main field and postharvest pests of staple maize in Africa (Boxall, 2002; Goergen et al. 2016), their effects on food systems have often been studied independently, even when they occupy the same ecological niche (Day et al. 2017; Rwomushana et al. 2018; Arthur et al. 2019; Muatinte et al. 2019). However, their successional attack on the different stages of maize for example shows that these two pests may have devastating negative complementary and interactive effects that represent a damage and loss continuum against food systems. The current study thus interrogate the food systems threats in Africa posed by *S. frugiperda* and *P. truncatus*, with special reference to impact on the maize crop cycle to demonstrate how the pest additive interactions through successional damage may exacerbate food losses. The objectives of this review were thus to document: (i) main maize invasive pests as the key drivers of food loss in Africa, (ii) drivers of pest invasions in Africa, (iii) invasive characteristics of *S. frugiperda* and *P. truncatus*; (iv) economic and ecological costs of *S. frugiperda* and *P. truncatus* as IAS; and (v) national and continental management strategies for pest invasions. Such insights could help in assessing efficacious management options for pest invasions, improve resilience and integrity of food production systems, consequently safeguarding food and nutrition security in Africa in response to SDGs 2 and 12.

Systematic literature search was conducted using different key words (including *S. frugiperda* in Africa, economic costs of *S. frugiperda*, damage due to *S. frugiperda*, *P. truncatus* in Africa, damage due to *P. truncatus*) and search engines such as Google scholar, Web of Science, Google, JSTOR Search and Scopus (Crowther and Lim, 2010; Snyder, 2019). Mendeley was then used to organise the downloaded articles and manage citations (Reiswig, 2010). A background of food security vulnerability in Africa was given first, second, potential drivers of biological invasions in Africa were elucidated (emphasising the role of *S. frugiperda* and *P. truncatus*), third, the economic and ecological consequences of these biological invasions to local economies and food security in general were discussed and the possible management strategies for these biological invasions.

In literature, crop pests have often been dealt with within the rigid framework of their host crop damage based on the alignment between crop and insect phenology. For example, both *S. frugiperda* and *P. truncatus* damage maize at different phases of the crop's life cycle, but most studies have dealt with *S. frugiperda* impact individually within the maize field production phase while *P. truncatus* has been studied individually within the limits of the postharvest phase. Thus, the respective economic loss impacts have been kept separate, although both impacts are on the same crop and experienced by the same farmer. Although the two pests damage maize at different stages of its production cycle, the underlying factor is the loss to the farmer and nation, and the cumulative impact of the loss to the farmer at these different phases of production cycle (pre- and post-harvest). The invasive insect pests multiply the loss impact that is experienced by the same grower. When the impact of invasive pests on vulnerable farming communities is analysed through the total loss impact lens, it provides a more realistic representation of the socio-economic and food and nutrition security impact of insect pest invasion in Africa. In the recent times, food and nutrition security has been subjected to high biosecurity threats from invasive pests driven by climate change (Pyšek and Richardson, 2010).

4.2. Vulnerability of food systems in Africa

Significant increase in food production in Asia, Latin America, the Pacific and the Caribbean has been realised in the recent past, leaving Africa and south Asia with the highest concentration of food insecurity in the world (Tian and Yu, 2019). The vulnerability of African food systems may partly emanate from the ever increasing abiotic and biotic shocks.

4.2.1. Abiotic factors and their effect on food systems in Africa

About 70% of the African livelihoods are directly dependent on agriculture (Debray et al. 2018). However, most croplands in Africa are characterised by poor and declining soil fertility (Mtambanengwe and Mapfumo, 2005) primarily due to long-term monocropping, especially under conventional tillage, removal of crop residues and lack of external nutrient inputs (Nezomba et al. 2018). Consequently, degraded soils are less responsive to inorganic soil amendments such as mineral fertilizers, hence poor maize crop yields ranging from 0.5 to 1.2 t ha^{-1} are reported: way below the potential for maize hybrids (FAOSTAT, 2022). Furthermore, changes in rainfall intensity and distribution patterns, as well as temperature increases, are the major abiotic factors affecting rain-fed agriculture in Africa (Debray et al. 2018; Masvaya et al. 2018). Temperatures in Africa are expected to rise by about 2.6°C by 2050 if climate change mitigation fails (Holtz and Golubski, 2021). This will result in reduced surface and ground water resources (IPCC, 2014). Extreme weather events such as heat waves, droughts, floods, and cyclones are also expected to increase (Milgroom and Giller, 2013; Stathers et al. 2013; Abegunde et al. 2019; Ofori et al. 2021). This will have direct impacts on crop yields, food prices and livelihoods (IPCC, 2014).

On the contrary, farmers are poorly resourced to adapt to their harsh and changing environments. For example, most African farmers use retained seed owing to high cost and limited access to certified seed (Denning et al. 2009; Mhango et al. 2013). Due to poor storage techniques and facilities, retained seed is usually attacked by storage insects, leading to low germinability, low plant vigour, poor crop stands and consequently low yield (Mhango et al. 2013; Chigoverah and

Mvumi, 2016; Chigoverah and Mvumi, 2018). Smallholder communities usually rely on agricultural extensification, where vast lands are cleared to enable agricultural production (Tittonell and Giller, 2012; Chigoverah and Mvumi, 2016). Extensive agricultural production can lead to deforestation, soil depletion and degradation. Furthermore, it can contaminate underground water resources through other agricultural inputs (e.g., agrochemicals) including other commercial activities such as mining (Reynolds et al. 2015; Technoserve, 2022). This adds to other negative environmental effects such as harm to non-target organisms and biodiversity losses (Sands et al. 2018; Ortiz et al. 2021). With increasing human population, land is continually becoming scarce to support such extensification systems. The majority of smallholder farmers in Africa also have limited access to requisite information, tools and technologies for insect pest identification and financial means of managing invasive insect pests (Bjornlund et al.2022; FAO, 2020). Coupled with the pressures of increasing human populations, this often offsets the balance between food production and demand (Tian and Yu, 2019). Biological invasions therefore represent an additional stress to an already burdened and fragile agricultural food system.

4.2.2. Biotic factors and their effect on food systems in Africa

Major biotic factors increasing the vulnerability of African agriculture relate to increased pest pressure in agricultural environments. Crop weeds and insect pressure are increasing due to climate and anthropogenic related changes. Range expansion and/or survival of insect pests are increasing owing to altered insect physiology and behaviour, as well as interactions within specific habitats (Gutierrez and Ponti, 2014). Insects being poikilothermic, depend on environmental temperatures for their development and survival (Chown and Nicolson, 2004). Insect pests are thus expected to have more generations and higher functional responses, hence increased crop damage with climate warming (Stathers et al. 2013) during both production and postharvest storage. This will likely increase associated cost of control, and losses (Sileshi et al. 2019).

4.3. Biological invasions: Donors, drivers and processes involved

4.3.1. Biological invasions

Biological invasions involve the successful introduction, establishment, and range expansion of a species in a non-native habitat, usually anthropogenically mediated (Diagne et al. 2020; Renault et al. 2022). Invasion records started around 6000 BC with the unintentional introduction of insect pests of stored grain such as *Sitophilus granarius* L. (Coleoptera: Curculionidae) and *Tribolium confusum* Jacquelin Du Val (Coleoptera; Tenebrionidae) from Eastern to Western Europe (Fried et al. 2017). Invasive insect pests have been introduced primarily through interventions aimed at helping local situations (e.g., disaster response) and/or through escape from native ranges (Kumschick and Richardson, 2013). Rarely, insect pests are introduced as contaminants of related commodities (Kumschick and Richardson, 2013). Due to their small sizes, insects are insidious and easily transported into new environments undetected through human activities (Gippet et al. 2019). Smuggling also plays a significant role in IAS introduction and remains one of the most common methods through which alien insect pests have been introduced, especially into developing countries where phytosanitary measures are still a major concern at ports of entry (Hallman, 2007). Deliberate smuggling of agricultural materials, such as seed, has been reported to have resulted in the introduction of various insect pests of stored maize grain in various regions (Hallman, 2007). In addition, the increased global connectedness and trade routes across both oceans and continents has also become the primary source of IAS introductions (McGeoch and Jetz, 2019; Sardain and Sardain, 2019). In particular, shipping, which accounts for 80% of global trade is believed to account for most of biological invasions (Sardain and Sardain, 2019). While several species and/or numbers may be introduced through transportation, only a few passes through all filters and become invasive (Blackburn et al. 2011). Similarly, the invasion process may also be delayed owing to the 'lag phase', that facilitate population build-up and local adaptation before spreading (Crooks, 2005). The development of regional and global trade agreements also increases the movement and exchange of commodities, which lead to an increase in the introduction of invasive species into new settings either as contaminants or hitchhikers (Ricciardi et al. 2017). To become invasive, organisms must overcome biogeographical barriers due to deliberate or accidental human actions and are able to spread rapidly to colonise new territories in the introduced region (Pyšek et al. 2020). The framework for biological invasions has been well explained by Blackburn et al. (2011) and involves transportation, introduction, establishment and spread.

As an invader, the advantages of *S. frugiperda* over native species are pivotal in its establishment. *Spodoptera frugiperda* was first detected on maize in Nigeria and São Tomé and Príncipe in 2016 (Goergen et al. 2016). The pest has spread across the African continent at alarming speed and is now near omnipresent across the continent (Kenis et al. 2022). The adult moth can self-disperse through flying over long distances to new environments. The presence of *S. frugiperda* in Egypt for example, means southern Europe is at risk of invasion as the adult moth can cover more than 500 km of flight in a single generation (Wang et al. 2023). In this regard, the top six countries at risk of invasion are Spain (39.1%), Italy (32.2%), Turkey (8.9%), France (6.8%), Greece (5.8%), and Portugal (5.1%), and their aggregated risk of invasion is 97.8% (Wang et al. 2023). The insect has high fecundity and a short life cycle which enhances its chances of survival. Additionally, *S. frugiperda* does not diapause, but migrates to warmer environments during winter (Wan et al. 2021). Furthermore, the insect can survive on a wide range of hosts other than the preferred maize and rice though the number of generations and individual strengths may be compromised (Montezano et al. 2018). Due to their high fecundity, insects are more likely to survive and spread quickly to newly introduced environments (Lieurance et al. 2022). There are various modes of dispersal of insects to new environments. These include, but not limited to, self-dispersal through adult flights, silking (in the case of *S. frugiperda*), and as ‘stowaway baggage’ (Blackburn et al. 2011). For *P. truncatus*, lack of, and/or failure of its natural enemies in invaded areas (Tigar et al. 1994; Holst and Meikle, 2003) and transportation of infested material (maize grain and dried cassava roots or empty bags) (Hodges et al. 1996), as demonstrated by the enemy release hypothesis (Keane and Crawley, 2002; Colautti et al. 2004; Venette and Hutchison, 2021) resulted in unregulated populations, wide dispersal and fast colonisation of hosts leading to high losses in maize and cassava (Richter et al. 1997). *Prostephanus truncatus* was first introduced in Africa in Tanzania and Togo (Dunstan and Magazini, 1981; Hodges et al. 1983; Hodges, 1986) as a pest in imported maize grain (Richter et al. 1997; Morey, 2023). At the time of the accidental introduction of *P. truncatus* into Tanzania, there were no suitable pesticides registered for its control as it required organophosphate-pyrethroid combinations rather than just the already available organophosphates which could effectively control all other storage insect pests (Golob, 1988).

4.3.2. ‘Donors’ of biological invasions

Though there is no consensus on the precise origin of IAS, it is widely accepted that the area of origin of pests corresponds to the centre of origin of the crops with which they are associated (Fried et al. 2017). China and the United States are touted as the major 'donors' of invasive crop insects due to massive agricultural production in these countries (Paini et al. 2016). It is also speculated that species from the Northern hemisphere are better competitors and consequently more effective invaders than those from the Southern Hemisphere (Darwin and Bynum, 2009; Van Kleunen et al. 2015) potentially owing to the climate variability hypothesis (Gutiérrez-Pesquera et al. 2016). *Spodoptera frugiperda* and *P. truncatus* are known to have originated from the tropical and sub-tropical regions of 'donor' meso-America and arrived in Africa in 2016 and the late 1970s, respectively (FAO, 2020; Tay et al. 2023). To date, *P. truncatus* has been reported in at least 21 countries (Quellhorst et al. 2021; Morey, 2023) while *S. frugiperda* has been reported in 47 countries (FAO, 2020; Kenis et al. 2022) across the African continent. *Spodoptera frugiperda's* invasion of Africa has been more rapid than *P. truncatus,* which arrived earlier but has not been reported in as many countries as the former, implying that *S. frugiperda* is more invasive than *P. truncatus.* However, we acknowledge that there could be other factors at play. For example, to our knowledge, *S. frugiperda* being a field pest, easily attracts attention from scientists and other stakeholders whereas grain storage tends to be 'hidden' from the public eye. Similarly, *S. frugiperda* invasion and spread also coincided with the boom in social media and the digital age which may have facilitated its faster publicity relative to the timing of *P. truncatus* invasion and spread.

4.3.3. Drivers of biological invasions

4.3.3.1. Anthropogenic activities

Increasing agricultural intensification, international trade of agricultural products (see Fig. 4.3), habitat modifications, anthropogenic climate change and the rise in human population size has led to a surge in invasive pest species, especially in tropical and subtropical environments (Levine and D'Antonio, 2003; Ellis et al. 2013; Pyšek et al. 2020; Nyamukondiwa et al. 2022). Furthermore, land use and land cover changes (e.g., forest clearing for agriculture or pastureland, urban expansion, or field abandonment) have played key roles in the introduction, establishment, and proliferation of invasive species as they contribute to ecosystem disturbance (e.g., fragmentation), thus creating dispersal corridors (Vilà and Ibáñez, 2011; Wang et al. 2016).

Human modification of environments to optimise crop production through tillage and mineral nutrient application increases nutrients and biomass of cultivated crops making them more attractive to pests than surrounding vegetation (Fried et al. 2017). Similarly, agricultural practices e.g., irrigation also creates conducive microhabitats with limited thermal and desiccation stress, likely modifying invasion ranges (Rendon and Walton, 2019; Liu et al. 2023). Additionally, human dietary shifts to fruits and vegetables and smallholder-based farming systems result in highly diverse agricultural ecosystems, which provide resource opportunities for polyphagous pests (Wan and Yang, 2016). Similarly, the mixed cropping and grain and tuber (cassava) storage systems by smallholder farmers make host switches by *P. truncatus* highly inevitable. Moreover, by using host wood and thatch as construction material for storage structures, this complicates management options for *P. truncatus* and increases its potential for establishment in new areas (Nang'ayo et al. 1993). As *S. frugiperda* and *P. truncatus* are both polyphagous, multiple cropping in most smallholder farming systems might have provided continuous food and winter habitats for the pests, providing niche resources to sustain populations and thus creating resilient bridgeheads for greatly extending their populations geographic range and temporal distribution (Wan and Yang, 2016). The prevalence of maize and other *S. frugiperda* host plants (see Montezano et al. 2018); associated with suitable agroecological conditions in most of the regions, makes it a serious (and most certainly perennial) threat to food security in Africa (Day et al. 2017; Baudron et al. 2019).

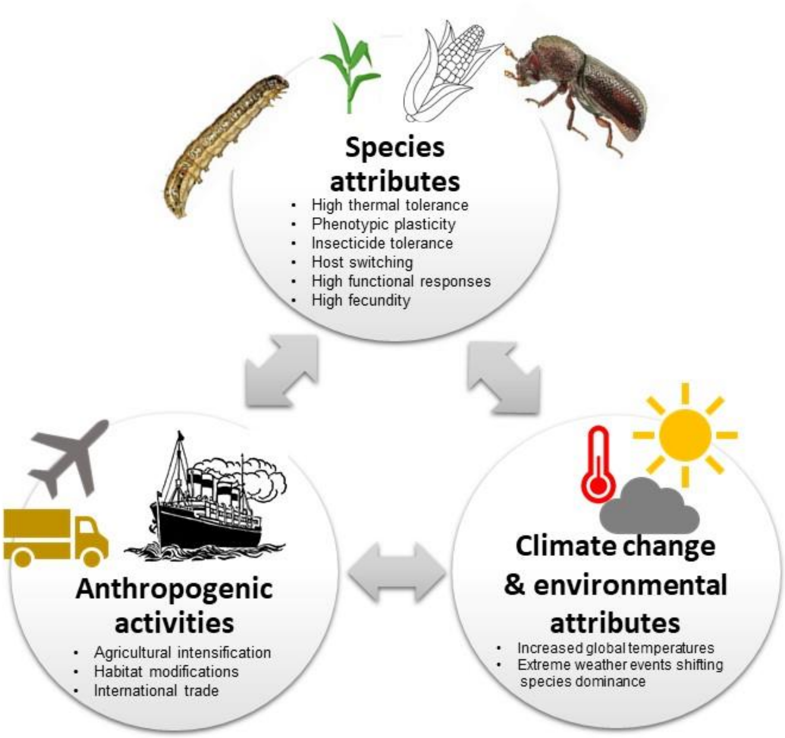

Figure 4. 3: Summary illustration on the potential drivers of *Spodoptera frugiperda* and *Prostephanus truncatus* biological invasion in Africa (see also Nyamukondiwa et al. 2022).

4.3.3.2. Climate change and environmental attributes

Global increases in mean temperatures and changes in precipitation patterns due to climate change, coupled with anthropogenic pathways described previously, have intensified biological invasions of pest insects (Hulme, 2009; Hill et al. 2016; Skendžić et al. 2021; Segaiso et al. 2022). Climate change has been reported to influence the distribution and abundance of invasive insects both directly (e.g., by altering where species and hosts can occur) and indirectly (e.g., via changes in population growth rates, propagule pressure, and spread), amongst other factors (Stathers et al. 2013; Jamieson et al. 2017; Gerken and Morrison III, 2022; Harvey et al. 2022). Recent evidence shows poleward shifts in species for more benign environments as climate warming persists (Gerken and Morrison III, 2022). As global mean temperatures and variability increases, the threat of invasive insect species will increase as tropical and subtropical insects expand their range into more temperate areas (Chown et al. 2007; Weldon et al. 2016). Extreme weather events also promote invasive pathways through the modification of species hierarchies across tropical ecosystems, resulting in shifting species dominance and invasions

(Nyamukondiwa et al. 2022). These shifts are likely to modify competitive interactions, resulting in native communities that are more or less susceptible to colonisation by new invaders or expansion by established invaders (Finch et al. 2021). Such changes to the bio-physical environments may result in changes in the abundance and geographic distribution of invasive species (Hulme, 2016; Walther et al. 2009).

Temperature forms the first abiotic 'ecological filter' for successful invasion and establishment (Crowl et al. 2008; Olyarnik et al. 2009). Some successful non-indigenous species are more tolerant to environmental and anthropogenic stressors than related native species, possibly stemming from evolutionary selection pressure (i.e., survival of only pre-adapted individuals for particular environmental conditions) during the invasion process (Briski et al. 2018). Owing to this is the notion that invasive alien species are more eurythermal, or able to maintain physiological functionality across variable temperatures (Tarusikirwa et al. 2020; Gerken and Morrison III, 2023). Rapid adaptation is recognised as an important component of successful invasions (Colautti and Lau, 2015). Phenotypic plasticity can be adaptive and has been reported to improve survival in both Lepidoptera (Stotter and Terblanche, 2009; Fischer et al. 2010; Chidawanyika et al. 2017) and Coleoptera (Chidawanyika et al. 2017; Nyamukondiwa et al. 2018). Desiccation stress, commonly associated with arid environments is one of the primary stressors influencing the distribution and behaviour of insects in the tropics (Keosentse et al. 2022). Thus, as arthropods move from more mesic to xeric environments, they are faced with stressful desiccating environments (Weldon et al. 2016; Tarusikirwa et al. 2021). Given the relationships between desiccation-stress, temperature-stress and other life history traits in arid ecosystems (Keosentse et al. 2022), assessed desiccation tolerance in *S. frugiperda* in different developmental stages showed no negative impact on *S. frugiperda* fecundity following exposure to desiccation pre-treatment. This desiccation resistance may have aided in the species survival and ultimate success in arid and semi-arid environments (Gibbs, 2002) as this contributed to unabated perpetual reproduction and fitness of the moth species under stressful arid environments.

The direct effects of evolutionary history, behaviour and physiology on the ecology, and species biological responses to rising global temperatures are increasingly being documented (Kearney et al. 2009; Gerken and Morrison III, 2023; Bodlah et al. 2023). Environmental conditions can alter the form, function and behaviour of organisms through physiological responses over short and long timescales, and even over generations (Hochachka and Somero, 2002; Srinivasan and Brisson, 2012). In order for invaders to become established in a recipient environment, they must first pass through the 'ecological filter' of that environment (Crowl et al. 2008; Nyamukondiwa et al. 2022). The ecological filter is composed of two overarching components, the biotic and the abiotic (Crowl et al. 2008; Kelley, 2014). Biotic factors include ability to compete with native species for both resources and niche possession and avoiding predation by local opportunistic predators (Levine et al. 2004; DeRivera et al. 2005). Temperature and relative humidity are the most important abiotic factors faced by invaders in new regions (Nyamukondiwa et al. 2010; Weldon et al. 2016; Chidawanyika et al. 2017; Tarusikirwa et al. 2020; Nyamukondiwa et al. 2022). They require the insect to adjust its physiological responses to adapt to prevailing conditions (Hochachka and Somero, 2002; Kelley, 2014; Nyamukondiwa et al. 2022). Failure to overcome both biotic and abiotic factors can prevent establishment or further range expansion.

Invasion success is also affected by intrinsic attributes of species and characteristics of the invaded habitat (Decker et al. 2012). Tropical climates typical in Africa are characterised by extreme weather events such as high temperatures and seasonal droughts, thus, for successful invasion, insect pests have to adapt to these extreme climate features (Nyamukondiwa et al. 2022). These climatic and weather changes not only affect the status of insect pests but also affect their population dynamics, distribution, abundance, intensity and feeding behaviour (Ayres and Schneider, 2009; Stathers et al. 2013; Khaliq et al. 2014; Singano et al. 2019). In Africa the highest densities of *P. truncatus* tend to occur in humid lowlands, in contrast to meso-America where the pest tends to occur in greatest numbers in cooler upland regions (Hill et al. 2022). Arthur et al. (2019) carried out a predictive model that found *P. truncatus* has been limited to tropical and subtropical regions but could likely spread to temperate regions as temperatures rise with climate change. On the other hand, African climate is conducive for *S. frugiperda* proliferation as the pest originates from tropical and subtropical South America with largely similar climate to tropical Africa (Day et al. 2017; Timilsena et al. 2022).

Climate change, particularly increasing temperatures, have both direct and indirect effects on insect development and survival. Firstly, climate change may have adverse effects on the activity and effectiveness of natural enemies through top-down effects (Chidawanyika et al. 2019). The most affected organisms by increasing temperatures are higher trophic levels, including natural enemies (e.g., predators and parasitoids) and this may affect their efficacy as biological control agents (reviewed in Chidawanyika et al. 2019). While both *S. frugiperda* and *P. truncatus* are known to have high thermal tolerance (Machekano et al. 2020; Nyamukondiwa et al. 2022; Segaiso et al. 2022) the abundance and efficacy of natural enemies can be negatively affected at higher temperatures as higher trophic levels are affected more disproportionally than lower trophic levels (Thomson et al. 2010), affecting antagonism and leading to invasive species proliferation. The rampant spread of especially *P. truncatus* and to a lesser extent *S. frugiperda* across Africa has been hypothesised to be largely aided by lack of adapted natural enemies during early stages of invasion (see Hodges et al. 1983; Tendeng et al. 2019) and thus greater losses have been reported.

Climate change also alters the interactions between the insect pests and their host plants. It also influences the range and quality of host species through interaction with edaphic conditions and nutrient supply status of host plants, thereby indirectly affecting their life history traits and survival chances. For instance, elevated temperatures increase the concentrations of plant secondary metabolites, particularly condensed tannins and total phenolics, which ultimately influence the thermal tolerance parameters of herbivorous insects that feed on them (Jamieson et al. 2017). For *S. frugiperda*, the effects of diet and temperature have been well-documented by (Mubayiwa et al. 2023). The rate of insect multiplication might also increase with an increase in carbon dioxide (CO_2) and temperature, owing to the bottom-up effects associated with increase in e.g., plant host growth under optimal high CO_2 and temperature environments. Similarly, large scale changes in rainfall associated with changing climates will have a major effect on the abundance and diversity of arthropods (Sangle et al. 2015).

4.3.3.3. Species and event attributes leading to biological invasions in Africa

4. 3.3.3.1. Shared attributes across aggressive invaders

Invasion success by IAS is not only influenced by characteristics of the invaded habitat e.g., agro-ecology, but also intrinsic attributes of invasive species have a significant contribution (Decker et al. 2012). Common shared attributes across aggressive invaders have been summarised by Nyamukondiwa et al. (2022) and include high basal thermal tolerance, phenotypic plasticity, desiccation tolerance, insecticide resistance, host switching, high functional responses, high propagule pressure, integrated stress resistance and others (also see Kelley, 2014; Wang et al. 2016; Tarusikirwa et al. 2021). On the contrary, native species usually have lower competitive ability; lower dispersal abilities and reproductive edge (Siliceo and Díaz, 2010; Sánchez-Ortiz et al. 2020). While these characteristics vary across taxonomic groups, notable trait overlaps are common across the most prolific insect pest invaders (Sakai et al. 2001; Tarusikirwa et al. 2022). For example, generalist predatory habits (Snyder and Evans, 2006), dynamic population growth after an initial lag period (Sakai et al. 2001) and superior competitive ability relative to native organisms (Callaway and Ridenour, 2004) are among several of the components that have been shown to facilitate the establishment of non-native species (Kelley, 2014).

4.3.3.3.2. Species and event attributes of *Spodoptera frugiperda*

In *S. frugiperda*, the adult insect can self-disperse through flying over long distances to new environments. High reproduction, shorter life cycles, no diapause and host plant switches allow species to thrive in diverse environments (Montezano et al. 2018; Wan et al. 2021). Notably, the most prolific invasive species can feed on broad diets, i.e., polyphagous (Ross et al. 2012; Christodoulides et al. 2017). This is particularly important during species introduction and ensures survival in new areas. For *S. frugiperda*, its ability to feed on many hosts (~353 plants species from 76 families) mainly from Poaceae, Asteraceae and Fabaceae families (Kassie et al. 2020) presents the pest with excellent host-switching opportunities. Maize is the preferred host plant. However, in its absence, the pest can survive on sorghum (*Sorghum bicolor* L. Moench), cotton (*Gossypium hirsutum* L.), wheat (*Triticum aestivum* L.), cabbage (*Brassica oleracea* L.), cassava (*Manihot esculenta* Crantz) tomato (*Solanum lycopersicum* L.), beans (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* L. walp.) (Sisay et al. 2023), banana (*Musa nana* Lour.) (Zhou et al. 2022) and other wild hosts (see also Montezano et al. 2018; Mubayiwa et al. 2023).

However, in Africa, *S. frugiperda* has been primarily reported to infest maize followed by sorghum (Hailu et al. 2021; Sisay et al. 2023).

Due to their high fecundity, insects are more likely to survive and spread to newly introduced environments (Lieurance et al. 2022). Following successful invasion, ecological, economic and human health issues arise as a result of the establishment of IAS. The history of a species in its native range is a good predictor of potential impacts in the introduced environment (Kumschick and Richardson, 2013). The high fecundity of *S. frugiperda* and its ability to migrate long distances are two of the species' traits that could also explain the speed at which it invaded the continent (Day et al. 2017; Baudron et al. 2019). Exceptionally high fecundity allows for species rapid establishment post-invasion (Rwomushana et al. 2018; Nguyen et al. 2021). In addition, adults have been known to migrate several hundreds of kilometres (Rose et al. 1975; Tay et al. 2022). The adult moths can fly continuously for over 24 h and cover over 400 km through self-powered flight (Chen et al. 2022). In terms of larval dispersal via ballooning, *S. frugiperda* was found to have a wider dispersal and plant damage potential than any of the indigenous stemborer species *Busseola fusca* (Lepidoptera: Noctuidae) and *Sesamia calamistis* (Lepidoptera: Noctuidae) (Sokame et al. 2020).

The high supply and frequency of propagule introductions might have increased the chance of successful invasion due to high genetic diversity, continual supplementation, and increased probability of finding host plants and introduction to a favourable environment (Colautti et al. 2006; Richardson and Pyšek, 2006; Catford et al. 2009). The invasion success of *S. frugiperda* has been attributed to high parental propagules and multivoltine nature (Midega et al. 2018; Sokame et al. 2020; Nyamukondiwa et al. 2022; Segaiso et al. 2022). In addition to the high genetic diversity found in this species, human-assisted long-distance movements can reciprocate introductions of genotypes from invasive populations to native populations (Tay et al. 2022). *Spodoptera frugiperda* can feed any part of the host plant, e.g., on leaves, tassels and ears on or before the soft dough stage. In addition, the insect has a relatively shorter lifespan (3-4 weeks) and can adjust number of larval instars depending on diet (Mubayiwa et al. 2023) compared to related species, e.g., stem borers. This enables it to complete several generations per season, and quickly develop insecticide resistance mechanisms as well as evading unfavourable habitats.

Successful management of *S. frugiperda* has historically relied upon application of synthetic insecticides and through cultivation of genetically engineered crops expressing insecticidal proteins (Bt crops) (Bernardi et al. 2015; Gutiérrez-Moreno et al. 2018). *Spodoptera frugiperda* has, however, developed resistance to both synthetic insecticides (e.g., organophosphates, carbamates, pyrethroids and diamides) and Bt crops, which risks undermining the benefits delivered by these important crop protection tools (Gutiérrez-Moreno et al. 2018). Also, the cryptic feeding behaviour of larvae can further limit pesticide effectiveness (Reavey et al. 2022). For *S. frugiperda*, there are up to 150 parasitoid species, with a large number of them (80 species) originating from South America (de Freitas et al. 2019; Kenis et al. 2022). These parasitoids includes *Telenomus remus* (Nixon), *Meteorus* sp., *Chelonus texanus* (Cresson), *Cotesia marginiventris* (Cresson), *Aleiodes* sp. (Meagher and Nagoshi, 2012; de Freitas et al. 2019) in the Americas. In Africa, over 30 *S. frugiperda* parasitoids have been identified *viz Coccygidium luteum* (Brullé), *Trichogramma* sp., *Telenomus* sp., *Drino quadrizonulla* (Thomson, 1869), *Metopius* cf. *discolor* (Tosquinet), *Charops* sp., *Cotesia icipe* (Fernandez and Fiaboe) and *Palexorista zonata* (Curran) (Kenis et al. 2022). Despite the availability of these natural enemies, *S. frugiperda* damage remains serious in Africa due to overuse of pesticides in agroecosystems that compromise the field efficacy of these biological antagonists coupled with environmental conditions permitting the moth's all-year round development.

4.3.3.3.3. Species and event attributes of *Prostephanus truncatus*

Prostephanus truncatus, though not as devastating in its native range in central America as it is in invaded areas (Tigar et al. 1994) causes much higher damage in the introduced regions in Africa primarily due to lack of and/or failure of its natural enemies (Holst and Meikle, 2003). As such, unregulated populations result in wide dispersal and fast colonisation of hosts leading to high losses in stored maize and dried cassava roots (Richter et al. 1997). As previously alluded to, at the time of the accidental introduction of *P. truncatus* in Tanzania, there were no suitable pesticides registered for control of the pest as it required organophosphate-pyrethroid combinations rather than just organophosphates which could effectively control all other storage insect pests (Golob, 1988). Competition is one of the key elements propelling invasive species (Baliota et al. 2022). Although some studies have found *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) to be the better competitor compared to *P. truncatus* (Baliota et al.

2022) most agree that the latter fares much better in conditions found in most storage facilities, i.e., high temperature and low relative humidity and has a competitive advantage as an invasive species in new areas with stored maize, even in the presence of *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) (Giga and Canhao, 1993; Quellhorst et al. 2020; Baliota et al. 2022). However, most of these studies were laboratory-based and therefore more investigation is required on the competition phenomenon as this could play out differently in nature or under simulation. Pesticide tolerance also add to superior attributes of *P. truncatus*. While neonicotinoids have proven efficacious against *P. truncatus* (Mlambo et al. 2018; Doganay et al. 2018), there has been evidence of tolerance to organophosphate and pyrethroid formulations (Rumbos et al. 2013; Quellhorst et al. 2021; 2023). *Prostephanus truncatus* also produces copious amounts of grain dust that dilutes applied pesticides; thus affecting pesticide efficacy (Mlambo et al. 2018; Mutambuki et al. 2019). The increased rates of pesticide degradation due to increasing temperatures (Mlambo et al. 2018), coupled with *P. truncatus*'s high thermal tolerance and insecticide resistance mechanisms enhances the chances of survival of the pest over other species sharing the same ecological niche with it. Studies have also shown that apart from maize, *P. truncatus* can breed on a wide range of other plant substrates (branches, roots and seeds), has adapted to alternate hosts e.g., cassava, and can persist in non-agricultural habitats (Hill et al. 2002; Nang'ayo et al. 1993; Arthur et al. 2019). Muatinte and Van den Berg (2019) listed 13 trees and 8 grass species on which *P. truncatus* bred and survived on in the wild. The tree species include *Brachystegia spiciformis* Benth, *Colophospermum mopane* (Kirk ex Benth.) and *Strychnos spinosa* Lam, and fresh and dry grass stems of species including *Pennisetum glaucum* (L.) R. Br, *Hyparrhenia hirta* (L.) Stapf, *Acroceras macrum* Stapf, *Digitaria eriantha* Steud and *Aristida congesta* Roem and Schult (Muatinte and Van den Berg, 2019; 2021). The beetle possesses α-amylase and proteases that aids in digestion of wide variety of diets including hard woody material (Vázquez-Arista et al. 1999; Mendiola-Olaya et al. 2000; Castro-Guillén et al. 2012). Species attributes of *S. frugiperda* and *P. truncatus* that aid their invasiveness are summarised in Table 4.1.

Table 4. 1: Summarised superior species attributes possessed by the *Spodoptera frugiperda* and *Prostephanus truncatus* that potentially enable them to outcompete native species in invaded territories (also see Kelley, 2014 and Nyamukondiwa et al. 2022).

S. frugiperda	*P. truncatus*
• High fecundity and absence of diapause	• High reproductive capacity
• Self-dispersal through adult flights and larval ballooning	• Self-dispersal by adult flight
• High tolerance to pesticides	• High basal heat tolerance
• Larval internal feeding and frass cover limits pesticides' contact and efficacy	• Sporadic and temporal occurrence, making it difficult to control
• Wide host range	• Alternates between cultivated and wild hosts, making it difficult to control
• Have predatory habits, allowing it to devour competitors	• Possesses α-amylase enzyme to aid in digestion of hard material such as timber
	• Produce copious amounts of dust during feeding, thus diluting pesticides and reducing their efficacy
	• Feeds from inside kernels thus evading contact pesticides

4.4. Impacts of *S. frugiperda* and *P. truncatus* biological invasions

4.4.1. Overview

Invasive alien species have environmental, economic and social impacts, disproportionally threatening livelihood and food security of smallholder farmers in low- and medium-income countries (Paini et al. 2016; Pratt et al. 2017; Tambo et al. 2020; Durocher-Granger et al. 2021). In most cases, farmers and governments often invest huge sums of money towards synthetic pesticides, the major and first control option used against invading pests (Wan et al. 2021; Timilsena et al. 2022), seldom trading-off other important sectors e.g., healthcare and education (Eade and Williams, 1995; Jensen, 2000). Given pesticide resistance, many of these insecticides are often ineffective (Gutiérrez-Moreno et al. 2018). Furthermore, resource-poor farmers in developing countries usually cannot afford personal protective equipment and lack knowledge and understanding of chemical pesticides and their safe use (Nyamutukwa et al. 2022), which compromise proper use and exposure to toxic substances, resulting in accidental poisonings. Widespread and indiscriminate use of chemical pesticides also undermine environmental quality (biodiversity loss and pollution of air and water) and the pest control services provided by natural enemies (Isman, 2006).

4.4.2 Economic costs of *S. frugiperda* and *P. truncatus* invasions

The impacts of *S. frugiperda* and *P. truncatus* can be defined and quantified as economic costs, i.e., expenditures to prevent, reduce or alleviate the losses caused by these pests (Zenni et al. 2021), or the marketing losses resulting from compromised quality. In Africa, IAS generally can cause up to 35% loss in national gross domestic product (GDP) (Yainna et al. 2022). Severe maize infestation by *S. frugiperda* can reduce per capita household income by 44% and increase a household's likelihood of experiencing hunger by 17% (Rwomushana et al. 2018). Infestation by *S. frugiperda* reduces maize yields by up to 54% (Day et al. 2017; Kumela et al. 2019; De Groote et al. 2020) and can cause up to US$13 billion per annum crop losses across Africa (Day et al. 2017). Various reports have recorded even higher estimated losses per annum (Rwomushana et al. 2018; 211). In Ghana and Zambia, the annual loss estimates for 2017 were US$177 million and US$159 million, respectively (Rwomushana et al. 2018). In Ethiopia, the pest caused an average annual loss of 36% in maize production, reducing yield by 0.225 million tonnes of grain between 2017 and 2019 (Abro et al. 2021). In Kenya, *S. frugiperda* caused losses of about 33% of the annual maize production, estimated at about 1 million tonnes, with large variations across regions (De Groote et al. 2020; Kenis et al. 2022). Rwomushana et al. (2018), extrapolated that the pest had the potential to cause an annual reduction in maize production in Zimbabwe of about 264,000 tonnes, translating into revenue loss of US$83 million. More costs related to *S. frugiperda* damage are highlighted in Table 4.2.

Table 4. 2: Summary table showing the estimated costs related to *Spodoptera frugiperda* in some African countries. The costs are related to field damage, cost of control (including pesticides) and related. This list may not be exhaustive but represent significant data obtained at the time of writing.

Reported loss/ costs (USD)	**Year**	**Loss/ cost description**	**Country**	**Reference**
40. 2 million* (134 000 tonnes maize)	2017	Field damage to crops, amount of food that can feed 1.1 million people.	Ethiopia	(Kassie et al. 2020)
2.5 - 6.2 million (8.3 – 20.6 tonnes maize)	2022	Estimated yield losses	12 African countries	(Day et al. 2017; FAO, 2020)
3 million	2017	For pesticides and provision for replanting. Cost of pesticides per household was US$14.20 without subsidies and $7.30 with subsidies.	Zambia	(Rwomushana et al. 2018; FAO, 2020)
159 million	2018	Value of maize field losses	Zambia	(FAO, 2020)
4 million		Procurement of plant protection products	Ghana	(FAO, 2020)
177 million	2018	Value of maize field losses	Ghana	(FAO, 2020)
$ 25.30	2017	The amount spent on pesticides per household for those without subsidies. For those who received subsidies, the cost was $13.30	Ghana	(Rwomushana et al. 2018)

* *Using an average regional price of USD 300 per tonne of maize.*

On the other hand, grain damage due to *P. truncatus* can level up to 100% and weight losses between 30-50% have been reported in stored maize (Tefera, 2012; Muatinte and Cugala, 2015; Mlambo et al. 2017; 2018). Costs related to damage and losses as well as costs of controlling *P. truncatus* in maize are scarce primarily because the costs cannot be isolated from those of co-occurring pests such as *S. zeamais* and *Tribolium* spp. When *S. frugiperda* and *P. truncatus* occur in the same environment, they have potential to further disrupt vulnerable Africa's food systems through synergistic interactions. Invasive species also comprise one of the most apparent risks of globalization of international trade to both agricultural and related products (Goodell et al. 2000). This is because IAS can disrupt trade across countries, particularly in developing African regions, where phytosanitary measures are relaxed and ineffective (Venette and Hutchison, 2021). When the losses caused by the *P. truncatus* became more apparent in literature, many African countries declared it a quarantine pest and prohibited importation of maize from infested countries or after transit through these countries (Schulten and Toet,1988). This approach, however justified at that time, not only caused a loss of export markets to African countries that had a surplus of maize (in particular, Tanzania), but also complicated logistics and increased costs of the provision of 'relief maize' by the international community after the drought in southern Africa in 1991/1992 (Tyler et al. 1994; Farrell and Schulten, 2002). Combined field and postharvest losses due to *S. frugiperda* and *P. truncatus* led to food shortages by removing part of supply from the market thus contributing to high food prices (Ngom et al. 2020).

4.4.3. Direct and indirect effects of *S. frugiperda* and *P. truncatus* on human health and nutrition

Economic losses experienced when invasive species affect food production also result in negative effects on human health, directly or indirectly. By contributing to huge losses in maize, both *S. frugiperda* and *P. truncatus* contribute to malnutrition negatively affecting the health of many people across the continent. Tambo et al. (2020) found that households affected by *S. frugiperda* were 12% more likely to experience hunger, as measured by the household hunger scale. Farm losses incurred have cascading effects of reducing agricultural production which is largely menial in Africa (World Bank et al. 2011), thus further compounding food insecurity challenges. Human health is also affected by product contamination in storage, i.e., infestation by *P. truncatus* can increase the moisture content of the stored grains, inadvertently creating a favorable environment for fungal growth, e.g., *Aspergillus flavus* which can produce some carcinogenic aflatoxins in food products (Ngom et al. 2020). Furthermore, insect feeding also causes nutritional postharvest losses reducing basic access to nutritious food for consumers (Bechoff et al. 2022; Ngwenyama et al. 2022). Cereal grains comprise 30–60% of the daily caloric intake for humans around the globe (Awika, 2011). Maize, for instance, is central to food and nutrition security for millions of people in Africa, which consists of 54 countries populated by over one billion people and accounts for 73% of calorific intake within the region (UNDP, 2015; Sisay et al. 2019; Tambo et al. 2019; Mutyambai et al. 2022). Consumption of insect damaged grain potentially having low nutritional value exposes the population to malnutrition (Durocher-Granger et al. 2021).

Initial detection of *S. frugiperda* and *P. truncatus* is usually followed by haphazard use of pesticides, also leading to increased human exposure to pesticides. For example, in 2017, Zimbabwe distributed nearly 102,000 L of pesticide valued at 1.97 million US dollars to farmers (Timilsena et al. 2022). The continuous and injudicious use of these chemical insecticides poses adverse risks to human and environmental health, including the loss of biodiversity e.g., natural enemies and pollinators (Durocher-Granger et al. 2021; Mutyambai et al. 2022). This also increases the costs incurred in mitigating and managing the pest, a feat that is often difficult for resource constrained African farmers (Machekano et al. 2018; Tarusikirwa et al. 2020).

4.4.4. Ecological costs of biological invasions

Biological invasions rank among the most significant threats to biodiversity and ecosystems and are considered the second most serious cause of species extinctions (Richardson et al. 2011; Castaño-Quintero et al. 2020). Their ecological impacts can be so severe that they are considered as one of the major drivers of biodiversity loss across the globe (Pyšek et al. 2020; CBD, 2022; Mačić et al. 2018). They are associated with an average of 25% decline in native species diversity and increasing abundances of non-native predators are linked to a 44% decline in native species population (Bradley et al. 2019). Indeed, the impact of invasion by a single non-native species on the function and structure of ecological communities can be devastating as they have detrimental effects on ecosystem functioning and the delivery of ecosystem services (Simberloff et al. 2013; Pyšek et al. 2020; Diagne et al. 2021). The interactions amongst species in an ecological community can be significantly altered as the introduction of an exotic species can influence species composition, richness and abundance; thereby disrupting the structure of local food webs and patterns of interspecific interactions (Ehrenfeld, 2010; Simberloff et al. 2013). Using data from InvaCost, a repository of costs of invasive alien species (Diagne et al. 2021), estimated the cumulative cost of biological invasions in Africa to range between US$18.2 billion to US$78.9 billion for the period from 1970 to 2020. Worryingly, the reported costs are mostly associated with the damage caused by invasive alien species without considering those of controlling the incursions. Consequently, the actual total costs were grossly under-estimated. The majority of reported costs are, however, skewed towards agriculture and health sectors, which are considered economic activities compared to ecosystem services (Zenni et al. 2021).

Field studies conducted in Uganda revealed that the invasion by *S. frugiperda* has caused the decline of stemborer incidences in maize and the displacement from the maize crop, as their preferred host plant, to sorghum (Hailu et al. 2021; Mutyambai et al. 2022). There is interspecific competition amongst these species at the larval stage in the utilisation of maize – the preferred host (Ntiri et al. 2019; Sokame et al. 2020). Such interactions are likely to influence community structure of these lepidopteran herbivores in areas where they co-exist (Mutyambai et al. 2022). Introduction of species into new environments can trigger rapid evolution, for example functional responses, and thus increasing the damage potential of alien invasive species (Jaric et al. 2019). Furthermore, multiple introductions of species from different biogeographical regions can result in cryptic interactions leading to admixture of genetic characteristics leading to changes in genomic structure of the IAS (Juric et al. 2019; Sherpa and Després, 2021; Wang et al. 2023). Rane et al. (2023), for example, associated multiple *S. frugiperda* introductions into Asia and Australia with genetic hybridisation, backcrossing and genome doubling (Yainna et al. 2022), linking these with the introduction of insecticide resistance alleles in established populations. Such genetic hybridisation complicates pest management, leading to increased crop losses.

Similarly, studies have shown that invasive species that occur in postharvest agricultural commodities are often more competitive and can overcome competition and even displace other native species (Athanassiou et al. 2014; Sakka and Athanassiou, 2018; Quellhorst et al. 2020; Baliota et al. 2022). Quellhorst et al. (2020), examined the competition between *S. zeamais* and *P. truncatus* on maize at four varying temperatures and found that increasing temperature resulted in elevated population growth of the invasive *P. truncatus* at the expense of *S. zeamais*. Other impacts noted included direct competition, changes to ecosystem functioning, hybridization and predation. Phylogenetic studies by Guntrip et al. (1996), revealed significant additive genetic and environmental effects enhancing some traits (e.g., body weight) in strains of *P. truncatus* from different geographical locations, increasing fitness and thus invasiveness in certain populations. Similarly, genetic diversity in *T. nigrescens* characterised by allele insertions and deletions at specific loci may explain the variable success of biological control of *P. truncatus* with predators from different geographical locations (Omondi et al. 2011). Ecosystem dynamics are altered through a variety of interacting, mutually reinforcing mechanistic pathways, for example, species' resource acquisition traits; population densities and the ability to engineer changes to physical environmental conditions (Ehrenfeld, 2010). Impacts to the environment such as pollution and development of pesticide resistance in pests arise through excessive and/or over application of synthetic pesticides in response to biological invasions (Venette and Hutchison, 2021). This has negative implications on ecological services as they can lead to death of non-target organisms, e.g., pollinators, predators and parasitoids (Blacquière et al. 2012).

4.5. Management strategies for *S. frugiperda* and *P. truncatus* biological invasions

4.5.1. Overview

Management of biological invasions can be divided into two stages: 1. prevention through quarantine measures, and 2. management through curative measures, which is a reaction to invasion following detection of ecological impacts (Cuthbert et al. 2022). Usually, preventive measures are the first line of defence and if the results are unsatisfactory, curative measures are employed. In practice, management of invasive species require the application of a combination of these approaches.

4.5.2. Prevention through quarantine measures

Investment in biosecurity measures is important in monitoring and preventing introductions (Epanchin-Niell et al. 2021). However, Ahmed et al. (2022), noted that the unpredictable nature of potential invasion makes preventive management "riskier" than control after establishment. The use of numerical trajectory models to predict the long-distance migration and possible destinations of insect pests is one example that can be used to monitor and detect invasions at early stages in areas under invasion risk (Wang et al. 2023). However, it is practically impossible to detect insect pests at the initial infestation site at a sufficiently early stage to have chances of eradicating the pest (Salama and Abd-Elgawad, 2003). Given that zero tolerance quarantine protocols require sampling every unit of imported goods, the default strategy therefore is to set acceptable tolerance limits (supported by technical information) for each pest sampled. In Africa, Salama and Abd-Elgawad (2003) presented a table to determine probabilities of detecting pest infestation levels when increasing numbers of samples are collected from an imported lot. Such a technique reduces labour, time, money and ensures certainty in the detection process. Budgetary constraints and bureaucracy, on the other hand, also tempt decision-makers to intervene in late-stage management of invasions (Ahmed et al. 2022). In most invaded countries therefore, management of *S. frugiperda* and *P. truncatus* is limited to eradication strategies following invasion and initial spread of the pests.

4.5.3. Curative measures

The use of synthetic pesticides to control both field and storage insect pests is dominant in Africa (Nyabako et al. 2021). In *S. frugiperda*, control is mainly dominated by the use of a combination of synthetic pesticides, cultural (early planting, varietal selection and field hygiene) and mechanical methods (Timilsena et al. 2022; Nyamutukwa et al. 2022; Tay et al. 2023). Since the invasion of the African continent by *S. frugiperda*, huge quantities of pesticides amounting to trillions of US dollars have been used to control the pest (Stokstad, 2017; Table 4.2). However, the use of synthetic pesticides is unsustainable due to high costs, resistance development, pest resurgence and negative effects to environmental and human health (Timilsena et al. 2022; Nyamutukwa et al. 2022). This calls for the development and use of alternative control options for example systemic seed treatments (Chinwada et al. 2023). Cultural control options such as varietal selection are key as the first line of defence against *S. frugiperda* and other pests. Host plant resistance is one of those methods that can be useful for *S. frugiperda* control (Kenis et al. 2022). There is thus need to identify and target those hosts/varieties for pest management. Crops grown under rainfed and mixed cropping systems were found to be less prone to attack by *S. frugiperda*, as rainwater tend to wash larval instars away (Mutyambai et al. 2022). This can be complemented by tillage systems where conventional tillage and frequent weeding was found to reduce *S. frugiperda* incidences through exposure of pupae to the soil surface, thereby exposing them to the direct sunlight and predation (Baudron et al. 2019; Mutyambai et al. 2022). On the other hand, intercropping with pumpkins was found to increase damage from *S. frugiperda* (Baudron et al. 2019). Mechanical and physical control methods are recommended under small-scale farming systems, as these methods are more practical on small pieces of land. These methods include handpicking and crushing the larvae and egg masses, and/or adding ash, saw dust or sand in plant whorls to desiccate the insects (Wan et al. 2021). In addition, intercropping with non-hosts such as common bean and push-pull strategies are being advocated for (Wan et al. 2021; Timilsena et al. 2022). Host plant resistance through cultivation of Bt crops has also been an option for the control of *S. frugiperda* (Bernardi et al. 2015; Gutiérrez-Moreno et al. 2018) however, reports suggest the pest has developed resistance to Bt maize (Gutiérrez-Moreno et al. 2018).

On the other hand, conventional synthetic insecticidal dusts have not guaranteed protection of stored maize grain against *P. truncatus* damage (De Groote et al. 2013; Ndegwa et al. 2016; Mlambo et al. 2017; Mutambuki et al. 2019) Neonicotinoid-based pesticides have been quite effective compared to organophosphate and pyrethroid active ingredients (Tsaganou et al. 2021). The use of entomopathogenic fungi such as *Beauveria bassiana* has been reported to be effective in controlling *P. truncatus* infestation on stored maize though it would require periodic re-treatment after every 4 weeks to maximize grain protection during prolonged storage (Luke et al. 2023). Combinations of enhanced diatomaceous earths (DEs) and natural products such as spinosad or low dose pyrethroids have also been proven effective both in the laboratory and in small scale grain storage systems (Machekano et al. 2017; 2019) but are not available on the market. Host plant resistance through selection and use of resistant varieties can be integrated with other control methods such as synthetic pesticides to improve *P. truncatus* management (Tefera et al. 2011). Recent research has thus focused on hermetic storage technologies which have brought the much-needed improved protection of stored grain commodities in much of Africa (Harish et al. 2014; Waongo et al. 2019; Baributsa et al. 2020; Ngwenyama et al. 2020) safeguarding food and nutrition security while simultaneously reassuring pesticide-free food (Ndegwa et al. 2016). Grain imports can also be phosphine-fumigated on-board to control all life stages of insect pests before destination arrival (Pimentel et al. 2007; Chidemo et al. 2023). Apparently, literature on economic impact of postharvest interventions are scarce, more so with specific reference to *P. truncatus*. In a comprehensive scoping study by Stathers et al. (2020), only 12.5% of the 334 studies reviewed, reported economic outcomes. This shows that more evidence is required in this area in future studies. A robust postharvest loss assessment system for Africa is provided by African Postharvest Loss Information Systems (APHLIS) online platform (Stathers et al. 2018; Anon, 2023). The platform provides loss estimates for different cereal grains by country, year, postharvest stage and the causes of postharvest losses (Rembold et al. 2011; Hodges et al. 2014). The platform is expanding to include nutritional and economic implications of postharvest weight losses (Anon, 2023).

To successfully regulate invasive species therefore, both quarantine and eradication measures through voluntary and enforced legislation are required (Wilson et al. 2011). The use of lists of quarantine species at border crossings to prevent the introduction of IAS should increase between counties (García-De-Lomas and Vilà, 2015). Furthermore, coordination across countries that share IAS is important as well as synchronising their regulations to prevent local spread. Postharvest wise, investment in road systems, infrastructure and logistics for grain movement, storage and processing are essential to reducing losses (Tian and Yu, 2019). Increased international trade agreements may offer an opportunity for individual nations to harmonise quarantine policies (Ricciardi et al. 2017). Comparison of the environmental conditions of native and introduced ranges is useful in determining the likelihood of an introduced species' establishment and invasiveness in novel ranges (Kumschick and Richardson, 2013). Using climate data from *P. truncatus* native range Arthur et al. (2019), predicted the beetle will likely spread and become more aggressive in Southern Africa due to similar climatic conditions, particularly high temperatures, compared to those found in Mexico and Central America, where the pest originated. Similarly, numerical trajectory models have placed southern Europe at risk of invasion by *S. frugiperda* from Egypt (Wang et al. 2023). Thus, through dynamic modelling of climate data and species spatial-temporal dynamics, and accounting for the lesser sensitivity of biological invaders relative to natives (Gu et al. 2023), models have become essential to the control of biological invasions (Buchadas et al. 2017).

4.6. Conclusions

Efforts to improve regional food security in Africa continue to be hampered by increasing threats of pest invasions across the food value chain. Climate change and increased anthropogenic activities, including trade and landscape modifications for agricultural purposes, are some of the major drivers of biological invasions in Africa. Since its introduction into Africa in 2016, *S. frugiperda* has become the most devastating field pest of maize – a staple food across sub-Saharan Africa and similar regions of the world. Similarly, *P. truncatus* exacerbates these food losses along the maize grain value chain, and the interaction between the two pests through cumulative synergistic damage on the same crop has led to aggravated staple food losses. In the case of *P. truncatus*, further economic losses are incurred through loss of goodwill in terms of trade between countries or the extra measures that have to be taken when importing grain from *P. truncatus*-infested countries. Ironically, concrete data on economic losses caused by *P. truncatus* are scanty; and hence need greater attention in future studies. Integrated pest management strategies are key to management of the two invasive species at national level whilst pest monitoring and phytosanitary compliance are key at regional and international level. The aggressive nature of the two invasive insect species, extensive damage and associated attributes leading to their superiority, offer insights to researchers and policymakers on issues relating to future research studies and legislation for the control of biological invasions and mitigating their economic, environmental and societal impacts. This information is vital for improving food and nutrition security nationally and continentally through increased yield and reduction of postharvest losses. The maintenance of resilient and integral food systems in highly vulnerable regions like Africa, e.g., through reducing the introduction and/or impacts of invasive agricultural pests is of paramount importance for the realisation of the United Nations Sustainable Development Goals.

4.7. References

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CHAPTER 5

Parental heat stress has transgenerational physiological- but not ecological-progeny fitness advantage in the larger grain borer[4].

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5.1. Introduction

Climate change has accelerated significantly over the last few decades, with clear trends in global temperature rise, shifting weather patterns, and increasing frequency and magnitude of extreme events (Karl and Trenberth, 2003; Seneviratne et al. 2021). These changes affect organisms across different levels of biological organization, with cascading long-term effects along generations over different timescales (Donelson et al. 2017; Pecl et al. 2017). Because their body temperature and physiological processes are directly influenced by the external ambient environment, temperature fluctuations especially impose significant thermal stress on ectotherms (Chown and Nicolson, 2004; Angilletta, 2009; Abram et al. 2016). While some species may adapt *in situ* or migrate, many others face increasing risk of decline or extinction (Moritz and Agudo, 2013). As such, *in situ* adaptation through phenotype physiological and/behavioral modification is an important topic in ecology, facilitating species resilience and persistence, while supporting ecosystem functioning under climate change (Fox et al. 2019; Kellermann and Van Heerwaarden, 2019). Indeed, an organism's fitness under climate change may be defined by how efficient it can integrate different sources of environmental information regarding the likelihood of success of phenotypic alternatives (Leimar and McNamara, 2015). The term plasticity is therefore used to describe how environmental conditions modify adaptive phenotypic expressions in living organisms (Moczek, 2010; Sgrò et al. 2016; Rodrigues and Beldade, 2020). This mechanism is near ubiquitous in insects (Moczek, 2010; Sgrò et al. 2016) and many ecologists agree that it allows for within- and across-generation adaptation and may cushion organisms against climate change (Seebacher et al. 2015; Rodrigues and Beldade, 2020; Harmon and Pfennig, 2021). However, a few studies have shown that there is limited potential for plasticity to buffer organisms against climate change owing to a low acclimation ability (Hoffmann et al. 2013; Van Heerwaarden et al. 2016; Van Heerwaarden et al. 2024). The mechanisms facilitating phenotypic plasticity have been widely documented (Whitman and Agrawal, 2009; Sgrò et al. 2016) however, despite a growing body of knowledge on climate change and effects on ecology, the mechanisms underlying insect responses to climate change remain complex and context-dependent (Mlambo et al. 2024a), influenced by species-specific traits, interactions with other organisms, and the macro and micro local environmental conditions. Understanding how climate change affects insect ecology across generations is therefore essential for predicting broader ecological outcomes and for developing conservation and management strategies for economically important insects under rapidly changing environments. Scientists have often used acute and chronic heat acclimation experiments whereby parental organisms are respectively subjected to short- and long-term heat respectively to induce acclimation responses and subsequently test whether the responses have been passed on to the progeny.

Environmental conditions experienced by offspring can interact with earlier experiences of parent generations to induce phenotypic alterations in organisms (Woestmann and Saastamoinen, 2016; Donelson et al. 2017). Such plastic responses are of particular interest as they can buffer organisms against immediate stress effects (Donelson et al. 2017) while simultaneously, providing time for more long-term evolutionary population responses (Sgrò et al. 2016; Donelson et al. 2017). While within-generation changes in phenotypes are important for short term adaptive responses, transgenerational plasticity allows organisms with short lifespans to rapidly adjust phenotypes across generations without changing their genetic makeup (Bell and Hellmann, 2019). This is a type of phenotypic plasticity where the environment experienced by a parent can influence the fitness traits of its offspring (Leimar and McNamara, 2015; Donelson et al. 2017). The process occurs stepwise following a parent receiving stressful environmental cues that induce acclimation (Bell and Hellmann, 2019), which are then expressed in offspring through epigenetic inheritance (Donelson et al. 2017). This epigenetic inheritance allows environmentally induced changes in gene expression to be transmitted by parents to offspring without changes in DNA sequence. Through this process, parents pass on ‘memories’ of environmental experiences to their offspring, allowing them to express phenotypes that improve survival and/or fitness under stressful and dynamic environments (Bell and Hellmann, 2019).

The larger grain borer, *Prostephanus truncatus* (Horn) is a serious invasive insect pest of stored maize in Africa (Hodges et al. 1983; Arthur et al. 2019; Mlambo et al. 2024b). The pest is native to Central America; in Africa it was first reported in Tanzania in 1970 (Hodges et al. 1983). Since then, the pest has spread to different African countries (see Quellhorst et al. 2021; Mlambo et al. 2024b) propelled by different anthropogenic activities and climatic conditions which resemble its place of origin (Arthur et al. 2019; Harman et al. 2024). *Prostephanus truncatus* thrives in diverse environments and can disperse between maize and cassava stores as well as non-agricultural forest woodlands which act as alternative hosts (Borgemeister et al. 1998; Nansen et al. 2002; Arthur et al. 2019). Prediction models suggest that *P. truncatus* will continue its range expansion accompanied by population growth and extensive damage with increased temperatures (Arthur et al. 2019; Nyabako et al. 2020; Harman et al. 2024). These predictions are in contrast the optimal developmental temperature hypothesis which suggests that an organism exhibits peak performance at a specific optimum temperature (Zamudio et al. 1995; Klepsatel et al. 2019). It is therefore important to understand the mechanism behind the success of *P. truncatus* in new and rapidly changing environments to provide insights on abundance modelling and integrated pest management options. Previous studies have determined within generation effects of increased temperatures on *P. truncatus* physiological responses (see Singano et al. 2020; Machekano et al. 2020; Mutamiswa et al. 2021). Mlambo et al. (2024a) further linked physiological responses to ecological performance and outlined fitness trade-offs following sub-lethal heat stress exposure. However, since *P. truncatus* can thrive in diverse environments for instance when beetles migrate from grain storage facilities to forests following pesticide application (Harman et al. 2025), it is unknown how parental environmental stress history shapes progeny fitness in the new environment and whether or not the fitness responses will be passed on to the subsequent generations. An understanding of this is important for integrated management of persistent pests.

While temperature variability is mainly influenced by seasonal climatic changes, habitat and microhabitat induced temperature fluctuations can also be detrimental to insects (Colinet et al. 2015). This is especially true for storage insect pests which suffer temperature increases due to stochastic processes and biological activity of grain e.g., respiration (Moses et al. 2015; Wu et al. 2020). Here we used ‘physiology’ to describe the physical functional properties of insects supporting life (Jurenka, 2021). On the other hand, we also used insect utilisation of host grain and/or interaction with its surrounding environment as a proxy for ecological fitness (Kingsolver, 1989; Fordyce, 2006; Abram et al. 2016). To complement previous studies, we evaluated physiological and ecological performance of *P. truncatus* to determine transgenerational effects of heat acclimation on its life history traits between F_2 and F_3 generations. Physiological traits were measured using critical thermal limits (critical thermal maxima [CT_{max}] and critical thermal minima [CT_{min}]) and Heat knockdown time (HKDT) as well as upper lethal temperatures (ULTs). These metrics are easy to measure and ecologically relevant (Chown and Nicolson, 2004; Gunderson and Stillman, 2015). Ecological performance was measured by assessing adult weight, days to progeny emergence, progeny production, percentage insect damage chaff, percentage grain damage and percentage grain weight loss following parental heat acclimation. These metrics represent the pest damaging potential and thus its ecological significance under natural conditions (Hodges et al. 1983; Boxall, 2002). The current study was therefore aimed at determining the effects of temperature on the transgenerational responses of *P. truncatus*. The objectives of the investigations were to determine the effects of *P. truncatus* parental acute heat acclimation on progeny (i) physiological fitness and (ii) ecological performance in F_1, F_2 and F_3 generations. In line with the beneficial acclimation hypothesis (see Huey et al. 1999; Wilson and Franklin, 2002), it is hypothesized that parental sublethal acute heat exposure will improve physiological and ecological performance of *P. truncatus* progeny in post acclimation filial generations. Understanding transgenerational responses is crucial for forecasting pest dynamics, anticipating stress resistance, and designing sustainable, long-term integrated pest control strategies under climate change.

5.2. Materials and methods

5.2.1. Treatments

Seven treatments, from parental to F_1-F_3 generations were evaluated (Table 5.1). These were formulated using a culture of *P. truncatus* that had been kept in the Eco-physiological entomology research laboratory at Botswana International University of Science and Technology for more than ten generations. This population was started from individual beetles trapped using pheromone-baited traps (active ingredients: 1-Methylethyl (E)-2-pentenoate and 1-Methylethyl (E, E)-2,4-dimethyl-2,4-heptadienoate) in Gaborone, Botswana (site of collection 24°35′01″ S; 25°56′49″ E). Wild collected individuals from the same site were regularly added to the parent culture to reduce inbreeding depression (Terblanche and Chown, 2007). The culture was maintained on shelled yellow maize grains (SeedCo variety 608, SeedCo Group, Gaborone, Botswana) in 1 litre Colsol jars with perforated lids to allow air circulation. These jars were kept in a Memmert climate chambers (HPP 260, Memmert GmbH + Co.KG, Germany) set at 32 °C, 65 ± 10% RH under a 12L:12D photoperiod. Acclimation treatments were exposed to acute heat (35 or 38℃; 80% RH) for a duration of 2 hours.

Table 5. 1: Treatments T_1–T_7 used to evaluate physiological and ecological performance of *Prostephanus truncatus* following acute heat acclimation. Acute acclimation conditions were derived from previous studies (see Chown and Nicolson, 2004). TGP = transgenerational plasticity.

Treatment	**Description**
T_1 (P_32°C)	Parent *P. truncatus* culture maintained at optimal conditions; 32°C, 65 ± 10% RH. This treatment acted as the control.
T_2 (F_1_35°C)	A sub-culture from P_32°C that was acclimated at 35°C, 80% RH for 2 hours and then maintained at 32°C, 65-80 % RH for subsequent TGP tests.
T_3 (F_1_38°C)	A sub-culture from P_32°C that was acclimated at 38°C, 80% RH for 2 hours and then maintained at 32°C, 65-80 % RH for subsequent TGP tests.
T_4 (F_2_35°C)	A subculture from F_1_35°C that was maintained at 32 °C, 65 ± 10% RH for subsequent TGP tests.
T_5 (F_2_38°C)	A sub-culture from F_1_38°C that was maintained at 32°C, 65 ± 10% RH for subsequent TGP tests.
T_6 (F_3_35°C)	A sub-culture from F_2_35°C that was maintained at 32 °C, 65 ± 10% RH for subsequent TGP tests.
T_7 (F_3_38°C)	A sub-culture from F_2_38°C that was maintained at 32°C, 65 ± 10% RH for subsequent TGP tests.

The acclimation conditions have been shown to induce beneficial acclimation responses in similar insects (Chown and Nicolson, 2004; Weldon et al. 2011; Cole et al. 2023; Mlambo et al. 2024a) and are also experienced under natural heat wave conditions in Botswana. For example, temperature highs often range between 36–40°C in summer (Moses, 2017; Nkemelang et al. 2018). After acclimation, insects were maintained at optimal conditions (32°C, 65 ± 10% RH) on shelled maize for subsequent bioassays.

5.2.2. Bioassays

Bioassays were run using adult 3–7 days old *P. truncatus* beetles. To get uniformly aged beetles, adult beetles were removed from each treatment following a 21-day window for mating and oviposition (Machekano et al. 2020). The beetles that emerged thereafter were collected as progeny for subsequent transgenerational plasticity experiments.

5.2.2.1. Thermal tolerance assays

Thermal tolerance was measured using critical thermal limits to activity (CT_{max} and CT_{min}), HKDT and ULTs. In this study, CT_{max} and CT_{min} were respectively defined as the maximum and minimum temperature at which individual adult *P. truncatus* lost coordinated muscle function and capacity to respond to mild stimuli from a thermally inert object (Nyamukondiwa and Terblanche, 2009). These limits represent ecologically relevant endpoints to key life activities, including e.g., locomotion, mating, oviposition and survival. Ten adult insects were each placed in individual transparent organ pipes of a double-jacketed chamber connected to a programmable water bath (heated and refrigerated circulating water bath with a temperature range of −25°C to +200°C; LAUDA Ecogold® RE 2025, Lauda-Königshofen, Germany) with a 1:1 water to propylene glycol solution running through the chamber to control the temperature (Chown and Nicolson, 2004; Chidawanyika and Terblanche, 2011). The rate at which temperature changes has significant effects on physiological and ecological responses (Leong et al. 2022), and indeed, critical thermal limits are affected by methodological context (Terblanche et al. 2007). As such, the temperature was ramped up (for CT_{max}) and down (for CT_{min}) from a set point of 32°C (optimum temperature for *P. truncatus*) at two rates, 0.25 and 0.5°C per minute (as in Mpofu et al. 2022) until critical thermal limits were recorded. Temperature readings were made from a thermocouple (type K 36SWG) connected to a digital thermometer (Fluke 54 series IIB) inserted in the control organ pipe of the chamber. Thirty replicated measurements were produced by repeating the procedure three times for each treatment.

Heat knockdown time assays were executed by acutely exposing adult beetles to constant 50°C using the Memmert climate chamber with a video recording camera (HD Covert Network Camera, DS-2CD6412FWD-20, Hikvision Digital Technology Co., Ltd, Hangzhou, China) connected to a computer to record the activity. Temperature of the climate chamber was allowed to stabilize at 50°C for 10 minutes after which thirty adult beetles each placed in 1.5 ml Eppendorf tubes were assayed. Heat knockdown time was recorded as the time in minutes at which an insect lost ability to self-right during exposure to acute heat stress (Machekano et al. 2020; Mutamiswa et al. 2021; Mlambo et al. 2024a).

ULTs were assayed following the direct plunge protocol (Terblanche et al. 2008; Chidawanyika and Terblanche, 2011). Three replicate perforated 60 ml plastic vials were used, each with an added wet cotton wool inside to maintain RH and prevent desiccation related mortality. Thereafter, 10 adult insects were added to each replicate vial. The three vials were then placed in a water-tight zip lock bag and plunged into a water bath set at different treatment temperatures at.38, 42, 46 and 50°C and time durations for 0.5, 1, 2, 3 and 4 hours. This resulted in three replicates for each treatment × temperature × time exposure combination. Following exposure, the insects were conditioned at optimum conditions of 32°C, 65 ± 10% RH for 24 hours to recover. Thereafter, survival was scored as those insects that exhibited either coordinated muscle function or normal behaviors e.g., feeding, walking, flying or self-righting (Nyamukondiwa and Terblanche, 2009).

5.2.2.2. Ecological performance assays

Ecological performance of *P. truncatus* following parental heat acclimations were assayed using 3–7 days old F_1–F_3 progeny beetles. Three replicates of 500 ml jars (5 cm diameter × 125 cm height) with 400 g sterilized and conditioned dried maize grains were prepared for each treatment (Table 1). The grains were sterilized by freezing at -18°C for 14 days and then conditioned at 32°C, 65 ± 10% RH for another 7 days (Hodges and Dobson, 1998; Mlambo et al. 2024a). Twenty beetles (10 male: 10 female) sexed following protocols by Shires and McCarthy, (1976) were placed in each jar. The jars were kept in a climate chamber at optimal conditions (32°C, 65 ± 10% RH) for 21 days after which adult beetles were removed from grains. The jars were kept under the same conditions for 35 days and checked daily to determine the number of days to F_1 emergence for each treatment. Individual weights of adult beetles were recorded 3–7 days after emergence. After the 35-day period which allowed all eggs to hatch; all progeny that had emerged were recorded. Further, whole sample analyses were done to determine insect feeding dust, grain damage and grain weight loss percentage, which are standard metrics for estimating postharvest pest grain damage (Boxall, 2002).

5.3. Data analyses

Datasets gathered were subjected to Kolmogorov-Smirnov and Lilliefors test for normality. CT_{max}, CT_{min}, grain damage, grain weight loss, insect feeding dust, number of progenies, adult individual weight and number of days to progeny emergence datasets were normally distributed (all $p > 0.05$). HKDT data did not satisfy normality tests ($p < 0.05$) and were square root transformed to compress the large values and reduce positive skewness (see Church, 1979). Thereafter, analysis of variance in Statistica 14 (Day and Quinn, 1989; De Sá, 2007) was used to compare treatment means on all data sets to determine if there were any significant differences between them. For CT_{max} and CT_{min}, ramping rates (0.25 and 0.5°C/ minute) were used as factor. In case of significant differences, post hoc analysis was performed using Tukey's HSD test to separate treatment means. Survival was plotted using Cumulative proportion surviving (Kaplan-Meier) by group analysis as a function of exposure time. Treatments were used as the censoring variables and temperature as the grouping variable.

5.3. Results

5.3.1. Physiological performance

5.3.1.1. Critical thermal limits

Critical thermal maxima ranged between 46 and 52°C for both the 0.25 and 0.5°C/minute ramping rates (Fig. 5.1). Significant differences in CT_{max} between ramping rates were observed for the 0.25°C/minute ($p < 0.05$) and not 0.5°C/minute rate ($p > 0.05$). As such, our transgenerational plasticity discussions are only based on the 0.25°C/minute heating rate for CT_{max}. For the 0.25°C/minute ramping rate, mean progeny CT_{max} increased significantly ($F_{6, 406} = 14.56$, $p < 0.001$) from 48.6 ± 0.07°C in parental control treatment (P_32°C) to around 49.5 ± 0.05°C which was then 'stable' and statistically not different across the subsequent F_1 to F_3 treatments. Furthermore, individual control CT_{max} values varied widely between 46.5 and 49.5°C whereas progeny individual CT_{max} (F_1–F_3 treatments) had a narrower range between 48.5 and 50°C with a few outlier values (3°C versus 1.5°C for parental and F_1–F_3 progenies respectively). On the contrary, 0.5°C/minute ramping rate did not influence progeny CT_{max} and both parent and progeny CT_{max} had a narrow range between 49.5 and 50°C (1°C for both parental and F_1–F_3 progenies).

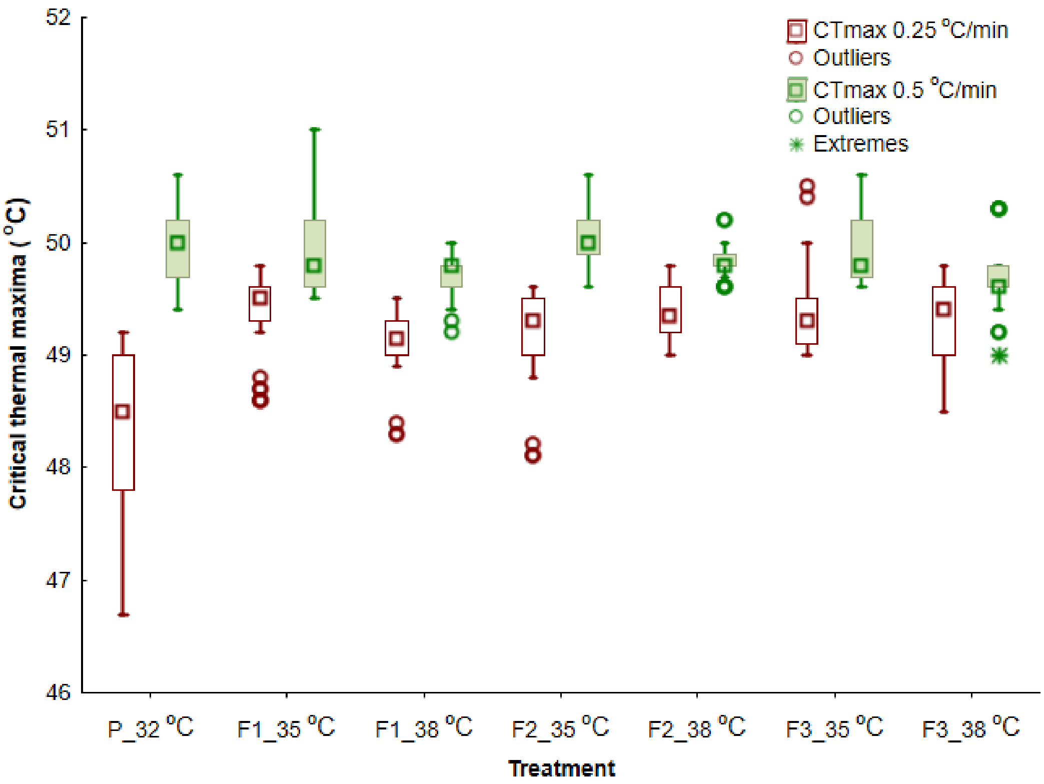

Figure 5. 1: Critical thermal maxima ranges recorded for *Prostephanus truncatus* using 0.25 and 0.5°C/minute ramping rates. P_32°C = a parent culture (control) maintained at 32°C, 65 ± 10% RH. F_1_35°C = a sub-culture of P_32°C that was acclimated at 35°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_1_38°C = a sub-culture of P_32°C that was acclimated at 38°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_2_35°C = a subculture of F_1_35°C that was maintained at 32°C, 65 ± 10% RH. F_2_38°C = a sub-culture of F_1_38°C that was maintained at 32°C, 65 ± 10% RH. F_3_35°C = a sub-culture of F_2_35°C that was maintained at 32°C, 65 ± 10% RH. F_3_38°C = a sub-culture of F_2_38°C that was maintained at 32°C, 65 ± 10% RH.

Critical thermal minima ranged from 2.5–5.0 and 3.0–7.0°C for the 0.25 and 0.5°C/minute ramping rates respectively (Fig. 5.2). Acute heat acclimation significantly increased progeny CT_{min} for the 0.5°C/minute cooling rate ($F_{6,\,406} = 25.12$, $p < 0.001$) but not the 0.25°C/minute rate ($p > 0.05$) in *P. truncatus*. As such, our transgenerational plasticity discussions are only based on the 0.5°C/minute cooling rate for CT_{min}.

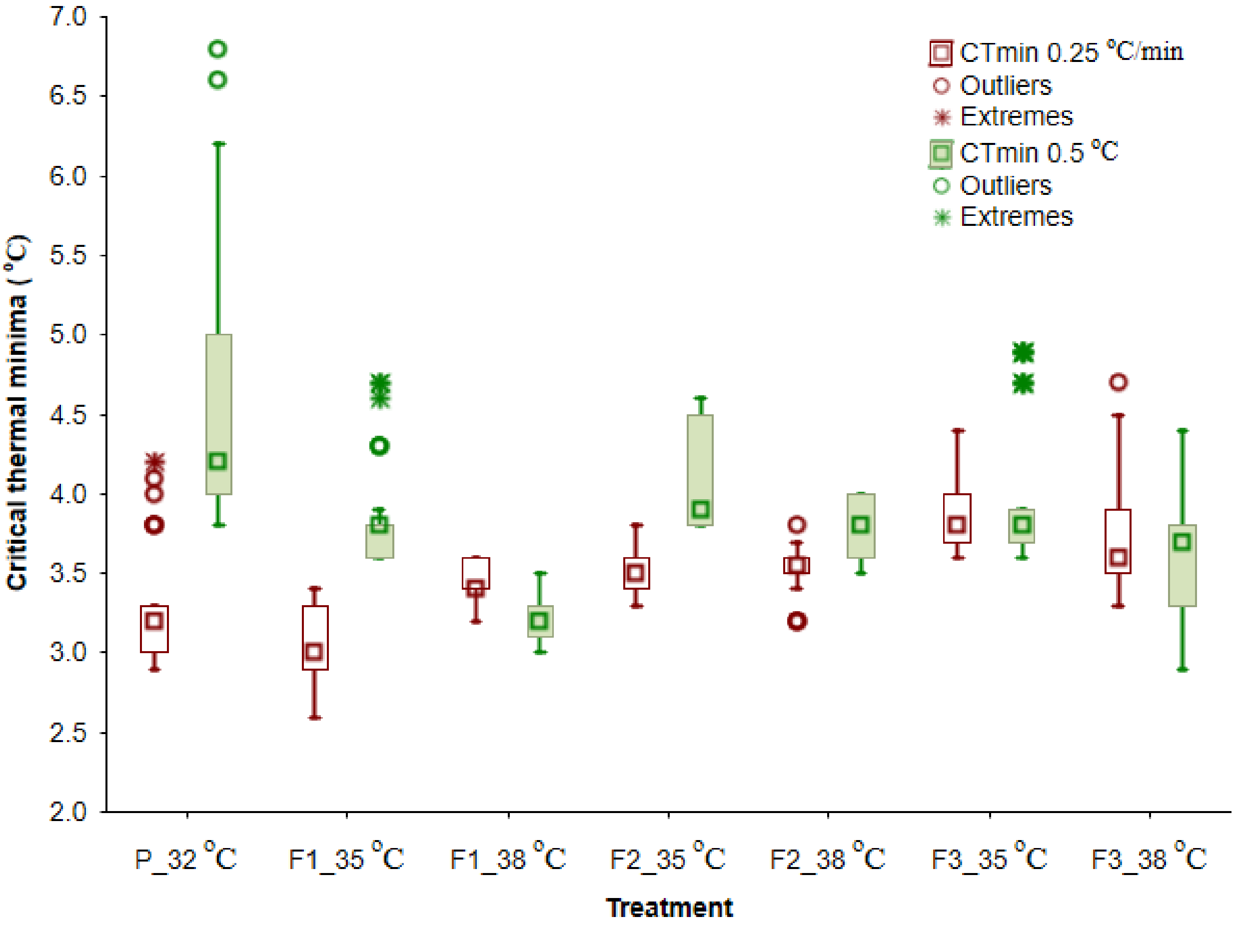

Figure 5. 2: Critical thermal minima ranges recorded for *Prostephanus truncatus* using 0.25 and 0.5°C/minute ramping rates. P_32°C = a parent culture (control) maintained at 32°C, 65 ± 10% RH. F1_35°C = a sub-culture of P_32°C that was acclimated at 35°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_1_38°C = a sub-culture of P_32°C that was acclimated at 38°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_2_35°C = a subculture of F_1_35°C that was maintained at 32°C, 65 ± 10% RH. F_2_38°C = a sub-culture of F_1_38°C that was maintained at 32°C, 65 ± 10% RH. F_3_35°C = a sub-culture of F_2_35°C that was maintained at 32°C, 65 ± 10% RH. F_3_38°C = a sub-culture of F_2_38°C that was maintained at 32°C, 65 ± 10% RH.

Mean progeny CT_{min} improved from around 4.2 ± 0.04°C in the control to between 3.1–3.9°C in F_1–F_3 treatments for the 0.5°C cooling rate. Increased cold tolerance was, however, accompanied with decreased thermal limit ranges from 3.7–6.7°C in the control to 3.0–4.5°C in F_1-F_3 progeny treatments (3°C versus 1.5°C for parental and F_1–F_3 progenies respectively). This trend was more pronounced in progeny treatments acclimated at 38°C (F_1_38°C, F_2_38°C and F_3_38°C) compared to those acclimated at 35°C. For the 0.25°C rate, individual progeny CT_{min} values remained 'stable' between 2.6 and 4.5 ± 0.03°C and were not statistically different from the control range of 2.8–3.3°C (0.5°C versus 1.9°C for parental and F_1–F_3 progenies respectively) (Fig. 5.2).

5.3.1.2. Heat knockdown time

Heat acclimation significantly decreased progeny heat tolerance (HKDT) in F_1–F_3 treatments ($F_{6, 203} = 26.73$, $p < 0.001$). Mean progeny HKDT ranged between 9.4 and 10.0 ± 0.08 minutes which was a significant decrease from 10.5 ± 0.08 minutes recorded for the control treatment (P_32°C). Mean progeny HKDT marginally increased from around 9.4 ± 0.07 in F_1 treatments to 9.6 ± 0.09 and 9.8 ± 0.11 minutes in F_2 and F_3 treatments respectively although this was not significantly different from the F_1 (Fig. 5.3).

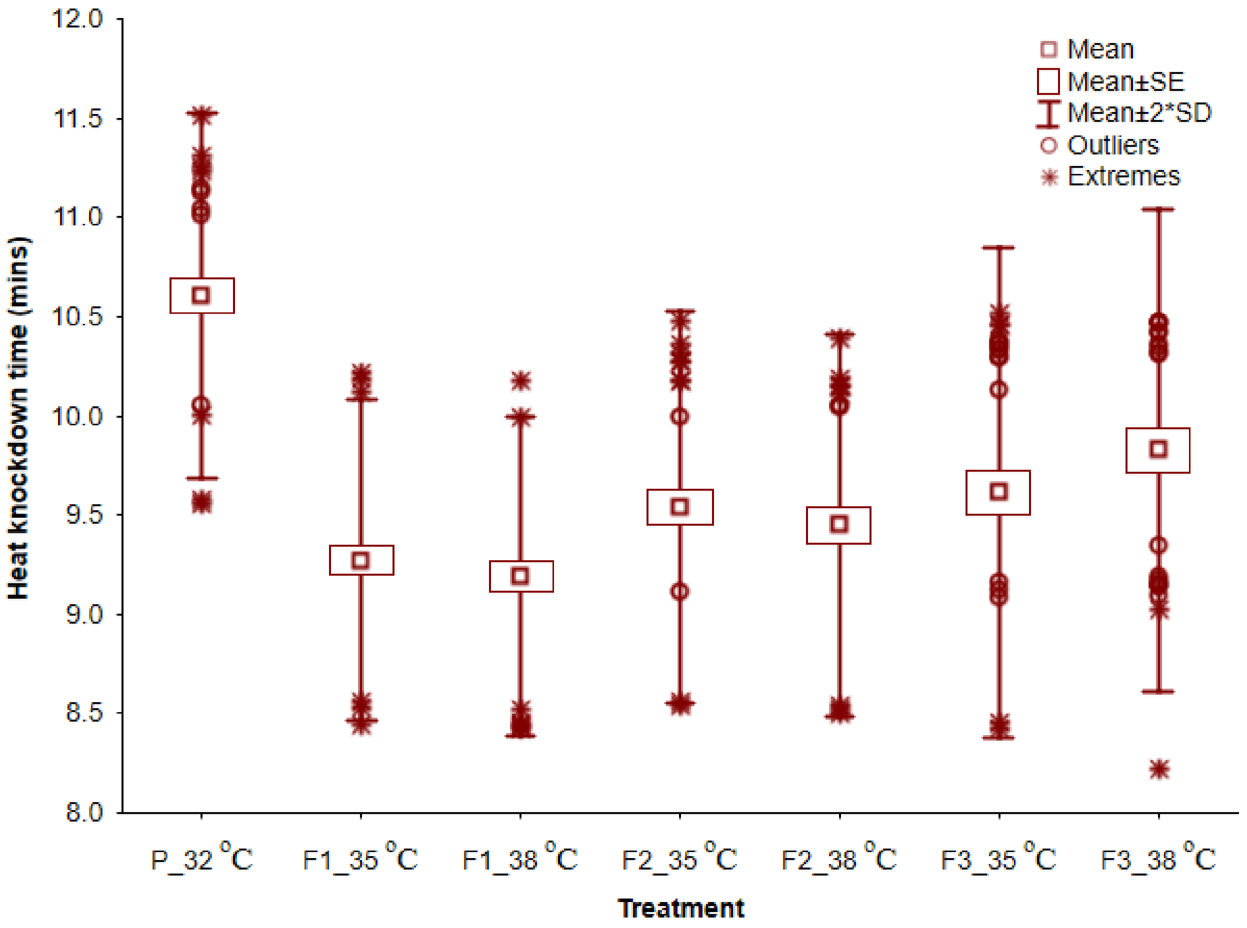

Figure 5. 3: Heat knockdown times recorded for *Prostephanus truncatus* at 50°C. P_32°C = a parent culture (control) maintained at 32°C, 65 ± 10% RH. F_1_35°C = a sub-culture of P_32°C that was acclimated at 35°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_1_35°C = a sub-culture of P_32°C that was acclimated at 35°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_1_38°C = a sub-culture of P_32°C that was acclimated at 38°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_2_35°C = a subculture of F_1_35°C that was maintained at 32°C, 65 ± 10% RH. F_2_38°C = a sub-culture of F_1_38°C that was maintained at 32°C, 65 ± 10% RH. F_3_35°C = a sub-culture of F_2_35°C that was maintained at 32°C, 65 ± 10% RH. F_3_38°C = a sub-culture of F_2_38°C that was maintained at 32°C, 65 ± 10% RH.

5.3.1.3. Upper lethal temperature survival

Progeny survival was significantly affected by exposure temperature and time combinations (χ^2 = 3.369085, df = 3, p = 0.033816). The probability of *P. truncatus* progeny survival at 38 and 42°C was high, exceeding 90% for up to 3 hours of exposure time. Progeny survival probability however dropped significantly after 0.5 hours of exposure at 46 and 50°C (Fig. 5.4). Probability of survival was lowest for 46 and 50°C × 4 hours duration treatments consistent with the notion mortality is a function of temperature severity × time of exposure.

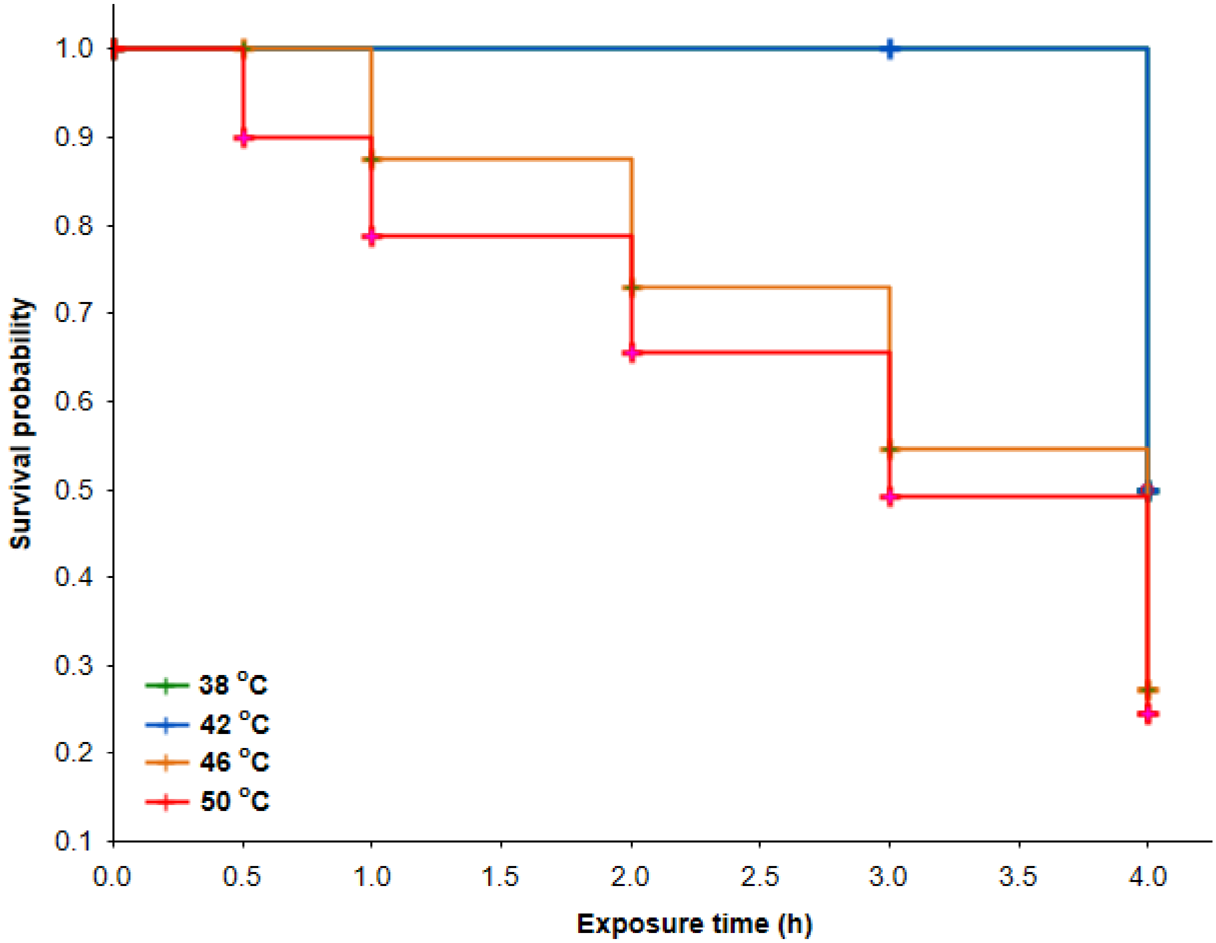

Figure 5. 4: Survival probability for *Prostephanus truncatus* upper lethal temperature limits when exposed to different temperature × time combinations vis 38, 42, 46 and 50°C for 0.5-, 1-, 2-, 3- and 4-hour exposure periods. Survival probabilities at 38°C (green) are superimposed behind 42°C (blue).

5.3.2. Ecological performance

Heat acclimation caused significant effects on the ecological performance of *P. truncatus* progeny (Table 5.2). First, F_1_35℃ and F_2_35℃ progeny weighed significantly higher ($F_{6, 209} = 3.89$, $p < 0.001$) than the control (P_32℃). Secondly, the number of progenies was significantly lower ($F_{6, 20} = 24.20$, $p < 0.001$) in F_1, F_2 and F_3 (for F_3_35℃) following parental heat acclimation. The number of progenies steadily increased with progression in generations and F_3_38℃ matched control treatment progenies. The number of days to progeny emergence significantly increased in F_2 treatments ($F_{6, 20} = 17.95$, $p < 0.001$) compared to the control although at F_3, number of days to progeny emergence reduced to match that of control treatment.

Table 5. 2: Progeny adult individual weight, number of progeny and number of days for progeny emergence data recorded for different treatments of *P. truncatus*. P_32℃ = a parent culture (control) maintained at 32℃, 65 ± 10% RH. F_1_35℃ = a sub-culture of P_32℃ that was acclimated at 35℃, 80% RH for 2 hours and then maintained at 32℃, 65 ± 10% RH. F_1_38℃ = a sub-culture of P_32℃ that was acclimated at 38℃, 80% RH for 2 hours and then maintained at 32℃, 65 ± 10% RH. F_2_35℃ = a subculture of F_1_35℃ that was maintained at 32℃, 65 ± 10% RH. F_2_38℃ = a sub-culture of F_1_38℃ that was maintained at 32℃, 65 ± 10% RH. F_3_35℃ = a sub-culture of F_2_35℃ that was maintained at 32℃, 65 ± 10% RH. F_3_38℃ = a sub-culture of F_2_38℃ that was maintained at 32℃, 65 ± 10% RH.

Treatment	**Adult individual weight (g)**	**Number of progeny**	**Number of days to progeny emergence**
P_32 ℃	0.0029 ± 0.13**a**	141.00 ± 9.64**c**	32 ± 0.00**a**
F_1_35 ℃	0.0033 ± 0.97**b**	53.33 ± 7.75**a**	32 ± 0.33**ab**
F_1_38 ℃	0.0032 ± 0.50**ab**	82.33 ± 3.76**ab**	30 ± 0.33**a**
F_2_35 ℃	0.0033 ± 0.80**b**	88.67 ± 1.86**b**	34 ± 0.33**bc**
F_2_38 ℃	0.0031 ± 0.60**ab**	85.33 ± 4.10**b**	36 ± 0.00**c**
F_3_35 ℃	0.0030 ± 0.67**ab**	93.67 ± 4.63**b**	32 ± 0.33**ab**
F_3_38 ℃	0.0031 ± 0.27**ab**	129.00 ± 6.81**c**	30 ± 0.67**a**
P value	$F_{6, 209} = 3.89$, $P < 0.001$	$F_{6, 20} = 24.20$, $P < 0.001$	$F_{6, 20} = 17.95$, $P < 0.001$

Parental heat acclimation also significantly affected progeny ecological performance in *P. truncatus*, measured as grain damage, grain weight loss and chaff production (Fig. 5.5). Grain damage ($F_{6, 14} = 110.34$, $p < 0.001$), grain weight loss ($F_{6, 14} = 45.66$, $p < 0.001$) and chaff ($F_{6, 14} =$

40.69, $p < 0.001$) were significantly reduced in F_1 treatments following parental acclimation. A steady increase in grain damage, weight loss and chaff were noted in F_2 and F_3 treatments and only chaff increased to match control (P_32°C) levels at F_3.

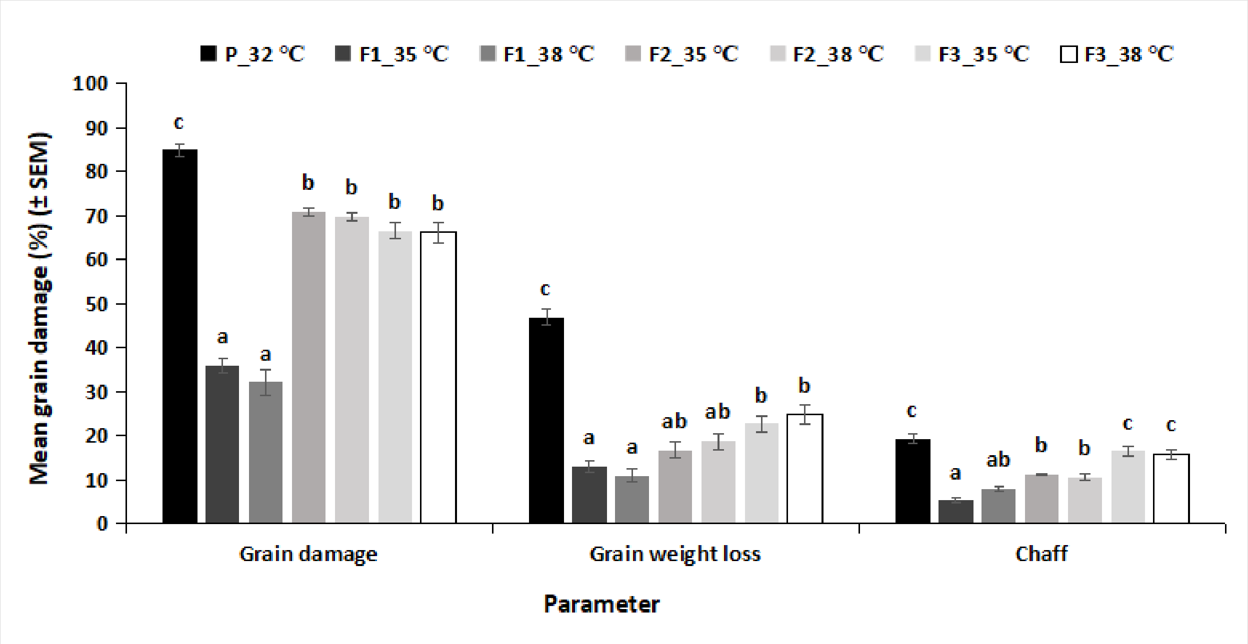

Figure 5. 5: Grain damage, weight loss and chaff percentage recorded for *Prostephanus truncatus*. P_32°C = a parent culture (control) maintained at 32°C, 65 ± 10% RH. F_1_35°C = a sub-culture of P_32°C that was acclimated at 35°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_1_38°C = a sub-culture of P_32°C that was acclimated at 38°C, 80% RH for 2 hours and then maintained at 32°C, 65 ± 10% RH. F_2_35°C = a subculture of F_1_35°C that was maintained at 32°C, 65 ± 10% RH. F_2_38°C = a sub-culture of F_1_38°C that was maintained at 32°C, 65 ± 10% RH. F_3_35°C = a sub-culture of F_2_35°C that was maintained at 32°C, 65 ± 10% RH. F_3_38°C = a sub-culture of F_2_38°C that was maintained at 32°C, 65 ± 10% RH.

5.4. Discussion

Transgenerational plasticity responses are an important mechanism to buffer insect fitness and survival under constantly changing environments due to climate change (Cavieres et al. 2020). This non-genetic inheritance is critical as it facilitates fast, flexible, and seldom reversible adaptation to environmental change that complements genetic inheritance as a driver of evolution. Ecologically, it allows parents to ‘prime’ their progeny for ‘expected’ environmental stress based on their own environmental history experiences (e.g., thermal stress, food availability, predation risk and related stresses) (Leimar and McNamara, 2015). Here, physiological- and ecological-performance of *P. truncatus* progeny across three generations following parental acute heat acclimation was evaluated. The results showed parental environmental heat acclimation history (i) had transgenerational physiological- but not ecological-progeny fitness advantage, (ii) decreased critical thermal limit ranges, consequently giving organisms a narrower thermal breath (iii) had transgenerational cross protective improvement in cold tolerance and that (iv) elicited transgenerational physiological responses that potentially last generations. This transgenerational plastic adaptation may help in understanding how species and ecosystems respond to environmental global change.

Critical thermal limits define temperature ranges within which an organism can survive and are thus crucial for predicting organisms' performance and/or vulnerability to climate change (Terblanche et al. 2007). We showed positive transgenerational plastic responses for CT_{max} following the 0.25°C/minute ramping but not the 0.5°C/minute. The transgenerational effects were still present in F_3 generation and significantly different from the parental treatment. This suggests that transgenerational memories may last for several generations. Similar trait-dependent transgenerational plasticity responses have been reported in aphids (Tougeron et al. 2020) and Lepidoptera species (Woestmann and Saastamoinen, 2016) allowing subsequent generations to cope with environmental stresses experienced by their parents (Sgrò et al. 2016). Increased CT_{max} was, however, associated with a narrower thermal limit range across the tested animals. While the control treatment (P_32°C) recorded a relatively wider thermal tolerance range of 3.0°C, the response of F_1–F_3 treatments following heat acclimation of parental cultures had a very narrow thermal tolerance range of 1.5°C. This represents a general 1.5°C increase in CT_{max} with acclimation. Such an increase in tolerable temperatures has been estimated to cause a 10–25% increase in insect damage on crops (Deutsch et al. 2018). Although progeny thermal tolerance improved in post acclimation treatments, Hoffmann et al. (2013) documented that ectotherms may reach their heat tolerance limits more quickly in tropical environments where they live closer to their limits, and temperature increases are expected to be disproportionally higher with climate change (IPCC, 2022). This scenario gives tropical species little scope for heat stress adaptation, and this may explain the narrower thermal tolerance range observed in the current study (see also Van Heerwaarden and Kellermann, 2020). Moreso, *P. truncatus* is known to have a high optimum developmental temperature around 32°C (Shires 1980; Hodges, 1986; Mutamiswa et al. 2021; Quellhorst et al. 2021) due to its tropical origin which may limit its tolerance for higher temperatures compared to other storage insect pests which generally have an optimum temperature around 25°C (Mason and McDonough, 2012). García-Robledo et al. (2016) reported a narrow CT_{max} range in rolled-leaf beetles (*Cephaloleia* and *Chelobasis* species) from high elevation geographies, further suggesting the limited heat stress maneuver under tropical climates. Piyaphongkul et al. (2012) also reported limited thermal tolerance range in tropical brown planthopper *Nilaparvata lugens* as these species are living close to their absolute upper thermal limits. Similarly, insects with high basal heat tolerance, similar to *P. truncatus* are likely to trade off their plasticity of heat tolerance (Nyamukondiwa et al. 2011), in consonance with the results reported here.

The thermal limitation hypothesis also suggest that tropical species have higher but narrower thermal limits (Kaspari et al. 2015; García-Robledo et al. 2016). Parental heat acclimation also improved progeny lower critical thermal limits to activity (CT_{min}) at 0.5°C/minute ramping rate. Studies on how ramping rates affects critical thermal limits have widely been discussed in literature (Terblanche et al. 2007; Chown et al. 2009; Sørensen et al. 2013; Allen et al. 2016; Jørgensen et al. 2021; Mpofu et al. 2022; Mlambo et al. 2024a). The increased cold tolerance following parental heat acclimation reported here demonstrates transgenerational cross tolerance (see Sinclair et al. 2013; Mpofu et al. 2024) where parental acclimation to one stressor (heat) improved progeny tolerance to a different stressor (cold) owing to shared stress resistance mechanisms or signaling pathways. The transgenerational plasticity for critical thermal limits likely improves the activity ranges of *P. truncatus* and can be a critical survival mechanism in the face of increasing temperature stress with climate change.

Parental heat acclimation reduced the time taken by *P. truncatus* progeny to be knocked down by acute heat stress (HKDT) across F_1–F_3 generations compared to the parental control treatment. Similar results have been reported on the Angoumois grain moth, *Sitotroga cerealella* (Mpofu et al. 2022). In contrast, studies done by Mutamiswa et al. (2021) showed a significant within generation increase in HKDT following acute heat acclimation for adult *P. truncatus*. Studies on transgenerational effects on insects are generally scant in literature. Most studies of transgenerational effects have been done on vertebrates, including migratory birds (Knudsen et al. 2011; Byholm et al. 2022) and rats (Robaire et al. 2022). This is the first report documenting transgenerational heat tolerance plasticity for this economic storage pest. Both HKDT and CT_{max} are standardized, easy and ecologically relevant measures for heat tolerance (Chown and Nicolson 2004). Heat knockdown time represents static and direct exposure to a specific temperature while on the other hand CT_{max} represents dynamic and indirect exposure to gradually increasing temperatures in a circulating water bath (Bak et al. 2020). This difference in protocols can therefore account for the differences in progeny responses to these different high temperature tolerance metrics (Terblanche et al. 2007). *Prostephanus truncatus* progeny had a higher chance of survival at 38 and 42°C for up to 3 hours than when exposed for longer durations. However, this survival significantly declined at 46 and 50°C. Similar results based on actual survival have been reported; 100% survival at 38°C for 2 hours and 0% survival at 42°C for 3 hours (Mlambo et al 2024). According to Fields (1992), lethal temperatures for stored-product pests start at 36°C at which point insect feeding stops. The degree of heat and exposure duration will determine time to death for insects, and no stored-product insects can survive beyond 1 hour at 50-60°C (Fields, 1992; Banks and Fields, 1995). High temperatures often ranging between 36–40°C have been reported in Botswana during heat wave conditions (Moses, 2017; Nkemelang et al. 2018). At this temperature range the reproduction of *P. truncatus* stops and individual insects die due to heat induced desiccation and lack of feeding (Fields, 1992). This is consistent with the findings of the current study that showed reduced insect grain damage and progeny production.

Postharvest grain loss assessments are standard ecologically relevant measures done to identify causes and extent of grain damage. This is often done by quantifying insect damaged grains, grain weight loss, insect feeding dust (chaff) and number of insect progenies (Hodges, 2013). Parental heat acclimation improved F_1 (F_1_35°C) and F_2 (F_2_35°C) adult individual weights, decreased number of progenies, and increased the number of days to progeny emergence in F_2 generation. Further, parental heat acclimation reduced progeny grain damage, grain weight loss and insect feeding dust in F_1, F_2 and F_3 generations. This shows that parental heat acclimation lowered progeny production and feeding capacity of *P. truncatus* in post acclimation generations hence less grain damage was incurred. High temperatures, thus, leveraged on *P. truncatus* management. Relyea (2002) asserts that transgenerational adaptation is a compromise owing to the costs associated with plasticity. The costs of transgenerational plasticity are unavoidable as, after heat stress related injury, organisms need to restore physiological and biochemical processes. Furthermore, these may also include costs of maintaining sensory and response pathways that induce plasticity and costs associated with developmental instability (Relyea, 2002; Colinet et al. 2015). In this regard, plastic phenotypes can integrate rate-dependent processes like body size and weight to fluctuate with environmental temperatures (Colinet et al. 2015). In the current study, adult individual weights of *P. truncatus* progeny significantly improved in F_1 (F_1_35°C) and F_2 (F_2_35°C) treatments. As demonstrated by Colinet et al. (2015), accelerated growth can be observed if the thermal stress experienced is close to the developmental threshold of the organism, as was the case in the current study. Parental heat acclimation of *P. truncatus* also increased number of days to progeny emergence and reduced progeny production. These trade-offs can be due to more energy being conserved to be channeled to support the induced phenotype (Pörtner et al. 2006; Moczek et al. 2011; Colinet et al. 2015). As such, grain damage, grain weight loss and chaff dust production which are used to measure damage caused by *P. truncatus* on grain, were also significantly low in F_1–F_3 treatments compared to the control. Ecological performance, however, steadily increased in F_2 and F_3 treatments although it remained significantly lower than controls except for chaff. This can be a result of phenotypes getting habituated and accustomed to the changing stressful environment (Horowitz, 2016).

In conclusion, the study showed that parental heat acclimation (i) had transgenerational physiological- but not ecological-progeny fitness advantage, (ii) decreased critical thermal limit ranges, (iii) had cross protective improvement in cold tolerance, (iv) elicited thermal plasticity responses that were dependent on the degree of temperature increase/decrease (ramping rates) and (v) elicited transgenerational physiological responses that manifested in many generations. This transgenerational plasticity facilitates species' flexible, non-genetic adaptation across generations, making it a critical survival mechanism in the face of global environmental change, especially for organisms inhabiting highly stochastic environments. It broadens the understanding of species' responses to stress, evolution of stress resistance, and management strategies in a rapidly changing climate environment. The current study provides insights into the likely status of *P. truncatus* with increased temperatures due to climate change.

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CHAPTER 6

Trait-dependent plasticity erodes rapidly with repeated intergenerational acclimation in an invasive agricultural pest[5]

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6.1. Introduction

Temperature is an important environmental factor that primarily affects the ecology of ectothermic organisms (Dillon et al. 2010). While climate is generally warming (Wong, 2023), fine-scale daily and seasonal fluctuations are concomitantly increasing and becoming more frequent and prolonged (Davis-Reddy and Vincent, 2017; Smith and Lancaster, 2020; Wong, 2023). These temperature fluctuations expose ectothermic organisms to constantly changing levels of thermal stress (Sørensen et al. 2019; IPCC, 2021; Ventura et al. 2023), which may inflict fitness costs (Klockmann et al. 2017; Heidi and Sorte, 2022; Mpofu et al. 2022), but seldom benefits (Roeder et al. 2021). Projections suggest that high and extreme temperatures are expected in tropical climates e.g., in sub–Saharan Africa (SSA) (Davis-Reddy and Vincent, 2017), where invasions by polyphagous agricultural and forest insect pests have increased food losses and burdened ecosystem services (Stathers et al. 2013; Singano et al. 2020). Interactions between climatic stressors and biological invasions could alter ecological and socio-economic impacts of insect pest species (Mlambo et al. 2024), leading to possible development of environmental stress adaption mechanisms to maintain ecological function. Therefore, ability to shift phenotypes in the short- to long-timescales when exposed to stressful environments may shape impacts and ecosystem function in the face of environmental change (Drown et al. 2021). This adaptation creates resilience in insect pests in a changing environment scenario where most recommended pest management methods are increasingly becoming climate-strained (Chidawanyika et al. 2012; Andrew and Hill, 2017; Matzrafi, 2019; Ma et al. 2021a).

Heat stress responses in arthropods are mediated by behavioural microhabitat selection (Pincebourde et al. 2016), genetic adaptation and physiological changes (e.g., through phenotypic plasticity) (Sgrò et al. 2016; Tarusikirwa et al. 2020; Waltzer et al. 2020). While genetic adaptation is important for long-term survival, behavioural changes and phenotypic plasticity are important for short-term responses to heat stress that present increased chances of surviving extremely high temperature environments (Horowitz, 2001; Malmendal et al. 2006). Some stress responses are rapidly triggered within-generation in minutes to hours or days (i.e., rapid and long-term acclimation), while some responses are gradual, extending and/or manifesting in successive generations (transgenerational plasticity [TGP]) (Kristensen et al. 2018; Cavieres et al. 2020; Lann et al. 2021). Thermal tolerance adaptation, however, often results in fitness costs (see e.g., Driessen et al. 2011; Segaiso et al. 2022) and trade-offs in biological performance of arthropod species (Dixon et al. 2009; Cavieres et al. 2020). Fitness costs manifest as both plasticity- and/or phenotypic-costs (Driessen et al. 2011).

Plasticity costs comprise of all investment costs of eliciting plastic responses compared to a fixed phenotype. For example, costs of acquiring information regarding the changing thermal conditions and maintaining the physiological mechanism for plasticity (Smith and Lancaster, 2020). However, phenotypic costs encompass investments made in terms of energy and resource expenditure to produce an inducible phenotype and is of significance especially in the expression of reversible traits such as body size (Driessen et al. 2011). Phenotypic adaptation is a recurrent process due to seasonal thermal fluctuations, and hence the costs of producing an induced phenotype are paid for repeatedly throughout the life cycle of ectotherms (Driessen et al. 2011). Despite the understanding that thermal acclimation induces both adaptation and fitness costs, little is known on (i) the effects of acclimation, either single or repeated, on the direction of heat tolerance traits; and (ii) the subsequent effects on ecological performance of individual insects, particularly commodity/plant damage in agricultural pests, which thus, require species-specific data for accurate estimations (Donelson et al. 2016; Cavieres et al. 2020).

Stored grain insect pests experience temperature rises in storage environments due to the enclosed nature of grain facilities as well as grain cell respiration, especially at high grain moisture content, and this constant exposure further induces inevitable acclimation to heat stress (Panigrahi et al. 2020; Wang et al. 2020). The larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera; Bostrichidae) is a devastating pest of stored maize grain and dried cassava roots originally from Central America and spread into Africa through grain trade as first reported in Tanzania in 1970 (Hodges et al. 1983). Maize grain damage as high as 100% and weight losses as high as 50% have been reportedly caused by *P. truncatus* as the range of synthetic pesticides commonly used by farmers are not effective against the pest (see Cugala et al. 2007; Mlambo et al. 2017; Mutambuki et al. 2019). Full details on the current global pest status of *P. truncatus* and its biological traits are provided in Quellhorst et al. (2021). As an ectotherm, *P. truncatus* relies on thermal tolerance mechanisms like acclimation capacity (Mutamiswa et al. 2021) as well as heat-shock responses to survive heat stress (Jian, 2019; Harvey et al. 2022; Zhu et al.

2022). However, the effects of heat stress tolerance and/or plasticity on biological performance of *P. truncatus* are unknown.

Here, the current study thus demonstrate the effects of single and repeated acute heat stress on the thermal fitness and ecological performance of *P. truncatus*, an invasive pest of significant biosecurity threat to stored maize grain and dried cassava roots as well as alternative hosts e.g., forest timber products (Hodges et al. 1983; Muatinte and Van den Berg, 2019). *Prostephanus truncatus* was chosen because of its high pest status and economic significance, invasive nature (Arthur et al. 2019; Quellhorst et al. 2021) and high heat tolerance (Fields et al. 1992; Mahroof et al. 2005), coupled with rapid responses to acclimation (Machekano et al. 2020; Mutamiswa et al. 2021). Critical thermal limits to activity (critical thermal maxima [CT_{max}], critical thermal minima [CT_{min}]), heat knockdown time (HKDT) and upper lethal temperature limits (ULTs) are standard metrics used to measure insect physiological thermal responses (Terblanche et al. 2011) and are reasonable proxies for estimating species ecological niches (Chown and Nicolson, 2004). These traits (CT_{max}, CT_{min}, HKDT, ULTs) are important measures of insect thermal tolerance and are measured using ecologically relevant static and dynamic standard protocols synonymous with pest experiences under natural environments (Gunderson and Stillman, 2015).

The study thus aimed to determine the effect of single and repeated acute heat acclimation on the intergenerational responses of *P. truncatus* in terms of physiological and ecological performance. Such investigation can form the basis for managing the pest, as it provides quantitative information on the direction and magnitude of thermal tolerance traits, fitness and/or benefits thereof and the likely impacts of resultant ecological performance from repeated stressful environmental exposure associated with climate change. Specifically, physiological (CT_{max}, CT_{min}, HKDT and ULTs) and ecological traits (feeding rates, fecundity, body weight) were measured following single (at F_1 generation) and repeated (at F_2 generation) acute heat acclimation. It was hypothesized that acute heat acclimation would improve these physiological and ecological traits in *P. truncatus* at both F_1 (with single acclimation) and F_2 (repeated acclimation).

6.2. Materials and methods

6.2.1. Insect rearing

A colony of wild *P. truncatus* was established through aggregated pheromone trapping from surrounding forests in Gaborone, Botswana (24°35′01′′S; 25°56′49′′E). An aggregation pheromone (active ingredients: 1-Methylethyl (E)-2-pentenoate and 1-Methylethyl (E, E)-2,4-dimethyl-2,4-heptadienoate) was obtained from NovAgrica (Hellas, South Africa) through the Ministry of Agricultural Development and Food Security in Gaborone, Botswana. This formed the parent culture, which was reared in 1 litre Consol jars with gauzed lids on cobbed yellow maize (SeedCo 608 variety, SeedCo Group, Gaborone, Botswana) at 32 ± 1°C and 80 ± 5% relative humidity (RH) [the optimum conditions for *P. truncatus* (Shires, 1980; Subramanyam and Hagstrum, 1991; Quellhorst et al. 2021)] in a climate chamber (HPP 260, Memmert GmbH + Co.KG, Schwabach, Germany) under a 12L: 12D photoperiod. Maize grain was sterilised by freezing at -18°C for two weeks and then equilibrated by holding at 32°C, 80% RH for seven days before being used for the trials (Hodges and Dobson, 1998; Mutamiswa et al. 2021). Grain moisture content was measured using a digital Unimeter (Agri-Enviro Solutions (Centurion, South Africa) and confirmed at 12.2% after equilibration. To get a uniformly aged batch of insects, adults were removed from the grain after 21 days and the first laboratory generation of uniformly aged adult insects that emerged thereafter was defined as the F_1. This F_1 generation was then exposed to acute heat acclimation treatments as described in section 6.2.3 for subsequent intergenerational plasticity experiments.

6.2.2. Bioassays

The current study tested intergenerational plasticity across two generations of adult stages (3-7 days old) of a laboratory-reared colony of *P. truncatus*. Specifically, to determine CT_{max}, CT_{min}, HKDT and ULTs (specific methods for each metric are detailed in section 6.2.2.1) for successive F_1 and F_2 generations of *P. truncatus* following F_1 and F_2 generational acute heat acclimation (for 2 h at 35°C and 38°C; 80% RH). The chosen acclimation temperatures are ecologically relevant and were simulated from conditions experienced by the insects in the natural collection sites (Nkemelang et al. 2018; Walzer et al. 2020). Furthermore, these temperature × time acclimation conditions are sufficient to elicit acclimation conditions in insects (Chown and Nicolson, 2004; Weldon et al. 2011; Enriquez et al. 2019; Cole et al. 2023). The study also assessed biological performance of *P. truncatus* following acclimation using adult individual weight, fecundity, maize grain damage, grain weight loss and amount of dust produced due to *P. truncatus* feeding activity. For comparison with test insects, an adult *P. truncatus* group maintained at 32 ± 1°C; 80 ± 5% RH served as a positive control.

Mixed sex adults in 1 L Console jars were exposed to acute heat shock acclimation at static 35°C and 38°C separately for 2 h in Memmert climate chambers. After acclimation, the insects were returned to the climate chamber at 32°C and 80% RH in labelled 1 L Consol jars and were provided with sterilised yellow maize cobs and left to oviposit under 12L: 12D photoperiod for 21 days. Adult insects were then removed from each jar to enable emergence of the F_1 generation following methods in Machekano et al. (2020) and Mutamiswa et al. (2021). Adult *P. truncatus* from each group (F_1) were then assayed for physiological (heat stress tolerance) and ecological performance (fecundity, adult body weights, grain damage, grain weight loss and insect feeding dust produced). A sub-culture was retained from the F_1 and re-acclimated at the same conditions to get the next filial generation (F_2) (Walzer et al. 2020) (Fig. 6.1). Although the acclimation temperatures differed for the two sub-cultured treatment groups (35 and 38°C), the rearing conditions for oviposition were the same (32°C and 80% RH). The acclimation temperatures of each F_1 sub-culture matched the F_2 acclimation temperatures (Fig. 6.1). Five treatments; *viz* Parent_32°C (T1 the control), F_1_35°C (T2), F_1_38°C (T3), F_2_35°C (T4) and F_2_38°C (T5) were thus evaluated (Fig. 6.1).

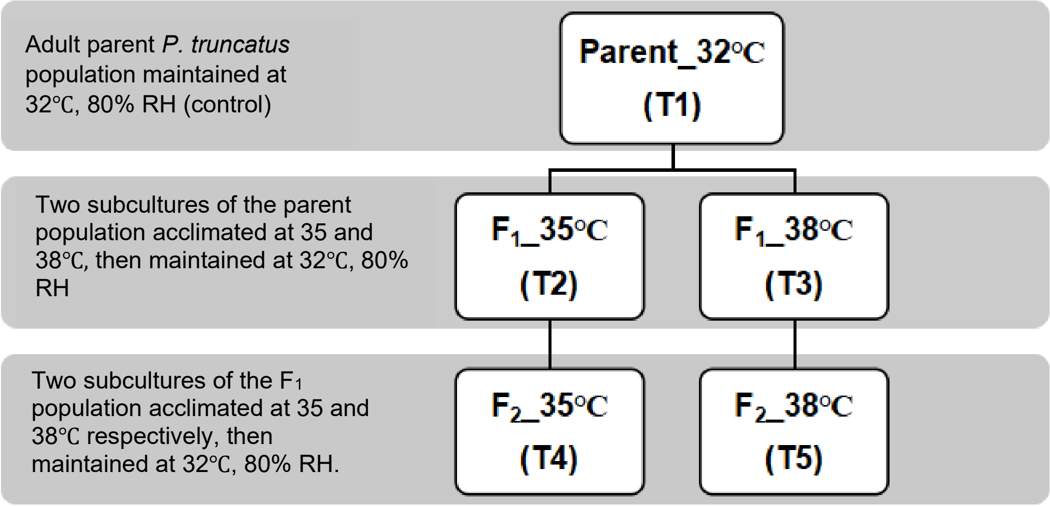


Figure 6. 1: Acute heat acclimation protocol (2 h exposure at the respective temperatures) and illustration of the treatments and rearing process from adult parent *Prostephanus truncatus* population to F_2 generation. T1–T5 = Treatments 1-5.

6.2.2.1. Critical thermal limits to activity (CTLs)

6.2.2.1.1. Critical thermal maxima (CT_{max}) and Critical thermal minima (CT_{min})

Two CTL (CT_{max} and CT_{min}) programmes were run using 0.25°C/min and 0.5°C/min ramping rates. These ramping rates were previously reported to resemble more ecologically relevant temperature changes and hence enable detection of variations in thermal limits to activity and survival of insects (Terblanche andMitchell, 2017). Most studies on CTLs have used the same ramping rate of 0.25°C/min and 0.5°C/min (Chown and Nicolson, 2004; Mutamiswa et al. 2021) while others, e.g., Mpofu et al. (2022) used even much lower rates of 0.06°C/min, all with mixed results. Our ramping rates thus allowed for CTLs comparison with much of the available literature (see discussions in e.g., Chown and Nicolson, 2004). Ten adult insects were each placed in individual transparent organ pipes of a double-jacketed chamber (LAUDA Ecogold® RE 2025, Lauda-Königshofen, Germany) connected to a programmable water-bath (refrigerated and heated circulating bath with a temperature range of ~25°C to + 200°C) with a 1:1 water to propylene glycol solution running through the chamber to control the temperature (Chidawanyika and Terblanche, 2011). These organ pipes are standard instruments used in physiological ecology studies to quickly assess critical thermal limits in small animals (especially ectotherms) but have also been used for small mammals (Chown and Nicolson, 2004).

From a setpoint temperature of 32°C which represent optimum conditions, temperature was ramped either up (CT_{max}) or down (CT_{min}) at the different ramping rates (0.25 or 0.5°C/min) until CT_{max} and CT_{min} were recorded, respectively. CT_{max} was defined as the maximum temperature at which insects lost coordinated muscle function to self-right and ability to respond to mild stimuli from a thermally inert object (Nyamukondiwa and Terblanche, 2009; Tarusikirwa et al. 2022). On the other hand, CT_{min} was recorded as the minimum exposure temperature at which insects lost coordinated muscle function (Terblanche et al. 2007). Temperature readings were made from a thermocouple (type K 36SWG) connected to a digital thermometer (Fluke 54 series IIB) inserted in the control organ pipe of the chamber. The water-bath had 11 organ pipes, thus allowing 10 insects and one control to be assayed at a run time. The procedure was therefore repeated three times to yield 30 replicates (n = 30) for each ramping rate, generation time and acclimation temperature.

6.2.2.1.2. Heat Knockdown Time (HKDT)

Heat knockdown time was assayed for adult *P. truncatus* by acutely exposing insects to 50°C using the Memmert climate chamber with a video recording camera (HD Covert Network Camera, DS-2CD6412FWD-20, Hikvision Digital Technology Co., Ltd, Hangzhou, China) connected to a computer for recording activity. This acute heat knockdown temperature (50°C) was used following the species basal heat results, i.e. CT_{max} data from Machekano et al. (2020). Furthermore, findings from Fields et al. (1992) indicate that temperatures of 50°C or beyond cause 100% mortality in stored product insect pests in less than an hour. Temperature of the climate chamber was allowed to stabilise at 50°C for 10 minutes before adult *P. truncatus* were placed each in 1.5 ml Eppendorf tubes in the climate chamber. Heat knockdown time, captured from the video recording system, was recorded as the time in minutes at which an insect lost activity following exposure to acute heat stress (Mutamiswa et al. 2018; 2021; Machekano et al. 2020). Thirty adult beetles were assayed per generation and acclimation temperature to obtain 30 replicates (n = 30).

6.2.2.1.3. Upper lethal temperatures (ULTs) survival

Prostephanus truncatus adult insects of mixed sexes were subjected to lethal temperature assays by direct plunge method (Chidawanyika and Terblanche, 2011) in a water-bath filled with a 1:1 mixture of water and propylene glycol (Terblanche et al. 2008; Machekano et al. 2020). Ten beetles were loaded in each of three 60 ml plastic vials with perforated lids to get a total of 3 replicates (*n* = 30). A wet cotton ball was placed in each vial to maintain RH and avoid confounding mortality related to desiccation (Stotter and Terblanche, 2009). The three vials were then placed in a water-tight zip lock bag and plunged into a water-bath for each temperature × time treatment. The insects were exposed to upper lethal temperatures of 38, 42, 46, 50 and 52°C for 0.5, 1, 2, 3 and 4 h, at varied temperature-time combinations until a range of insect mortality from 0 to 100% was recorded. The temperatures (38 and 42°C) partly represent conditions experienced in the insect collection sites (Byakatonda et al. 2018; Mguni, 2020) and are above the optimum temperatures for development of storage insects (Fields, 1992; Agrafioti et al. 2019). After exposure, the insects were transferred to sterilised maize grain stored at fixed conditions of 32°C, 80% RH, i.e., optimal conditions for *P. truncatus* for recovery. After 24 h, survival was scored on test adults for each temperature-time treatment. Survival was recorded as a coordinated response to mild stimuli from prodding (with a camel hairbrush) and/or normal insect behaviour such as feeding, self-righting, walking or flying post-treatment (Stotter and Terblanche, 2009 Nyamukondiwa and Terblanche, 2009).

6.2.2.2. Ecological performance

Body weight, fecundity, maize grain damage, grain weight loss and weight of dust generated due to insect feeding were used to assess ecological intergenerational performance of *P. truncatus* following heat acclimation. Twenty sexed beetles (10 male: 10 female) were placed in 500 ml rearing jars with sterilised maize grain (500 kernels) and left for 21 days to mate and oviposit under 12L:12D photoperiod in a Memmert climate chamber at 32°C, 80% RH. The beetles were sexed to ensure chances of mating in each treatment. However, the results (fecundity and adult individual weight) were not sex aggregated. Each treatment was replicated three times (*n* = 3). Sex determination was done by examining clypeal tubercles of live beetles under a light microscope (Shires and McCarthy, 1976). The clypeal tubercles are more pronounced and further apart in females than males (Shires and McCarthy, 1976). After 21 days, adult insects were removed from the jars. The total number of emerged progeny recorded after 35 days following the first emergence was recorded as fecundity (Masasa et al. 2013; Gvozdenac et al. 2018). Emerging insects were weighed to 1 mg at 5 day intervals using a precision balance (PGW 453e, Adam Equipment™, Johannesburg, South Africa). At the end of the experiment, i.e., after 56 days, grain damage, grain weight loss and weight of insect feeding dust were assessed. The count and weigh assessment method was used for grain damage and grain weight loss determination as follows:

Grain damage = $\frac{Nd}{Nd+Nu} \times 100$

Grain weight loss = $\frac{NdWu-NuWd}{((Nd+Nu)\times wu)} \times 100$

where Nd = number of damaged grains, Nu = number of undamaged grains, Wu = weight of undamaged grains and Wd = weight of damaged grains (Boxall, 2002).

6.2.3. Data analyses

Normality tests were performed on all data sets using Kolmogorov-Smirnov and Lilliefors test. CT_{max}, CT_{min} and HKDT data did not meet the assumptions for normality and were analysed using Kruskal-Wallis Analysis of Variance (ANOVA) and Median Test whilst all the other data sets having satisfied the normality tests ($p > 0.05$), were then analysed using one way ANOVA in Statistica 13 to determine if there were any significant differences between treatments (which were the basis of explanatory variables) (Table 6.1). In the case of significant differences, post-hoc analysis was done using Fisher's LSD test to separate treatment means. A generalised linear model with a beta distribution was used to analyse survival rates as a function of two factors: exposure temperature and exposure time, as well as their interaction (Brooks et al. 2017), in R version 4.3.1 (R Core Team, 2023). Survival rates were transformed to remove extreme values (0 and 1) to meet the beta distribution assumptions:

$$s_t = (s_i(n-1) + 0.5)/n$$

where s_i is the survival rate and n is the total sample size. Analysis of deviance was used to report the main effect coefficients with Type III sums of squares (Fox and Weisberg, 2019). Estimated marginal means were used to compute pairwise comparisons post-hoc (Lenth, 2023).

Table 6. 1: A summary of response and explanatory variables used in each data analysis model.

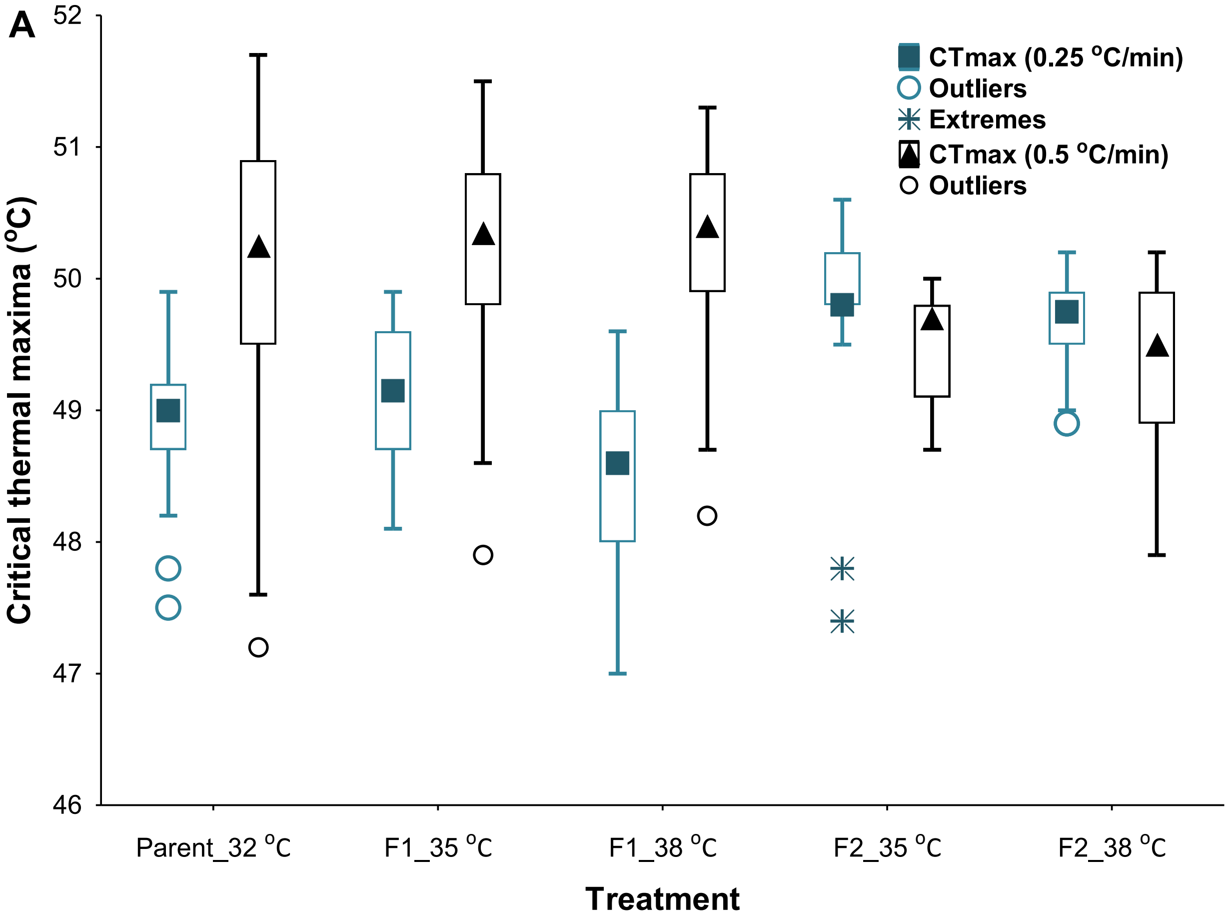
Model	Variables	
	Explanatory variable(s)	**Response variable(s)**
Kruskal-Wallis	Treatments (×5), ramping rates (×2)	CT_{max}, CT_{min}
ANOVA	Treatments (×5)	HKDT
One way ANOVA	Treatments (×5)	HKDT, fecundity, grain damage, grain weight loss, insect feeding dust
Generalised linear model	Exposure temperature (×5), exposure time (×5)	Survival rate

6.3. Results

6.3.1. Effects of acclimation on CT_{max} and CT_{min}

Heat tolerance (CT_{max}) in *P. truncatus* was not significantly influenced by single (at F_1) and repeated (at F_2) heat acclimations (Kruskal-Wallis test: $H_{(4)} = 4.881$; $P = 0.300$). In F_1, the slower ramping rate (0.25°C/ minute) caused a reduction in heat tolerance while the higher ramping rate (0.5°C/ minute) improved heat tolerance. The reverse was true in the F_2 generation, where the more gradual ramping rate improved CT_{max} and the rapid rate decreased CT_{max} resulting in convergence of CT_{max} ranges between 48 and 52°C for both rates (Fig. 6.2A). This, however, did not significantly improve heat tolerance of acclimation treatments when compared to the parent population.

For CT_{min} however, heat treatment significantly influenced tolerance (Kruskal-Wallis test: $H_{(4)} = 35.120$; $P < 0.001$). The trend was especially apparent for the slowest ramping rate compared to the higher rate. In the interaction, the 0.25°C/ minute ramping rate improved cold tolerance in F_1 but the 0.5°C/ minute rate did not. In the F_2 generation, cold tolerance significantly improved for both ramping rates to a range of 3-5°C (Fig. 6.2B).


A
52
51
50
49
48
47
46
Critical thermal maxima (°C)
CTmax (0.25 °C/min)
Outliers
Extremes
CTmax (0.5 °C/min)
Outliers
Parent_32 °C
F1_35 °C
F1_38 °C
F2_35 °C
F2_38 °C
Treatment

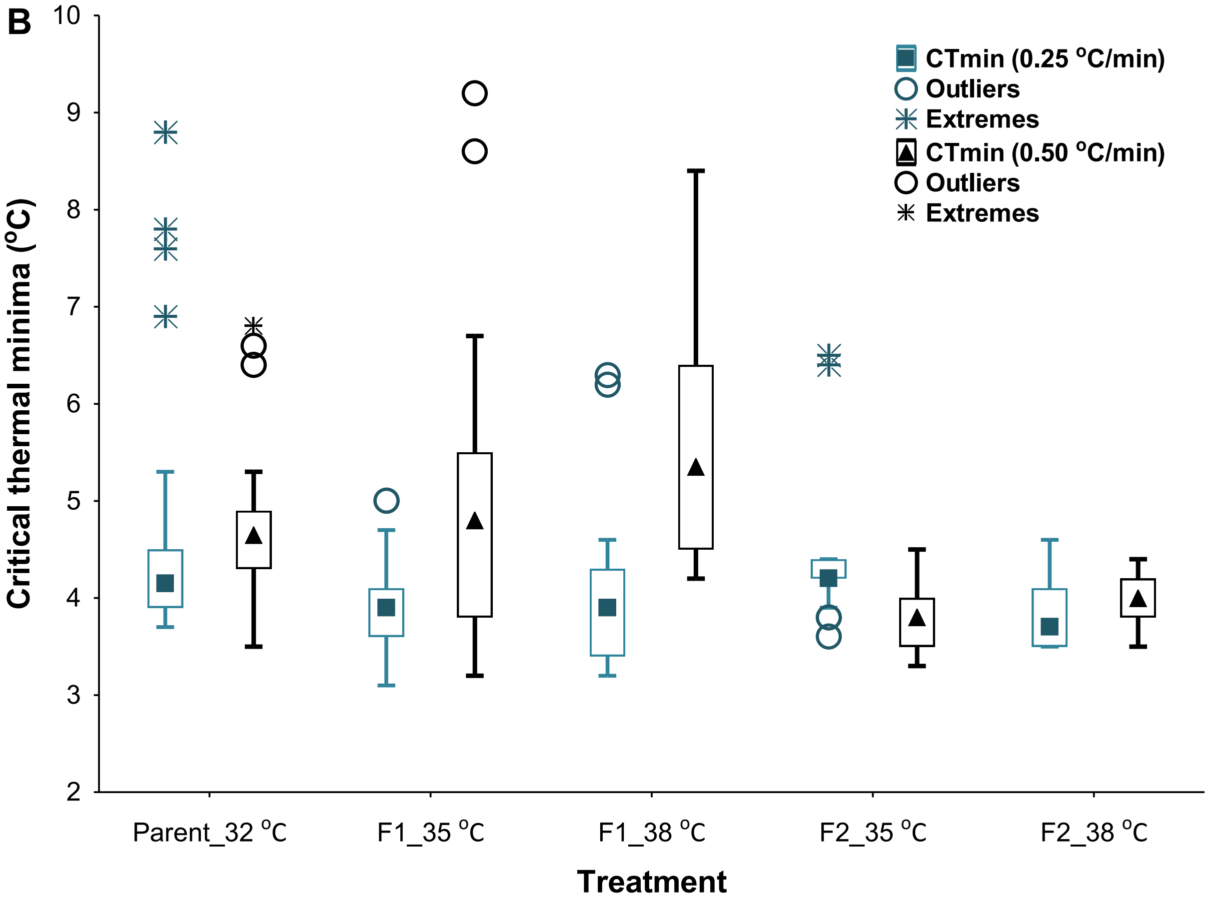


Figure 6. 2: Box and whisker plots showing critical thermal limits for adult *Prostephanus truncatus* after acclimation (n = 30): (**A**) median critical thermal maxima for treatments across 0.25 and 0.5°C/minute ramping rates (**B**) median critical thermal minima values for treatments across 0.25 and 0.5°C/minute ramping rates. Parent_32°C = *P. truncatus* parent control population (32°C, 80% RH); F_1_35°C = *P. truncatus* F_1 generation acclimated at 35°C for 2 h; F_1_38°C = *P. truncatus* F_1 generation acclimated at 38°C for 2 h; F_2_35°C = *P. truncatus* F_2 generation acclimated at 35°C for 2 h; F_2_38°C = *P. truncatus* F_2 generation acclimated at 38°C for 2 h. All treatments were maintained at 32°C, 80% RH after acclimation.

6.3.2. Effects of acclimation on HKDT

Acute heat acclimation significantly improved HKDT (Kruskal-Wallis test: $H_{(4)} = 104.141$; $P < 0.001$) in *P. truncatus* in the F_1 generation. However, these beneficial HKDT acclimation effects were quickly reversed and/or lost by repeated acclimation in the F_2 generation for both acclimation temperatures (35 and 38°C for 2 h). Heat knockdown time significantly improved from a mean of 10 minutes for the parent population to 11. 5 minutes in the respective F_1 generations. In the F_2 generations, however, HKDT was significantly reduced to between 6 and 8 minutes, representing a HKDT cost to repeated acclimation (Fig. 6.3).

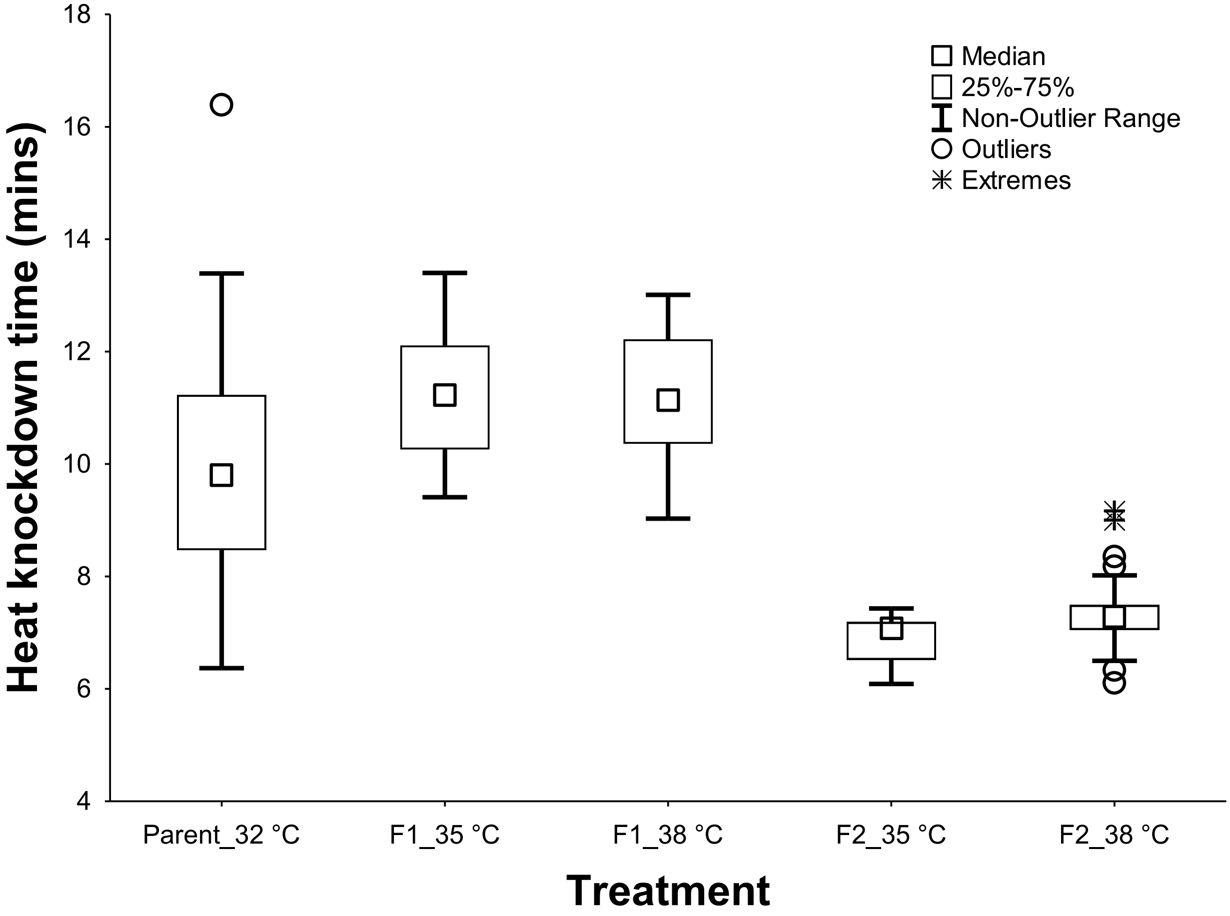


Figure 6. 3: Box and whisker plots showing median heat knockdown time (in minutes at 50°C) of adult Prostephanus truncatus control group and acclimation treatments (n = 30).Parent_32 °C = P. truncatus parent control population (32°C, 80% RH); F_1_35°C = *P. truncatus* F_1 generation acclimated at 35°C for 2 h; F_1_38°C = *P. truncatus* F_1 generation acclimated at 38°C for 2 h; F_2_35°C = *P. truncatus* F_2 generation acclimated at 35°C for 2 h; F_2_38°C = *P. truncatus* F_2 generation acclimated at 38°C for 2 h. All treatments were maintained at 32°C, 80% RH after acclimation.

6.3.3. Effect of ULTs on survival

Prostephanus truncatus survival rates were mediated by a significant interaction between temperature and exposure time ($\chi^2 = 97.531$, df = 16, $p < 0.001$). This was principally because there was no survival above 50°C, which dissolved any influence of exposure time, whereas below 50°C, exposure time always mediated survival. At 38°C, survival after 4 h and 3 h was significantly lower than 30 min and 1 h, and 2 h exposures (all $p < 0.001$). On the other hand, at 42°C, survival at 2, 3, and 4 h was significantly lower than 30 min and 1 h (all $p < 0.001$). At 46°C, survival at 1, 2, 3, and 4 h were significantly lower than 30 min (all $p < 0.001$). Therefore, as temperature increased, the threshold for significant survival differences among exposure times shortened, whereby shorter exposure times approached complete mortality (Fig. 6.4).

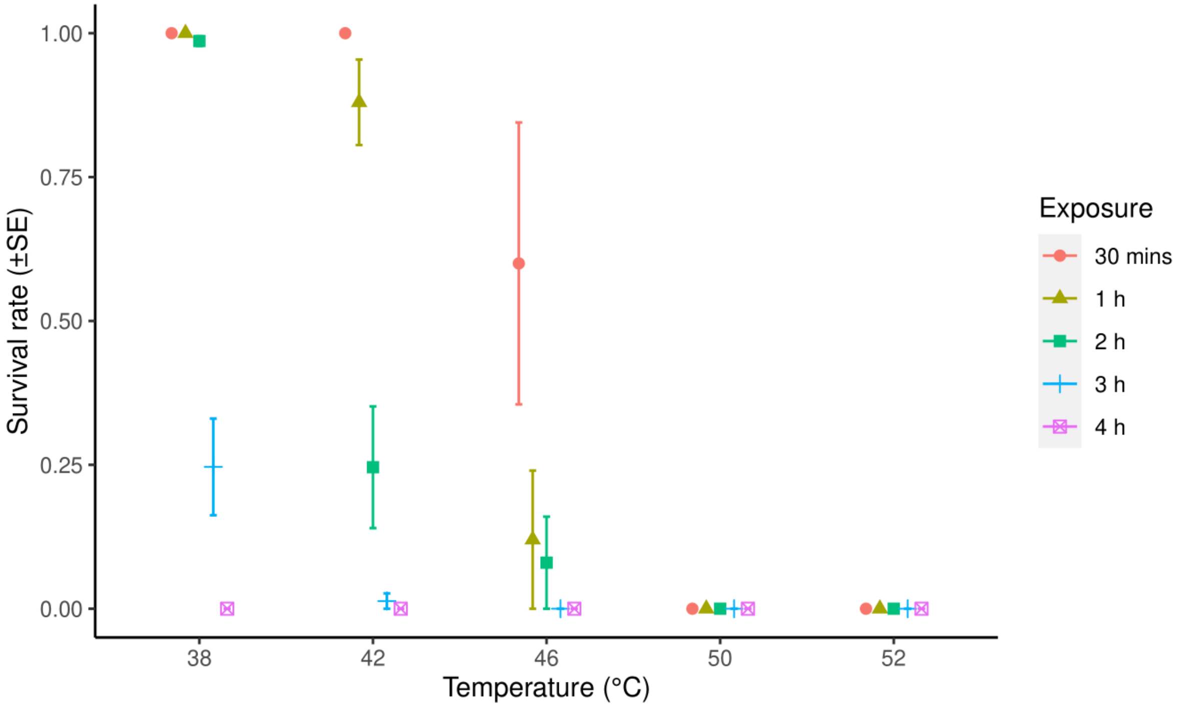


Figure 6. 4: Survival rates recorded for 3–7 days old adult *Prostephanus truncatus* (n = 3). Treatment combinations were: (Exposure temperatures; 38, 42, 46, 50, 52°C) × (Exposure durations; 30 mins, 1, 2, 3, 4 h)

6.3.4. Effects of acclimation on ecological performance of *P. truncatus*

6.3.4.1. Adult weights

Body weights of *P. truncatus* adults significantly improved ($F_{4,\ 145} = 5.020$; $p = 0.001$) in the F_1 generation following acclimation at both 35 and 38°C. With repeated acclimation, however, body weights of F_2 individuals significantly reduced for the 38°C acclimation treatment whereas the 35°C maintained higher adult body weights. Individual weights of Parent_32°C were recorded as

2.3 ± 1 mg and this was significantly lower than F_1_35°C and F_1_38°C weights, which ranged from 2.52 to 2.70 ± 1 mg. In the F_2 generation, adult body weights of F_2_38°C decreased to 2.3 ± 1 mg whereas for F_2_35°C body weights were maintained at 2.7 ± 1 mg (Fig. 6.5).

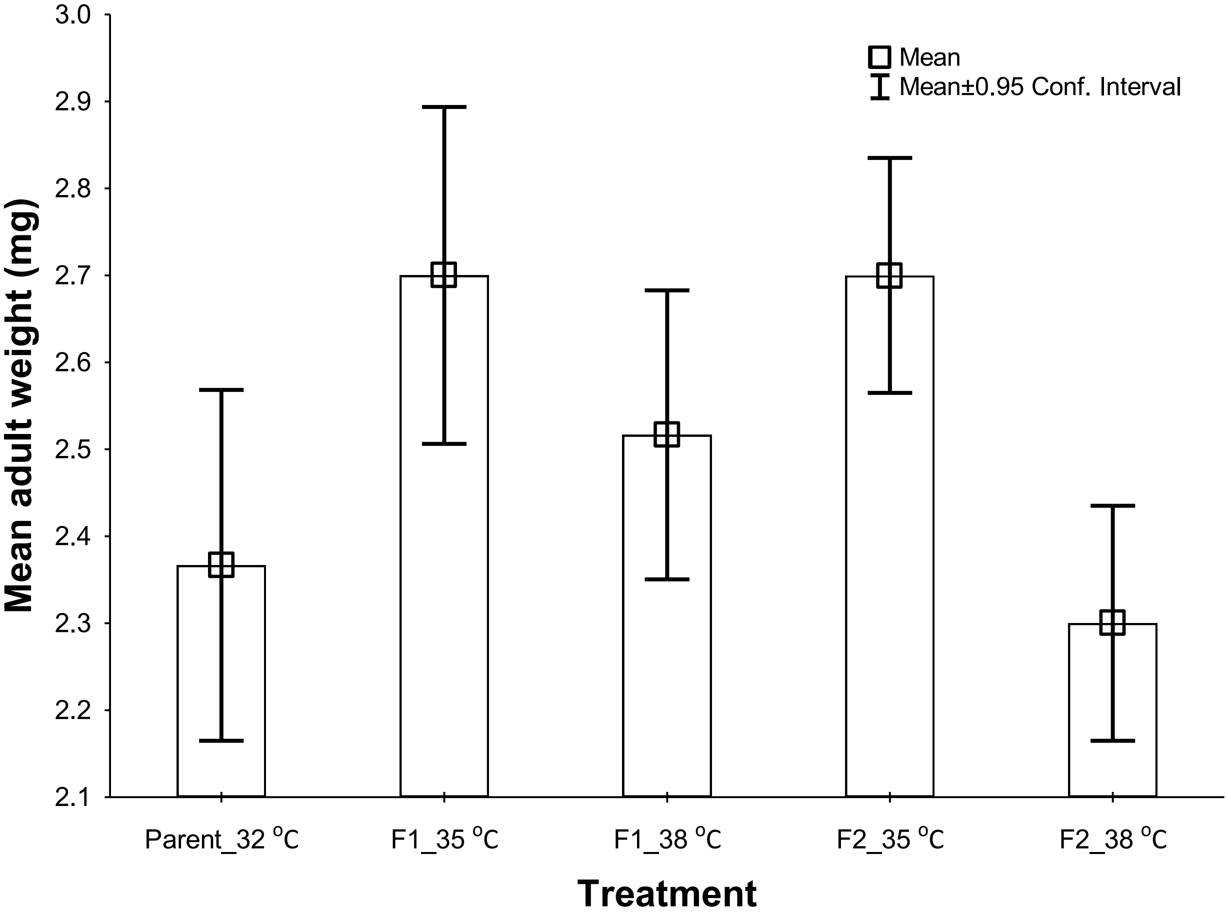


Figure 6. 5: Effects of *Prostephanus truncatus* acclimation at 35 and 38°C on adult weights recorded over two generations. The values presented are means ± SEM at 95% confidence interval (n = 30). Parent_32°C = *P. truncatus* parent control population (32°C, 80% RH); F_1_35°C = *P. truncatus* F_1 generation acclimated at 35°C for 2 h; F_1_38°C = *P. truncatus* F_1 generation acclimated at 38°C for 2 h; F_2_35°C = *P. truncatus* F_2 generation acclimated at 35°C for 2 h; F_2_38°C = *P. truncatus* F_2 generation acclimated at 38°C for 2 h. All treatments were maintained at 32°C, 80% RH after acclimation.

6.3.4.2. Fecundity, grain damage, grain weight loss and insect feeding dust.

Generally, ecological performance of *P. truncatus* significantly decreased (all $p < 0.05$) in F_1 generation following a single heat acclimation and then improved for some traits in the F_2 generation following repeated acclimation (Table 6.2). Fecundity ($F_{4, 10} = 40.42$; $p < 0.05$), grain damage ($F_{4, 10} = 48.74$; $p < 0.05$), grain weight loss ($F_{4, 10} = 6.310$; $p = 0.008$) and insect feeding dust ($F_{4, 10} = 9.799$; $p < 0.05$) were all significantly lowered by single acclimation in the F_1 generation. Generational repeated acclimation resulted in improved F_2 ecological performance in *P. truncatus* for some traits relative to F_1 but not the control population. For example, F_2_38 °C significantly increased fecundity (106. 67 ± 14.62 adults), grain damage (52.28 ± 2.87%) and grain weight loss (10.40 ± 1.97%) compared to F_1 populations and F_2_35°C. Thus, an interaction between repeated acclimation and the degree of acclimation temperature mediated ecological performance in F_2 treatments. For all parameters, parent control populations had the highest ecological performance; fecundity (194.33 ± 16.46 beetles), grain damage (61.30 ± 3.89%), grain weight loss (15.52 ± 1.00%) and insect feeding dust (9.50 ± 0.92%).

Table 6. 2: Ecological performance of *Prostephanus truncatus* measured in terms of fecundity, insect feeding dust, grain damage and grain weight loss following acclimation at 35 and 38°C recorded over a 56-days (n = 30). Parent_32°C = *P. truncatus* parent control population (32°C, 80% RH); F_1_35°C = *P. truncatus* F_1 generation acclimated at 35°C for 2 h; F_1_38°C = *P. truncatus* F_1 generation acclimated at 38°C for 2 h; F_2_35°C = *P. truncatus* F_2 generation acclimated at 35°C for 2 h; F_2_38°C = *P. truncatus* F_2 generation acclimated at 38°C for 2 h. All treatments were maintained at 32°C, 80% RH after acclimation.

Treatment	**Fecundity**	**Grain damage (%)**	**Weight loss (%)**	**Insect feeding dust (%)**
Parent_32°C	194.33 ± 16.46^c	61.30 ± 3.89^c	15.52 ± 1.00^c	9.50 ± 0.92^b
F_1_35°C	33.33 ± 3.53^a	23.60 ± 1.96^a	5.03 ± 1.62^a	4.18 ± 0.13^a
F_1_38°C	58.33 ± 2.60^a	27.52 ± 0.33^a	8.25 ± 1.73^{ab}	4.34 ± 0.22^a
F_2_35°C	58.67 ± 1.45^a	29.21 ± 1.47^a	8.25 ± 1.20^{ab}	5.20 ± 0.58^a
F_2_38°C	106.67 ± 14.62^b	52.28 ± 2.87^b	10.40 ± 1.97^b	4.38 ± 1.17^a
$F_{4, 10}$	$p < 0.0001$	$p < 0.0001$	$p = 0.01$	$p < 0.01$

6.4. Discussion

The current study aimed to determine the effect of single and repeated acute heat acclimation on the intergenerational responses of *P. truncatus* in terms of physiological and ecological performance. Firstly, the study showed that the responses are non-linear, trait- and generation-dependant. For example, acute heat acclimation improved specific traits while it decreased or had no effect on other traits at both F_1 and F_2 levels. Second, the study also showed trait-dependant erosion of beneficial as well as detrimental ecological effects following acclimation. For example, F_1 single acclimation significantly improved HKDT but these beneficial acclimation effects were eroded by repeated acclimation. On the other hand, ecological costs on fecundity, adult body weight and feeding rates (measured as grain damage) in F_1 were recovered in F_2. Third, ramping rates significantly influenced CT_{max} estimates. Single and repeated acclimations did not significantly affect CT_{max} values. However, ramping rate effects were significant in interaction between generations and temperatures. Slower ramping rate reduced CT_{max} estimates in F_1 generation although repeated acclimation in F_2 generation improved heat tolerance. Similarly, acute heat acclimation improved cold tolerance for the slower ramping rate in F_1 generation and also for the higher ramping rate in F_2 generation following repeated acclimation.

Critical thermal limits are measured during a gradual increase in body temperature and are ecologically important measures of insect thermal tolerance as they represent limits to activity for organisms as experienced with changes in climatic patterns in the natural environment (Gunderson and Stillman, 2015). Although acclimation is intended to improve thermal tolerance traits by broadening the thermoregulation temperatures (Horowitz, 2001), in the current study, single and repeated acclimations were trait-dependant, as some traits (e.g., CT_{max}) were negatively affected by acclimation and ramping rate. This resulted in loss of plasticity, which is consistent with observations by Brennan et al. (2020) who reported that plasticity is lost in the long term (F_2 generation in this case) as animals adapt to changing conditions. Furthermore, Gunderson and Stillman (2015) found that heat acclimation marginally improves heat tolerance because tropical ectotherms have a narrow thermal window due to their inherent high basal heat tolerance. In contrast, Mutamiswa et al. (2021) reported improved heat tolerance in *P. truncatus* following acclimation within generation. Ramping rates also had significant effects on CT_{max} and CT_{min} and this is in concurrence with findings on storage pests from other studies (e.g., Machekano et al. 2020; Mpofu et al. 2021).

The results highlight that thermal tolerance in *P. truncatus* is highly influenced by interaction between temperature and ramping rates and the beetle is more susceptible to gradual changes in extreme temperatures (0.25°C/minute) compared to rapid changes (0.5°C/minute) in extreme temperatures, consistent with the notion that slower rates of stress results in more and cumulative heat stress damage (Jøgensen et al. 2021). Similar observations were noted by Machekano et al. (2020). CT_{max} ranged between 47 and 52°C, CT_{min} (3-10°C), HKTD (5-14 minutes; rarely exceeding 15 minutes) and in ULTs *P. truncatus* survival was mediated by exposure duration with 0% survival achieved at 46°C for as little exposure as 3 h. These findings could find application in grain heat treatment protocols for phytosanitary disinfestation. Previous studies have shown that heat acclimation improved cold tolerance in the fruit fly, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) (Bubliy and Loeschcke, 2005), consistent with the current findings. Single acclimation improved HKDT in the F_1 generation and this was lost in the F_2 generation for both acclimation temperature regimes. Improvement in HKDT results in F_1 following single acclimation is consistent with the beneficial acclimation hypothesis (Wilson and Franklin, 2002). However, repeated acclimation at F_2 may result in cumulative or additive stress that may offset acclimation benefits (Jøgensen et al. 2021). A 100% survival rate was recorded at 38°C up to 2 h exposure. At that same exposure temperature, survival then declined to 25% at 3 h and 0% at 4 h exposure durations. Similar results have been reported in Machekano et al. (2020) who then proposed thermal (physical) control of *P. truncatus* at lower ramping rates to moderate exposure temperatures × long exposure durations i.e., 45.5°C for 4 h in stored grain to save energy. Lethal temperatures kill insects by mechanisms such as disruption of lipid structure in membranes, rate imbalances, and desiccation, in addition high temperatures cause a decrease in relative humidity and a depletion in grain moisture content (Fields et al. 1992).

The effects of acute heat acclimation on the ecological traits of *P. truncatus* also varied with acclimation temperature and with single F_1 versus F_2 repeated acclimation. Ecological performance generally declined in F_1 generation following a single acclimation and only improved in F_2_38°C in the F_2 generation. Heat acclimation significantly reduced the *P. truncatus* fecundity in F_1 generation, which then resulted in reduced grain damage, grain weight loss and insect feeding dust generated in the respective treatments. The F_2_38°C treatment recorded significantly higher fecundity, grain damage and grain weight losses compared to F_1_35°C, F_1_38°C and F_2_35°C which points to a regain in ecological traits following repeated acclimation, leading to improved performance. Cavieres et al. (2020) demonstrated similar results in which a trade-off between thermal tolerance and fecundity was observed in a parental fly population, resulting in "partial compensatory responses" in the offspring. This is because reproduction is the most heat sensitive life history trait in insects and has a very narrow thermal tolerance range (Ma et al. 2021b). Besides negatively affecting fecundity, Huang et al. (2007) also found that heat hardening depresses adult feeding and this can partly explain the low grain damage and weight losses recorded for acclimation treatments in this study. Bubliy and Loeschcke, (2005) postulated that ectotherms generally respond to extreme heat by lowering metabolism to conserve resources, further supporting the low ecological performance seen in the current study. Results of individual weight analysis are inclined to a similar trend, where F_2_38°C recorded weights similar to the parent_32°C which were significantly lower than F_1_35°C, F_1_38°C and F_2_35°C. This observation, as articulated by Walzer et al. (2020), manifests as intergenerational responses speeding up development in F_2 generations and causing larger body sizes compared to initial (parent) generations.

The results on *P. truncatus* adult individual weights ranged from 2.3–2.7 ± 1 mg following acute heat acclimation treatments. These individual adult weights were in the lower range as those (3.05–3.6 mg) reported in Haines (1981) possibly due to a different host (cassava) used by the former. Further, fecundity ranged 30–194 ±16 adults, grain damage (23–61 ± 3.89%), grain weight loss (5–15 ± 1.00%) and insect feeding dust (4–9 ± 0.92%) were recorded over a 56-day period on maize grain. Comparable results of progeny production, maize grain damage and insect feeding dust production in *P. truncatus* were reported by Altunç et al. (2023). However, Altunç et al. (2023) only investigated progeny production without heat acclimation. At optimum conditions of 32°C and 80 % RH, *P. truncatus* complete its life cycle in 25–27 days (Hodges, 1983; Shires, 1987; Muatinte et al. 2014; Quellhorst et al. 2021). At these conditions, a single female lays around 20 eggs at a time depending also on the food available (Quellhorst et al.

2021) and up to 300 eggs in a lifetime (Suma and Russo, 2005). At 32°C and 80% RH, Quellhorst et al. (2019) demonstrated that *P. truncatus* produces significantly higher progeny, grain damage, grain weight losses and insect feeding dust compared to lower (20°C) or 'excessive' (35°C) temperatures. However, these experiments were done in interaction with the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae) to mimic where these two coexist. Hence, the individual effects of *P. truncatus* may be difficult to tease apart using results by Quellhorst et al. (2019). The current study is thus the first reporting of *P. truncatus* performance as a single species under repeated generational heat hardening and the effects thereof on maize grain. Insect feeding dust was significantly higher in the control treatment F_1_32°C which also had the highest progeny for all treatments. This may mean that reproduction may be lower under higher stressful temperatures, and with repeated bouts of heat stress. This is likely a result of trade-offs in life history traits, for example, *P. truncatus* may trade off reproduction for heat stress protection mechanisms that may require large energy reserves (Neven, 2000). Altunç et al. (2023) linked high insect feeding dust production to high reproduction in *P. truncatus* as the feeding dust is meant for protection and development of the larvae (see also Quellhorst et al. 2021).

Various researchers have posed the question of what temperature increases under climate change would mean to insect pests of stored grain (e.g., Stathers et al. 2013; Arthur et al. 2019; Singano et al. 2020; Nyabako et al. 2021). Most of the conclusions pointed to increased reproduction, damage and range expansion of stored grain insect pests. The current study demonstrates that acute heat acclimation has negative effects on physiological and ecological functions of *P. truncatus* to a limited number of generations; at least one generation based on our data. This, however, is not a model to interpret what would happen with different other insect pests of stored grain or insect pests from different taxa as is the case in normal stored-grain ecosystems. As such, further studies including transgenerational plastic responses and extending the investigations beyond 2 generations and in the presence of other different cosmopolitan or invasive insect pests of stored grain are recommended to determine the effects of changing climatic conditions on physiological and ecological performance under competition as is the case in natural habitats. One of the few studies on stored grain thermal responses is Mpofu et al. (2022) who investigated transgenerational responses to heat and fasting acclimation in the

Angoumois grain moth, *Sitotroga cerealella* Olivier (Lepidoptera: Gelechiidae) and concluded that acclimation resulted in fitness costs on the moth. Mutamiswa et al. (2021) reported improved heat tolerance in *P. truncatus* following heat (and fasting) acclimation. Mpofu et al. (2022) and Mutamiswa et al. (2021), however, did not (i) repeat the acclimations generationally and (ii) did not focus on the effects of acclimation on ecological performance. The current study did not extensively investigate the number of days to progeny emergence and beetles' longevity following heat acclimation, which are important parameters that would otherwise improve our understanding of the effects of changing climatic conditions on the biology of *P. truncatus*. Furthermore, this study indicate potential improvements on existing heat-based phytosanitary disinfestation protocols, especially on pests *P. truncatus* that are hard to control with conventional synthetic pesticides. The study points to opportunities for pest physical control options through cooling or heating, e.g., by solarisation to suppress beetle populations, especially with increased warming (also discussions in Fields et al. 1992; Abdelsamea et al. 2023).

In conclusion, the study found that: (i) intergenerational responses to single or repeated heat acclimation in *P. truncatus* are trait- and generation-dependent, (ii) while acclimation improved HKDT at F_1, repeated acclimation significantly reduced F_2 HKDT, suggesting plasticity erosion with repeated acclimation, (iii) single acclimation negatively affected ecological performance (fecundity and grain damage potential) of *P. truncatus* in the F_1 generation. However, repeated acclimation led to adaptation in F_2 generation and thus regaining ecological performance to near parental, (iv) thermoregulation in *P. truncatus* is significantly affected by ramping rates and their interaction with acclimation temperature and/or generation. *Prostephanus truncatus* will therefore continue to be a serious threat under climate change as repeated bouts of extreme heat experienced in the natural environment will result in adaptation to stress, leading to improved intergenerational ecological performance and enhanced survival of this important agricultural and forest invasive pest.

6.5. References

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CHAPTER 7

Temperature, host density and maternal host preference effects on progeny fitness of the invasive larger grain borer[6]

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7.1. Introduction

Insect pests exist in complex environments where biotic resources (e.g., diets) widely vary in type, quality and quantity across ecosystems and seasons (Altieri, 1999). Furthermore, abiotic stresses (Outhwaite et al. 2022) and competitive interactions across conspecifics and sympatric heterospecifics (Fisher et al. 2021) may also dictate the fitness of organisms under competitive and rapidly changing environments. The dietary diversity of resources has significant effects on the ecology of parental and progeny of oviparous insects (Burian et al. 2017). In the field, plant quality affects offspring fecundity, size, and survival of insect pests such as aphids (Ríos-Martínez and Costamagna, 2018). As such, maternal investment is a significant component of securing field fitness for the next generation. Defined as any parental expenditure of time, energy, or resources aimed at benefiting the offspring, maternal investment comprises organismal actions such as selection of oviposition host, the protective covering of eggs (e.g., in fall armyworm [Kenis et al. 2022]), the 'decision' to produce a few large eggs or many smaller ones based on prevailing food resource quality and quantity (Koch and Meunier, 2014; Macartney et al. 2022). Such actions may influence the fitness survival fate of organisms under complex and rapidly changing environments. Indeed, it is increasingly evident that many maternal effects are shaped by natural selection, acting as an adaptive mechanism for offspring phenotypic responses to changing environments (Mousseau and Fox, 1998; Uller et al. 2013; Crino et al. 2024).

The larger grain borer, *Prostephanus truncatus* Horn (Coleoptera: Bostrichidae) is an economic insect pest of maize grain, dried cassava (Shires, 1980; Quellhorst et al. 2021) and a wide range of other stored products e.g., sorghum (Osipitan et al. 2012). The Bostrichid pest has spread to many counties following its accidental introduction in Africa in the early 1980s (Athanassiou et al. 2017; Arthur et al. 2019; Muatinte and Van den Berg, 2019; Sadiku et al. 2019; Loko et al. 2020). While members of the Bostrichidae family are commonly known for wood-boring, *P. truncatus* together with the lesser grain borer, *Rhyzopertha dominica* (F.) have evolved successfully as colonisers of stored grains including maize (Jia et al. 2008). *Prostephanus truncatus* alternates between maize grain, cassava and wild host tree and grass species, such as *Brachystegia spiciformis* Bent., *Colophospermum mopane* (J. Kirk ex Benth.), *Commiphora rostrata* Engl., *Commiphora baluensis* Engl, *Delonix regia* (Bojer) Raf. and *Acacia polyacantha*

Willd. (Nang'ayo et al. 2002; Muatinte and Van den Berg, 2019). This constant and frequent switching between wild and cultivated host plants may happen as 'forced choices' without prior ancestral exposure history (Nang'ayo et al. 2002; Nansen and Meikle, 2002). Although host-switching plays an important role in the survival and dispersal of the *P. truncatus*, it may come with fitness trade-offs. The performance of a newly introduced population under new stressful environments (e.g., dietary conditions) thus defines its survival and reproductive capacity and mediates its fitness traits (Papanikolaou et al. 2019). The physiological and ecological fitness traits associated with each individual host for *P. truncatus* and the costs or benefits associated with host-switching between *P. truncatus* parents and offspring are not well understood. Further, as temperatures increase with climate change, the effects that the increased temperatures have on *P. truncatus*' feeding rates are not known (Quellhorst et al. 2020). These physiological and ecological responses are important in integrated management of the pest.

Besides responding to new hosts, insects are faced with the simultaneous need to adapt to increasing temperatures due to climate change (Skendžić et al. 2021). Thermal responses delineate insect physiological fitness through critical thermal limits to activity and further expound insect feeding rates under climate change (Lutterschmidt and Hutchison, 1997; Terblanche et al. 2007). *Prostephanus truncatus* is known to have a high optimal temperature for development and progeny production at 32℃ although its highest damage levels are spread out from 27–32 ℃ at 80% relative humidity (RH) (Shires, 1980; Harman et al. 2024). It is imperative therefore to measure and understand the interactions between maternal host preference, feeding rates and static and dynamic thermal tolerance metrics which resemble pest experiences under natural environments (Chown and Nicolson, 2004; Gunderson and Stillman, 2015). For this purpose therefore, Critical thermal maxima (CT_{max}) and Heat knockdown time (HKDT) were employed as relevant proxies for measuring insect physiological responses to thermal stress (Lutterschmidt and Hutchison, 1997).

Ecologists have often used different fitness traits to measure how well an organism is adapted to its environment. For example, Lampasona et al. (2022) defined fitness on the basis of organismal weight, developmental period, and survival rates. Here, the current study used fitness traits defined by Lampasona et al. (2022) to determine the trophic interaction strengths and effects of maternal investment on progeny fitness in *P. truncatus*. The study sought to understand whether *P. truncatus* adults would prefer and or perform better under one host over the other and how such maternal investment would influence progeny fitness. In the current study, insect physiological fitness was defined as functional properties of insect tissues and organs (Jurenka, 2021) and ecological traits as insect fitness through interaction with their surrounding environment (Abram et al. 2017). The objectives of this study were to (i) determine feeding rates of *P. truncatus* populations in relation to host (diet) density, host type and increasing temperature regimes; (ii) determine *P. truncatus* host preference for oviposition; and (iii) determine whether maternal experience or environment affects progeny fitness. The study hypothesised that (i) feeding increases with host-insect density and temperature (non-competitive *P. truncatus* interaction), (ii) that maize grain is the most preferred host for *P. truncatus* oviposition; and (iii) maternal experience increases progeny fitness. Such information is crucial in explaining the ecological and economic impacts of invasive insect pests of quarantine importance under rapidly changing biotic and abiotic complex environments.

7.2. Materials and methods

7.2.1. Test insects

Prostephanus truncatus was cultured from pheromone-baited trap catches in the forest surrounding the Department of Plant Health offices in Gaborone, Botswana. This outbred culture was maintained on dried maize cobs for over six generations with regular addition of wild collected individuals to minimise inbreeding depression (Terblanche and Chown, 2007). The colony was reared at 32°C; 65% RH under a 12L:12D photoperiod in Memmert climate chambers (HPP 260, Memmert GmbH + Co.KG, Germany). In cases where sex was an important factor in experiments, beetles were sexed using gross morphology under a stereo microscope, following methods by Shires and McCarthy (1976). Females are differentiated from males by having more pronounced and spaced clypeal tubercles than males (Shires and McCarthy, 1976).

7.2.2. Test hosts

Four different host plants were used comprising (i) peeled and dried cassava tubers, (ii) sliced and dried mopane wood, (iii) dried and shelled maize, and (iv) sorghum grains. The wild host, mopane wood, was chosen based on its abundance in savanna ecosystems (Makhado et al. 2014), while the cultivated hosts were chosen based on their importance as staple crops in Africa (Knox et al. 2012). Maize and cassava are the preferred hosts for *P. truncatus* whilst mopane wood is a confirmed wild host (Muatinte and Van den Berg, 2019). Sorghum was also added as trends show its increasing cultivation as a 'climate-smart' crop (Hadebe et al. 2017), and that it is also affected by *P. truncatus* (Osipitan et al. 2012).

Cassava and mopane wood were chopped into small pieces of ~5cm × 3cm and 3cm × 3cm length and diameter respectively. Test hosts were dried and sterilised by freezing at -18℃ for two weeks and then acclimatised to subsequent experimental conditions for 7 days following methods by Hodges and Dobson (1998). Moisture content was measured using the oven dry method (Bergman, 2021) and was estimated 10.3 and 12.4% for cassava and mopane wood, respectively. Maize and sorghum grain moisture content was measured using the Unimeter digital grain moisture meter (Agri-Enviro Solutions, South Africa) and was estimated at ~12. 3 and 11.8%, respectively.

7.3. Experimental procedure and measurements

Three experiments were conducted i.e., (i) feeding rate tests, (ii) host suitability for oviposition tests, and (iii) progeny physiological and ecological fitness tests following different maternal host experiences.

7.3.1. Feeding rates of *P. truncatus* under varying host densities and increasing temperature regimes.

Trophic interactions were determined using a 3 × 4 × 3 factorial experimental approach, with 3× population density levels (5, 10, 20 adults [3–7 days old]); 4× host density levels (50, 100, 200, 400 g for dried maize and 25, 50, 100, 200g for cassava) and 3× temperature levels (29, 32 [control] and 35°C [and 65% RH]) in Memmert climate chambers. Treatment combinations were set up and replicated three times in 500 ml glass jars with perforated metal lids to allow free air circulation. The experiment was left undisturbed for 21 days after which adult insects were removed from each treatment. Weight of the remaining host material (grain) was recorded and returned to respective treatments at the prescribed conditions for further 35 days to allow all eggs to hatch (Masasa et al. 2013). The amount of food removed and the total number of emerged progenies were recorded for each treatment.

7.3.2. Host suitability for oviposition test

A suitability test was conducted to assess *P. truncatus'* host preference for oviposition amongst maize, cassava, sorghum and mopane wood. Three 5 litre plastic containers with perforated lids to allow for air circulation were prepared. In each container, 200g of each test host was added and thoroughly mixed. Fifty sexed adult beetles (25 males: 25 females) that had emerged from maize grain were added in each plastic container. The containers were sealed and kept in a Memmert climate chamber set at 32°C; 65% RH under 12L:12D photoperiod. Four treatments were thus created (Table 7.1).

Table 7. 1: Summary of the four treatments evaluated to determine *P. truncatus'* host suitability for oviposition.

Treatment	**Description**
F_1 Maize	F_1 progeny emerging from dried maize grain host
F_1 Cassava	F_1 progeny emerging from dried cassava host
F_1 Sorghum	F_1 progeny emerging from dried sorghum grain host
F_1 Mopane	F_1 progeny emerging from dried mopane host

After an oviposition period of 21 days, adult insects were removed from the containers. The test hosts were put in separate 500 ml jars (in three replications) and incubated at the same conditions for 35 days. The number of F_1 progeny that emerged from each treatment over the 35-day period was recorded.

7.3.3. Effects of maternal experience on progeny fitness

Cultures of *P. truncatus* were reared separately on maize, cassava and mopane wood for two generations (F_1 and F_2) in 1 litre glass jars. Set conditions in Memmert climate chambers were 32℃, 65% RH and 12L:12D photoperiod. F_1 progeny (3–7 days old) emerging from each host were weighed individually and exposed to a fresh host in sets of 20 sexed adults (10 male:10 female) in 500 ml glass jars (Fig. 7.1).

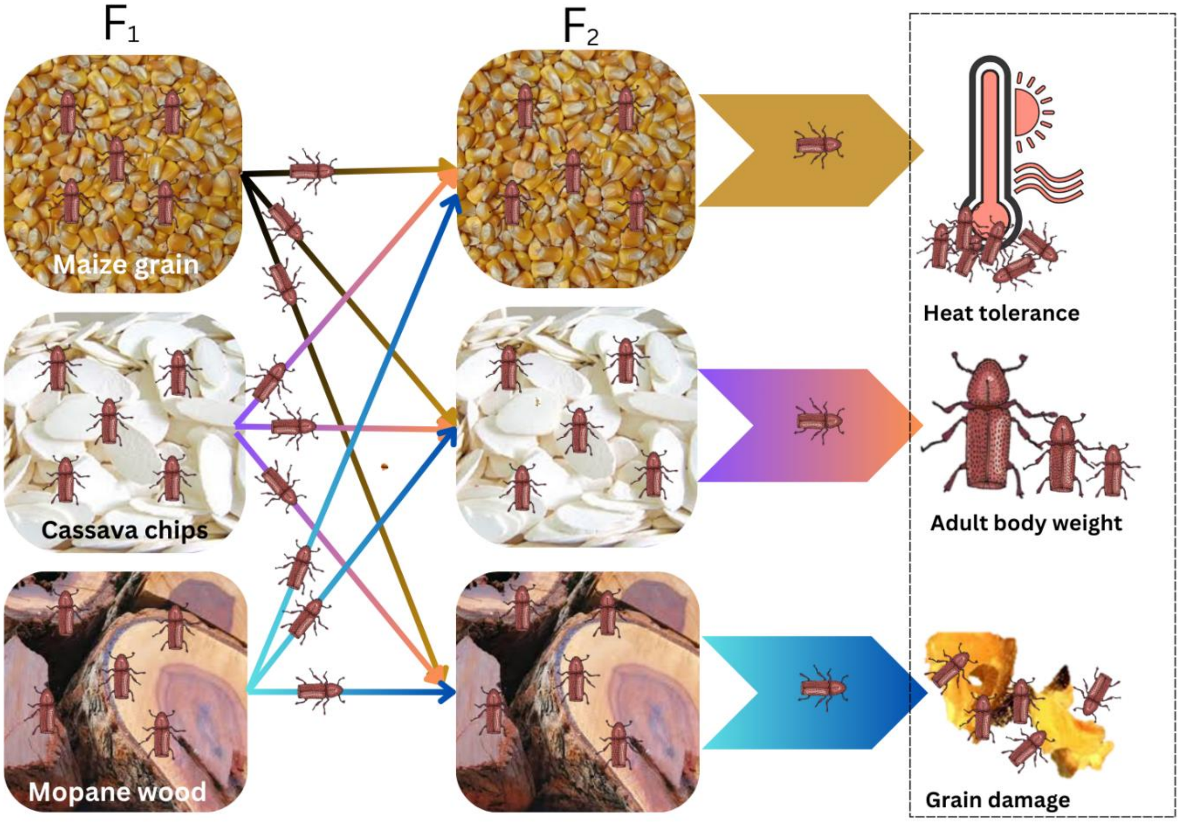

Figure 7. 1: Treatment combinations used to assess the effects of maternal investment on progeny fitness in terms of ecological and physiological traits. F_1 parents represent F_1 progeny that emerged from the respective hosts (maize grain, cassava chips and mopane wood) and were then placed into different host combinations (indicated with arrows) to emerge as F_2 progeny. Ecological and physiological experiments were then done using the F_2 progeny.

The jars were sealed with tight metal lids with small perforations to allow free air circulation. Nine treatment combinations (Fig. 7.1) were thus prepared, and these were replicated three times. A *P. truncatus* culture reared on mopane wood, however, did not produce progeny for subsequent tests within the expected period and the mopane host treatment was thus excluded for further testing the effects of maternal host on progeny fitness resulting in a 2 × 2 experiment. The jars were kept in a Memmert climate chamber at the same conditions at 32°C, 65% RH and 12L:12D photoperiod. A mating and oviposition period of 21 days was allowed, after which adult insects were removed from the jars. Ecological and physiological traits of 3–7 days old F_2 progeny emerging from each of the treatments were then assayed. Ecological traits were estimated using adult weight, maize grain damage and grain weight loss caused, following methods by Boxall (2002). Briefly, 20 unsexed 3–7-day old adult beetles emerging from each treatment were used to assess grain damage and grain weight loss. These newly emerged beetles were transferred to fresh 200g maize grain in separate 500 ml jars and kept at 32°C, 65% RH and a 12L;12D photoperiod for a storage period of 35 days, after which grain damage and weight loss were assessed using the count and weigh method (Boxall, 2002).

Heat tolerance, comprising critical thermal maxima (CT_{max}) and heat knockdown time (HKDT) were estimated to assess physiological traits of F_2 progeny from each treatment. These traits represent standard metrics for measuring insect responses to heat stress and are ecologically relevant (Lutterschmidt and Hutchison, 1997). For CT_{max}, 10 adult beetles were each placed in a double-jacketed chamber submerged in a programmable water bath (LAUDA Ecogold® RE 2025, Lauda-Königshofen, Germany) at a ramping rate of 0.25°C/ minute. CT_{max} was recorded as the temperature at which insects loose coordinated muscle function and ability to respond to mild stimuli from a thermally inert object (Nyamukondiwa and Terblanche, 2009). The experiment was repeated three times to obtain 30 replicates. Heat knockdown time assays were conducted at 50°C in a Memmert climate chamber with a video recording camera (HD Covert Network Camera, DS-2CD6412FWD-20, Hikvision Digital Technology Co., Ltd, Hangzhou, China) which was connected to a computer to record the activity. Thirty beetles were placed in perforated Eppendorf tubes and acutely exposed to 50°C. Heat knockdown time was recorded as the time (in minutes) at which an insect lost activity due to heat stress (Mlambo et al. 2024).

7.3.4. Data analyses

For the feeding rates experiment, generalised linear models (GLMs) assuming a binomial error distribution, were used to analyse rounded (to nearest g) feeding rates of *P. truncatus* in relation to its density, resource supply, and temperature, with separate models for maize and cassava. A third GLM was fitted to compare feeding rates on maize and cassava at matched resource supplies (50, 100, 200g), using the same aforementioned predictor variables. Progeny numbers were included as a covariate in each model.

For the host preference experiment, quasipoisson GLMs were used to assess the effects of host choice on the numbers of progeny produced, owing to residual overdispersion. For the effects of maternal experience on progeny fitness experiment, thermal fitness (F_1/F_2 adult weight, CT_{max}, and HKDT) were analysed using linear models in relation to treatment and were log-transformed to improve homoscedasticity where needed. Numbers of progeny produced were analysed using quasipoisson GLMs. Ecological outcomes (% chaff, grain damage, and grain weight loss) were analysed using beta regression as a function of treatment.

In all models, non-significant terms were removed backward, stepwise to reach the most parsimonious suite of terms. Analysis of deviance was used to assess the main effects of models with more than two categorical predictor levels, with estimated marginal means used for post-hoc comparisons following Tukey adjustments as needed. Model assumptions were tested through residual simulations in comparison to model outcomes. All datasets were analysed in R version 4.3.1 (R Core Team, 2023).

7.4. Results

7.4.1. Feeding rates of *P. truncatus* on different maize and cassava densities at increasing temperature regimes

Feeding rates on maize were significantly positively affected by progeny numbers, but not initial population densities (Table 7.2). Maize feeding also differed owing to a two-way interaction between host density and temperature (Table 7.2). Overall, feeding rates tended to decline with both increase in host density and temperature. However, the effects of temperature reduced the importance of host density in driving consumption, and even shifted the direction of the effect. For cassava, a significant three-way interaction was shown according to population density, host density, and temperature, with temperature warming eroding the effects of population and host densities. Progeny significantly increased feeding rates which ranged from 0.01–0.08g) (Table 7.2). Feeding rates between maize and cassava significantly differed at matched densities, with higher consumption of dried cassava relative to maize grain across the temperature treatments overall. This was further mediated by a significant three-way interaction among population density, temperature, and host type (Table 7.2), with temperature effects heightened by increasing population densities, especially in maize (Fig. 7.2). Host density had a significant negative effect on feeding rates overall. Feeding rates averaged 0.01g for maize and above 0.04g for cassava.

Table 7. 2: Binomial generalised linear model outputs considering *P. truncatus* feeding rates towards maize and cassava in relation to consumer density, resource supply temperature, and progeny numbers. Feeding rate was defined as the amount of feed consumed in relation to resource supply and *P. truncatus* density. A separate GLM was fitted to compare feeding on maize and cassava at matched resource supplies (50, 100, 200g).

Model	**Term**	**z-value**	**p-value**
Maize consumption	Consumer density (*P. truncatus*)	0.106	0.916
	Host density (maize)	4.193	< 0.001
	Temperature	5.492	< 0.001
	Progeny	6.998	< 0.001
	Consumer density × Host density	0.741	0.458
	Consumer density × Temperature	0.706	0.48
	Host density × Temperature	4.044	< 0.001
	Consumer density × Host density × Temperature	1.956	0.05
Cassava consumption	Consumer density	0.937	0.349
	Host density (cassava)	1.817	0.069
	Temperature	0.331	0.741
	Progeny	2.124	0.034
	Consumer density × Host density	2.181	0.029
	Consumer density × Temperature	0.926	0.355
	Host density: Temperature	1.959	0.05
	Consumer density × Host supply × Temperature	2.116	0.034
Combined consumption	Consumer density	2.556	0.011
	Host supply	5.624	< 0.001
	Temperature	4.419	< 0.001
	Resource type	2.71	< 0.001
	Progeny	4.035	< 0.001
	Consumer density × Host density	0.387	0.699
	Consumer density × Temperature	2.452	< 0.001
	Consumer density × Host type	3.834	< 0.001
	Host density × Temperature	0.138	0.89
	Host density × Host type	1.284	0.199
	Temperature × Host type	2.281	< 0.001
	Consumer density × Host density × Temperature	0.564	0.573
	Consumer density × Host density × Host type	0.112	0.911
	Consumer density × Temperature × Host type	3.606	< 0.001
	Host density × Temperature × Host type	0.191	0.849
	Consumer density × Host density × Temperature × Host type	1.905	0.057

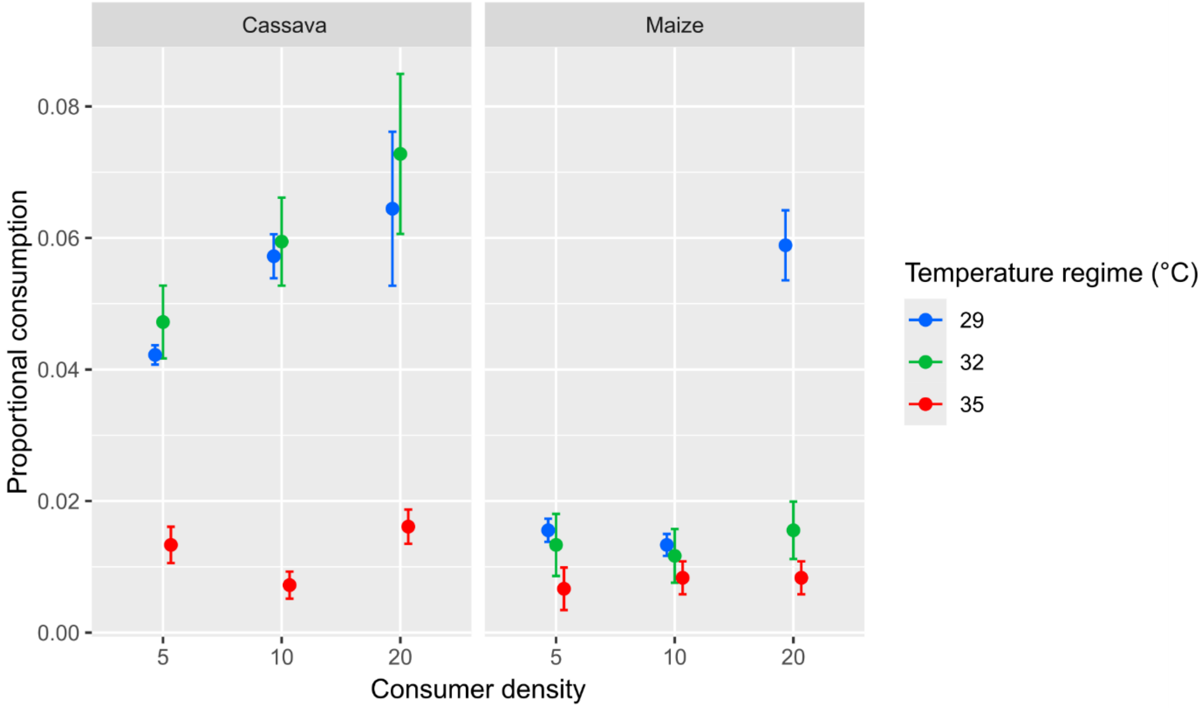

Figure 7. 2: Feeding rates (grams consumed divided by grams supplied) of *P. truncatus* towards maize and cassava at different consumer densities and temperatures (n = 3). Means are shown alongside standard errors.

7.4.2. Host suitability for oviposition

Progeny production differed significantly among the four hosts ($\chi^2 = 96.866$, $p < 0.001$). Cassava tubers and maize grain were statistically similar ($p = 0.229$), whereas they both facilitated significantly more progeny than mopane and sorghum ($p < 0.05$), which were in turn similar ($p = 0.446$) (Fig. 7.3). Progeny numbers between 75 and 200 were produced from cassava and maize grain hosts whilst less than 25 emerged on sorghum grain and mopane wood.

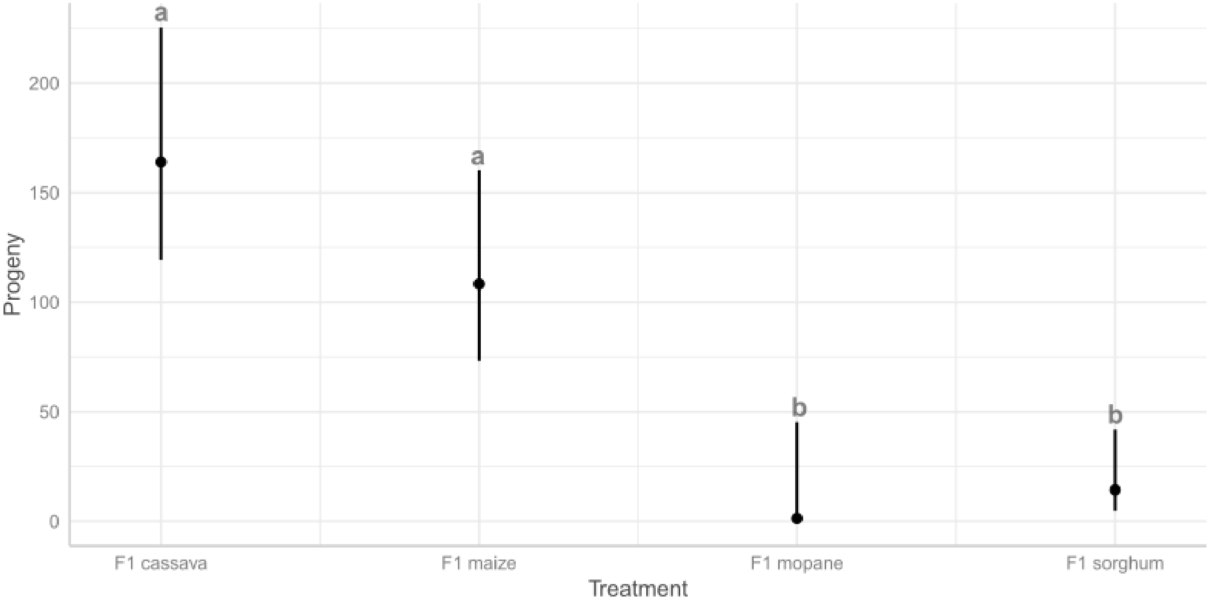

Figure 7. 3: Model output for progeny production of *P. truncatus* towards various resources (n = 3). Means are shown alongside standard errors. F_1 cassava = F_1 progeny emerging from dried cassava host, F_1 maize = F_1 progeny emerging from dried maize grain host, F_1 mopane = F_1 progeny emerging from dried mopane wood host, and F_1 sorghum = F_1 progeny emerging from dried sorghum grain host.

7.4.3. Effects of maternal experience on progeny physiological and ecological fitness.

7.4.3.1. Heat tolerance

CT_{max} ranged between 48 and 50°C and did not differ significantly amongst treatments ($F_{3,\ 116} = 2.502$, $p = 0.063$). In contrast, HKDT differed significantly ($F_{3,\ 116} = 15.506$, $p < 0.001$), with consecutive consistent host exposure/experiences (cassava-cassava and maize-maize) having a higher fitness (greater HKDT ranging from 7.5–8.5 minutes) than mixed host experiences in general (Fig. 7.4). With the exception of maize-maize vs cassava-maize, these ‘consistent-mixed’ differences were always statistically clear ($p < 0.05$). Maize-cassava always had significantly lowest heat tolerance (lowest HKDT, $p < 0.05$).

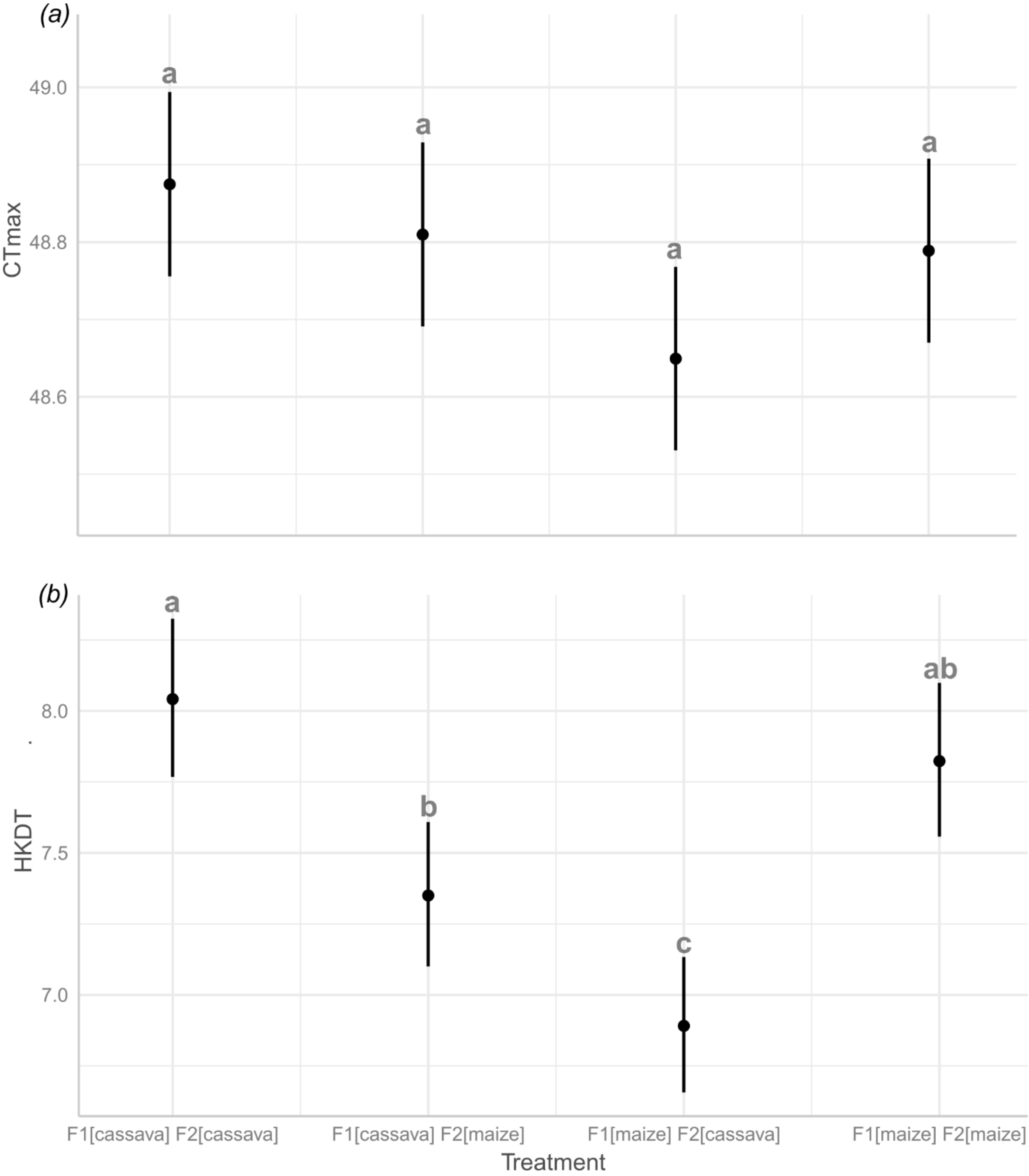

Figure 7. 4: Model outputs assessing CT$_{max}$ (a) and heat knock-down time (HKDT; b) of F$_2$ *P. truncatus* towards various host plant resource combinations across generations (n = 30). Means are shown alongside standard error. F$_1$ [cassava] F$_2$ [cassava] = F$_1$ progeny emerging from dried cassava host and then exposed to cassava again to produce the F$_2$ generation; F$_1$ [cassava] F2 [maize] = F$_1$ progeny emerging from dried cassava host and then exposed to maize host to produce F$_2$ generation; F$_1$ [maize] F$_2$ [cassava] = F$_1$ progeny emerging from dried maize grain

host and then exposed to cassava host to produce F_2 generation; and F_1 [maize] F_2 [maize] = F_1 progeny emerging from dried maize grain host and then exposed to maize host again to produce the F_2 generation.

7.4.3.2. Ecological performance

F_1 adult weights were significantly higher following the maize treatment ($z = 2.384$, $p > 0.05$) compared to cassava. The maize host caused the highest adult weights, ranging from 0.0033g to slightly above 0.0034g per individual. Cassava caused *P. truncatus* weights below 0.0032g per individual. F_2 adult weights also differed significantly among host treatment combinations ($\chi^2 = 3.039$, $p = 0.032$), with weights tending to be highest in maize-maize groups. However, pairwise comparisons lacked statistical clarity ($p > 0.05$) (Fig. 7.5).

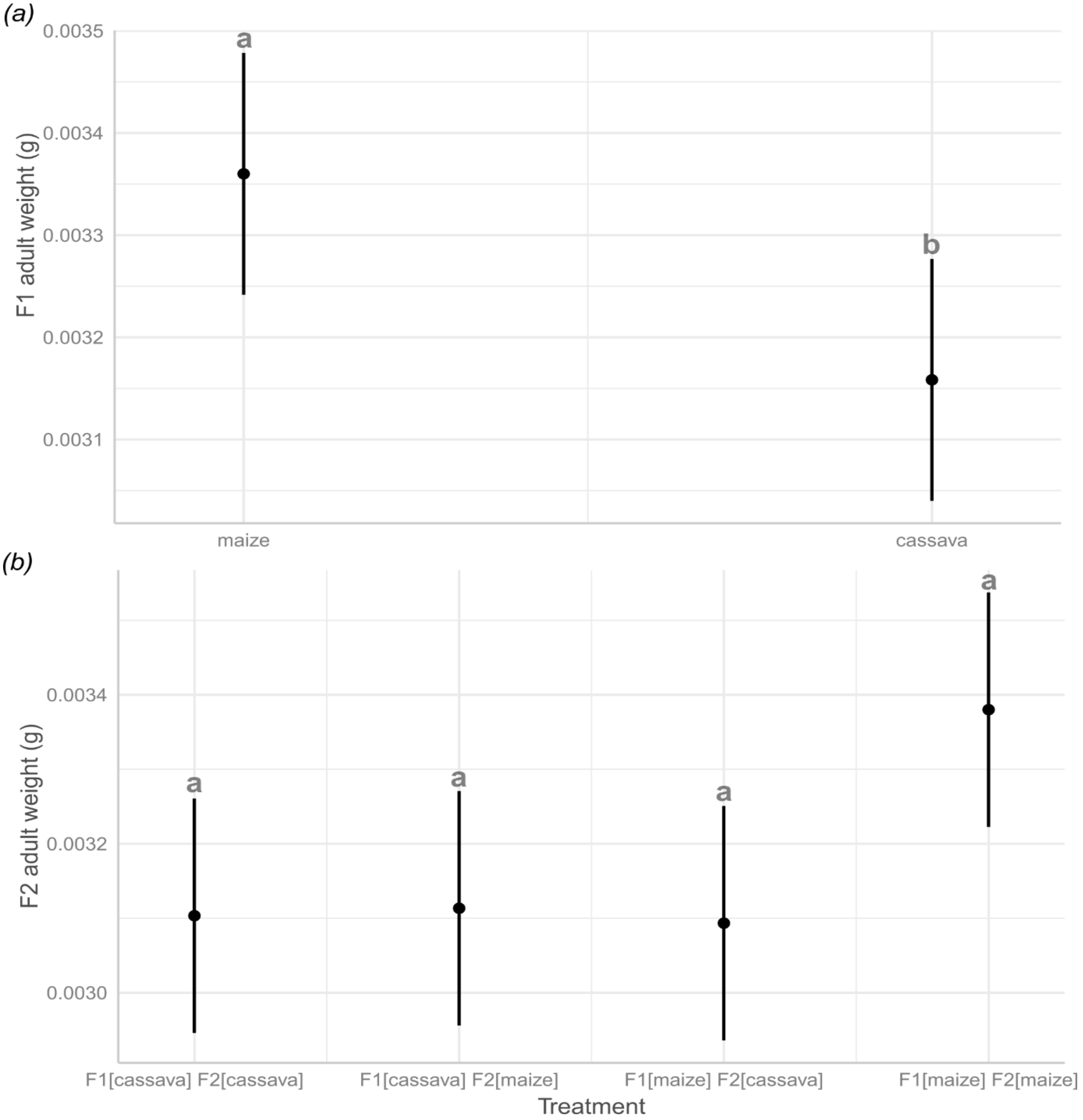

Figure 7. 5: Model outputs for adult weight of F_1 (a) and F_2 (b) *P. truncatus* towards various host plant resources across generations (n = 30). Means are shown alongside standard error. F_1 [cassava] F_2 [cassava] = F_1 progeny emerging from dried cassava host and then exposed to cassava again to produce the F_2 generation; F_1 [cassava] F2 [maize] = F_1 progeny emerging from dried cassava host and then exposed to maize host to produce F_2 generation; F_1 [maize] F_2 [cassava] = F_1 progeny emerging from dried maize grain host and then exposed to cassava host to produce F_2 generation; and F_1 [maize] F_2 [maize] = F_1 progeny emerging from dried maize grain host and then exposed to maize host again to produce the F_2 generation.

Progeny production differed significantly among cross-generational host exposures ($F_{3,\ 8}$ = 12.190, p = 0.002), with significantly more progeny (averaging 125) produced in maize-maize compared to all other groups which averaged between 25 and 75 progenies (Fig. 7.6a).

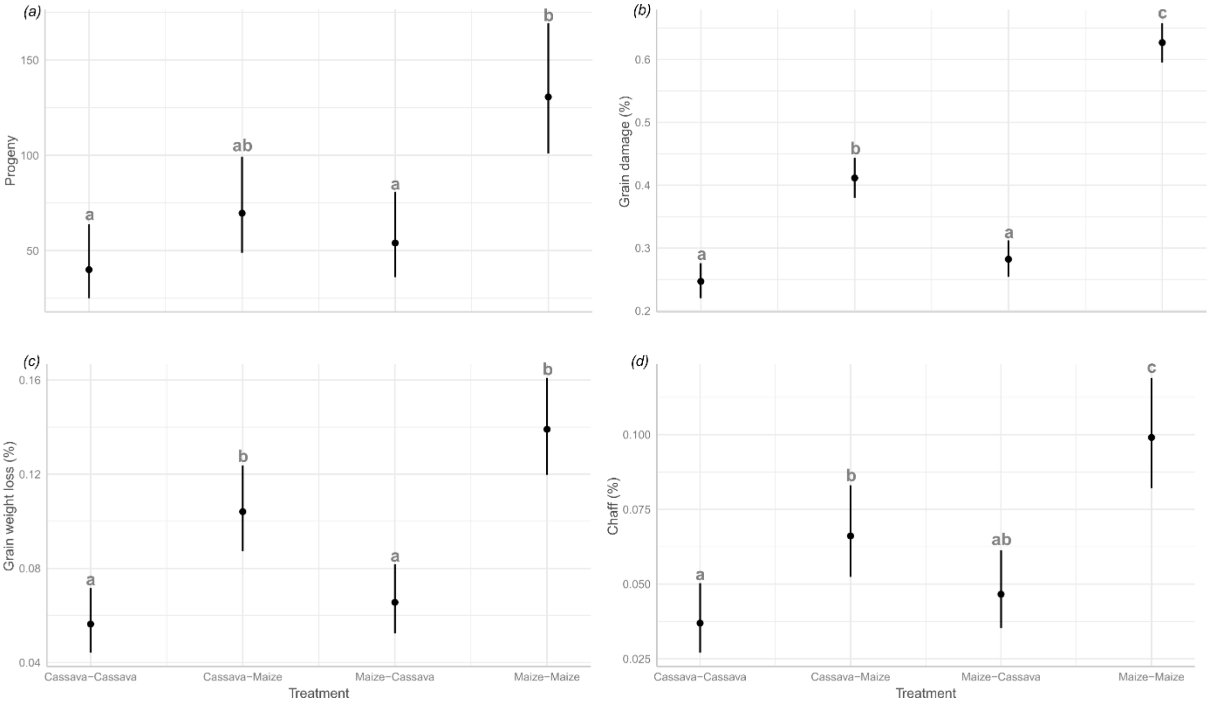

Figure 7. 6: Model outputs for (**A**) numbers of progeny produced, (**B**) grain damage, (**C**) grain weight loss and (**D**) grain chaff percentage recorded for *P. truncatus* following exposure to different host combinations (n = 3). F_1 [cassava] F_2 [cassava] = F_1 progeny emerging from dried cassava host and then exposed to cassava again to produce the F_2 generation, F_1 [cassava] F_2 [maize] = F_1 progeny emerging from dried cassava host and then exposed to maize host to produce F_2 generation, F_1 [maize] F_2 [cassava] = F_1 progeny emerging from dried maize grain host and then exposed to cassava host to produce F_2 generation, F_1 [maize] F_1 [maize] = F_1 progeny emerging from dried maize grain host and then exposed to maize host again to produce F_2 generation.

Grain damage differed significantly among treatments (χ^2 = 40.387, p < 0.001) (Figure 7.6b), with *P. truncatus* exposed to maize-maize causing significantly the highest grain damage (p < 0.001) above 60% followed by cassava-maize (p < 0.001) with 40%, while maize-cassava and cassava-cassava were similar (p = 0.316) with damage levels below 30%. Grain weight loss also differed significantly among groups ($\chi^2 = 20.639$, $p < 0.001$), with maize-maize and cassava-maize significantly higher (with losses averaging between 10 and 15%) than maize-cassava and cassava-cassava ($p < 0.01$; Fig. 7.6c) with < 8% weight losses. Chaff production was also significantly affected by treatment ($\chi^2 = 16.823$, $p < 0.001$), with maize-maize significantly highest overall ($p < 0.05$) with 10% average chaff %, cassava-maize higher than cassava-cassava ($p < 0.05$), and the two other groups more similar ($p > 0.05$; Fig 7.6d) with < 5% chaff.

7.5. Discussion

Parental environmental history can provide some cues that influence progeny development and fitness. As such, parental environmental experiences may have both costs and benefits to offspring fitness (Uller et al. 2013; Koch and Meunier, 2014; Lord et al. 2021; Lampasona et al. 2022). Recent empirical evidence suggest that maternal effects often facilitate transgenerational phenotypic plasticity - a mechanism in which the mother's environmental experiences shape the phenotypes of their offspring (Mousseau, 1991; Sgrò et al. 2016; Lord et al. 2021). Further, in oviparous insects, females lay eggs which hatch into progeny on maternally chosen hosts. Such maternal decisions influence progeny knowledge and choices of suitable and alternate hosts as well as oviposition sites in the environment (Slater et al. 2019). Here, the study showed (i) that *P. truncatus* feeding rates vary with temperature, consumer and host plant (maize and cassava) density; (ii) the suitable host for *P. truncatus* oviposition and (iii) how maternal experience shapes progeny physiological and ecological fitness. The results showed that *P. truncatus* maize feeding rates generally declined as host density and temperature increased. On cassava, feeding rates were influenced by a significant three-way interaction among population density, host density and temperature. As reported by Bell and Watters (1982), temperature and food density (among other factors) influence *P. truncatus* oviposition and progeny production, thus affecting feeding rates on maize. Feeding rates were higher at 29℃ and declined at 32℃ going to 35℃. This is likely a result of the trade-off between these two traits. For example, maintaining the beneficial change in heat tolerance at these stressful temperatures may come at the detrimental change in feeding trait (cost) (Stearns, 1989; Zera and Harshman, 2001); suggesting a negative association between heat tolerance and feeding in *P. truncatus*. This result concurs with observations by Papadimitriou et al. (2024) that temperatures between 25 and 32℃ produce the highest feeding rates (grain damage) partly due to high progeny production which contributed to increased damage at the prescribed conditions. In response to stressful high temperatures, ectotherms usually lower their feeding rates to conserve energy by reducing metabolism (Bubliy and Loeschcke, 2005); which is consistent with reduced grain damage at higher temperatures observed in the current study. Although feeding and the resultant damage occurred at higher temperatures (35 and 38°C), population growth rates and progeny were limited (Papadimitriou et al. 2024). According to Fields (1992), development in storage insect pests stops at ≥35°C in response to heat stress, desiccation and moisture depletion in the food. Feeding rates on maize were not affected by the initial density of *P. truncatus*. This observation demonstrates that a small colony of *P. truncatus* has the same potential as a large colony to build up large populations in a short space of time causing elevated damage given a favourable host and temperature conditions (Scholz et al. 1997; Hodges et al. 1998). This is also because the pest is known to exist in high densities in maize kernels and this increases the damage (Sakka and Athanassiou, 2018; Baliota et al. 2022).

We observed higher feeding rates on cassava relative to maize at matched host densities. This may be due to the greater palatability of cassava compared to maize based on texture. Reports show ranges of 30-40 and 50-70% maize and cassava losses, respectively; for the same storage duration (Harman et al. 2024) suggesting a preference of the pest for cassava. Similar observations have been reported by Sadiku et al. (2019) who showed higher pest damage, weight loss, feeding dust and *P. truncatus* progeny in cassava relative to maize, and wood, (e.g., *Albizzia glaberrima*, *Gmelina arborea* and *Tectona grandis*). Farm losses in mixed cropping systems where farmers produce both maize and cassava will, therefore, promote *P. truncatus* perpetuation and cross infestation between stores resulting in potentially huge farmer losses. Further, the high optimum developmental temperatures for *P. truncatus* at 32°C will not only increase its range expansion due to climate change resilience, but also enable its survival in previously unsuitable environments as average global temperatures increase (Arthur et al. 2019).

The host suitability for oviposition tests demonstrated that cassava and maize were the preferred suitable hosts for *P. truncatus* oviposition compared to sorghum and mopane wood. The oviposition habit of *P. truncatus* demands the appropriate selection of host in terms of size, shape, and hardness (Jie et al. 1998; Quellhorst et al. 2021). The natural size of stored cassava and maize grain give female beetles sufficient space to tunnel, oviposit and remain in a single grain or piece of cassava before moving on to other grains or cassava tuber (Jie et al. 1998). Various authors have shown that maize and cassava are the preferred hosts that support feeding, development and progeny production (Shires, 1980; Hodges, 1986; Sadiku et al. 2019; Quellhorst et al. 2021). In free choice test studies, Popoola (2018) showed that cassava and maize were the most preferred hosts, in consonance with the current study. Female *P. truncatus* beetles lay more eggs in response to the quality and quantity of host available (Hodges, 1986). In the current study, there were no significant differences in progeny produced on maize and on cassava although Nyakunga (1982) and Jin et al. (1998) observed that oviposition and progeny production was higher on maize than cassava. Other hosts such as sorghum grain and mopane wood have been reported as potential alternative hosts and reservoirs of *P. truncatus* propagules, although support for progeny production is limited (Nang'ayo et al. 2002; Mailafiya et al. 2007; Osipitan et al. 2012; Muatinte et al. 2014; Muatinte and Van den Berg, 2019). On sorghum for example, Mailafiya et al. (2007) reported few progenies between 1 and 13 from an initial population of 100 unsexed beetles. The small structural size of sorghum grain has insufficient tunnelling depth due to small kernel size and thus may affect its suitability as a *P. truncatus* host (Mailafiya et al. 2007). Similarly, Athanassiou et al. (2017) reported that development of *P. truncatus* on non-host grains was marginal to negligible. However, Muatinte and Van den Berg (2019) reported a total of 144 progenies on a naturally infested firewood piece of mopane.

The role of parental experience in determining the subsequent success of stored-grain pests through adaptation to heterogeneous environments, e.g., new hosts and temperature conditions have received little attention in literature. Scant evidence exists showing that the ability of females to adjust their egg number and size in relation to host quality may explain their success across different environments (Jin et al. 1998; Awmack and Leather, 2002). Furthermore, when faced with resource limitation, females can switch hosts and facilitate their offspring fitness upon facing related stresses through transgenerational phenotypic plasticity (Harmon and Pfennig, 2021). Indeed, our maternal experience experiments showed that physiological fitness in *P. truncatus* progeny was significantly affected by maternal host choices. Consistent exposure to a host (either cassava-cassava or maize-maize) conferred significantly greater fitness through high heat tolerance measured as HKDT compared to mixed exposure combinations (maize-cassava,

cassava-maize). Indeed, feeding status is one of the factors affecting within-individual variability of physiological tolerance in insects (Bowler and Terblanche, 2008; Nyamukondiwa and Terblanche, 2009). Offspring fitness is usually higher when environments persist across generations due to adaptive matching of parental and offspring cues (Uller et al. 2013; English et al. 2016). Consequently, offspring produced by mothers on non-optimal hosts also exhibit poor fitness due to carry-over effects (Uller et al. 2013). Critical thermal maxima were, however, not significantly different across the treatments.

There are no previous studies which have determined effects of host on *P. truncatus* fitness or effects of host on fitness in storage insect pests across generations. However, the current results demonstrate that consistent exposure to either maize or cassava conferred higher heat tolerance as observed with higher HKDTs recorded for these treatments. Parental F_1 exposure to mopane wood failed to produce progeny. This may suggest that mopane tree, which is abundant in the natural habitat, may not be a very suitable host for the larger grain borer due to its hardness - and that its use as a host may be more of chance, or an alternative host when more optimal hosts are unavailable - and that this may come at a huge fitness and or survival cost, consistent with the current observation. As discussed by Nansen and Meikle (2002), the *P. truncatus* would seem to prefer soft, starchy wood compared to hard wood (further discussions in Nang'ayo et al. 1993; 2002).

Maize grain further aided highest ecological performance in *P. truncatus* as the highest F_1 and F_2 individual adult weights were recorded on maize-maize compared to maize-cassava, cassava-cassava and cassava-maize host exposure combinations. This result is not surprising as previous studies have shown similar trends. For example, although maize and cassava are both optimal hosts for *P. truncatus,* studies show higher body weight for larger grain borer feeding on maize relative to cassava (Jin et al. 1998). The reasons for this are unknown but could be due to poor nutrition and the sub-lethal toxic effects of cassava (Jin et al. 1998). Moreso, feeding consistently on maize host resulted in higher progeny and higher feeding rates, as evidenced by higher grain damage, grain weight loss and grain chaff percentage produced- suggesting that previous parental experience is key for offspring fitness in the same environment. This was followed by cassava-maize exposure combination while cassava-cassava exposure resulted in consistently the least ecological performance. According to Ashra and Nair (2022), insects show metabolic plasticity in their ecological responses to different hosts and thus drive adaptation to food hosts. Secondary metabolites such as antifeedants, oviposition deterrents, antinutritive and antidigestive compounds mediate plant defense against insect feeding and therefore reduces host preference while simultaneously conferring fitness costs in insects (War et al. 2020). In the current study, shifting from maize to cassava host or maintaining *P. truncatus* on cassava host was associated with low feeding and low progeny fitness costs, likely because of the low nutrition and sub-lethal toxins associated with the host (Jin et al. 1998). Insects may thus experience the ecological trade-offs associated with different diets across ontogeny, and therefore make ecological decisions for example being 'extremely specialized on a particular host' based on these past experiences (Fordyce, 2006; English et al. 2016). This underlines the importance of maternal choices in determining the fitness of filial generations in new or stressful environments (Papanikolaou et al. 2019).

Maternal flexibility in insects, e.g., altering reproductive traits to better cope with suboptimal environments (e.g., host quality and/or density and temperature) may facilitate offspring survival through transgenerational plasticity. The current study showed that (i) increased host density and temperatures interactions negatively affected consumer feeding; (ii) parental optimal host experiences conferred the highest physiological and ecological performance in *P. truncatus,* (iii) while host switching is possible, it negatively affected offspring physiological and ecological performance and (iv) although feeding was restricted at higher temperatures, consistency in maternal host preference among maize and cassava will increase fitness in *P. truncatus*, and as such maintaining its survival and spread under changing climate. This work is significant in explaining the role of maternal effects and plasticity in aiding adaptation to novel environments and may help explain invasive species success in new resource constrained environments and also assist in designing pest management programmes in specific habitats. While results for the current study showed compromised physiological and ecological performance under host plant switching treatments, future work should focus on repeated sub-optimal host exposure or preconditioning (e.g., going beyond F_2) on life history traits. As such, increasing the number of repeated generations may offer insights into *P. truncatus* adaptation to diverse hosts and likely more long-term effects to fitness and pest status.

7.6. References

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CHAPTER 8

Prostephanus truncatus outcompetes *Sitophilus zeamais* under varying temperatures and introduction order on stored maize grain[7].

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8.1. Introduction

Competition among coexisting organisms often influences their fitness, abundance, and diversity in nature (Reitz and Trumble, 2002; Kaplan and Denno, 2007). Two theories have been advanced to define competition - the neutral theory and the niche theory (Venner et al. 2011). The theories propose that resource competition is a result of niche overlap and a rise in population densities of coexisting organisms (Klomp, 1963; Venner et al. 2011; Bird et al. 2019). The effects of simultaneous infestation of grain by different insect pests needs an in-depth understanding as it can affect either the establishment of coexisting insects due to competition or exacerbate grain damage and losses due to additive damage (Athanassiou et al. 2017; Quellhorst et al. 2020). Resource competition is especially interesting when invasive species are involved because of their inherent adaptation to competition and efficient resource utilisation in a given niche; often resulting in suppression of endemic species (Kavallieratos et al. 2017; Song et al. 2021) and changes in local pest biodiversity dynamics (Venner et al. 2011). In a normal pest succession in storage systems, once primary pests inflict damage on whole grain, secondary pests find it easier to attack and additive damage often occurs resulting in higher losses (Trematerra et al. 2015). Primary pests are those that can inflict damage on whole grain whereas secondary pests infest already infested and/or damaged grain. Given this succession feeding behaviour, primary and secondary insect pests thus often elicit synergistic grain damage (Athanassiou et al. 2017). Interspecific interactions occur when primary insect pests share the same ecological niche (Vowotor et al. 2005). This type of interaction is important because the primary colonisers will be vying for the same "internal kernel part" for feeding and oviposition (Crombie, 1944; Sakka and Athanassiou, 2018; Ngom et al. 2020). Climate change has given rise to increased populations of insect pest species, coupled with reduced resources and this creates enormous pressure on food resources through competition. For grain, this co-infestation may have synergistic effects on grain damage (Arthur et al. 2019). As such, this has sparked increased interest in studying how these developments have amplified grain storage losses and shaped grain storage ecosystems (Quellhorst et al. 2020).

Maize and sorghum are some of the world's most important grains, particularly in sub-Saharan Africa (SSA), where they are grown primarily for food and secondarily for animal feed

(Tuinstra, 2008; Shiferaw et al. 2011; Akplo et al. 2023). However, stored maize and sorghum grains are often damaged by numerous insect pests that coexist in storage ecosystems. Depending on the fate of the interactions, this often results in huge qualitative and quantitative grain losses (World Bank et al. 2011; APHLIS, 2020). Insect pests of stored maize include primary colonisers such as the maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera; Curculionidae); the larger grain borer, *Prostephanus truncatus* Horn (Coleoptera: Bostrichidae); the lesser grain borer, *Rhyzopertha dominica* Fabricius (Coleoptera: Bostrichidae), the Angoumois grain moth, *Sitotroga cerealella* Olivier (Lepidoptera; Gelechiidae); the rice weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae) and secondary pests such as the rust-red flour beetle, *Tribolium castaneum* Herbst (Coleoptera; Tenebrionidae), rusty grain beetle, *Cryptolestes ferrugineus* Stephens (Coleoptera; Laemophloeidae), the saw-toothed grain beetle, *Oryzaephilus surinamensis* Linnaeus (Coleoptera; Silvanidae) and the confused flour beetle*, Tribolium confusum* Jacquelin du Val (Tenebrionidae; Coleoptera) (Haines, 1991; Mvumi et al. 2003; Stathers et al. 2013; Trematerra et al. 2015; USDA, 2016). Whilst most of these insect species are cosmopolitan, *P. truncatus* is an invasive alien species accidentally introduced in Africa from Central America through grain trade (Hodges et al. 1983; Addo et al. 2010). *Sitophilus zeamais* is globally cosmopolitan and was regarded as the most important pest of stored maize in Africa until the introduction of *P. truncatus* (Holst and Meikle, 2000). *Sitophilus zeamais* thrives best at 27°C and 40% RH (Quellhorst et al. 2020) and relatively higher grain moisture content from around 10.5% (Hodges et al. 1983). Humidity response trials conducted by Victor and Ojaruega, (1993) highlighted that *S. zeamais* favours low RH ranging from 30 to 50%. On the other hand, *P. truncatus* favours high temperatures around 32°C and 80% RH (Shires, 1979) and can thrive on grain with as little as 9% moisture content (Hodges et al. 1983) potentially aided by microbial gut symbionts. Empirical evidence suggest related grain storage beetles such as *R. dominica* and *O. surinamensis*, possess high desiccation tolerance attributed to microbial gut symbionts that confer ecological adaptation (Engl et al. 2018).

Sitophilus zeamais and *P. truncatus* both infest maize grain whilst in the fields at physiological maturity starting from moisture content of about 20% when they lay eggs on the cobs and the infestation will manifest with emergence and perpetuation of adult insects during grain storage (Stathers et al. 2013; Ngom et al. 2020). *Prostephanus truncatus* feeding is characterised by production of copious grain feeding dust and thus is often associated with *T. castaneum* which feeds on the flour dust produced (Nyabako et al. 2020; Shah et al. 2021). The female *P. truncatus* beetle chooses its oviposition sites carefully to prevent intra- and interspecific competition although high populations can build up on small quantities of grain affecting progeny production (Nansen and Meikle, 2002). In natural settings, male beetles release a pheromone to attract females when they encounter a suitable host and only stop this release when females arrive so as to limit intraspecific competition (Fadamiro et al. 1998). *Prostephanus truncatus* can burrow through hard material and prefers the bottom of grain stack for leverage (Nansen and Meikle, 2002). Nwosu et al. (2015) also noted that adult *S. zeamais* and *P. truncatus* favour large, flattened maize grains because they offer more room for better grain perforation.

As temperatures rise due to climate change, it is critical to assess the status of significant pests of stored maize such as *S. zeamais* and *P. truncatus*. A recent review reported that *S. zeamais* can outcompete *P. truncatus* at 25°C, but the latter is superior in terms of population growth rates at 30 and 35°C (Quellhorst et al. 2020). Previous studies on the interaction of these two species following simultaneous introduction in varying proportions at 30°C and 70% RH were inconclusive as both populations exhibited similar convex curves associated with increased reproduction (Giga and Canhao, 1993). Given *P. truncatus*'s optimum developmental temperature of 32°C and 80% RH (Shires, 1979) and high thermal tolerance (Machekano et al. 2020; Mutamiswa et al. 2021), it is not surprising that it outcompetes *S. zeamais* at higher temperatures. According to Baliota et al. (2022), *P. truncatus* faces relatively low competition costs despite colonizing environments already occupied by other storage pests due to its invasive nature. As the geographical range of *P. truncatus* continues to expand due to climate change, the pest is likely to become problematic even in previously unsuitable environments (Arthur et al. 2019). The gradual advance in climate change effects will give rise to the emergence of "winners of climate change" being those insects that can adjust, adapt, and compete at more stressful thermal and resource-limited environments and "losers of climate change" being those whose populations will be negatively affected by these factors (Jackson et al. 2022). Insects as ectotherms are of particular interest in this context as their body temperature closely tracks ambient temperatures and are thus negatively affected by stressful sub-optimal temperatures

(Chown and Nicolson, 2004; Roeder et al. 2021; Lamarre et al. 2022). Simultaneously, their resource utilisation and functional responses are largely a function of temperature and metabolic rates (Archer et al. 2019; Uiterwaal and Delong, 2020) and increasing RH improves species performance at high temperatures (Papanikolaou et al. 2018). The current study therefore sought to evaluate intra- and interspecific competition between *S. zeamais* and *P. truncatus* using simultaneous and delayed introduction scenarios on stored maize over a range of temperatures from 25 to 35°C at constant RH in replacement series designed to elucidate the effects of population density on competition. Specifically, to test whether: (1) temperature and population density have an effect on progeny production of coexisting populations of *S. zeamais* and *P. truncatus*, (2) grain damage, grain weight losses, insect feeding dust and beetle boring holes increase with increased population densities of *S. zeamais* and *P. truncatus* at higher temperatures, and (3) the establishment dynamics of coexisting species when one of the beetles arrived earlier than the other on grain. It was hypothesised that (i) *P. truncatus* will outcompete *S. zeamais* with increase in temperature and population density, (ii) grain damage will increase with increasing parental densities and (iii) beetles that arrive on grain first have a niche occupation and an establishment advantage. Such information is important in unravelling the fate of competing conspecifics and sympatric heterospecifics infesting grain under changing and stressful climate and food resource environments.

8.2. Materials and methods

8.2.1. Collection and rearing of insects.

Colonies of *P. truncatus* and *S. zeamais* were reared separately in climate chambers (HPP 260, Memmert GmbH + Co.KG, Germany). The *P. truncatus* specimens were obtained from the Botswana Ministry of Lands and Agriculture in Gaborone having been trapped from surrounding areas (24°35′01′′S; 25°56′49′′E). A colony of *S. zeamais* that had been kept in the Eco-physiological entomology laboratory at Botswana International University of Science and Technology was used. The outbred colony has been maintained on shelled maize for over 10 generations with regular supplementation of naturally collected specimens to increase genetic diversity. *Sitophilus zeamais* was reared on shelled maize grain (variety SeedCo 608) at 27°C; 65% RH whilst *P. truncatus* was reared on cobbed yellow maize (variety SeedCo 608) at 32°C; 80% RH. The photoperiod was set at 12L: 12D for all the insects.

8.2.2. Experimental set-up

Two experiments on competition between *S. zeamais* and *P. truncatus* were conducted separately using dried yellow maize grain (variety SeedCo 608) at 25, 30 and 35°C at a constant RH of 65%. In Experiment 1, species were introduced simultaneously whilst in Experiment 2, one species was introduced first and the other species was introduced 10 days later. Woven polypropylene mini-bags (20 cm high x 5 cm wide) specially designed to resemble storage bags used by farmers were employed. First, dried grain was sterilised by freezing at minus 20°C for 14 days and then loaded into the woven polypropylene mini-bags up to the 15 cm mark leaving 5 cm of free space at the top. The average mass of grain in each mini-bag was 65 ± 5g which was approximately 200 grains. The loaded mini-bags were left to acclimatise to experimental temperatures in a climate chamber for one week. Grain moisture content measured after acclimatisation was 12.4% (Unimeter digital grain moisture meter, Agri-Enviro Solutions, South Africa). Proportions of unsexed 7- 14 days old *S. zeamais* and *P. truncatus* adults were then added to each treatment as shown in Table 1 (Intra- and interspecific competition following simultaneous introduction of species) and Table 2 (Interspecific competition following delayed introduction of one species) at constant total parental densities of 20, 40 and 80 adult insects as modified from Giga and Canhao (1993). The polypropylene mini-bags were sealed by folding the top and punching with staple pins. The bags were packed in vertical order in a transparent 4 L plastic container (34 cm x 42 cm x 10 cm: length, width and height) and placed in climate chambers.

8.2.2.1. Experiment 1: Simultaneous introduction of adult insect species

Nine treatments, each replicated three times, were evaluated (Table 8.1). Treatments 1–3 represent *P. truncatus* intraspecific competition, 4–6 represent interspecific competition whilst treatments 7–9 represent *S. zeamais* intraspecific competition at 20, 40 and 80 total parental densities.

Table 8. 1: Treatments evaluated to determine intra- and interspecific competition between *S. zeamais* and *P. truncatus* following simultaneous introduction of adult species.

Treatment	Total insect density per 65 ± 5 g of grain	Treatment description	Type of competition
1. Pt[20]	20	Twenty *P. truncatus*	
2. Pt[40]	40	Forty *P. truncatus*	Intraspecific
3. Pt[80]	80	Eighty *P. truncatus*	
4. Pt[10] + Sz[10]	20	Ten *P. truncatus* + ten *S. zeamais* introduced simultaneously	
5. Pt[20] + Sz[20]	40	Twenty *P. truncatus* + twenty *S. zeamais* introduced simultaneously	Interspecific
6. Pt[40] + Sz[40]	80	Forty *P. truncatus* + forty *S. zeamais* introduced simultaneously	
7. Sz[20]	20	Twenty *S. zeamais*	
8. Sz[40]	40	Forty *S. zeamais*	Intraspecific
9. Sz[80]	80	Eight *S. zeamais*	

Note: Population density of 20 was regarded as low, 40 as medium and 80 as high density.

8.2.2.2. Experiment 2: Delayed introduction of one of the 2 insect species

The experiment determines the effect of an insect's first arrival on grain on the outcome of competition (Baliota et al. 2022). Six treatments, each replicated three times, were evaluated (Table 8.2). In treatment 1–3, proportions of *S. zeamais* were introduced first then equal proportions of *P. truncatus* were introduced 10 days later and the reverse was done for treatment 4-6.

The two experiments were allowed to run for 65 days (as in Quellhorst et al. 2020; Baliota et al. 2022; Emre et al. 2023) without interruption after which grain from each treatment was sieved through 1 mm and 2 mm nested test sieves (Endecotts Ltd, England) to separate insects and chaff from grain. The 65 days window was sufficient to give at least one generation for each of the test species; allowing all eggs to hatch; simultaneously avoiding overlap with emergence of F_2 generation given the developmental times (under the chosen temperatures) of the two species (Shires, 1980; Danho et al. 2002; Masasa et al. 2013).

Table 8. 2: Treatments evaluated to determine interspecific competition between *S. zeamais* and *P. truncatus* following staggered introduction of species.

Treatment	**Total insect density per 65 ± 5g of grain**	**Treatment description**
1. [10]Sz^{1st} [10]Pt^{2nd}	20	Ten *S. zeamais* introduced first + ten *P. truncatus* introduced 10 days later
2. [20]Sz^{1st} [20]Pt^{2nd}	40	Twenty *S. zeamais* introduced first + twenty *P. truncatus* introduced 10 days later
3. [40]Sz^{1st} [40]Pt^{2nd}	80	Forty *S. zeamais* introduced first + forty *P. truncatus* introduced 10 days later
4. [10]Pt^{1st} [10]Sz^{2nd}	20	Ten *P. truncatus* introduced first + ten *S. zeamais* introduced 10 days later
5. [20]Pt^{1st} [20]Sz^{2nd}	40	Twenty *P. truncatus* introduced first + twenty *S. zeamais* introduced 10 days later
6. [40]Pt^{1st} [40]Sz^{2nd}	80	Forty *P. truncatus* introduced first + forty *S. zeamais* introduced 10 days later

Note: Population density of 20 was regarded as low, 40 as medium and 80 as high density.

8.2.3. Data collection

At the end of 65 days, data on number of progenies, insect grain damage, grain weight loss, insect feeding dust and number of beetle boring holes were collected. The total number of adult insects, both live and dead was recorded and used to determine the number of progenies. Number of damaged and undamaged grains as well as their respective weights was also recorded. The data were used to calculate grain damage and grain weight loss as per the count and weigh method (Boxall, 2002). Beetle boring holes which could be seen on the surface of polypropylene bags were counted and recorded at the end of the storage period. These holes are produced by the habitual boring and feeding characteristic of *P. truncatus* but can also be an indicator of beetles dispersing from storage bags in search of more food resources (Hodges, 2002). Data were tested for normality and homogeneity before analysis. Conforming data were analysed using a factorial design with treatment and temperature as independent variables. All data were analysed using analysis of variance in Statistica 13 (Demidova et al. 2016).

8.3. Results

8.3.1. Competition following simultaneous introduction of *S. zeamais* and *P. truncatus*.

8.3.1.1. Number of progenies

The number of progenies were significantly influenced by treatment ($F_{8,\,54} = 12.254$; $p < 0.001$), temperature ($F_{2,\,54} = 27.234$; $p < 0.001$) and treatment × temperature ($F_{16,\,54} = 2.6923$; $p = 0.003$) interactions. First, progenies for both species were high in intraspecific treatments compared to interspecific treatments highlighting the effects of niche competition for progeny production. Progenies were suppressed in all treatments at 35°C. However, at 25°C and 30°C, *P. truncatus* produced significantly higher progeny in interspecific interactions, (30 at 25°C, 40 at 30°C) compared to *S. zeamais* (3 at 25°C, 3 at 30°C) (Fig. 8.1).

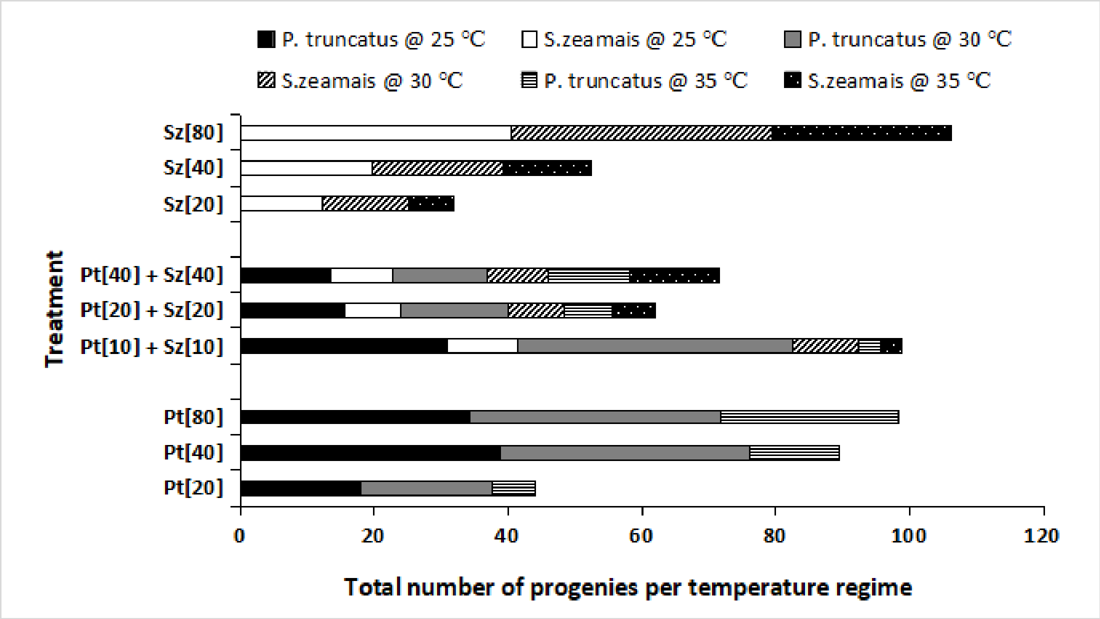

Figure 8. 1: *Sitophilus zeamais* and *Prostephanus truncatus* progenies recorded after 65 days of grain storage at 25, 30 and 35 °C at 65 % RH following simultaneous introduction of species (n = 3). Pt[20] = 20 *P. truncatus* in intraspecific competition, Pt[40] = 40 *P. truncatus* in intraspecific competition, Pt[80] = 80 *P. truncatus* in intraspecific competition, Sz[10] + Pt[10] = 10 *S. zeamais* + 10 *P. truncatus* in interspecific competition, Sz[20] + Pt[20] = 20 *S. zeamais* + 20 *P. truncatus* in interspecific competition, Sz[40] + Pt[40] = 40 *S. zeamais* + 40 *P. truncatus* in interspecific competition, Sz[20] = 20 *S. zeamais* in intraspecific competition, Sz[40] = 40 *S. zeamais* in intraspecific competition, Sz[80] = 80 *S. zeamais* in intraspecific competition.

8.3.1.2. Insect grain damage

Insect grain damage was significantly affected by a three way interaction between treatment, temperature and treatment × temperature interaction. Treatments recorded significantly different grain damage levels ($F_{8, 54} = 140.19$; $p < 0.001$). In intraspecific treatments, *P. truncatus* caused significantly higher levels of grain damage (50–85% at 25°C, 55–80% at 30°C and 25–60% at 35°C) compared to *S. zeamais* (20–40% at 25°C, 17–30 % at 30°C and 15–25% at 35°C) at similar insect densities especially at the highest population density of 80 (Fig. 8.2). Grain damage levels of interspecific treatments were not significantly different from those of *P. truncatus* intraspecific treatments although they were significantly higher than those for *S. zeamais* intraspecific treatments. Overall, grain damage was significantly higher in *P. truncatus* intra- (25–85%) and interspecific competition (22–85%) with *S. zeamais* treatments. Furthermore, temperature had significant effects ($F_{2, 54} = 166.31$; $p < 0.001$) on grain damage. Higher levels of grain damage up to 85% were recorded at 25 and 30°C compared to the maximum of approximately 60% damage at 35°C. Treatment × temperature interaction ($F_{16, 54} = 7.1275$; $p < 0.001$) also significantly influenced grain damage.

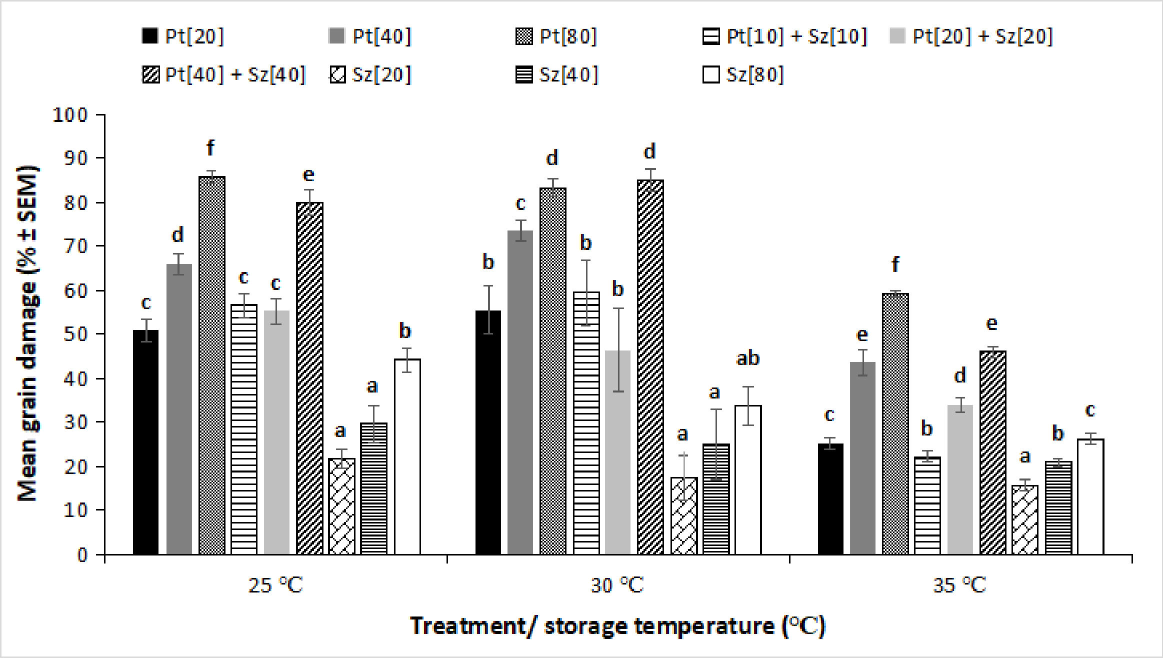

Figure 8. 2: Mean insect grain damage (% ± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following simultaneous introduction of species (n= 3). Pt[20] = 20 *P. truncatus* in intraspecific competition, Pt[40] = 40 *P. truncatus* in intraspecific competition, Pt[80] = 80 *P. truncatus* in intraspecific competition, Pt[10] + Sz[10] = 10 *S. zeamais* + 10 *P. truncatus* in interspecific competition, Pt[20] + Sz[20] = 20 *S. zeamais* + 20 *P. truncatus* in interspecific competition, Pt[40] + Sz[40] = 40 *S. zeamais* + 40 *P. truncatus* in interspecific competition, Sz[20] = 20 *S. zeamais* in intraspecific competition, Sz[40] = 40 *S. zeamais* in intraspecific competition, Sz[80] = 80 *S. zeamais* in intraspecific competition.

8.3.1.3. Grain weight loss

Grain weight loss differed significantly between treatments due to treatment effects, temperature effects and interaction between treatment effects and temperature effects. First, treatment effects caused significant differences ($F_{8,\ 54} = 142.47$; $p < 0.001$) in grain weight loss. Grain weight losses were higher in *P. truncatus* intraspecific and interspecific competition at 25 and 30°C compared to *S. zeamais* intraspecific competition treatments especially at highest population density. The *S. zeamais* intraspecific competition treatments recorded weight losses below 15% across all treatments and storage temperatures whereas losses as high as 50% were recorded in *P.*

truncatus intra and interspecific competition treatments (Fig. 8.3). Temperature effects significantly affected grain weight loss ($F_{2, 54} = 229.91$; $p < 0.001$) as losses were greatly suppressed at 35°C in all treatments. Treatment × temperature interactions further significantly ($F_{16, 54} = 16.905$; $p < 0.001$) affected grain weight loss.

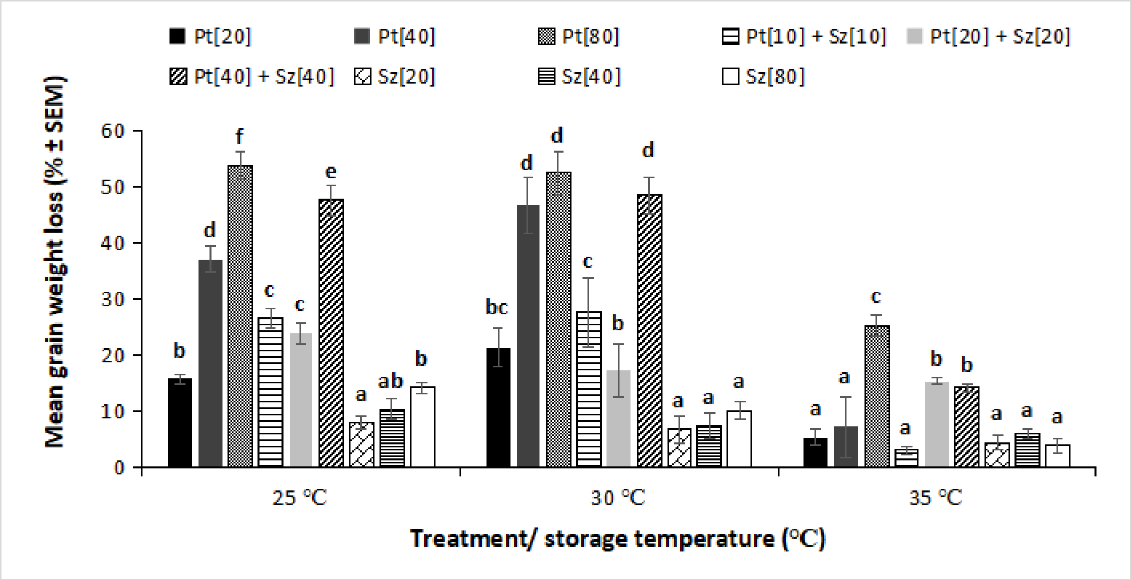

Figure 8. 3: Mean grain weight loss (% ± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following simultaneous introduction of species (n= 3). Pt[20] = 20 *P. truncatus* in intraspecific competition, Pt[40] = 40 *P. truncatus* in intraspecific competition, Pt[80] = 80 *P. truncatus* in intraspecific competition, Pt[10] + Sz[10] = 10 *S. zeamais* + 10 *P. truncatus* in interspecific competition, Pt[20] + Sz[20] = 20 *S. zeamais* + 20 *P. truncatus* in interspecific competition, Pt[40] + Sz[40] = 40 *S. zeamais* + 40 *P. truncatus* in interspecific competition, Sz[20] = 20 *S. zeamais* in intraspecific competition, Sz[40] = 40 *S. zeamais* in intraspecific competition, Sz[80] = 80 *S. zeamais* in intraspecific competition.

8.3.1.4. Insect feeding dust

Production of insect feeding dust was significantly affected by treatment ($F_{8, 54} = 150.73$; $p < 0.001$), temperature ($F_{2, 54} = 215.49$; $p < 0.001$) and treatment × temperature ($F_{16, 54} = 24.856$; $p < 0.001$) interactions. Whilst insect feeding dust was greatly suppressed below 10 % in all treatments at 35°C, dust was significantly higher in *P. truncatus* intraspecific (8–35%) and interspecific interactions with *S. zeamais* (8–26%) at 25 and 30°C compared to treatments for *S. zeamais* intraspecific competition (2–4%) (Fig. 8.4).

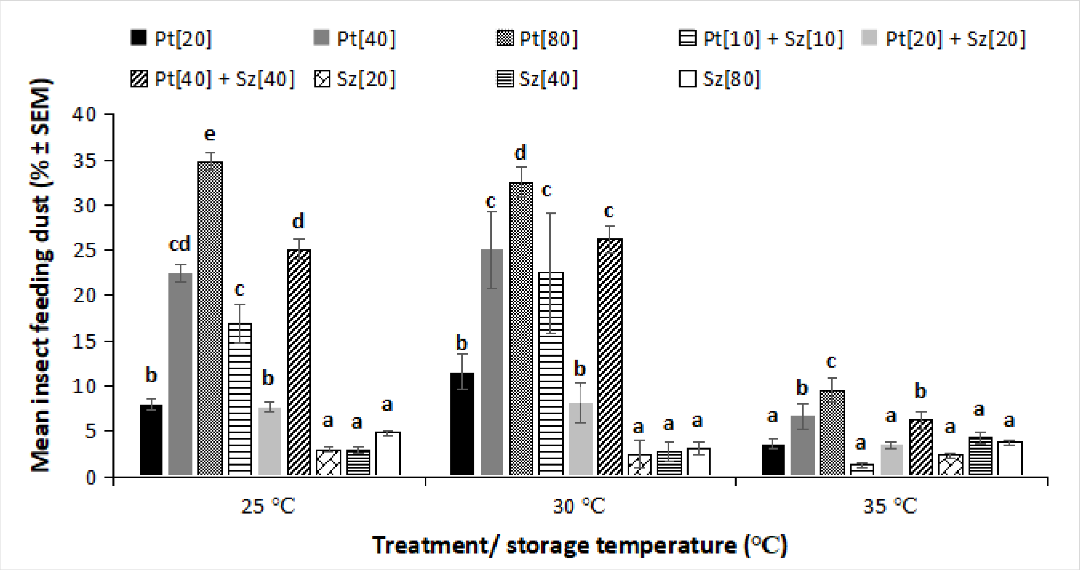

Figure 8. 4: Mean insect feeding dust (% ± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following simultaneous introduction of species (n= 3). Pt[20] = 20 *P. truncatus* in intraspecific competition, Pt[40] = 40 *P. truncatus* in intraspecific competition, Pt[80] = 80 *P. truncatus* in intraspecific competition, Pt[10] + Sz[10] = 10 *S. zeamais* + 10 *P. truncatus* in interspecific competition, Pt[20] + Sz[20] = 20 *S. zeamais* + 20 *P. truncatus* in interspecific competition, Pt[40] + Sz[40] = 40 *S. zeamais* + 40 *P. truncatus* in interspecific competition, Sz[20] = 20 *S. zeamais* in intraspecific competition, Sz[40] = 40 *S. zeamais* in intraspecific competition, Sz[80] = 80 *S. zeamais* in intraspecific competition.

8.3.1.5 Beetle boring feeding holes

Beetle boring feeding holes were significantly influenced by treatment ($F_{8,\ 54} = 58.539$; $p < 0.001$), temperature ($F_{2,\ 54} = 122.08$; $p < 0.001$) and treatment × temperature ($F_{16,\ 54} = 15.237$; $p < 0.001$) interactions. Boring was only observed at 25 and 30°C and the highest boring activity (40–60 holes) was observed in *P. truncatus* intraspecific interactions at the highest insect density of 80 (Pt[80]) (Fig. 8.5). *Sitophilus zeamais* intraspecific treatments recorded significantly low number of feeding holes (below 10) compared to *P. truncatus* intra and interspecific competition treatments (above 10) at 25 and 30°C. The highest parental density of *S. zeamais* intraspecific interaction (Sz[80]) even recorded significantly lower number of feeding holes (< 5 holes) compared to the lowest parent density of *P. truncatus* (Pt[20] = > 10 holes) at both 25 and 30°C.

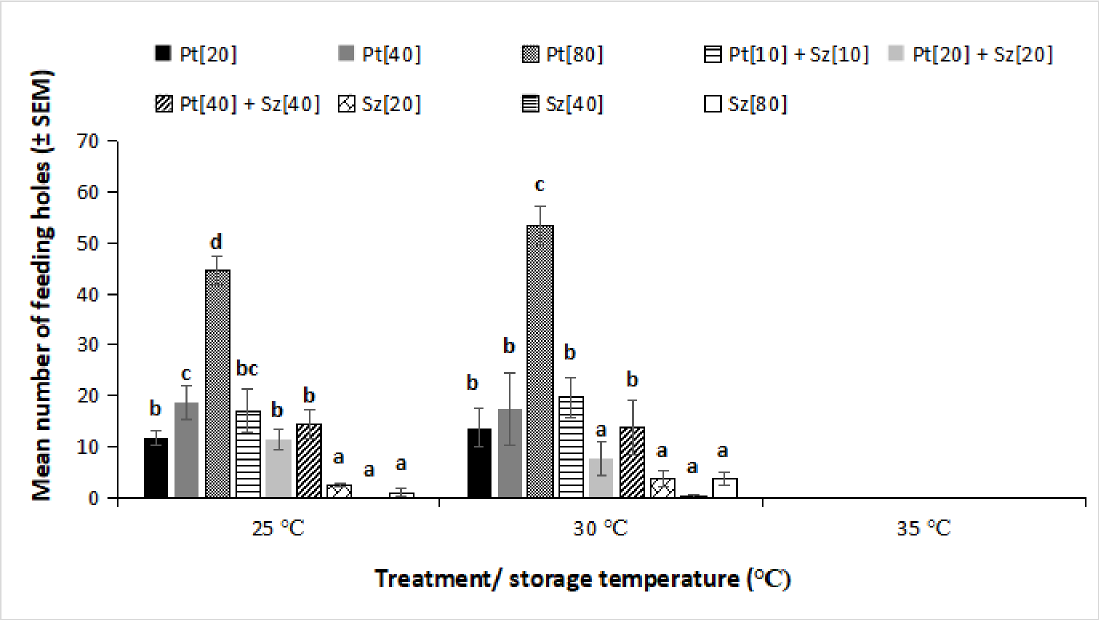

Figure 8. 5: Mean number of beetle feeding holes (± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following simultaneous introduction of species (n= 3). No feeding holes were recorded at 35°C. Pt[20] = 20 *P. truncatus* in intraspecific competition, Pt[40] = 40 *P. truncatus* in intraspecific competition, Pt[80] = 80 *P. truncatus* in intraspecific competition, Pt[10] + Sz[10] = 10 *S. zeamais* + 10 *P. truncatus* in interspecific competition, Pt[20] + Sz[20] = 20 *S. zeamais* + 20 *P. truncatus* in interspecific competition, Pt[40] + Sz[40] = 40 *S. zeamais* + 40 *P. truncatus* in interspecific competition, Sz[20] = 20 *S. zeamais* in intraspecific competition, Sz[40] = 40 *S. zeamais* in intraspecific competition, Sz[80] = 80 *S. zeamais* in intraspecific competition.

8.3.2. Competition following delayed introduction of one of the insect species

8.3.2.1. Number of progenies

Progeny production was significantly influenced by treatment ($F_{5,\ 36} = 248.75$; $p < 0.001$), temperature ($F_{2,\ 36} = 72.494$; $p < 0.001$) and treatment × temperature ($F_{10,\ 36} = 7.4689$; $p < 0.001$) interactions. Progeny production was highly suppressed at the lowest (20) population density in both introduction scenarios. Furthermore, number of progenies was restricted at 35°C (Fig 8.6).

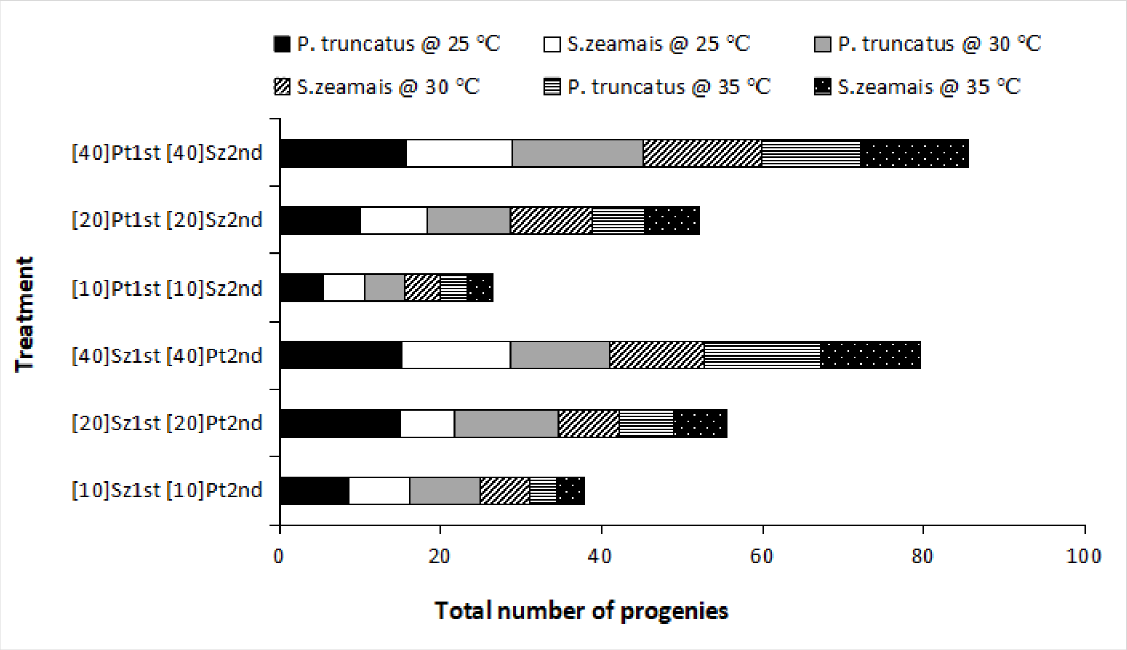

Figure 8. 6: Mean *Sitophilus zeamais* and *Prostephanus truncatus* progenies recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following delayed introduction of one species (n= 3). [10]Sz 1st [10]Pt 2nd = 10 *S. zeamais* introduced first and 10 *P. truncatus* introduced 10 days later, [20]Sz 1st [20]Pt 2nd = 20 *S. zeamais* introduced first then 20 *P. truncatus* introduced 10 days later, [40]Sz 1st [40]Pt 2nd = 40 *S. zeamais* introduced first then 40 *P. truncatus* introduced 10 days later, [10]Pt 1st [10]Sz 2nd = 10 *P. truncatus* introduced first then 10 *S. zeamais* introduced 10 days later, [20]Pt 1st [20] Sz 2nd = 20 *P. truncatus* introduced first then 20 *S. zeamais* introduced 10 days later, [40]Pt 1st [40]Sz 2nd = 40 *P. truncatus* introduced first then 40 *S. zeamais* introduced 10 days later.

8.3.2.2. Grain damage

Grain damage was influenced by significant 3-way interaction between treatments ($F_{5, 36}$ = 971.32; $p < 0.001$), temperature ($F_{2, 36}$ = 1603.0; $p < 0.001$) and treatment × temperature ($F_{10, 36}$ = 74.711, $p < 0.001$) interactions. First, grain damage increased with increasing parent density from low (20) to medium (40) density at 25 and 30°C. However, further increasing insect species density from 40 to 80 did not result in increased damage in both scenarios where either *S. zeamais* or *P. truncatus* was introduced first. Notably, grain damage was significantly low when *P. truncatus* was introduced first ([10]Pt 1st [10]Sz 2nd) compared to when *S. zeamais* was introduced first ([10]Sz 1st [10]Pt 2nd) across all storage temperatures for the lowest population density. Damage was suppressed at 35°C in all treatments (Fig. 8.7).

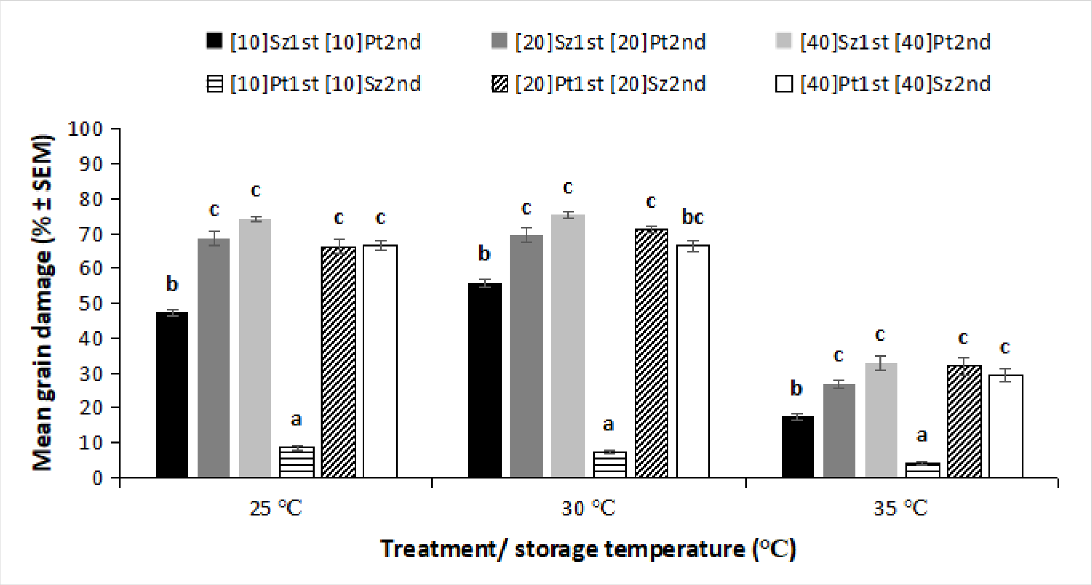

Figure 8. 7: Mean insect grain damage (% ± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following delayed introduction of one species (n= 3). [10]Sz 1st [10]Pt 2nd = 10 *S. zeamais* introduced first and 10 *P. truncatus* introduced 10 days later, [20]Sz 1st [20]Pt 2nd = 20 *S. zeamais* introduced first then 20 *P. truncatus* introduced 10 days later, [40]Sz 1st [40]Pt 2nd = 40 *S. zeamais* introduced first then 40 *P. truncatus* introduced 10 days later, [10]Pt 1st [10]Sz 2nd = 10 *P. truncatus* introduced first then 10 *S. zeamais* introduced 10 days later, [20]Pt 1st [20] Sz 2nd = 20 *P. truncatus* introduced first then 20 *S. zeamais* introduced 10 days later, [40]Pt 1st [40]Sz 2nd = 40 *P. truncatus* introduced first then 40 *S. zeamais* introduced 10 days later.

8.3.2.3. Grain weight loss

Grain weight loss followed a similar trend to grain damage. Losses were significantly different between treatments owing to interactions between treatment × temperature ($F_{10, 36} = 166.52$; $p < 0.001$). Grain weight loss was also significantly influenced by temperature ($F_{2, 36} = 314.22$; $p < 0.001$); whereas losses were high at 25 and 30°C (up to 40% at medium and high parent densities) they were significantly suppressed below 12% at 35°C in all treatments. Further, treatment effects significantly ($F_{2, 36} = 314.22$; $p < 0.001$) affected grain weight losses; whereby losses were equally highest at medium (40) and high (80) parent densities (36-40%) compared to 3–20% for lowest (20) insect densities ([10]Sz 1st [10]Pt 2nd and [10]Pt 1st [10]Sz 2nd). Grain weight losses were suppressed below 15% in all treatments at 35 °C (Fig. 8.8).

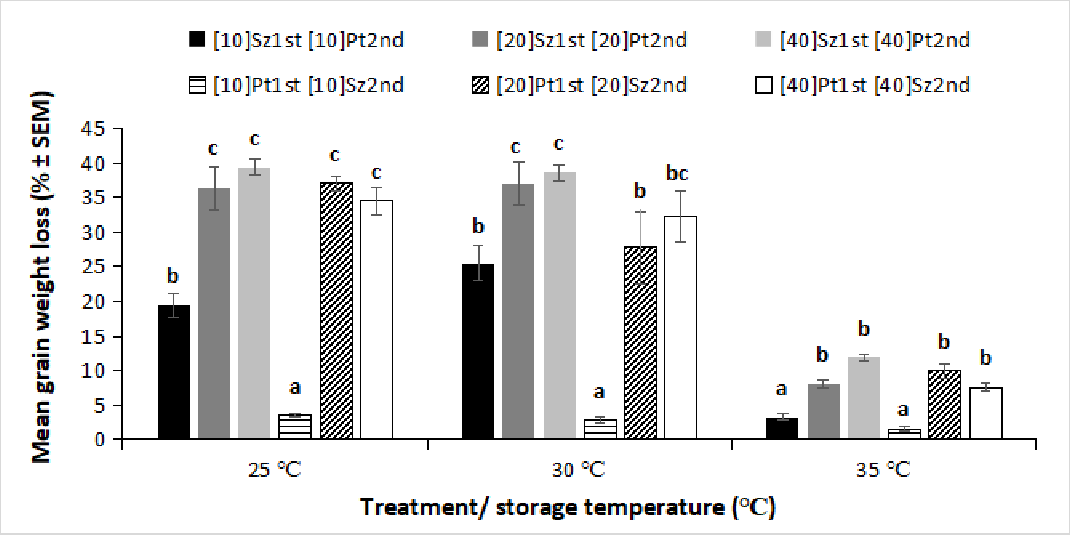

Figure 8. 8: Mean grain weight loss (% ± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following delayed introduction of one species (n= 3). [10]Sz 1st [10]Pt 2nd = 10 *S. zeamais* introduced first and 10 *P. truncatus* introduced 10 days later, [20]Sz 1st [20]Pt 2nd = 20 *S. zeamais* introduced first then 20 *P. truncatus* introduced 10 days later, [40]Sz 1st [40]Pt 2nd = 40 *S. zeamais* introduced first then 40 *P. truncatus* introduced 10 days later, [10]Pt 1st [10]Sz 2nd = 10 *P. truncatus* introduced first then 10 *S. zeamais* introduced 10 days later, [20]Pt 1st [20] Sz 2nd = 20 *P. truncatus* introduced first then 20 *S. zeamais* introduced 10 days later, [40]Pt 1st [40]Sz 2nd = 40 *P. truncatus* introduced first then 40 *S. zeamais* introduced 10 days later.

8.3.2.4. Insect feeding dust

Treatment ($F_{5, 36} = 75.408$; $p < 0.001$), temperature ($F_{2, 36} = 283.60$; $p < 0.001$) and treatment × temperature ($F_{10, 36} = 14.049$; $p < 0.001$) interactions all significantly affected production of insect feeding dust. Treatment effects significantly suppressed feeding dust below 5% at the lowest insect density (20) when *P. truncatus* ([10]Pt 1st [10]Sz 2nd) was introduced first. On the other hand, medium (15–20%) and high (17–20%) parent densities recorded equally and significantly high insect feeding dust at 25 and 30°C. Temperature effects resulted in suppressed feeding dust in all treatments at 35°C (5% and below) compared to 25 and 30°C (up to 20%). Overall, insect feeding dust between 10 and 25% was produced at 25 and 30°C while at 35°C dust was limited at ≤ 6% (Fig. 8.9).

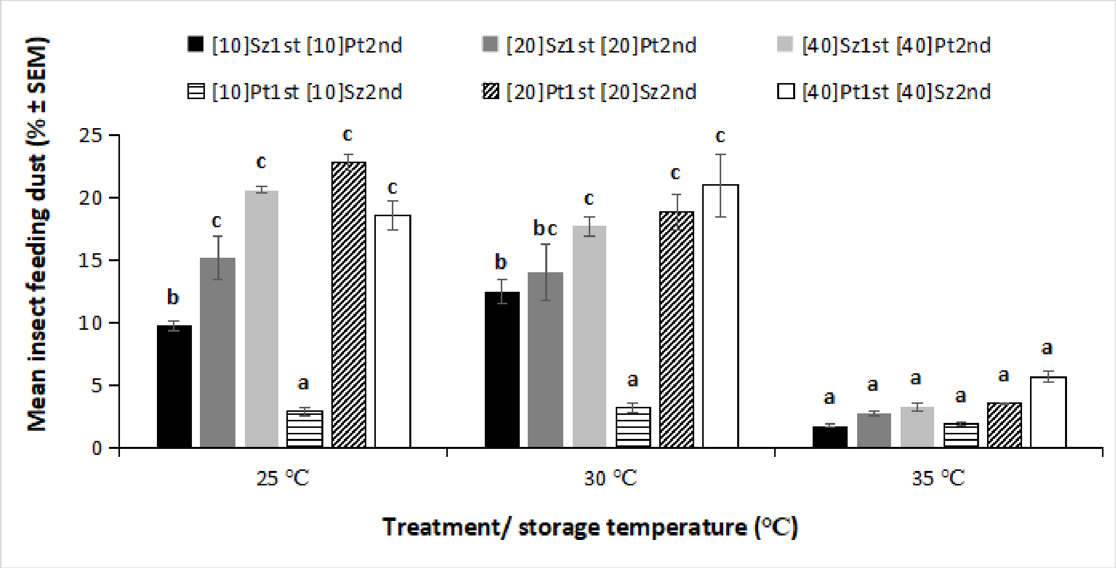

Figure 8. 9: Mean insect feeding dust (% ± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following delayed introduction of one species (n= 3). [10]Sz 1st [10]Pt 2nd = 10 *S. zeamais* introduced first and 10 *P. truncatus* introduced 10 days later, [20]Sz 1st [20]Pt 2nd = 20 *S. zeamais* introduced first then 20 *P. truncatus* introduced 10 days later, [40]Sz 1st [40]Pt 2nd = 40 *S. zeamais* introduced first then 40 *P. truncatus* introduced 10 days later, [10]Pt 1st [10]Sz 2nd = 10 *P. truncatus* introduced first then 10 *S. zeamais* introduced 10 days later, [20]Pt 1st [20] Sz 2nd = 20 *P. truncatus* introduced first then 20 *S. zeamais* introduced 10 days later, [40]Pt 1st [40]Sz 2nd = 40 *P. truncatus* introduced first then 40 *S. zeamais* introduced 10 days later.

8.3.2.5 Beetle boring feeding holes

Beetle boring was significantly different between treatments ($F_{5,\ 36}$ = 25.881; p < 0.001) and further influenced by temperature ($F_{2,\ 36}$ = 116.32; p < 0.001) and treatment × temperature interactions ($F_{10,\ 36}$ = 7.3337; p < 0.001). Feeding holes increased significantly with increased temperature (and parent density) from a range of 2–20 holes at 25°C to 35–65 holes at 30°C and were highly suppressed at 35°C due to failure of beetles to survive (Fig. 8.10). At 25°C, the middle and high parental densities recorded the highest number of feeding holes regardless of which species was introduced first. At 30°C however, introduction of *P. truncatus* first before *S. zeamais* ([20]Pt 1st [20]Sz 2nd and [40]Pt 1st [40]Sz 2nd) recorded the highest number of holes for both middle and high parent densities.

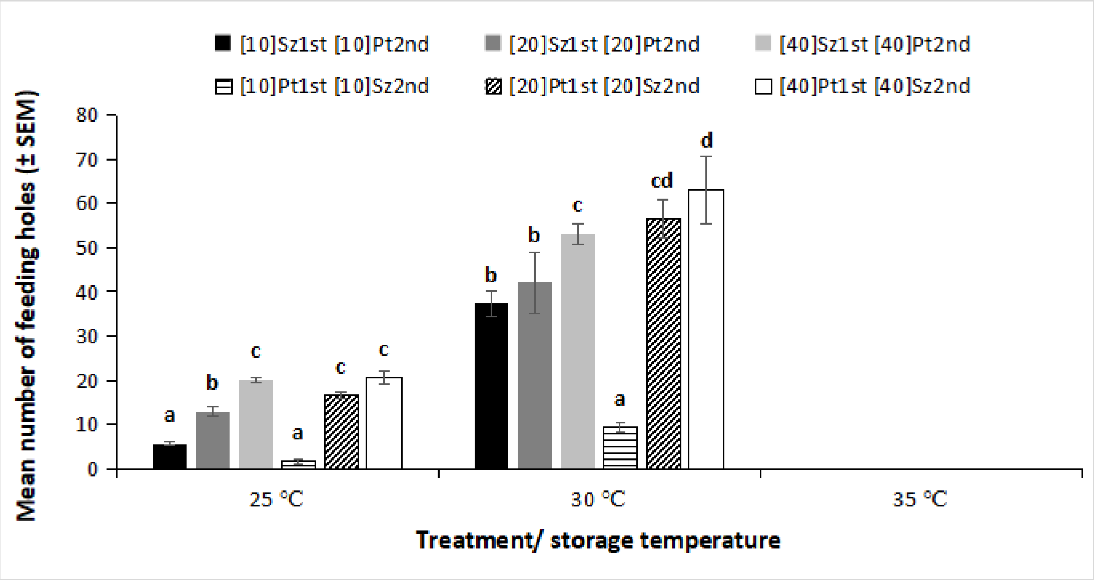

Figure 8. 10: Mean number of beetle boring exit holes (± SEM) recorded after 65 days of grain storage at 25, 30 and 35°C at 65% RH following delayed introduction of one species (n= 3). No feeding holes were recorded at 35°C. [10]Sz 1st [10]Pt 2nd = 10 *S. zeamais* introduced first and 10 *P. truncatus* introduced 10 days later, [20]Sz 1st [20]Pt 2nd = 20 *S. zeamais* introduced first then 20 *P. truncatus* introduced 10 days later, [40]Sz 1st [40]Pt 2nd = 40 *S. zeamais* introduced first then 40 *P. truncatus* introduced 10 days later, [10]Pt 1st [10]Sz 2nd = 10 *P. truncatus* introduced first then 10 *S. zeamais* introduced 10 days later, [20]Pt 1st [20] Sz 2nd = 20 *P. truncatus* introduced first then 20 *S. zeamais* introduced 10 days later, [40]Pt 1st [40]Sz 2nd = 40 *P. truncatus* introduced first then 40 *S. zeamais* introduced 10 days later.

8.4. Discussion

The current study aimed to determine effects of intra- and inter-specific competition in *P. truncatus* and *S. zeamais* at different temperature regimes, parental densities and when the insect species were introduced on maize grain simultaneously or when one species was introduced 10 days after the other. First, in simultaneous introduction of species, the highest significant grain damage, grain weight losses, insect feeding dust and beetle boring feeding holes were found in *P. truncatus* intra- and interspecific interactions with *S. zeamais* at medium (40) and high (80) parental densities; compared to *S. zeamais* intraspecific treatments. Grain damage (20–85%), weight loss (2–50%), feeding dust (2–35%) and boring holes (10–50 holes) were significantly higher in *P. truncatus* intra- and interspecific interactions compared to *S. zeamais* intraspecific interactions (15–44%; 2–14%; ≤ 5%; ≤ 5 holes respectively) for the same parental densities. These results indicate the invasiveness of *P. truncatus* as it outcompetes *S. zeamais* at similar temperatures (25 and 30°C) and parental densities. Although both *P. truncatus* and *S. zeamais* seemed to perform well at 25 and 30°C, the levels of ecological damage were remarkably different, and it would suggest high damage levels in interspecific interactions were largely a contribution of the *P. truncatus* species in the treatments. Similar conclusions were reported by Quellhorst et al. (2024). Further, the number of holes on the surface of polypropylene bags (bag damage) were significantly high in *P. truncatus* intraspecific interactions suggesting high resource competition compared to *S. zeamais* intraspecific interactions at similar parental densities. According to Hodges (2002), bag damage increases in response to increased population densities as beetles disperse to look for new food resources. The results for beetle boring therefore give an indication that resource competition was high in *P. truncatus* intraspecific treatments especially at high parental densities. This is further supported by the significantly high levels of grain damage, grain weight losses and number of progenies recorded for the same treatments at medium and high densities in both experiments.

The damage indices of *P. truncatus* are characterized by extensive habitual adult tunneling and larval feeding from inside the grain which transforms kernels into dust (Tefera et al. 2011; Papadimitriou et al. 2024). In the process of feeding, *P. truncatus* produced copious amounts of feeding dust (Hodges, 1983; Nyabako et al. 2020), leaving grains unfit for human consumption (Dunstan et al. 1983; Boxall, 2002). The habitual boring and extensive feeding characteristic further cause high levels of grain weight losses observed in the current study and supported by other researchers (see Mlambo et al. 2018; Sakka and Athanassiou, 2018; Papadimitriou et al. 2024). Reports show that grain losses have since doubled in locations where *P. truncatus* was reported due to excessive damage (Hodges, 1986; Muatinte et al. 2019; Quellhorst et al. 2021). Mukundi et al (2010) reported similar results showing that damage and losses due to *P. truncatus* are at least twice as much as those caused by *S. zeamais* under similar conditions. Furthermore, increased *P. truncatus* grain damage is attributed to high densities of the pest that can coexist within each grain kernel (Vowotor et al. 2005). Guntrip et al. (1996) asserted that *P. truncatus* lays fewer eggs in low insect densities and oviposition increases with increased insect densities. Our low parental density (20) matched densities used in Sadiku et al. (2017) although they used equal ratios of sexed beetles as opposed to unsexed beetles in the current study. Compared with the current study, higher numbers of progenies for *P. truncatus* (77 adults) and *S. zeamais* (99 adults) were reported in interspecific treatments after 70 days of grain storage and even much higher progenies in intraspecific interactions (109 and 174 adults for *P. truncatus* and *S. zeamais* respectively (Sadiku et al. 2017).

The effects of temperature on the performance of *P. truncatus* and *S. zeamais* were distinct. Ecological performance of both species was high at 25 and 30°C and highly suppressed at 35°C highlighting the effects of temperature on progeny production and the resulting grain damage and grain weight losses. This result on temperature points to the optimal developmental temperatures which are 25–30°C at 75% RH for *S. zeamais* and 32°C at 80% RH for *P. truncatus* (Shires, 1970; Mason and Macdonough, 2011; Fields and Muir, 2018; Quellhorst et al. 2021). *Prostephanus truncatus* has a higher optimal developmental temperature and can tolerate higher temperatures compared to *S. zeamais* and this has been pinpointed as one of the major "species attributes" for *P. truncatus'* invasiveness (Aurthur et al. 2009; Mlambo et al. 2024). As highlighted by Fields (1992), high development for storage insect pests is observed at 25–33°C and development stops at 35°C due to desiccation, increased fluidity of membranes and rate imbalances in cells causing reduced egg laying, hatchability and insect death. At these extreme temperatures, relative humidity, grain moisture content and pest biology play crucial roles in mediating survival. *Prostephanus truncatus* is highly tolerant to dry conditions where it can survive and breed on grains with as low as 9% moisture content whilst *S. zeamais* requires at least 10.5% moisture content for development (Hodges et al. 1983). During the dry season, *P. truncatus* faces less competition to exploit the same food resources for feeding and oviposition as other pests e.g., *S. zeamais* are restricted by the low RH and moisture content of grains (Hodges et al. 1983). Competition increases during the rainy season in response to high moisture and RH conditions favouring the proliferation of storage insect pests (Hodges et al. 1983). Furthermore, immature stages of both *P. truncatus* and *S. zeamais* can escape some degree of extreme heat as they develop inside grain kernels (Hodges et al. 1983). *Prostephanus truncatus* produced similarly high number of progenies in both intra- and interspecific interactions whilst *S. zeamais* only produced higher progenies in intraspecific treatments. This highlights that progeny production in *P. truncatus* is not always limited by competition as does with *S. zeamais*. Different instars of *P. truncatus* feed on different parts of grain (differential feeding on the germ and endosperm) and this reduces competition for food (Quellhorst et al. 2021). Further, the beetles can reduce competition by dispersing through tunneling out of storage bags in search of new food resources (Quellhorst et al. 2021).

Results of delayed introduction of species highlight a 3-way interaction between treatments, temperature and treatment × temperature in influencing competition. First, number of progenies, grain damage, grain weight loss, insect feeding dust and beetle boring feeding holes increased with increased insect densities from low ([10]Sz 1^{st} [10]Pt 2^{nd}; [10]Pt 1^{st} [10]Sz 2^{nd}) to medium ([20]Sz 1^{st} [20]Pt 2^{nd}; [20]Pt 1^{st} [20]Sz 2^{nd}) density treatments. However, there were no significant differences between medium and high density treatments in both scenarios whether *P. truncatus* or *S. zeamais* is introduced first. Notably however, the least ecological performance was recorded at the lowest insect density when *P. truncatus* was introduced first ([10]Pt 1^{st} [10]Sz 2^{nd}) as compared to when *S. zeamais* is introduced first ([10]Sz 1^{st} [10]Pt 2^{nd}). This anomaly was not consistent with other treatments where there were no significant differences in ecological performance observed regardless of which species was introduced first. Ecological performance of both species was suppressed at 35°C similar to what was observed with simultaneous introduction. Overall, comparable ecological performances were observed in simultaneous and delayed introduction of the species. In simultaneous introduction, number of progenies were approximately 40 for both *P. truncatus* and *S. zeamais*), grain damage level (5–85%), grain weight loss (2–58%), insect feeding dust (2–35%) and number of feeding holes (2–53 holes) whereas in delayed introduction of one species number of progenies were around 16 for each species, grain damage (5–75%), grain weight loss (2–40%), insect feeding dust (2–20 %) and number of feeding holes (5–60 holes).

Quellhorst et al (2020), found that *P. truncatus* has higher ecological impacts at higher temperatures of 25–30°C whilst *S. zeamais* performs better at 20–25°C in simultaneous introduction of species. The current study did not include treatments at 20°C as average ambient temperatures in sub-Saharan Africa are expected to rise (Serdeczny et al. 2017). However, *P. truncatus* outcompeted *S. zeamais* at both 25 and 30°C with negligible competition costs in interspecific interactions. Giga and Canhao (1993) concluded that *S. zeamais* outcompete and suppress *P. truncatus* at 25°C. However, at 30°C, the outcome was inconclusive. Contrary to their findings, our findings suggest that *P. truncatus* outcompetes *S. zeamais* at both 25 and 30°C and both species are highly suppressed at 35°C due to heat desiccation and denaturation of proteins leading to insect death within days (Fields, 1992). Giga and Canhao (1993) found that competition increased with increased parent population densities, which is partially in line with current observations for low to medium densities although there was a saturation in performance at medium to high densities. Studies by Sadiku et al. (2017) on the interspecific interactions between *P. truncatus* and *S. zeamais* concluded that interspecific interaction of the two species reduced progeny production in both species. In the current study, similar patterns were noted, particularly at higher parental densities, interspecific treatments produced fewer number of progenies than those at low parent densities. Mukundi et al (2010) found that *S. zeamais* produced higher number of progenies compared to *P. truncatus* irrespective of the initial parent population which is contrary to the current study. Rugumamu (2005) found higher grain damage and weight losses in interspecific interactions between *P. truncatus* and *S. zeamais* compared to single infestations, suggesting synergistic interactions in simultaneous introductions. On the contrary, our results do not suggest synergistic interactions as ecological damage in interspecific treatments was either at par or below that of *P. truncatus* intraspecific interactions. Baliota et al (2022) studied competition between *P. truncatus* and *S. oryzae* on maize at 26 and 30°C and found that *P. truncatus* was the dominant species regardless of the presence of *S. oryzae* or being introduced after the later. This result concurs with our study findings although we evaluated competition with *S. zeamais* as opposed to *S. oryzae*. *Sitophilus zeamais* is known to be problematic on maize whilst *S. oryzae* is notorious on sorghum and wheat and these differences in preference can confound our evaluation of the competing abilities of the pests with *P. truncatus* on maize. Vowotor et al (2005) studied the association of *P. truncatus* and *S. zeamais* on shelled maize in field experiments and found that the two species are not associated with each other; only a few *S. zeamais* would be found amongst high densities of *P. truncatus* and *vice versa*. The current study did not directly study association however, the two species coexisted and, in some cases, produced equal number of progenies.

In conclusion, the results showed that (i) *P. truncatus* outcompetes *S. zeamais* at 25 and 30°C at low, medium and high parental densities, (ii) ecological performance of both *P. truncatus* and *S. zeamais* was suppressed at 35°C, (iii) *P. truncatus* has high ecological performance in both intra- and interspecific interactions with *S. zeamais*, (iv) ecological performance of *P. truncatus* gets saturated at medium to high densities, (v) *P. truncatus* caused high ecological damage regardless of being introduced first or later, and (vi) *P. truncatus* dispersed through tunneling in response to competition.

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CHAPTER 9

General Discussions

9.1. Discussion

The gradual advance in climate change coupled with agricultural intensification and increased global trade are megatrends that have facilitated the movement and introduction of invasive insect pests into new geographical regions where they have become biosecurity threats. Interactions between these megatrends exacerbate biosecurity threats by facilitating movement, introductions, adaptation and expanded ranges of invasive species. Understanding these megatrends, e.g., species dispersal pathways, environmental and species physiological attributes, species spatial and temporal distribution as well as the ecological impacts of invasive species in introduced environments are crucial in developing models for early warning and control. In most cases however, there is lack and/or limited species-specific bio-physical data to inform modeling hindering pest management.

The current study was aimed at determining the occurrence of *P. truncatus* in Botswana, the role of abiotic stress responses as mechanisms of survival under changing environments and the implications thereof to population dynamics and pest management. It was hypothesised that *P. truncatus* is likely present and widely distributed in Botswana and that stress response mechanisms affect *P. truncatus*' life history traits and overall fitness. Results obtained showed that (i) *P. truncatus* is present but still spatially constrained, (ii) smallholder farmers rely on traditional storage techniques as opposed to synthetic pesticides or modern postharvest grain protection technologies, e.g., hermetic storage facilities which makes them vulnerable to *P. truncatus*, (iii) climate change and anthropogenic activities are major trends that have facilitated global movement and establishment of invasive alien species, (iv) heat acclimation responses in *P. truncatus* are trait- and generation-dependant, (v) intergenerational repeated heat acclimation erodes thermal plasticity in *P. truncatus*, (vi) heat acclimation had transgenerational physiological- but not ecological-progeny fitness advantage, (vii) parental optimal host experiences conferred the highest physiological and ecological performance in *P. truncatus,* (viii) *P. truncatus* outcompetes *S. zeamais* at 25 and 30°C in low, medium and high parental densities and (ix) *P. truncatus* outcompete *S. zeamais* regardless of being introduced simultaneously or later in grain, suggesting its significance for grain storage under changing climates.

The occurrence of *P. truncatus* had been anecdotal in Botswana. The current study reported the first record of *P. truncatus* in Botswana (Mlambo et al. 2024a, Chapter 2). Although confirmed, the surveillance results showed that *P. truncatus* is still spatially-constrained and thus not yet widely distributed across the country. Furthermore, surveillance studies also showed that this pest has not yet been reported on stored grain yet. The occurrence of *P. truncatus* in Botswana is not alarming as its neighbouring countries and agricultural trade partners such as South Africa, Zambia, Namibia, Zimbabwe, Malawi, Mozambique have all reported the occurrence of the pest as far back as 2007 (Quellhorst et al. 2021; Mlambo et al. 2024a). Although the pest has not been confirmed on stored grain yet, the current farmer grain storage practices dominated by botanical ashes e.g., *Combretum imberbe* wood ash (Keosentse et al. 2018 unpublished data) expose their grain to damage by storage insect pests. Botanical pesticides, although widely used, have no guaranteed protection of stored grains (Isman, 2006; Mlambo et al. 2018; Duguma, 2020) mainly due to lack of standardisation in their preparation, the need for frequent reapplication to maintain efficacy and in some cases, high volumes are required for small amounts of grains (see Stevenson at al. 2014; Sola et al. 2014; Parwada et al. 2018). Alternative grain storage techniques e.g., the use of synthetic pesticides and hermetic storage facilities which have demonstrated moderate to high efficacy depending on type (see Chigoverah and Mvumi, 2016; Ndegwa et al. 2016; Mlambo et al. 2018; Mutambuki et al. 2019; Mubayiwa et al. 2021), are not popular in Botswana. This leaves farmers vulnerable if *P. truncatus* is reported on grains. Efforts aimed at training extension staff, farmers and border control agents to recognise and understand the dangers that *P. truncatus* pose to stored grains are required. Further, deliberate efforts by government to subsidise and/or encourage the use of- and research on improved efficacious grain storage methods as well as coordination and harmonisation of phytosanitary standards with regional and international standards are required.

The context of new environments in which *P. truncatus* is introduced need to be understood in terms of farmers' knowledge, practices and perceptions on pest management (Chapter 3). Besides megatrends which have facilitated movement and establishment of invasive species, species attributes of *P. truncatus* e.g., high reproductive capacity and high thermal and pesticide tolerance which are advantageous in increased temperature and highly regulated environments favour its spread and ecological dominance over native species (Mlambo et al. 2024b; Chapter 4). Thermal stress is one factor that can affect pest populations under climate change. This study demonstrated that mechanisms such as transgenerational plasticity (Chapter 5) and intergenerational adaptation (Mlambo et al. 2024c; Chapter 6) mediate *P. truncatus* survival. Although the mechanisms of heat stress adaptation are trait and generation dependent, the general trend showed that heat stress adaptation in succeeding generations lead to increased progeny physiological fitness (Mlambo et al. 2024c). Transgenerational plasticity is a mechanism by which parents pass on memories of environmental stress to their offspring allowing them to express phenotypes that improve fitness (English et al. 2016). Although transgenerational plasticity improved physiological fitness, it significantly reduced *P. truncatus* progeny ecological performance (Chapter 5). This highlighted the costs of plasticity whereby individual beetles would invest more resources to sustain the plastic phenotype at the expense of progeny production and this 'development instability' retarded feeding (Relyea, 2002; Colinet et al. 2015). Ecological performance of *P. truncatus* will therefore be retarded to compensate for heat stress tolerance resulting in reduced number of progenies, grain damage and grain weight losses at higher sub-optimal temperatures.

The current study also highlighted the fitness costs associated with different diet (host) diversity (Chapter 7). First, maternal host preference in *P. truncatus* conferred the highest progeny physiological and ecological fitness compared to either non preferred hosts and/or host switching. Feeding consistency on maize or cassava chips, increased progeny fitness whereas a switch between the two drastically reduced progeny fitness. This information is crucial in integrated targeted pest control where the farming system models e.g., mixed cropping can be used to control *P. truncatus* at its weakest point or host. Maternal experiences are crucial in preparing shaping progeny fitness through investment in decisions that influence progeny fitness once hatched. The study showed that the decision of female *P. truncatus* beetles to lay more eggs on either maize grains or cassava tubers is based on either maternal experience or preference based on perceived adaptive cues and thus led to progeny fitness through adaptive matching of parent and offspring cues transferred through transgenerational plasticity (more discussions in Uller et al. 2013; English et al. 2016).

The fate of interactions among *P. truncatus* conspecifics or with other different storage pests e.g., *S. zeamais* can be synergistic or antagonistic resulting in increased or decreased grain damage respectively. Chapter 8 recognised that primary storage insect pests can arrive on grain at the same time or one after the other and these scenarios can define which insect performs better in terms of feeding and oviposition (Athanassiou et al. 2017; Sakka and Athanassiou, 2018). Chapter 8 highlighted that *P. truncatus* outcompetes *S. zeamais* at 25 and 30°C in low, medium and high initial parental densities regardless of being introduced simultaneously or later. Although interspecific interactions between *P. truncatus* and *S. zeamais* were not additive, it did little to affect the proportion of damage caused by *P. truncatus* alone. As such high damage levels were recorded across intra- and interspecific interactions in both simultaneous and staggered introduction scenarios. These results concur with findings that suggest that *P. truncatus* causes 2–3 times more damage than native species; hence grain losses on farms have since doubled in invaded environments (Mutambuki and Ngatia, 2012). Chapter 8 further demonstrated that temperatures of 35°C were extreme for both *P. truncatus* and *S. zeamais* and this suppressed feeding and progeny production. Extreme heat is detrimental to ectotherms (Chown and Nicolson, 2004; Jackson et al. 2022) and can be used in physical control (see more discussions in Machekano et al. 2020). Indeed, this is also confirmed in storage insect pests where desiccation and metabolic imbalances lead to insect death at temperatures ≥35°C (Fields and Muir, 2018).

These findings are an 'eye-opener' for farmers and stakeholders in Botswana and SSA at large as they highlight the (i) expanding geographical range of *P. truncatus* in the region, (ii) critical performance temperature ranges of *P. truncatus* and associated insect pests of stored grains, (iii) thermal stress response mechanisms that mediate *P. truncatus* survival under environmental change, (iv) physiological and ecological fitness associated with different *P. truncatus* hosts and (v) fate of interspecific interactions between *P. truncatus* and *S. zeamais* as a model for competition on stored grains. This information is important first in decision making on the most efficacious grain storage practices and techniques to guarantee protection of stored grains. Second, the information is important for targeted integrated pest management for example, *P. truncatus* can be targeted on its weakest host and at extreme temperatures. Third, the information provides insights in developing abundance prediction models.

9.2. Conclusions

The current study confirms the presence of *P. truncatus* in Botswana (in line with hypothesis 1), albeit still being spatially restricted. Although the pest has not established in agricultural landscapes, farmers are vulnerable to the pest due to current grain storage facilities being used; the prevailing high temperatures favourable for *P. truncatus* and also lack of information on improved postharvest management practices (Hypothesis 2). Laboratory assays showed that thermal plasticity play an important role in conferring fitness traits in *P. truncatus* through transgenerational and intergenerational responses (Hypothesis 3). Further, maternal experiences and/or host preference also play an important role in progeny fitness through transgenerational matching of parent and offspring adaptive cues (Hypothesis 4). The ecological performance of *P. truncatus* was demonstrated to be high at 25 and 30°C in response to temperature, host type and density and intra- and interspecific interactions (Hypothesis 5) which suggest that losses can be high at these prevailing temperatures when grain is not securely stored. Under extreme temperatures in excess of 35°C, *P. truncatus* population growth stops, and individual insects die due to desiccation (Hypothesis 6). The study provides insights into the ecology and physiology of *P. truncatus* which are important in designing models for early warning and control as well as integrated national and regional pest management strategies against the pest.

9.3. Recommendations

The occurrence of a quarantine pest jeopardizes Botswana's trade, including the trade in host plant and/plant products (e.g., grain exports). This calls for concerted efforts to monitor the pest at strategic locations such as land border posts, inland trade routes and bulk grain storage depots to control the pest before it is widely spread or causes extensive damage. Furthermore, it is important to train both extension services and farmers to identify the pest and recognise the dangers it poses to stored maize grains. The study recommends deliberate efforts by Government of Botswana and development agents to introduce improved, affordable and efficacious grain storage technologies to smallholder farmers to guarantee effective protection of stored grains. Further, the study recommends research on pesticide efficacy trials to evaluate the efficacy of current synthetic grain protectants against *P. truncatus* so as to recommend the best control methods to farmers and these should be readily available in cases of outbreaks and/or geographic expansion.

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