Mathematical modelling of population dynamics of khapra beetle (*Trogoderma granarium*)

by

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A thesis submitted to the Faculty of Graduate Studies of

The University of Manitoba

in partial fulfilment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biosystems Engineering

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ABSTRACT

Trogoderma granarium Everts (Coleoptera: Dermestidae), generally known as the khapra beetle, is found in the hot and dry regions of North Africa, the Middle East, and India. It is not established elsewhere and is classified as a quarantine pest in Canada and several other countries. It is one of the economically important quarantine pests that mainly feeds on food grain and proteinaceous materials. Its total lifespan lasts approximately 40 to 45 d under favourable environmental conditions. Extreme temperatures, high RH, high larval densities, or low food quality can induce a larval diapause, where the insect can survive for up to a few years, occasionally feeding and molting. The diapausing larvae are resistant to heat, cold, and insecticides, that aids in surviving the adverse conditions. Ecological modelling is a helpful tool to study the population dynamics of biological systems. The objective of this study was to develop mathematical models to calculate the survival and development of the khapra beetle under different environmental conditions such as temperature, RH, and food quality. The developed models were used to estimate the development and survival of the khapra beetle under Canadian grain storage conditions.

The factors affecting the development and mortality of the khapra beetle were reviewed, and appropriate assumptions were made for developing the mathematical equations using the Physi-Biological age method. This method is based on temperature-driven development rate, and factors such as RH and food quality were considered as multipliers. Mathematical equations were developed to calculate the development and mortality of adults, eggs, larvae, pupae, and oviposition and diapause under different environmental conditions. Algorithms were developed to simulate the population dynamics for each day and coded in C++. The developed models were validated against the literature data and evaluated using linear regression, R^2 and MSE. Population dynamics were simulated under Canadian grain storage conditions, and it was found that the diapausing larvae survived the extremely cold conditions found in Canadian grain. In contrast, insects in other stages did not survive. The surviving larvae developed to pupae and adults, and females began laying eggs once the temperature became warmer in the grain bins.

Keywords: *Trogoderma granarium*, Mathematical modelling, Physi-Biological age, Population dynamics, Same shape concept

DEDICATION

Dedicated to my mother Bagyalakshmi and my father Rajendran
for the inspiration, motivation, countless sacrifices, and
always believing in my potential to be successful

ACKNOWLEDGEMENTS

First and foremost, I would like to express my gratitude and respect to my advisor, Dr. Fuji Jian, for his exemplary guidance, support and for enriching me with the knowledge required for my research work all through the course of my study.

I would like to express my deepest gratitude to Dr. Paul Fields for providing the necessary assistance and motivation to complete my thesis work successfully.

I would like to thank Dr. Digvir Jayas, my co-advisor, for his leadership, inspiration and guiding me in due course of this project work. I would like to thank Dr. Vincent Hervet for his advice and valuable feedback. I thank Agriculture and Agri-food Canada for the financial support.

I sincerely thank Anukiruthika Thangarasu, Rahul Tripathi, Vimala Bharathi S K and the Professors, technicians and graduate students working in CWB Center for Grain Storage Research for their constant support and help throughout my study. A special thanks to Praveen Kumar for helping me with coding. I am thankful to my friends Abhinav Tiwary, Chitra Sivakumar, Darsana Divagar, Lavanya Ganesan, Mehul Patil, Prabakaran Santhanam, Raghuram Atmuri, and Sristi Mundhada for their immense support.

Last but not least, a special thanks to Dr. Jeyan Arthur Moses, my family and friends in India for their moral support and for inspiring me to succeed in life.

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LIST OF ABBREVIATIONS AND SYMBOLS

B_n	Physi-Biological age
cm	Centimeter
CO_2	Carbon di-oxide
d	Day
m	Meter
mg	Milligram
mL	Millilitre
mo	Month
MSE	Mean squared error
R^2	Coefficient of determination
RH	Relative humidity
SD	Standard deviation
T	Temperature in °C
wk	Week
yr	Year
ϕ	Relative humidity

1. INTRODUCTION

The total production of grain in Canada amounted to 86 million tonnes in 2019-2020. Wheat and canola are the two most important crops in terms of production (Reports and Statistics Data for Canadian Principal Field Crops, 2020). After harvesting, the grains are stored temporarily on farms before being transported to country grain elevators, which send grains to terminal elevators for export outside the country or domestic customers in the food and feed industry (White et al., 2011). During processing, the food grains are subjected to various unit operations like cleaning, dehusking, milling, packaging, storage, and distribution (Moses et al., 2015). Storage is an intermediate processing step that usually occurs immediately after harvesting as well as at many points during post-harvesting processing and handling. The quality of grain is the most important criterion that dictates the end-use, grading value, and marketability (Tipples, 1995). Several abiotic factors such as temperature, relative humidity, moisture content and CO_2 concentration, as well as biotic factors including insects, mites, fungi, and rodents influence the stored grain quality (Jayas, 2012; Jian and Jayas, 2012; Moses et al., 2015). Among the biotic factors, insects and mites cause significant damage to the stored and processed grain in terms of quality and quantity (Sinha et al., 1969). Further, infested grain may lead to several health hazards like illness and allergies when humans and animals ingest them (Athanassiou et al., 2016; Pasek, 1998).

Khapra beetle (*Trogoderma granarium* Everts, Coleoptera: Dermestidae) is one of the most economically significant stored product insects, originated from the Indian sub-continent (Barnes and Grove, 1916; Rahman et al., 1945). It is well established in the hot and dry regions of the world, especially in the Middle Eastern countries, South Asian countries, and parts of northern Africa (Athanassiou et al., 2016; Day and White, 2016). The larvae of the khapra beetle feed on cereal seeds, grain products and oilseeds (Athanassiou et al., 2016; Pasek, 1998). The damage is mainly caused by feeding and the presence of insects and their frass contaminates the product, making it unfit for consumption. The khapra beetle is termed a ‘dirty feeder’ as an individual partially damages multiple seeds to complete development (Stibick, 2009). Under conditions such as limited food resources, they can consume all the parts of the food grain except husk (Kavallieratos et al., 2017). It is important to establish safe storage and handling methods during grain processing to prevent the infestation of khapra beetles in grain (Karunakaran et al., 2001). In this regard, various quarantine regulations are practiced in North and South America, China, and

Australia (Athanassiou et al., 2019). Although the khapra beetle is absent in these countries, khapra beetle is regularly found in imported commodities and packing material. Chemical fumigation is commonly used to control the insect. The chemical control can be less effective as some strains have developed resistance to the common fumigants (Cao et al., 2002; Rajendran, 2002; Rajendran and Parveen, 2005; Shivananjappa, 2019); thereby, eradication is difficult in quarantine and non-quarantine countries.

Currently, the khapra beetle is found occasionally in imported goods but is not established in Canada, perhaps due to the cold temperatures. But, the chances of survival cannot be overlooked in the feed mills, flour mills and other heated food processing facilities, just like other stored product pests (Ameen, 2012; Wilches et al., 2016). It is classified as a quarantine pest, and if found, the infestations are vigorously controlled. Knowledge about the potential prevalence of this pest under Canadian conditions is needed to prevent its damage if it ever becomes established in the country. Hence, it is crucial to predict this pest's survival and population dynamics under Canadian conditions. Ecological modelling is a valuable tool to understand and predict the population dynamics of any living organism in an ecosystem. Several mathematical models have been developed to predict the development and life cycle of different insect species. However, mathematical models to predict the population dynamics of the khapra beetle have not been developed. This study aimed to develop and validate mathematical equations of population dynamics of the khapra beetle. Validated models were used to predict the survival possibility of the khapra beetle under Canadian grain storage conditions.

2. REVIEW OF LITERATURE

2.1 Scientific classification of khapra beetle

The major pests infesting grain are beetles, mites, and moths. Approximately 600, 335 and 70 species of beetles, mites, and moths, respectively, are identified as stored product pests in addition to the psocids (Rajendran, 2002). Beetles are classified in the order Coleoptera, the most diverse order comprising 40% of all known insects. Many beetles are pests of agriculture, horticulture, and forest ecosystems. Dermestidae is a family of Coleoptera that has about 50 genera and 1000 species (Rees, 2004). They feed on dried plants, tree barks, dead animals, cotton, fibres, and wool (Hinton, 1945; Peacock, 1993). *Trogoderma* species are notable pests that mainly feed on grain and dry plants or animal materials. Many species remain unknown, while the most common ones, including *T. anthrenoides*, *T. glabrum* and *T. inclusum*, are classified as carpet and cabinet beetles. *Trogoderma variabile* is another dermestid beetle that affects stored products, and its ecology is relatively similar to the khapra beetle (Barak, 1991; Rees, 2004).

2.1.1. Prevalence of the khapra beetle

Khapra beetle, *T. granarium*, is one of the most economically significant insect pests affecting cereal grain in India, Pakistan, Egypt, and Turkey. It is recognized as one of the top 100 worst invasive species on earth (Lowe et al., 2000). More than 30 countries, including Australia, Brazil, Canada, China, New Zealand, Russia, and United States, have quarantine regulations on all grain from the exporting countries that have khapra beetles (Fig. 2.1) (Athanassiou et al., 2019). The khapra beetle is found in hot arid climates or storage structures with high temperatures and low relative humidity (Banks, 1977). Thus, these prime factors result in outbreaks in countries with similar conditions (Rees and Banks, 1998).

Globalization, commerce, and international travellers increase the risk of distributing the khapra beetle worldwide (EPPO, 2013). The khapra beetle was successfully established in other countries due to its diapausing ability (Banks, 1977). Major grain trading countries such as the USA and Australia follow rigorous protocols to prevent the establishment of this pest. For instance, the khapra beetle was found to have significant infestations in California, Arizona and New Mexico in 1953, and a 13-yr eradication plan was implemented with a total cost of 15 million USD in 1966 (equal to 133 million USD in 2021) (Armitage, 1958; Pasek, 1998; Shivananjappa, 2019).

Khapra beetle is not established in Canada, and phytosanitary certificates are mandatory from the importing countries. Cargos with khapra beetle are returned to the original point or destroyed (ISPM, 2016).

Figure 2.1. Geographical distribution of khapra beetle (adapted with permission from Athanassiou et al., 2019)

2.1.2. Damage and losses due to khapra beetle infestation

Khapra beetle infests more than 100 commodities, including cereal grain, nuts, seeds, fabrics, animal feed, dried meat, dried blood, dead insects, other plant-based and animal-based artifacts in museums (Athanassiou et al., 2016; Hinton, 1945; Pasek, 1998). Heavy losses of up to 75% of the total commodity can decrease the overall quality, such as bioavailability of carbohydrates, protein, crude fat (Jood and Kapoor, 1993; Rahman et al., 1945). The adults do not damage the grain, but the larva mainly consumes the grain embryo and germ (Athanassiou et al., 2016). The whole kernel is not damaged by the young larvae, which feed on broken kernels or

dust, but heavy infestations and the presence of other insect species help in damaging the sound grain (Kavallieratos et al., 2017; Pruthi and Singh, 1950). The larvae shed skin, hair, and feces, thereby contaminating the commodities. The feeding activity of the larvae can result in severe health hazards upon consumption with infested grains that have mouldy and rotten odour (Athanassiou et al., 2016; Pasek, 1998). Apart from the direct contamination of stored grain, larvae can penetrate through packaging materials like polyethylene and laminates. Grain infestation close to grain dryers and stored grain malt has been reported in Japan and Northern Europe. They referred to the khapra beetle as the 'pest of maltings'(Banks, 1977; Burges, 1959b; Eliopoulos, 2013; Mason, 1921; Voelkel, 1924), because it was found in the hot dry areas of the building where barley was malted for the beer industry. Its larval diapause enables survival for several years after initial infestations in ships, rail cars, and other grain transportation equipment.

2.1.3. Control methods

The most effective way to control the khapra beetle is by using fumigation with methyl bromide or phosphine (Bell et al., 1984; Mahmood et al., 1996; Lindgren and Vincent, 1959; Vincent and Lindgren, 1972). More than double the amount of methyl bromide is required to control the khapra beetle than most other insects (Bogs, 1976; Bond, 1984; Day and White, 2016). Even though phosphine fumigation requires a longer exposure time than methyl bromide, it is more widely used; since methyl bromide has been banned in many countries because of its ozone-depleting properties (Ahmad and Sarfraz, 2000; Ahmedani et al., 2007; Bell and Wilson, 1995; Bell et al., 1984; Borah and Chahal, 1979; Hole et al., 1976; Lindgren et al., 1958; MBTOC, 2014). Fumigation using sulfuryl fluoride was effective even at low doses (Rajendran et al., 2008; Sriranjini and Rajendran, 2008; Su and Scheffrahn, 1990). Contact insecticides such as malathion, chlorpyriphos, lindane and deltamethrin are also used but are not very effective due to resistance to these pesticides (Champ and Dyte, 1976; Eliopoulos, 2013; Khosla et al., 2005; Kumar et al., 2010; Lindgren and Vincent, 1959; Singh and Yadav, 1994). Low-temperature treatment is another method, but prolonged exposure of up to 70 d at -15°C is needed to control diapausing cold-acclimated larvae (Wilches, 2016; Wilches et al., 2017). Exposure to high-temperature treatment such as 50°C and above completely killed the khapra beetle in a few hours (Fields and White, 2002; Wilches, 2016; Wilches et al., 2016; Wilches et al., 2019). But, maintaining high temperatures constantly in all parts of the building is difficult and costly and is not practical to

disinfest commodities. Other monitoring and management methods like insect traps, radiation, and modified atmosphere storage using elevated levels of CO_2 or N_2 could be alternatives to control the khapra beetle (Al-Hadidi, 2002; Khatoon and Heather, 1990; Lindgren and Vincent, 1970; Navarro et al., 2002; Reichmuth et al., 1992; Spratt et al., 1985).

2.2. Morphology and biology of khapra beetle

2.2.1. Morphology

The adult khapra beetle is oval-shaped and is reddish-brown. Female beetles are usually lighter coloured than dark brown or black males. Females (2.1 to 3.4 mm long and 1.7 to 1.9 mm wide) are larger than males (1.4 to 2.3 mm long and 0.75 to 1.1 mm wide), as they usually have one more larval instar than males (EPPO, 2013). Females tend to lay eggs in a cylindrical cluster of 5 eggs. Eggs are milky white in the early stages that eventually turn to pale yellowish when about to hatch (Fig. 2.2). The egg is round-ended at one side, and the other side is pointed with spine-like projections. An egg weighs roughly 0.02 mg, and it is 0.7 mm long, and 0.25 mm wide (OEPP/EPPO, 1981). The larvae are yellowish-white in colour with a brown head (Botha et al., 2005). A fully matured larval stage after the fourth instar measures approximately 6 mm long and 1.5 mm wide with distinct yellowish-brown colour hair (OEPP/EPPO, 1981). The conversion to pupa begins from this point as the skin hardens and begins to split with the development of hard exarate.

2.2.2. Identification

The antennae of adults are yellow, 10 or 11 segmented and are clustered with four segments in female, five segments in male, thereby showing sexual dimorphism. A shallow notch is found in the inner margin of the eyes, and there is a median ocellus. The yellowish-brown coloured legs contain a short and a long spine at the base of tarsal claws. The reproductive organs should be examined thoroughly for correct identification as the khapra beetle appears like *T. inclusum* and *T. variabile*. A broad pronotum is closely attached to the elytra and is dark brown or black. The khapra beetle larvae are further differentiated by the barbed hairs present on certain abdominal tergites in pairs of tufts. The larva's body has nidisetae, spicisetae and hastisetae, where hastisetae are clusters of short pointed hair on the terminal segments. Definitive identification requires dissection and mounting larval mouth parts on slides. The challenges associated with correct

identification make it difficult and hence to adopt suitable quarantine actions (Barak, 1991; EPPO, 2013; ISPM, 2016; OEPP/EPPO, 1981; Pasek, 1998; Rees, 2004).

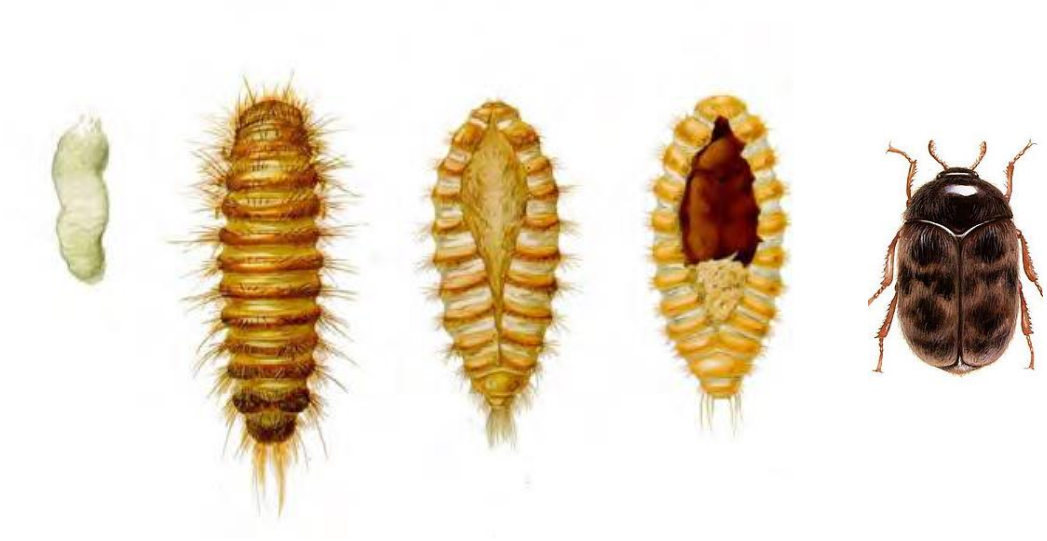

Figure 2.2. Life stages of khapra beetle.

From left to right - egg, larva (final instar), pupa (in the skin of final instar), adult beetle (about to escape from the cuticle of the pupa), adult khapra beetle (reproduced with permission from Botha et al., 2005)

2.2.3. Biology and life cycle

The longevity of adult khapra beetles is usually between 5 and 20 d. Each female can lay approximately 26 to 80 eggs under various temperatures (Burges, 1957; Hadaway, 1956; Odeyemi and Hassana, 1993; Riaz et al., 2014) and lay up to 130 eggs if the females came out of larval diapause and have mated several times (Karnavar, 1972). However, there is a 25% decrease in fecundity if the mating is delayed by 15 to 20 d (Banks, 1977; Day and White, 2016). Eggs usually start hatching in approximately 8 to 25 d. The larval stage lasts for 3 to 6 wk under optimal environmental conditions with adequate food and non-diapausing conditions (Burges, 1957; Lindgren and Vincent, 1959). Females have six instars, and males have five instars, with the total number of larval instars can be from 4 to 8 under various temperatures (Burges, 1957; 1962). Pupae remain in the burst skin of the larvae. Usually, the development time of pupae is shorter than the other stages, with a duration of 4 to 10 d for both males and females (Burges, 1957).

Unlike other species of *Trogoderma*, adults of *T. granarium* do not fly even though the wings develop fully (Banks, 1977; Hadaway, 1956). The duration of the adult male beetles is 7 to

12 d depending on rearing conditions, whereas the mated and unmated female beetles live for 4 to 7 d and 20 to 30 d, respectively. Under optimal conditions, the development period from egg to adults lasts approximately 39 to 45 d (EPPO, 2013). But unfavourable environmental conditions can slow down their development to more than 6 yr due to the larval diapause (Bell, 1994; Burges, 1962; Nair and Desai, 1973). Adults are bigger and lay more eggs if larvae have gone through the diapause (Nair and Desai, 1972). Temperature, relative humidity, light, climate and host species are the most critical factors that affect the growth and survival of *T. granarium* (Ramzan and Chahal, 1986).

2.2.4. Diapause in khapra beetle

The worldwide distribution of the khapra beetle is aided by the ability of its larvae to undergo an inherently designed physiological condition called diapause. In general, diapause can be obligate or facultative, and in both cases, the metabolism is slowed to survive hostile environmental conditions such as high densities, inadequate food, extreme temperatures, and relative humidity (Burges, 1963). Diapausing khapra beetle larvae have been shown to survive for over 7 yr without food, and the number of instars increases to as many as 15 in some cases (Athanassiou et al., 2019; Burges, 1962a). Respiration decreases to very low levels during diapause, and the beetles develop increased heat and cold tolerance. Diapausing larvae also develop resistance against insecticides and fumigants like phosphine and methyl bromide (Bell, 1994; Burges, 1962a; Witches et al., 2016). The diapausing larvae of khapra beetles do not feed except for the occasional brief scavenging excursions and are hidden in cracks, allowing them to live for multiple years. Phosphine levels as high as 1.5 mg/mL with an exposure period of 6 d are required to achieve 100% mortality of diapausing larvae at 20°C or lower temperatures (Bell and Wilson, 1995; Bell et al., 1983; Bell et al., 1984).

2.3. Factors affecting the development and mortality

2.3.1. Effect of temperature

Unlike other stored product pests, the khapra beetle can survive a wide range of temperatures and is remarkably tolerant to extreme temperatures (Wilches, 2016; Wilches et al., 2017). The ideal temperature required for the growth of khapra beetle is 25 to 37°C (Lindgren and Vincent, 1959; Lindgren et al., 1955), with reproduction occurring at temperatures as low as 21°C

and as high as 41°C (Burges, 1962). The total development time from egg to adult is approximately 220 d at 21°C (EPPO, 2013). If the average monthly temperature is greater than 27°C, the khapra beetle can develop to the next generation within a couple of months. The time required for establishing the population increases when the average temperature decreases to 21°C. Riaz et al. (2014) and Yadav and Srivastava (2017) have studied the effect of temperature on the development and survival of khapra beetle, including adult longevity, fecundity, oviposition period, incubation period, duration of egg hatching, mortality at each stage, length of larval and pupal periods. Adults do not lay eggs if the temperature is less than 20°C and higher than 45°C, and no larvae pupated at these temperatures, thereby going into diapause. The oviposition does not vary much between 20°C and 45°C and eventually stops if the temperature is below 20°C (Odeyemi and Hassana, 1993). The mortality of eggs is about 50% at 20°C. The larval lifespan is the quickest at 35°C when the total development happens in 15 days (Hadaway, 1956). Wilches et al. (2017; 2019) have studied the time required to kill 99.9% of the insects at extreme temperatures and found that the diapausing acclimated larval population is completely killed in 13 days at -20°C.

2.3.2. Effect of relative humidity

Relative humidity can affect the growth, physiology, length of incubation of eggs, and hatching of eggs. Khapra beetle is well established in the dry regions of the world, and it can survive in foods with moisture content as low as 2%. However, relative humidity levels of near 50% help the growth of larvae mainly due to the high water content available in the food. Therefore, the ideal development range is between 40 and 70% RH, and there is a slight decline in growth outside this range. Hadaway (1956) and Burges (1959a) found that the length of the pupal stage is not significantly affected by variations in humidity. Also, the air moisture is not so essential, but the high moisture foods aids in the quick growth of larvae. The larvae of *T. granarium* avoided the humid air with RH > 70% (Spangler, 1965) and are hygro-negative (Yinon and Shulov, 1967). The number of eggs laid was significantly different at different humidities as the females preferred the low RH over high RH (Odeyemi and Hassana, 1993).

2.3.3. Effect of food quality

A poor food source may negatively affect the morphology, fecundity, longevity, and development time of the insect (Sarfraz et al., 2006). Quality, quantity, and diet type directly influence survival and reproduction during the development period (Scriber and Slansky, 1981;

Rao et al., 2004). The adults do not feed, whereas larvae can feed on 96 commodities including wheat, maize, sorghum, rice, rye, triticale, oats, barley, gram, pulses, millets, nuts, coconut, walnuts (Athanassiou et al., 2016; Borzoui et al., 2015; Golizadeh and Abedi, 2016; Hagstrum et al., 2013; Majd-Marani et al., 2018; Mohammadzadeh and Izadi, 2018). Unlike other species of *Trogoderma*, the larvae of the khapra beetle can feed solely on grain for its entire development time (Pasek, 1998). The khapra beetle prefers cereals and pulses, especially wheat over oilseeds (Athanassiou et al., 2016; Punj, 1968). The presence of broken kernels increases the rate of development, even though the larvae can feed on the whole kernels during the posterior part of the larval stage (Kavallieratos et al., 2017).

2.3.4. Factors influencing diapause

Multiple factors are responsible for diapause initiation during the fifth larval instar in the khapra beetle (Wilches, 2016; Wilches et al., 2017). Diapause induction and termination are not completely understood, but factors such as temperature, relative humidity, larval density, diet quality and fecal pellets can individually or collectively induce diapause (Bell, 1994; Burges, 1962; Burges, 1963; EPPO, 2013; Nair and Desai, 1972; Wilches et al., 2016). The following three actions have been suggested by Burges (1962; 1963) to prevent diapause initiation. The most effective method recommended is to keep the temperature on the higher end of the optimal growth range, usually between 35 and 40°C. Another method is to maintain the temperature to at least 21°C for 30 d. A high-quality diet can also terminate diapause, but not as efficiently as the above-mentioned methods. Nair and Desai (1973) found that rapidly increasing the temperature outside the optimal growth range in the absence of challenging environmental conditions and supplying a highly nutritious diet to avoid larva overcrowding could help discontinue the diapause. However, some individuals in a cohort usually enter diapause regardless of the conditions (Wilches et al., 2017).

2.4. Mathematical modelling

A model refers to a set of mathematical equations and its logic instructions. In other words, a computer program that explains the mathematical descriptions, logic, and solutions (Fort, 2020). Modelling, in general, has four key stages: observing the system, modelling, simulation and verification (Longstaff, 1991). At first, data and real-world information are collected about the system. Then, collected data are analyzed and filtered to develop empirical equations by using the

data. The developed equations predict the anticipate behaviour. Different models are used for specific purposes, such as a conceptual model that aids in understanding real-world problems, a graphical model used to visualize things, and a mathematical model used to explain the applied problems. Mathematical models are precise, non-ambiguous, and can be summarized to compact equations using an algorithmic approach. It helps to understand, develop scientific relationships and for decision making. Complex numerical calculations can be performed with the help of computers, and challenging research experiments can be virtually performed by computer simulation (Fort, 2020; Jian et al., 2018a).

2.4.1. Simulation

While modelling refers to the logical development of mathematical equations, simulation deals with obtaining results by applying the developed model. A simulation is a valuable tool that can be used to modify and improve the developed model. It helps understand the system and the sensitivity of various factors. Thus, simulation is a cost-effective method as extrapolation or optimization can be done instantaneously without performing actual experiments. Also, in this case, the khapra beetle does not occur in Canada and it is classified as a quarantine pest. In Canada, it requires to be maintained in a facility certified Plant Pest Containment Level 2 or 3, which there are few, making the studies difficult. Hence, computer simulation is a useful tool in predicting the prevalence of this pest under Canadian conditions with the aid of mathematical models. The simulated results are validated with the available information for verification of the developed models.

2.4.2. Ecological modelling

Krebs (1972) defines ecology as a science that deals with the distribution and abundance of living organisms and their interactions with biotic and abiotic factors. Lotka (1925) and Volterra (1926) models were the first ecological models that predict competition and predation. Since then, researchers have developed various models to study community ecology (studying the organization, function, and interactions of different species in a specific location) (Levin, 1976) and population ecology (population dynamics of one particular species). These models explain the trends in nature qualitatively and are used to explain why that pattern occurs. It also helps in predicting future behaviour or pattern that is not yet seen (Fort, 2020). Recently, modelling the population dynamics of insects have become important in studying climate change (Bale et al.,

2002; Fagan et al., 2014; Gregory et al., 2009; McLaughlin et al., 2012; Powell and Logan, 2005), protecting endangered species (Bewick et al., 2016; McLaughlin et al., 2012; Zipkin et al., 2012), global food security (Abbott and Dwyer, 2007; Gregory et al., 2009), and protect from disease (Sutherst, 2004). The published models focus primarily on the factors such as temperature, insect density and interactions with other species (Bewick, 2016). However, multiple factors should be included in insect modelling to understand the combined effects of population dynamics or climate change (Bewick, 2016; Johnson et al., 2015).

2.4.3. Population dynamics models

Population dynamics models are simplified into sub-models such as development, oviposition, and mortality. They are numerically developed by several components such as birth and death models, deterministic age-dependent models, and stochastic models of population growth (Berry, 1987). The three major types of population dynamics models include non-linear, degree-day models and distribution delay models (Jian et al. 2018a). The structure of the model can be based on individual conditions or can follow a cohort, Leslie matrix or simulation. The key factors are analyzed initially, and then unstructured models including exponential and logistic equations, discrete-time models and distribution delay models are commonly used for predicting population dynamics (Kot, 2001).

Temperature, relative humidity, stages of the insect, crowding, interactions with other species, and food supply levels are the fundamental physical parameters. Their variations can predict insect generation time and occurrence with high accuracy (Bale et al., 2002). Several empirical and semi-theoretical models have been developed based on the effect of temperature. Population dynamics models usually tend to ignore the unique morphological and biological characteristics of the individuals in a group. The contribution of an individual insect to the demographics of the population is highly variable; hence it does not depict the true nature of the population. Integrated population models were developed to reduce this gap, thereby predicting the population demographics more precisely (Bewick, 2016; Plard et al., 2019). Another approach to represent reality is to study the chaos responsible for the variation in characteristics between the lab experiments and real-world situations. As a result, complex models can be developed and validated (Jian et al., 2018b).

2.4.4. Ecological models for stored product insects

Prediction of insect development and occurrence in a grain storage ecosystem is essential for integrated pest management. Duration of storage, grain temperature, relative humidity, method of sampling, locations within the bin, the geographical location of the farm, availability of food, presence and type of dockage, insect density, sex ratio and oviposition behaviour are the factors that influence the population of insects in the stored grain products (Hagstrum, 2000; Sinha, 1975; Surtess, 1965). Ecosystem models were developed to notify the insect infestation in stored products in granaries (Kawamoto et al., 1990). Simulation models have been developed for predicting the population dynamics of stored product insects like *Cryptolestes ferrugineus* and its management (Kawamoto et al., 1989; Kawamoto et al., 1992). The approaches used in the models developed for the management of stored product insects were reviewed. A new method called the 'expert system' was designed to predict population growth and provide pest management protocols (Flinn and Hagstrum, 1990; Longstaff, 1991). Degree-day models were developed for estimating the development rates of different stored product insects and moths under different temperatures, RH, and food (Subramanyam et al., 1991; Subramanyam and Hagstrum, 1993). A simulation model was developed to predict *Rhyzopertha dominica* population distribution and density in grain bins (Flinn et al., 2004).

Linear and non-linear models developed for predicting the minimum temperature required for the development of several stored product beetles, mites, moths, and psocids were reviewed (Stejskal et al., 2019). A distribution delay model was used to compute the ageing rate and survival of adults of rusty grain beetles (*C. ferrugineus*) at various temperatures, relative humidity levels and food sources (Jian et al., 2007). Kaliyan et al. (2007) developed and validated a model for predicting the survival of larvae of Indianmeal moth (*Plodia interpunctella*) under varying low temperatures. A dynamic non-linear model was developed by Boina et al. (2008) to predict the logarithmic survival of mature larvae of *Tribolium confusum* as a function of time and temperature during heat treatments in food processing industries. Jian et al. (2013) developed new thermal death models to predict mortality of young larvae and adults of *T. castaneum* in raised temperatures during structural heat treatments, thereby characterizing thermotolerance of the insect. Bingham et al. (2017) have developed and validated a thermal death kinetic model to predict the mortality of young *Tribolium castaneum* larvae at high temperatures. Jian et al. (2018b) have developed a

new mathematical model combining key factor analysis and degree-day model to predict the population dynamics of *C. ferrugineus*. The model developed by Jian (2021) is based on the same shape concept of organisms.

2.4.5. The same shape concept

The experimental data collected at constant environmental conditions can be used to predict the population demographics at variable environmental conditions using the concepts of rate summation (Curry et al., 1978) and the same shape (Sharpe et al., 1977; Wagner et al., 1984). The same shape concept is based on the stochastic analysis of the mortality and development of an insect in response to temperature using the physiological time scale. The distribution of normalized development time of a cohort is obtained by multiplying the development time by the mean development rate of a cohort. These normalized development time distributions have the same shape under different temperatures. Figure 2.3. explains the cumulative probability distributions of development times under different temperatures and normalized distributions to form a single curve. Hence, one standard curve is used to describe the distributions at all temperatures. An insect species of the same age within a stage are grouped to form a cohort. Population dynamics can be modelled by calculating the change in population over time in each cohort. New cohorts are added by emergence from one stage into the next as well as from adult reproduction (Fig 2.4). The population is updated in each cohort at the end of the time interval and grouped based on the same physiological age to form new cohorts (Curry et al., 1978). Statistically, small variations in the same shape occur due to long sample intervals, different sample sizes and extreme temperatures. These variations can be minimized by careful experimental design and by introducing special conditions in computer programming (Wagner et al., 1984). The framework for updating the population using the numerical solution of the continuous model at discrete time increments is similar to the Leslie matrix method (Wagner et al., 1984).

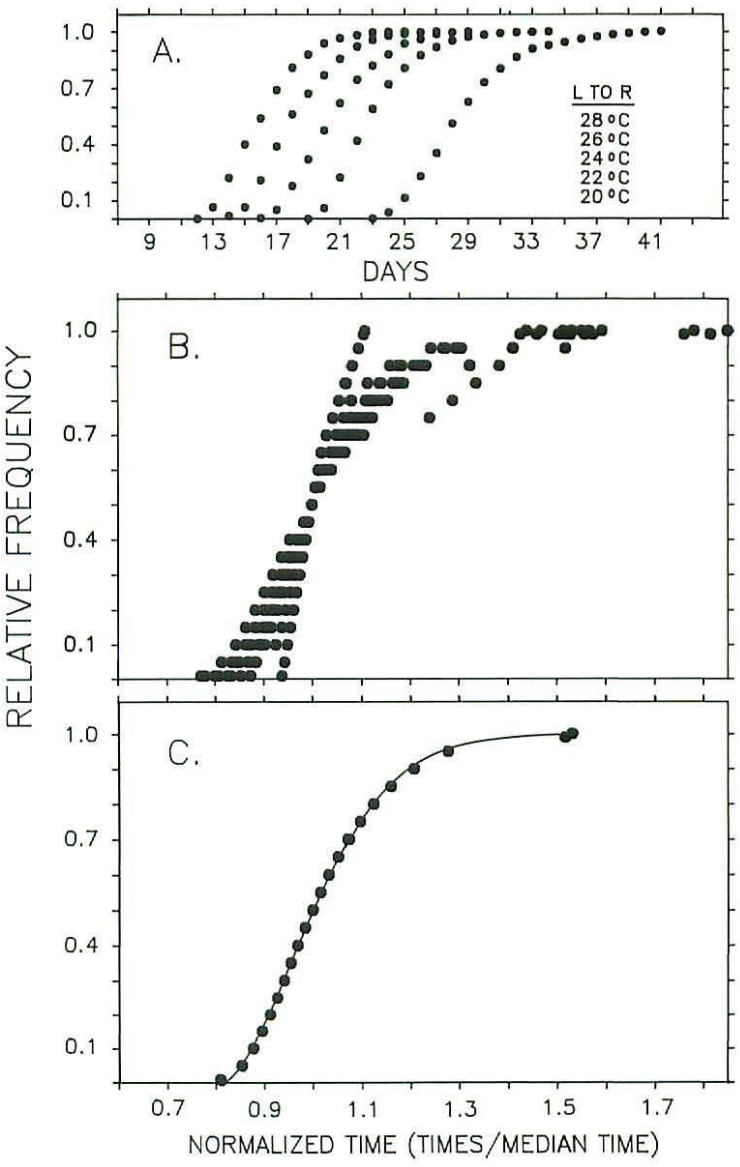

Figure 2.3. Cumulative probability distributions for the sorghum midge: (A) cumulative probability distributions of development times at five constant temperatures, (B) normalized development times at the 1st, 5th, l0th , . . . , 95th, 99th, and l00th percentile of all ten distributions in the data set, and (C) the cumulative Weibull distribution fit to the weighted mean times at each percentile. Data from Baxendale (1983). (reproduced with permission from Wagner et al., 1984)

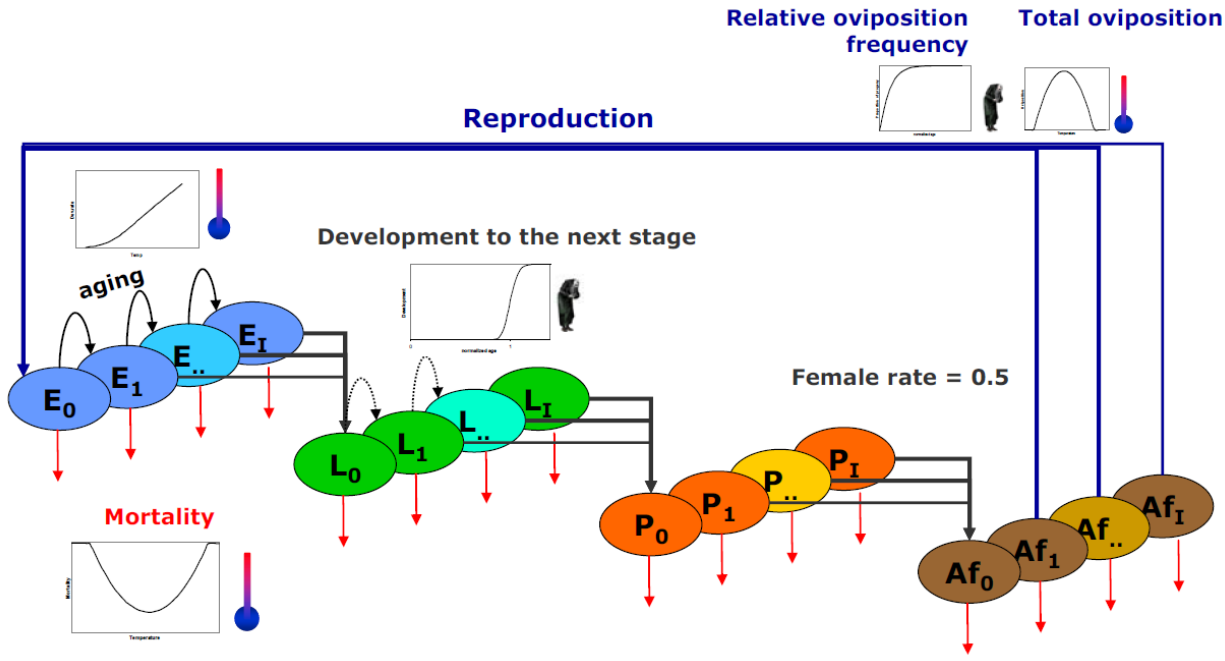

Figure 2.4. A schematic outline of population dynamics model using cohort updating method. (reproduced with permission from Sporleder et al., 2009)

2.4.6. Physi-Biological age model

Temperature is the key factor influencing the development rate at any stage of an insect. This temperature-driven development rate is modified by including other factors such as RH and food quality. The Physi-Biological age method (Jian, 2021) was used to create a population dynamics model and calculate the interaction effects of all physical factors. The assumptions made in this method are similar to the ones used in the degree-day model, but it includes the biological age of the organism in addition to the environmental conditions present in the system. The Physi-Biological age is calculated as a function of chronological or real time, rate of development under given environmental conditions and the maximum lifetime of the organism under least environmental, physical, and ecological stress. The optimum temperatures and RH for development were not considered for the maximum lifetime as insect metabolism is high at those conditions, resulting in a very short lifetime. Similarly, the environmental stress is high at extreme temperatures, therefore not considered for the calculation of maximum lifetime. The principal examples of physical stresses are food quality and diet. Insect density would be an example of ecological stress. Insect development at a particular environmental condition with the maximum lifetime is mapped to the insect development at other environmental conditions. Hence, the insect

development time is distributed for any environmental conditions using the calculated Physi-Biological time and it is based on the same shape concept. This method is chosen over other modelling techniques as it is more theoretically robust and simple. Unlike other modelling techniques, this method could accurately predict the development under varying environmental conditions and its interaction effects.

2.5. Knowledge gap

A model was developed to predict the possible arriving source of khapra beetle through international shipping networks to Australia (Paini and Yemshanov, 2012). This model did not consider the biology and characteristics of the khapra beetle, as the research objective was to enhance inspection protocols at the expected points of entry. Papanikolaou et al. (2019) have published a research article on demographic analysis of khapra beetle with the combination of deterministic and stochastic models. They used the models to predict the survival and reproduction rate of the khapra beetle at different temperatures. Demographic parameters including net reproduction rate, intrinsic and finite rate of increase, mean generation time and doubling time were calculated using experimental data and exponential, Weibull, log-normal and log-logistic models. This model did not consider the conditions outside the optimal temperature range and factors such as relative humidity. In Canada, mean daily temperatures are mostly less than 30°C. Hence it is vital to develop a model that can predict the demographics of the khapra beetle under Canadian conditions. Also, modelling individual stages of growth and the diapause characteristics of larvae is inevitable to ensure safe international trade and understanding the effects of climate change.

2.6. Objectives

The objectives of this study were to:

1. Collect pertinent information and identify primary factors influencing the demographics of *T. granarium.*
2. Develop mathematical models to predict the population dynamics of *T. granarium.*
3. Validate the developed mathematical models using the literature data.
4. Predict whether *T. granarium* can survive Canadian grain storage conditions by conducting a simulation using the validated models.

3. METHODOLOGY

3.1. Data used to develop the model

Based on the literature review, temperature, and relative humidity (RH) are the two most significant factors affecting the development and mortality of the khapra beetle. Food quality is another factor that affects the development of larvae. Hence, the present work considered only these three factors for the development of models. I assumed that factors such as insect density and photoperiod would not significantly influence the development and mortality of the khapra beetle, and these factors were not considered in the developed models in this study. These factors could be considered in future models. Various studies have investigated the effect of different temperature and relative humidity ranges on population growth and mortality. For the model development of mortality and development time of four stages, i.e., egg, larva, pupa, and adult of the khapra beetle; at the various temperatures from 20°C to 40°C, I used data from Riaz et al. (2014). Data published by Hadaway (1956) were used to model the effect of RH. Diapause induction and termination data published by Burges (1963) and Shivananjappa et al. (2020) were used to model diapausing larvae. Additional data provided by Wilches et al. (2017) and Wilches et al. (2019) for larval mortality at extreme temperatures were used for model development. The developed models were calibrated and then validated by using the data from other published sources.

3.2. General procedure of model development

It was assumed that the sex ratio of khapra beetles was 1:1 (Rahman et al., 1943). The development rate and mortality of females are the determining steps in producing eggs as the males can mate with several females and would not be a limiting factor. Therefore, the lifespan and mortality of female adults were used for developing the model. Multiple regression was conducted to fit the above-mentioned data. Appropriate equations were chosen based on the physical meaning of parameters used in the regression equations, coefficient of determination (R^2), number of arbitrary parameters and significance of each parameter. The equation with the highest R^2 and the smallest number of parameters was chosen provided the equation had a physical meaning. Linear regression was used to compare the predicted values and measured values. A slope close to 1 represents the agreement between the measured and predicted values. The model underestimates or overestimates if the slope is significantly greater than or less than one, respectively.

Physi-Biological age was calculated by using the method developed by Jian (2021) as:

$$B_n = B_{n-1} + \sum_{t=0}^{t} RM\Delta t \quad (1)$$

Where

B_{n-1} and B_n are the Physi-Biological age at t-1 and t chronological time respectively (Physi-Biological time scale, d).

R is the mean rate of development under a given environmental condition (chronological time scale, d^{-1}).

M is the maximum lifespan under the least environmental, physical, and biological stress (chronological time scale, d).

Here, temperature and RH are considered environmental stress. Published experimental data on mean development rate versus constant temperatures were regressed. This equation gives the mean development rate for an insect cohort per unit time at a given temperature, or the fraction of development completed per unit time. These fractions are accumulated under different temperatures on each day and are used as the independent variable in the normalized probability function. The normalized function estimates the fraction of the cohort that completes development at each accumulated rate. In summary, the development rate model determines the speed of cohort development as a function of temperature, and the normalized probability function determines the proportion of the cohort completing development as a function of accumulating rates.

3.2.1. Adult mortality model

The mean ageing rates of the adult khapra beetle from 15°C to 45°C at 60 ± 5% RH (Riaz et al., 2014) were regressed using a quadratic equation (Eq. 2) as the data followed a U – shape:

$$AR_T = a_1 - (0.0128 \times T) + (b_1 \times T^2) \quad (2)$$

Where AR_T is adult ageing rate (d^{-1}); T is the temperature (°C); a_1 and b_1 are constants (Table 3.1).

The mean ageing rate of adult beetles at 2% to 73% RH and 25°C to 40°C were published by Hadaway (1956). The ratio of the mean ageing rate at 60% RH to the mean ageing rate at other RH was calculated at each temperature. An exponential decay equation (Eq. 3) was used to regress the ratio of adult ageing rate:

$$AR_\phi = a_2 \times \exp(-0.005 \times \phi) \quad (3)$$

Table 3.1 Value of constants in the developed models for *Trogoderma granarium*

Eq. #	Model	Parameters	R^2
2	[1]T on adult ageing rate (AR_T)	a_1 = 0.2345±0.0036; b_1 = 0.0002±0.0000	0.956
3	[2]RH on adult ageing rate (AR_ϕ)	a_2 = 1.3965±0.0169	0.974
5	Cumulative adult mortality ($AM_{T\phi}$)	a_3 = 20.0000±0.0240; b_3 = 2.9395±0.0211	0.999
8	T on oviposition number (O_T)	a_4 = 31.1956±0.3532	0.972
9	RH on oviposition number (O_ϕ)	a_5 = 1.0006±0.0158; b_5 = 61.9034±1.6865	0.953
10	[3]B_n on oviposition number (O_B)	a_6 = 1.0055±0.0024; b_6 = 1.7852±0.0199; c_6 = 12.0294±0.0235	0.999
11	T on egg development rate (ER_T)	a_7 = 32.2344±0.6925	0.864
12	Cumulative egg hatching ($EH_{T\phi}$)	a_8 = 100.3890±0.1457. b_8 = 30.6514±0.0166; c_8 = 1.8382±0.0142	0.999
15	T on egg mortality (EM_T)	a_9 = -0.3491±0.0008	0.972
16	RH on egg mortality (EM_ϕ)	a_{10} = 1.2486±0.0215	0.871
17	B_n on egg mortality (EM_B)	a_{11} = 1.0968±0.0316; b_{11} = 10.1134±0.4282; c_{11} = 24.2404±0.7555	0.992
18	T on larva development rate (LR_T)	a_{12} = 25.4533±0.6555; b_{12} = 0.0530±0.0037; c_{12} = 34.6305±1.1122	0.974; 0.752
19	RH on larva development rate (LR_ϕ)	a_{13} = 0.6349±0.0090	0.988
22	Cumulative larval life ($LL_{T\phi}$)	a_{14} = 35.1205±0.0144; b_{14} = 1.7637±0.0127	0.999
25	T on larva mortality (LM_T)	a_{15} = -0.3385±0.0046; b_{15} = 0.0052±0.0001	0.941
26	RH on larva mortality (LM_ϕ)	a_{16} = 0.9855±0.0009; b_{16} = 1.0444±0.0019	1.0000
28	B_n on larva mortality (LM_B)	a_{17} = 1.0956±0.0305; b_{17} = 10.7861±0.442; c_{17} = 25.8640±0.7799	0.992
30	T on pupa development rate (PR_T)	a_{18} = 0.1291±0.0033; b_{18} = 32.5965±0.4274	0.943
31	Cumulative pupal life (PL_T)	a_{19} = 12.3500±0.0153; b_{19} = 1.1758±0.0134	0.999
34	T on pupa mortality (PM_T)	a_{20} = -0.7074±0.0068; b_{20} = 0.0114±0.0002	0.996
35	B_n on larva mortality (PM_B)	a_{21} = 1.1249±0.0508; b_{21} = 4.2830±0.2789; c_{21} = 10.1655±0.4962	0.993

[1]T – effect of temperature; [2]RH – effect of RH; [3]B_n – effect of Physi-Biological age.

Where $AR\phi$ is the ratio of adult ageing rate (day/day) at different RH; ϕ is RH (%), and a_2 is a constant (Table 3.1).

From Eqs. 1 and 2, the ageing rate of adults at any temperature and RH ($AR_{T\phi}$) can be calculated as:

$$AR_{T\phi} = AR_T \times AR_\phi \quad (4)$$

The mean maximum lifespan of female adults was 19.6 d, at 60% RH and 25°C (Riaz et al., 2014); therefore, the M of adults was assumed to be 20 d. Physi-Biological age (B_n) of adults at 25°C and 60% RH were calculated using Eqs. 1 to 4 and regressed with their corresponding cumulative mortalities:

$$AM_{T\phi} = \frac{100}{1 + e^{-\frac{B_n - a_3}{b_3}}} \quad (5)$$

Where $AM_{T\phi}$ is the cumulative percentage of mortality of adults at B_n at any temperature and RH; a_3 and b_3 are constants (Table 3.1). Eq 5, which was developed using the mortality of adults at 25°C and 60% RH, was used to calculate adult mortalities at any temperature and RH (Jian, 2021).

3.2.2. Oviposition model

Based on the oviposition data published by Yadav and Srivastava (2017), females lay eggs for 60% of their total lifespan at 30°C and 60% RH. Hence, the Physi-Biological age at this condition was calculated. It was assumed that female beetles could lay eggs up to 24 d of their Physi-Biological age (B_n). B_n for adults was calculated from the Eqs. 1 to 4 and regressed using a linear equation with the cumulated number of oviposition (O_{CN}) at the given condition:

$$O_{CN} = b_o \times B_n \quad (6)$$

Where b_o is the slope of the regression equation for oviposition and was further assumed as:

$$b_o = O_T O_\phi O_B \quad (7)$$

Where O_T, O_ϕ and O_B are the effects of temperature, RH and Physi-Biological age on oviposition, respectively.

It was assumed that $O_\phi = O_B = 1$, therefore calculated b_o (= O_T) was regressed with the reported temperatures at 60 ± 5 % RH (Riaz et al., 2014; Burges, 2008), and the Gaussian peak equation was the best found:

$$O_T = 3.6 \times \exp\left(-0.5 \times (T - a_4)/5.3\right)^2 \quad (8)$$

Where a_4 is a constant given in Table 3.1.

Odeyemi and Hassana (1993) published the cumulated number of eggs laid per female at various temperatures and RH combinations from 27 to 35°C and 20 to 100% RH. The ratio of b_o value at different RH to the b_o value at 60% RH was calculated and regressed. The three-parameter Gaussian peak equation was the best equation found to estimate the O_ϕ at different RH:

$$O_\phi = a_5 \times \exp\left(-0.5 \times (\phi - b_5)/52\right)^2 \quad (9)$$

Where a_5 and b_5 are the parameters presented in Table 3.1.

Initialize $O_B = 1$ at 30°C and 60% RH and calculate O_{CN}. The ratio between this calculated O_{CN} and the reported cumulated number of oviposition was calculated. This ratio was regressed with B_n to predict the effect of Physi-Biological age on oviposition number (O_B):

$$O_B = \frac{a_6}{1 + e^{-\frac{B_n - b_6}{c_6}}} \quad (10)$$

Where a_6, b_6 and c_6 are constants (Table 3.1).

The calculated O_T, O_ϕ and O_B from the above equations were substituted in Eq. 6 to calculate the cumulated number of eggs laid per female at any temperature and RH.

3.2.3. Egg development model

Riaz et al. (2014) have studied the time required for eggs to hatch into larvae at different temperatures from 20 to 40°C at 60 ± 5 % RH. Mean egg development rate (ER_T) was the reciprocal of mean egg development time and was calculated at different temperatures using these published data. The calculated ER_T was regressed with the reported temperatures using a quadratic equation:

$$ER_T = \frac{0.15}{1 + \left(T - a_7/6\right)^2} \quad (11)$$

Where a_7 is a constant given in Table 3.1.

Hadaway (1956) found that there was no significant effect of humidity on the egg hatching time. The maximum egg incubation time was 30.6 d at 40°C and 60% RH (Riaz et al., 2014).

Physi-Biological age (B_n) of eggs at 40°C and 60% RH were calculated using Eqs. 1 and 11 and regressed with their corresponding cumulative hatching percentage:

$$EH_{T\phi} = \frac{a_8}{1 + e^{-\frac{B_n - b_8}{c_8}}} \quad (12)$$

Where $EH_{T\phi}$ (%) is the cumulative hatching percentage of eggs at B_n at any temperature and RH; a_8, b_8 and c_8 are constants (Table 3.1). Equation 12 was used to calculate the cumulative hatching percentage of eggs at any temperature and RH.

3.2.4. Egg mortality model

The maximum mortality is achieved when the Physi-Biological age of the egg reaches 44 d at 20°C and 60% RH (Riaz et al., 2014). The published cumulated egg mortalities were regressed with the respective calculated B_n of the egg by using the method published by Jian (2021) as:

$$EM_{Cumulated} = b_e \times B_n \quad (13)$$

Where, b_e is the slope of the regression equation for mortality of egg and $EM_{Cumulated}$ is the cumulated mortality of eggs at the given temperature and RH and was further assumed as:

$$b_e = EM_T EM_\phi EM_B \quad (14)$$

Where EM_T, EM_ϕ and EM_B are the effects of temperature, RH and Physi-Biological age on egg mortality, respectively.

Assuming $EM_\phi = EM_B = 1$, the calculated b_e (= EM_T) values were regressed with the reported temperatures at 60 ± 5% RH (Riaz et al., 2014) using the quadratic equation:

$$EM_T = 5.1 + a_9 T + (0.006 \times T^2) \quad (15)$$

Where parameter a_9 is a constant (Table 3.1).

The total egg mortality at several temperatures and RH combinations were published by Hadaway (1956). The ratio of b_e at various RH to b_e at 60% RH was calculated at each temperature and regressed with the reported RH using a linear model.:

$$EM_\phi = a_{10} - (0.004 \times \phi) \quad (16)$$

Where the parameter a_{10} is presented in Table 3.1.

It was assumed that EM_B = 1 at 40°C and 60% RH and $EM_{Cumulated}$ was calculated. The ratio between this calculated $EM_{Cumulated}$ and the reported cumulated mortality was calculated. This ratio was regressed with B_n to predict the effect of Physi-Biological age on cumulated mortality (EM_B):

$$EM_B = \frac{a_{11}}{1 + e^{-\frac{B_n - b_{11}}{c_{11}}}} \quad (17)$$

Where a_{11}, b_{11} and c_{11} are constants (Table 3.1).

The calculated EM_T, EM_ϕ and EM_B from the above equations were substituted in Eq. 14 to calculate the cumulated mortality of egg at any temperature and RH.

3.2.5. Larval development time model

The time required for the newly emerged larvae to pupae was studied by Riaz et al. (2014) at 25 to 40°C and 60 ± 5% RH. Wilches et al. (2017) reviewed the survival rates of diapausing larvae at sub-zero temperatures from 0 to -20°C and Wilches et al. (2019) at 45 to 60°C. The larvae go into diapause below 25°C and above 40°C after 40 d from hatching. The model did not account for the number of instars for the calculation of larval development time. The larva mean development rate (LR_T) was calculated and regressed with the reported temperatures using the Gaussian peak equation:

$$LR_T = \begin{cases} 1/[276 + (a_{12} \times T) + (0.6 \times T^2)] & T < 25°C \\ b_{12} e^{\left[-0.5\left(\frac{T - c_{12}}{8.2}\right)^2\right]} & 25°C \leq T \leq 40°C \\ 1/[55.7660 + (-1.1124 \times T)] & T > 40°C \end{cases} \quad (18)$$

Where the parameters a_{12}, b_{12} and c_{12} are given in Table 3.1.

Using the published data for the larval development time at different temperatures and RH combinations (Hadaway, 1956), the ratio of larval development time at other RH to larval development time at 60% RH was calculated at different temperatures from 25°C to 40°C. The calculated ratio of larval development time ($LR\phi$) was regressed with the reported RH using the exponential rise equation:

$$LR_\phi = a_{13} + (0.4 \times (1 - \exp(-0.03 \times \phi)) \quad (19)$$

Where the parameter a_{13} is given in Table 3.1.

Using the data published by Shivananjappa et al. (2020), the effect of food quality on cumulative pupation of larvae was calculated using the exponential rise equation:

$$LR_F = 1.1453 \times (1 - e^{-0.02 \times F}) \quad (20)$$

Where LR_F represents the effect of food quality (% fresh food) on the development of larvae, and F represents the percentage of fresh food available for the larvae.

From Eqs. 18, 19, and 20, the development rate of larvae (LR) at any temperature, RH and food quality can be calculated as:

$$LR = LR_T \times LR_\phi \times LR_F \quad (21)$$

The maximum larval development time was 35.1 d at 25°C and 60% RH (Riaz et al., 2014). Physi-Biological age (B_n) of eggs at 25°C and 60% RH were calculated using Eqs. 1 and 21 and regressed with its corresponding cumulative percentage of larval development time:

$$LL_{T\phi} = \frac{100}{1 + e^{-\frac{B_n - a_{14}}{b_{14}}}} \quad (22)$$

Where $LL_{T\phi}$ (%) is the cumulative percentage of larvae that pupate at B_n at any temperature, RH, and food quality, a_{14} and b_{14} are constants (Table 3.1).

3.2.6. Larval mortality model

The larval mortality reaches the maximum when the Physi-Biological age of the larvae reaches 47 d (Riaz et al., 2014). The published cumulated larval mortalities were regressed with the respective calculated B_n of the larvae by using the method published by Jian (2021) as:

$$LM_{Cumulated} = b_l \times B_n \quad (23)$$

Where b_l is the slope of the regression equation for egg and was further assumed as:

$$b_l = LM_T LM_\phi LM_F LM_B \quad (24)$$

Where LM_T, LM_ϕ, LM_F and LM_B are the effects of temperature, RH, food quality, and Physi-Biological age on larval mortality, respectively.

The b_l values were regressed with the respective published temperatures at 60 ± 5% RH using a quadratic equation (Riaz et al., 2014):

$$LM_T = \begin{cases} 5.7 + (a_{15} \times T) + (b_{15} \times T)^2 & 25°C \leq T \leq 40°C \\ 2.13 & T < 25°C \text{ and } T > 40°C \end{cases} \quad (25)$$

Where parameters a_{15} and b_{15} are constants (Table 3.1).

The total mortality of larvae at several temperatures and RH combinations was published by Hadaway (1956). The ratio of b_l at various RH to b_l at 60% RH was calculated at each temperature and regressed with the reported RH using the exponential decay equation:

$$LM_\phi = a_{16} + b_{16} \times \exp(-0.06 \times \phi) \quad (26)$$

Where the parameters a_{16} and b_{16} are given in Table 3.1.

The effect of food quality on larval mortality (LM_F) was published by Shivananjappa et al. (2020):

$$LM_F = 12.4332 \times e^{(-0.04 \times x)} \quad (27)$$

It was assumed that $LM_B = 1$ at 25°C and 60% RH to calculate $LM_{Cumulated}$ using Eq. 24. The ratio between this calculated $LM_{Cumulated}$ and the reported cumulated larval mortality was calculated. This ratio was regressed with B_n of larvae to predict the effect of Physi-Biological age on cumulated mortality (LM_B):

$$LM_B = \frac{a_{17}}{1 + e^{-\frac{B_n - b_{17}}{c_{17}}}} \quad (28)$$

Where a_{17}, b_{17} and c_{17} are constants (Table 3.1).

The calculated LM_T, LM_ϕ and LM_B from the above equations were substituted in equation 24 to calculate b_1. Equation 23 was used to calculate the cumulated mortality of larvae at any temperature, RH, and food quality for both the diapausing and non-diapausing larvae.

3.2.7. Larval diapause model

It was assumed that 90% of the larvae undergo diapause when the temperature goes below 25°C and above 40°C. At these temperatures, the remaining 10% of the larvae continue in the non-diapausing state and follow the above-mentioned larval development time models. Diapause induction was assumed to be only 10% of larvae at temperatures between 25°C and 40°C (Riaz et al., 2014). Thus, the rest of the larvae follow the larval development time models.

Shivananjappa et al. (2020) studied the diapause termination of larvae that endured 3 and 14 months in diapause. Here, diapause termination refers to the emergence of pupae from larvae. Initially, the cumulative percentage of diapause termination (DT) was regressed with the Physi-Biological age of larvae when the optimal conditions were recovered, i.e., $B_{n(opt)}$ using an exponential rise equation:

$$DT = 3.4 + [\alpha \times (1 - \exp(-0.02 \times B_{n(opt)})]$$

Here, the parameter 'α' was regressed with the Physi-Biological age of the larvae that endured diapause, i.e., $B_{n(dia)}$, using a linear equation:

$$\alpha = 79 - 0.04 \times B_{n(dia)}$$

Therefore, the cumulative percentage of diapause termination was calculated as:

$$DT\ (\%) = 3.4 + (79 - 0.04 \times B_{n(dia)}) \times (1 - \exp\ (-0.02 \times B_{n(opt)}) \quad (29)$$

Where $B_{n(opt)}$ represents the Physi-Biological age of larvae when the optimal conditions recovered; $B_{n(dia)}$ represents the Physi-Biological age of the larvae that endured diapause.

3.2.8. Pupal development time and mortality model

Vir (1980) and Riaz et al. (2014) studied the pupal development time and total pupal mortalities at different temperatures. A Gaussian peak equation was regressed for pupal development rate (PR_T) with the reported temperatures between 25 to 40°C (Riaz et al., 2014):

$$PR_T = a_{18} e^{\left[-0.5\left(\frac{T - b_{18}}{8.2}\right)^2\right]} \quad (30)$$

Where the parameters a_{18} and b_{18} are given in Table 3.1. Riaz et al. (2014) found no pupal development if the temperature was below 20°C and above 40°C. Hadaway (1956) found that RH did not affect pupal development time as well as pupal mortality. Therefore, RH was not considered.

The maximum pupal development time was 12.3 d at 25°C and 60% RH (Riaz et al., 2014). Physi-Biological age (B_n) of eggs at 25°C and 60% RH were calculated using Eqs. 1 and 30. The calculated B_n was regressed with its corresponding cumulative percentage of pupal development time:

$$PL_T = \frac{100}{1 + e^{-\frac{B_n - a_{19}}{b_{19}}}} \quad (31)$$

Where $PL_{T\phi}$ (%) is the cumulative percentage of pupal development time completed at B_n at any temperature, a_{19} and b_{19} are constants (Table 3.1). Equation 31 was used to calculate the cumulative percentage of pupae that emerged into adults at any temperature (Jian, 2021).

The mortality of pupa was maximum at the Physi-Biological age of 18 d (Riaz et al., 2014). The published cumulated pupal mortalities ($PM_{Cumulated}$) were regressed with the respective calculated B_n of the pupae by using the method published by Jian (2021) as:

$$PM_{Cumulated} = b_p \times B_n \quad (32)$$

Where b_p is the slope of the regression equation for pupa and was further assumed as:

$$b_p = PM_T PM_B \quad (33)$$

Where PM_T and PM_B are the effects of temperature and Physi-Biological age on mortality of pupae.

The b_p values were regressed with the respective published temperatures at 60 ± 5% RH using a quadratic equation (Riaz et al., 2014):

$$PM_T = 11 + (a_{20} \times T) + (b_{20} \times T)^2 \quad (34)$$

Where parameters a_{20} and b_{20} are constants (Table 3.1).

It was assumed that $PM_B = 1$ at 25°C and 60% RH to calculate $PM_{Cumulated}$ using Eq. 32. Then, the ratio between this calculated $PM_{Cumulated}$ and the reported cumulated pupal mortality was calculated. This ratio was regressed with B_n of pupae to estimate the effect of Physi-Biological age on cumulated mortality (PM_B):

$$PM_B = \frac{a_{21}}{1 + e^{-\frac{B_n - b_{21}}{c_{21}}}} \quad (35)$$

Where a_{21}, b_{21} and c_{21} are constants (Table 3.1).

The calculated PM_T and PM_B from the above equations were substituted in Equations 32 and 33 to calculate the cumulated mortality of pupae at any temperature and RH.

3.3. Simulation procedure

The mathematical equations developed for different stages were validated by simulating the results at each temperature, relative humidity, and food quality combinations. The predicted values were compared with the data available in the literature. The programming language C++ was used to code this simulation. The overall procedure to simulate the population dynamics is given in Fig. 3.1. Temperature, RH, food quality, and initial insect number were the inputs on the simulated day 1 and were used to calculate the number of insects at each stage at the end of day 1. On day 2, these variables were again input, and the number of insects calculated at the end of the previous day is used as the initial insect number for the next day. The Physi-Biological age of the adults was calculated for each chronological day (time-step = 1) starting from day 1. On each day, the rate of development, Physi-Biological age, mortality, and the number of insects developing to the next stage was calculated in the same order. The estimated number of insects at each developmental stage and Physi-Biological age was updated at the end of the day before advancing to the next day. The algorithm for calculating the number of adults, eggs, larvae, and pupae each day is given in Figs. 3.2 to 3.5.

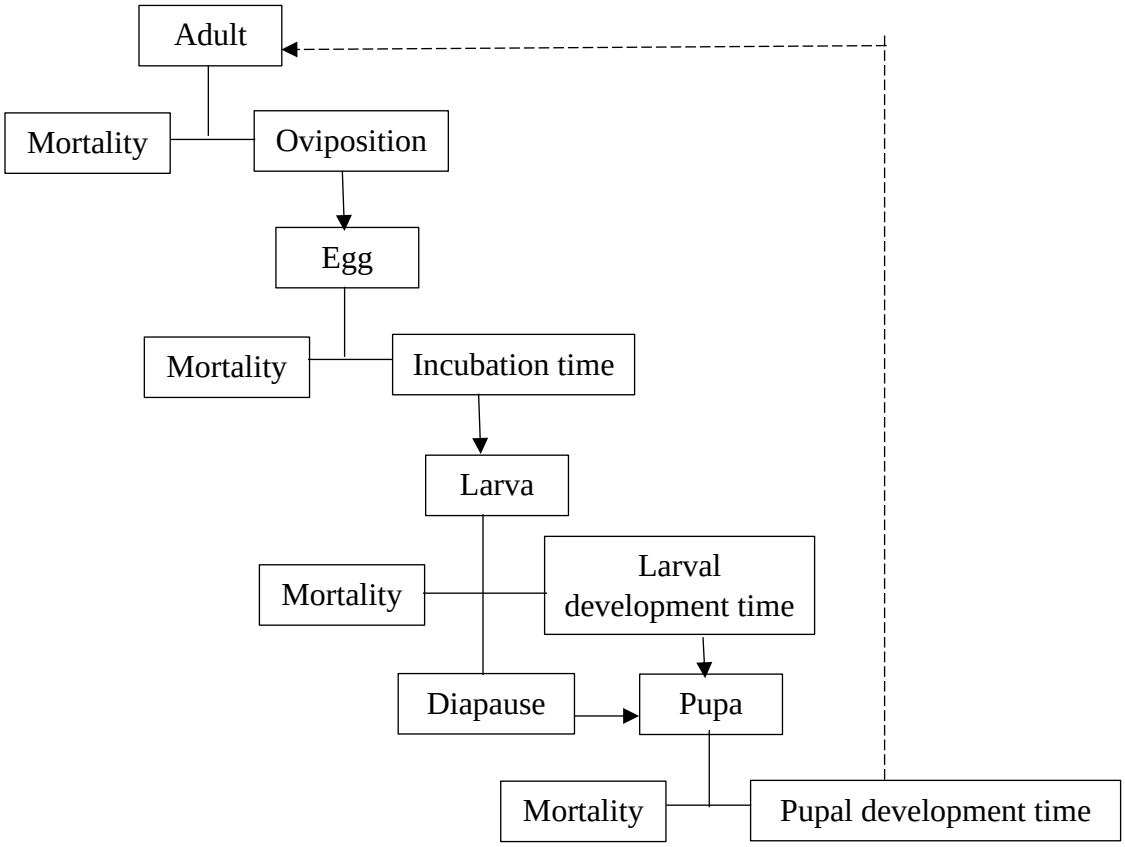

Figure 3.1. Flow chart of population dynamics of *Trogoderma granarium*

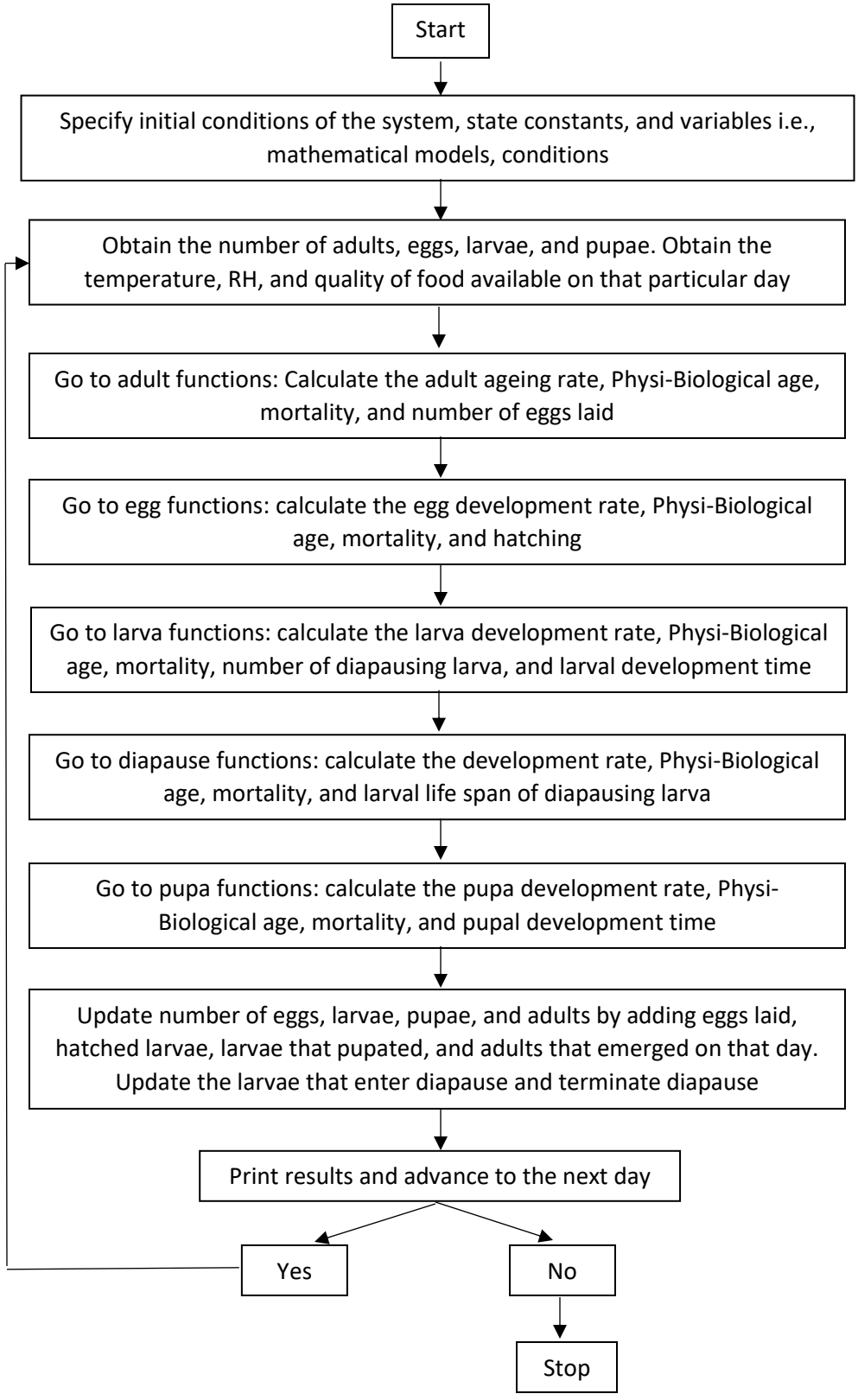

Figure 3.2. Overview of the flow of population dynamics of *Trogoderma granarium*

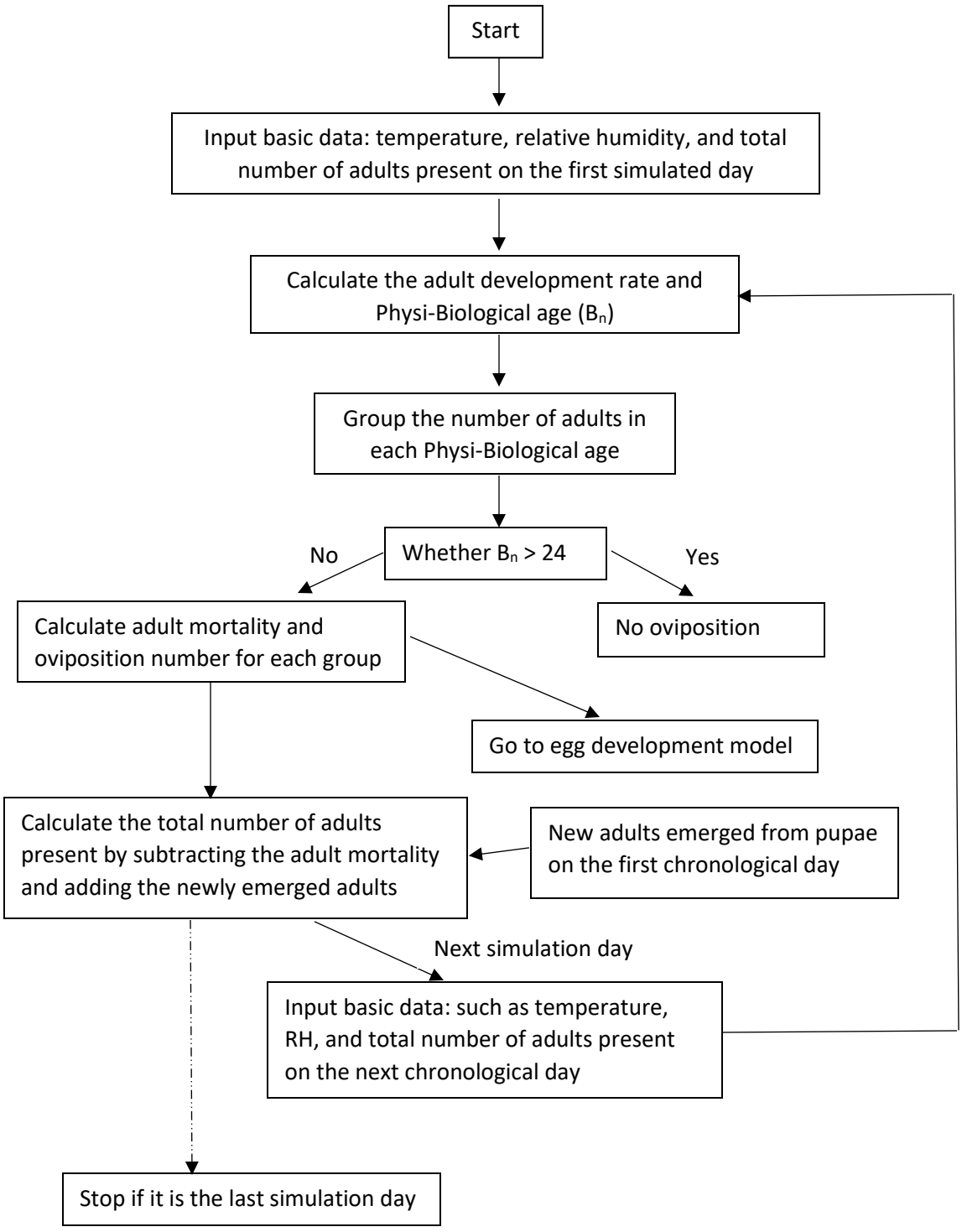

Figure 3.3. Algorithm for the calculation of the number of adults

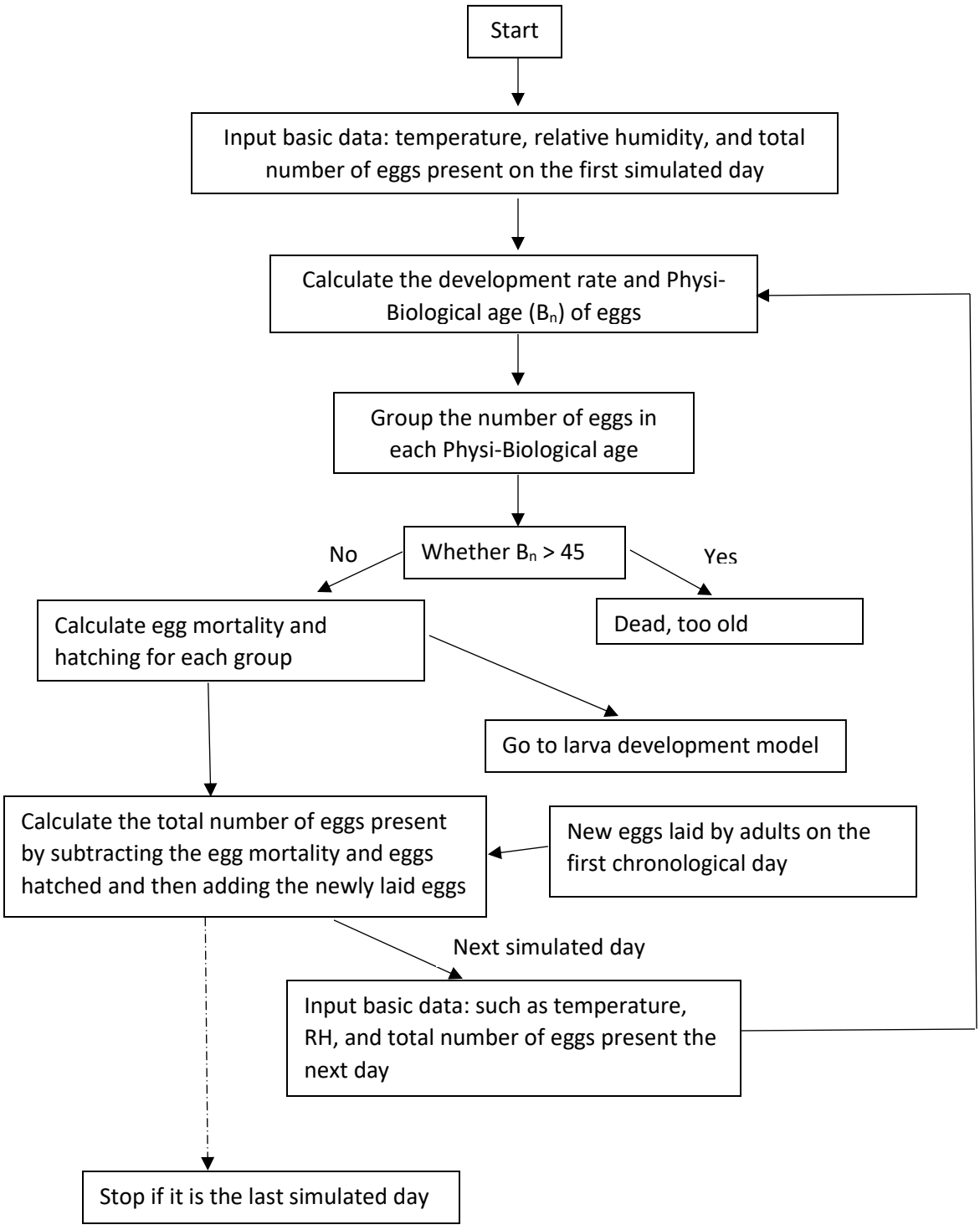

Figure 3.4. Algorithm for the calculation of the number of eggs

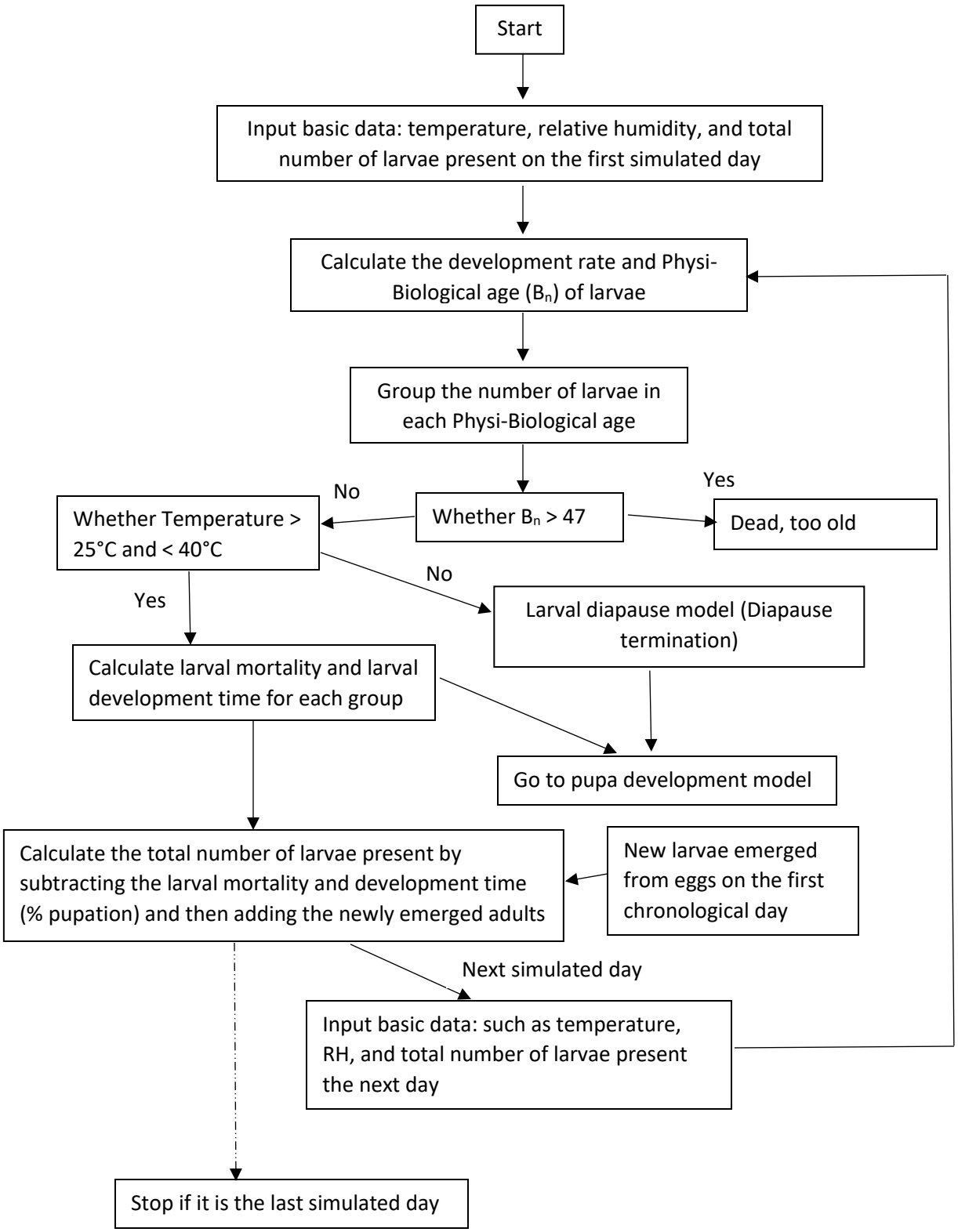

Figure 3.5. Algorithm for the calculation of the number of larvae

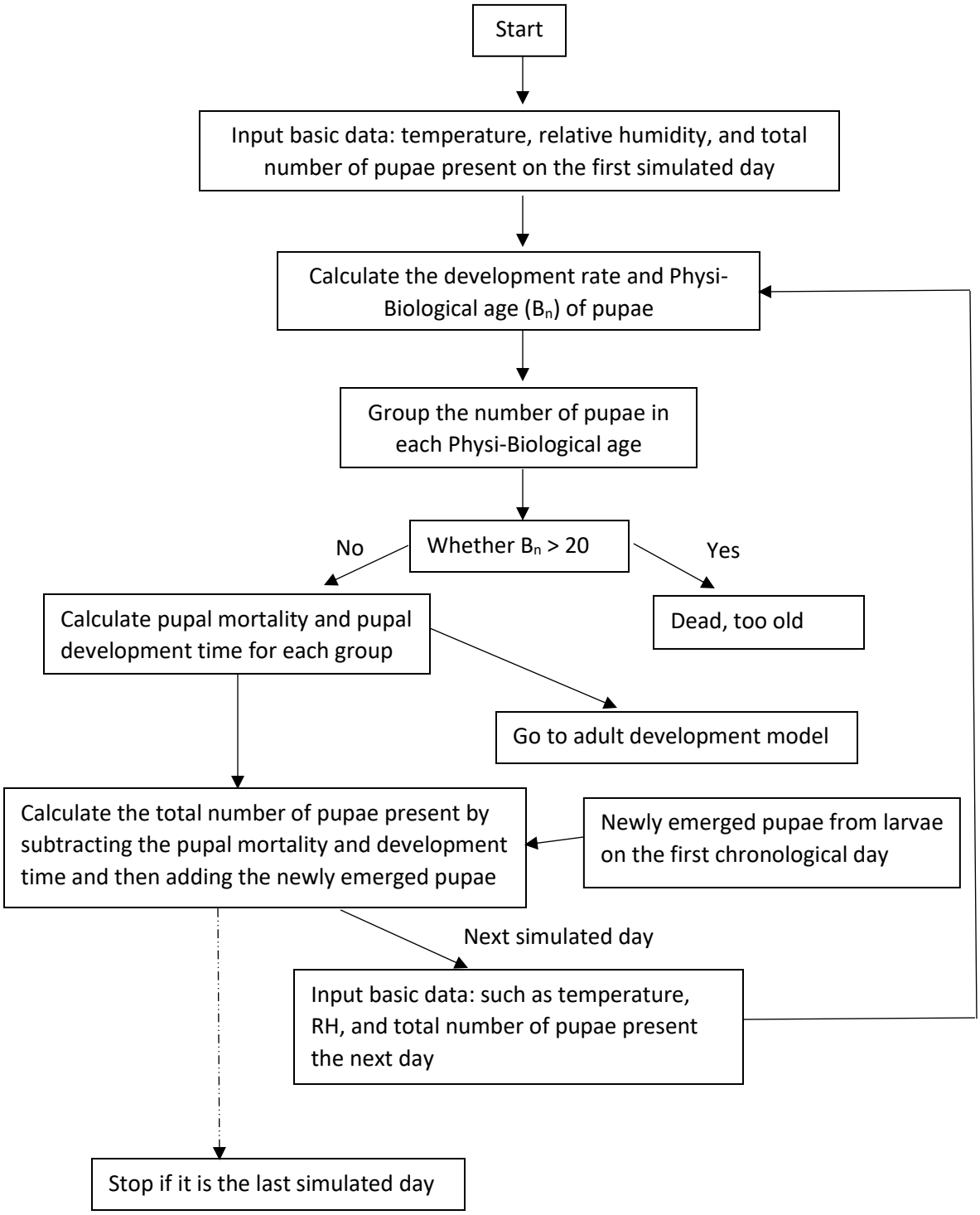

Figure 3.6. Algorithm for the calculation of the number of pupae

3.3.1. Simulation cases

The algorithms developed were coded in C++ to simulate the population dynamics of the khapra beetle in each stage of the insect (Figs. 3.2 to 3.6). Five cases were considered for simulating the population dynamics of *T. granarium* at: 1) different temperatures, i.e., -15°C, 0°C, 15°C, 30°C and 45°C.; 2) different RHs, i.e., 25% and 75%; 3) different food qualities, i.e., 25% and 75% fresh food; 4) varying temperatures and relative humidity in a given environmental condition such as grain bin; 5) conditions in the food processing facilities and warehouses. It was assumed that number of adults, eggs, larvae, and pupae available at the start to be 100 each for all the cases. The food quality was assumed to be 100% fresh throughout the first two cases. The temperature was assumed to be 30°C for the second and third cases, and 60% RH was assumed for the first and third cases. The quality of food in terms of the percentage of fresh food was considered a factor for both diapausing and non-diapausing larvae. Food quality was not considered for other stages because only larvae consume food. Different situations were considered for simulating the population dynamics in processing facilities and warehouses: 1) elevators where the temperature will be equivalent to the ambient; 2) processing areas or control rooms with constant temperatures; 3) inside the insulated or protected warehouses, feed mills, or flour mills where the temperature is modified.

3.3.2. Simulating Canadian grain storage conditions

Population dynamics of khapra beetle were simulated in a grain bin in Winnipeg, Manitoba conditions for 1 yr. The temperatures measured along the center axis of a 5.56 m diameter grain bin (Muir et al., 1980) and near the wall of a 3.76 m diameter grain bin (Jian et al., 2005) were used for the simulation. The temperature at the center was as high as 21°C during late summer following harvest and the onset of the fall period. The temperature reached 0°C at the end of winter months before gradually increasing over the spring and summertime. The wall temperatures were close to the ambient temperatures. Therefore, the grain close to the walls reached -12°C during winter. Temperatures at the wall reached slightly higher temperatures than in the center during the summer months, peaking at 27°C in July. The simulation started in September during the harvest year as the grain are usually harvested and stored in the bin during the beginning of the fall season. It was assumed that the fresh food availability is 100% throughout for simulating the conditions of a large bin.

4. RESULTS AND DISCUSSION

4.1. Model validation

4.1.1. Validation of adult mortality and oviposition number models

The model developed to predict the ageing rate of adults was verified with the literature data (Riaz et al., 2014) for a wide range of temperatures from 10 to 50°C (Fig. 4.1). The developed model predicted that the ageing rate of adult beetles was high when the temperature was below 10°C and above 50°C. Ageing rate of adult beetles reached the minimum at 30°C, and the ageing rate increases if the temperature decreases or increases gradually from 30°C, which was verified by the literature data (Burges, 2008). The cumulative percentage of mortality published by Riaz et al. (2014) was used to verify the adult mortality model calculated for the Physi-Biological age at different temperatures (Fig. 4.2). Linear regression between the predicted and measured values showed that the adult mortality models predicted the measured mortalities very well (Table 4.1).

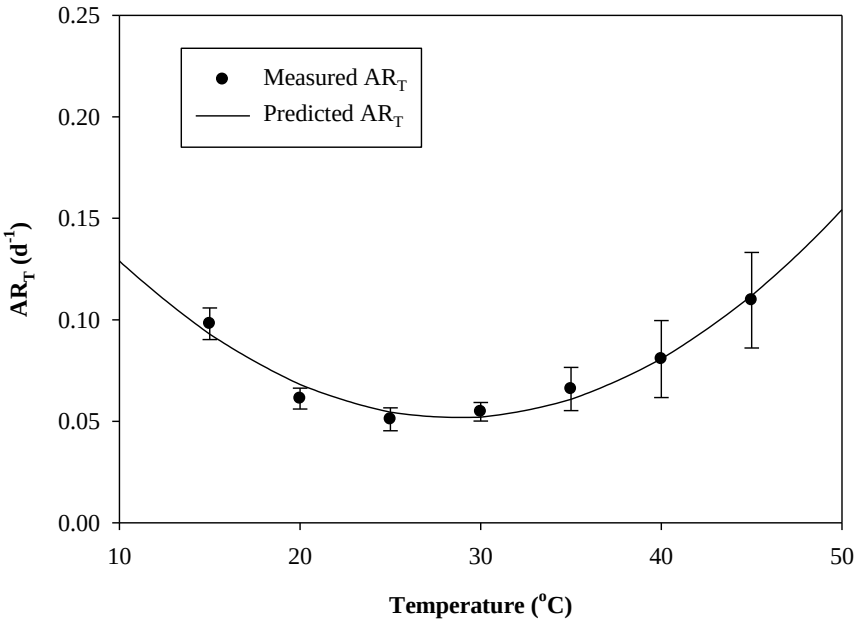

Figure 4.1. Ageing rate (AR_T) (d^{-1}) of adults at different temperatures and 60% RH. The measured AR_T was calculated from the data reported by Burges (2008).

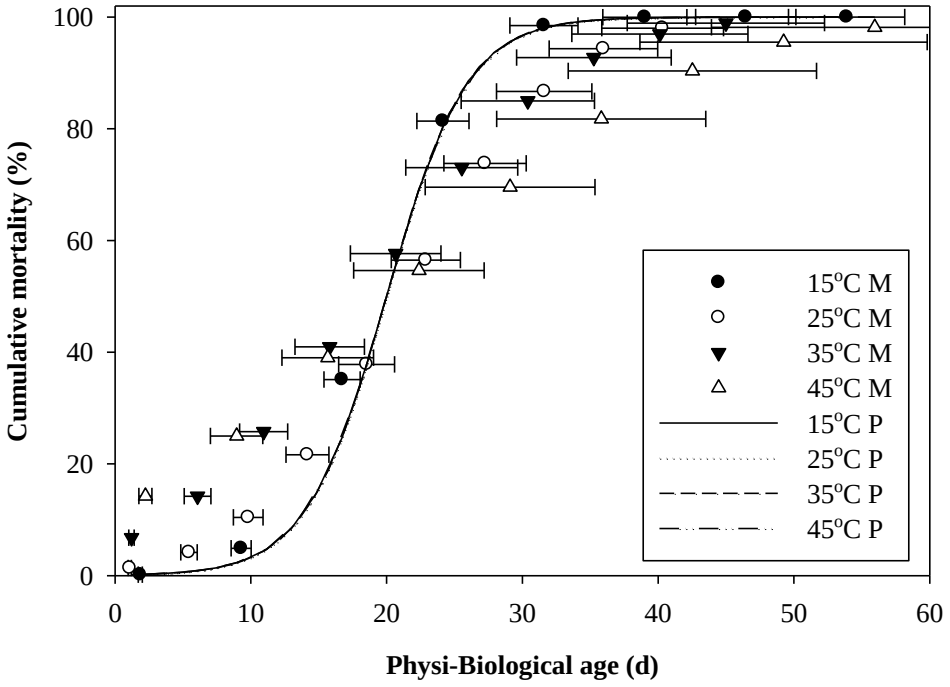

Figure 4.2. Cumulative mortality (%) of adults at different temperatures and 60% RH. In the graph, M and P are measured and predicted cumulative mortalities, respectively. The measured cumulative mortalities were calculated from the data reported by Riaz et al. (2014).

The oviposition model predicted that no eggs were laid at temperatures below 15 and over 45°C. Also, the cumulative number of eggs laid at 30°C was 80 per female, and the oviposition number decreased gradually till 20°C, which followed the measured data of Burges (2008) (Fig. 4.3). The effect of temperature and RH on oviposition models underestimated the data published by Odeyemi and Hassana (1993) at 20, 40, 60, 80 and 100% RH and 27 and 35°C; Shulov, (1955) at 0 to 100% RH and 20 to 45°C; Falah and Azher (2020) at 20 to 50% RH and 35°C (Table 4.1); the Mean Square Error (MSE) is almost negligible for the RH models on adult mortality and oviposition.

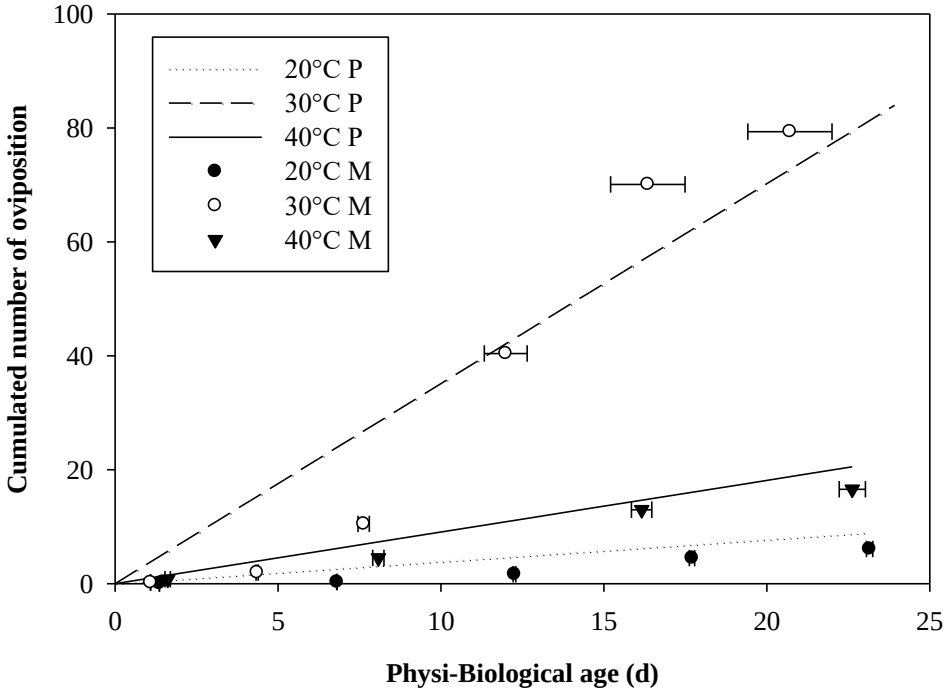

Figure 4.3. Cumulative number of eggs laid per female at different temperatures and 60% RH. In the graph, M and P are measured and predicted cumulative number of oviposition, respectively. The measured values were calculated from the data reported by Burges (2008).

4.1.2. Validation of egg development and mortality models

The data published by Voelkel (1924) were used to verify the developed models for *T. granarium* eggs. The egg development rate and cumulative percentage of hatching predicted by the equations were close to the reported values (Fig. 4.4 and 4.5). According to the developed egg mortality model, the eggs died immediately when the temperature was below 15°C or exceeded 45°C, agreeing with published data (Hinton, 1945; Yadav and Srivastava, 2017). The standard deviation (SD) was not published; hence mean mortalities were used for validating the model (Fig. 4.6). The effect of RH on the egg mortality model overpredicted the measured data. Still, the effect of temperature on egg mortality and hatching underpredicted the data published by Shulov (1955) at 0 to 100% RH and 25 to 40°C (Table 4.1). The low R^2 value was mainly due to the model overpredicted the egg hatching at the initial period.

Table 4.1 Model evaluation by linear regression between measured and predicted values

Model	Slope [a]	MSE	R^2
Adult mortality at different temperatures	0.9926±0.1266	1.4473	0.923
Adult mortality at different RHs	0.9753±0.1109	0.0012	0.975
Oviposition number at different temperatures	1.0633±0.1045	41.6756	0.972
Oviposition number at different RHs	1.0138±0.1297	0.0010	0.953
Egg mortality at different temperatures	1.0212±0.1312	24.8702	0.953
Egg mortality at different RHs	0.9158±0.2406	0.0026	0.879
Egg hatching at different temperatures	1.2261±0.6050	58.1000	0.673
Larval mortality at different temperatures	0.9867±0.0538	203.1974	0.980
Larval mortality at different RHs	1.0000±0.0018	0.0000	1.000
Larval mortality at different food qualities	0.9623±0.0536	0.2945	0.991
Larval development time at different temperatures	0.8503±0.2095	10.1717	0.846
Larval development time at different RHs	1.1167±0.0262	0.0000	0.999
Larval development time at different food qualities	0.9889±0.0261	1.0004	0.998
Larval diapause termination at different temperatures	0.9877±0.0603	47.9060	0.865
Pupal mortality at different temperatures	0.9999±0.0335	4.3634	0.997
Pupal development time at different temperatures	1.0251±0.1120	0.2190	0.966

[a] Slope value close to 1 indicates agreement between predicted and measured values. The measured values are the values reported in the literature.

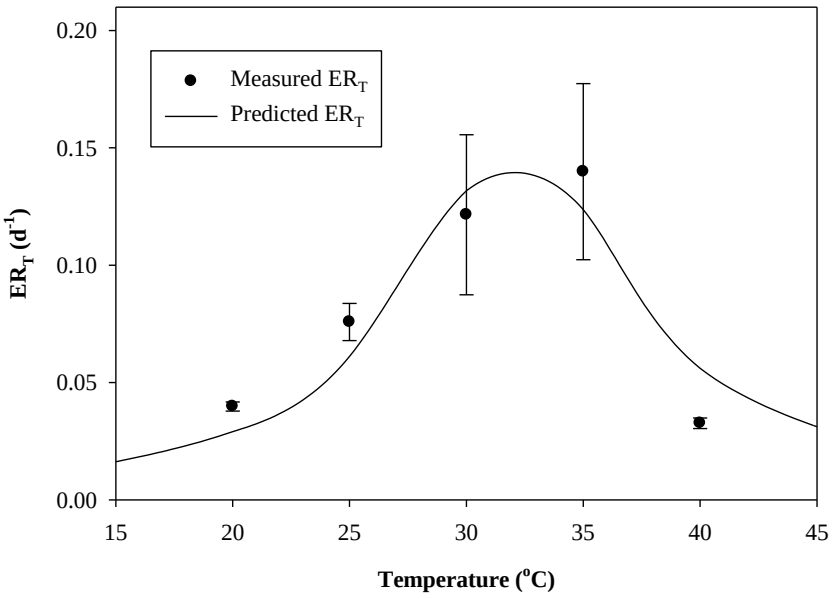

Figure 4.4. Egg development rate (ER_T) (d^{-1}) at different temperatures and 60% RH. The measured ER_T was calculated from the data reported by Voelkel (1924).

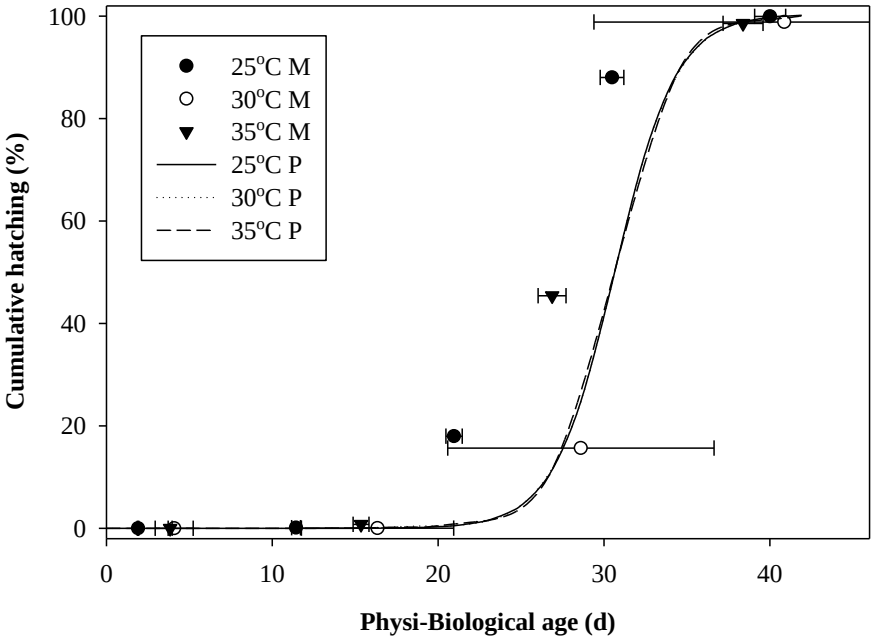

Figure 4.5. Cumulative hatching percentage of eggs at different temperatures and 60% RH. The measured values were calculated from the data reported by Voelkel (1924) and Shulov (1955).

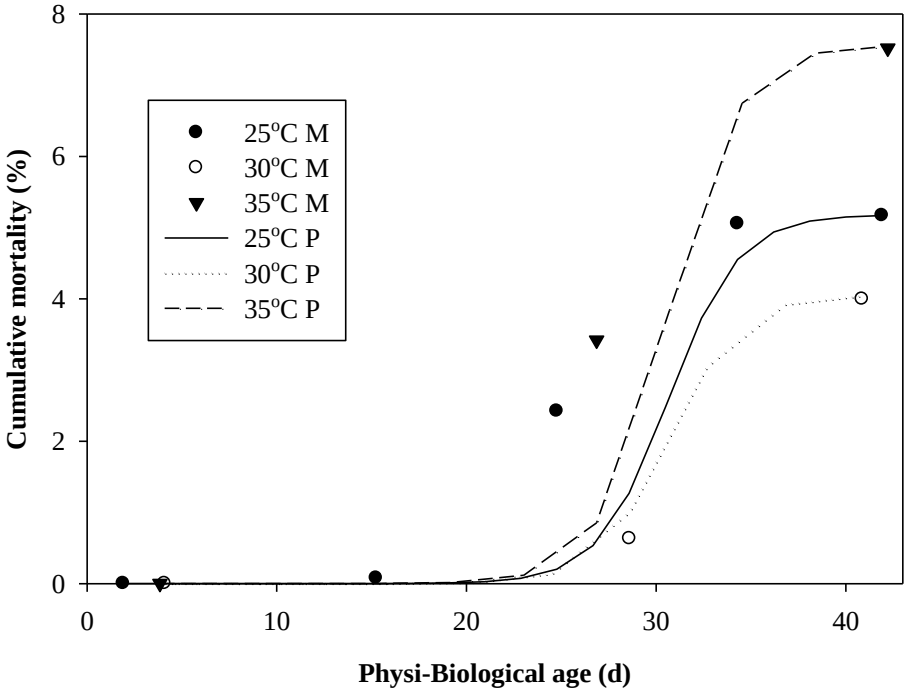

Figure 4.6. Cumulative mortality (%) of eggs at different temperatures and 60% RH. The measured values were the mean mortality values (without SD) reported by Hinton (1945); Yadav and Srivastava (2017).

4.1.3. Validation of larval development, mortality, and diapause models

The larval development rate equations at different temperatures were validated by the literature data (Fig. 4.7). The cumulative percentage of development at different temperatures was calculated for the temperatures between 25 and 40°C using the developed models, and it was close to the published data (Fig. 4.8). The larval mortality model at low temperatures such as -5°C and -15°C (Fig. 4.9) was validated using the data from the literature (Lindgren and Vincent, 1959). The model predicted the larval mortality for temperatures less than 25°C to as low as -20°C as the diapause acclimated larvae instantly die at or below -20°C (Wilches et al., 2017). For the temperatures from 25 to 40°C, the developed model was close to the data reported in the literature (Fig. 4.9) (Burges, 2008; Vir, 1980). The equation developed for the higher temperatures from 40°C to 50°C was validated using the literature data (Bains et al., 1974). The larval mortality model predicted 100% mortality at the end of day 1 if the temperature was above 50°C and below -20°C.

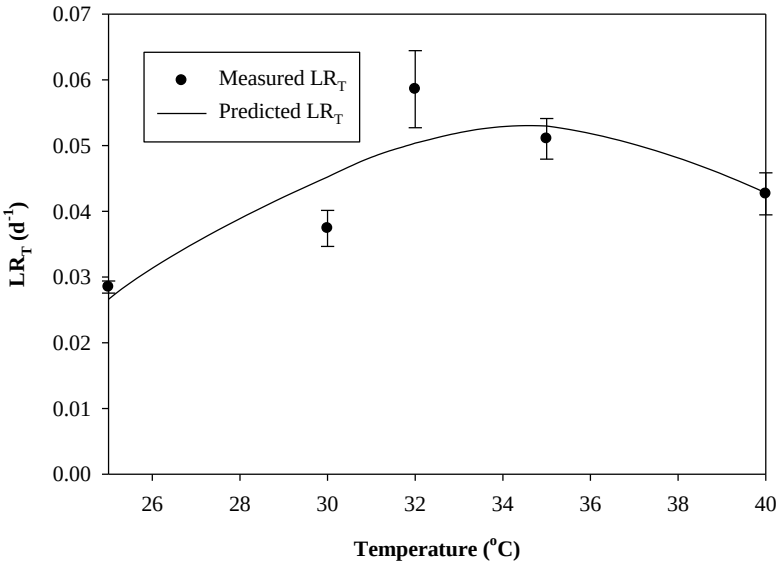

Figure 4.7. Larval development rate (LRT) (d-1) at different temperatures and 60% RH. The measured LRT was calculated from the data reported by Riaz et al. (2014).

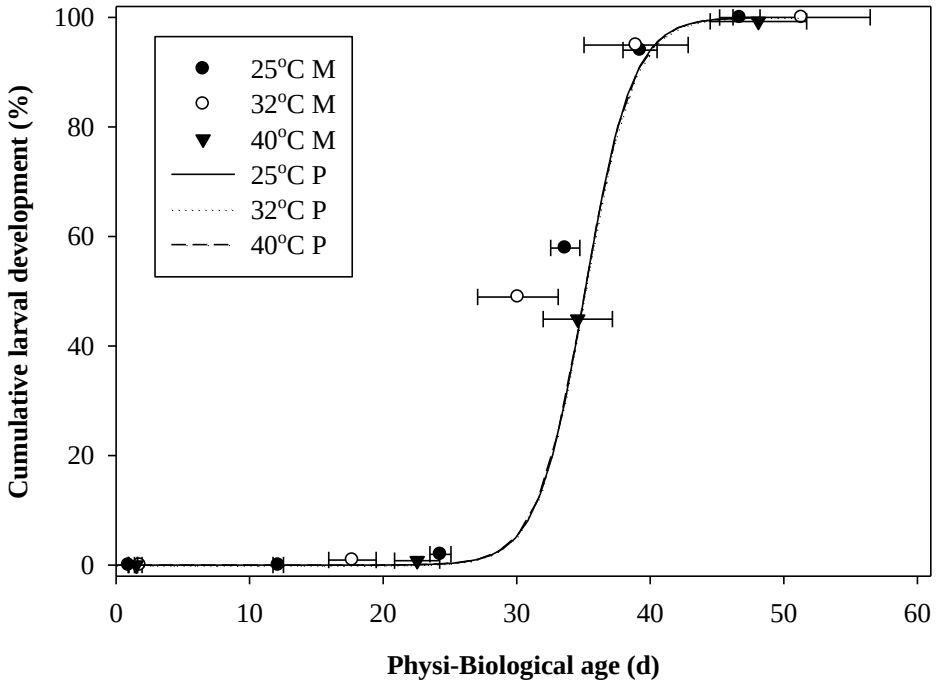

Figure 4.8. Cumulative development (%) of larvae at different temperatures and 60% RH. The measured values were calculated from the data reported by Riaz et al. (2014) and Vir (1980).

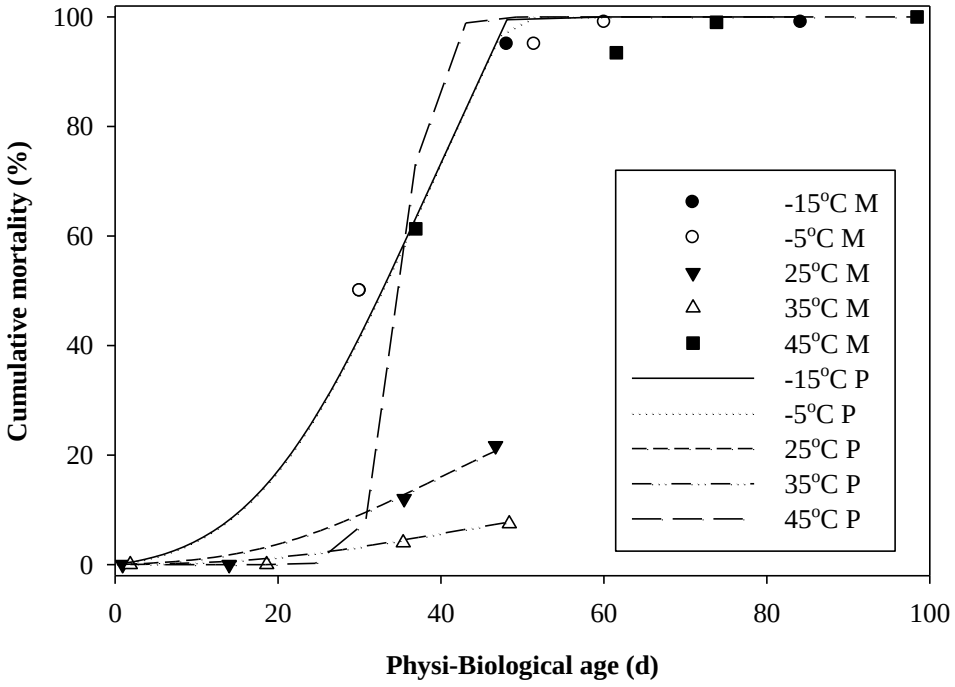

Figure 4.9. Cumulative mortality (%) of larvae at different temperatures and 60% RH. In the graph, M and P are measured and predicted cumulative mortalities, respectively. The M values were the mean mortality values (without SD) reported by Lindgren and Vincent (1959) for 25 and 35°C; Burges (2008) and Vir (1980) for -15 and -5°C; and Battu et al. (1975) for 45°C.

The effect of temperature and food quality on larval mortality and larval development time overestimated the literature data published by Odeyemi and Hassana (1993) at 20, 40, 60, 80 and 100% RH and 20, 27 and 35°C; Falah and Azher, (2020) at 20 to 50% RH and 35°C (Table 4.1) (Figs. 4.8 and 4.9). The MSE value was zero for the models to calculate the larval mortality and lifespan at different RH. The models developed for larval diapause overpredicted the published data. The duration of diapause lasts for several months or even years, thereby decreasing the model's accuracy (R^2 = 0.865) (Table 4.1). The effect of food quality on larval lifespan and mortality models were very close to the measured data from the literature (Table 4.1).

4.1.4. Validation of pupal development and mortality models

The mean development rate of pupa followed a bell shape with the maximum at 31°C. The development rate was close to zero at temperatures less than 15°C and greater than 50°C. Thus, the developed model predicted the development rate of pupa closely to match multiple sources of the published data over a wide range of temperatures (Fig. 4.10) (Vir, 1980; Voelkel, 1924; Yadav and Srivastava, 2017). The cumulative percentage of development of larvae to adults predicted by the developed models overlapped with the measured data from the literature (Fig. 4.11). The cumulative pupal mortality was close to 0 at 30°C, and it was generally less than 20% for temperatures between 20°C and 40°C. The mortality of pupae increases rapidly outside this range. The developed model predicted this trend precisely (Fig. 4.12), and it was validated for a wide range of temperatures (Saxena et al., 1992). Linear regression between the predicted and measured values showed that the developed pupal mortality model marginally overpredicted the measured data and the development time model under-predicted the measured data (Table 4.1).

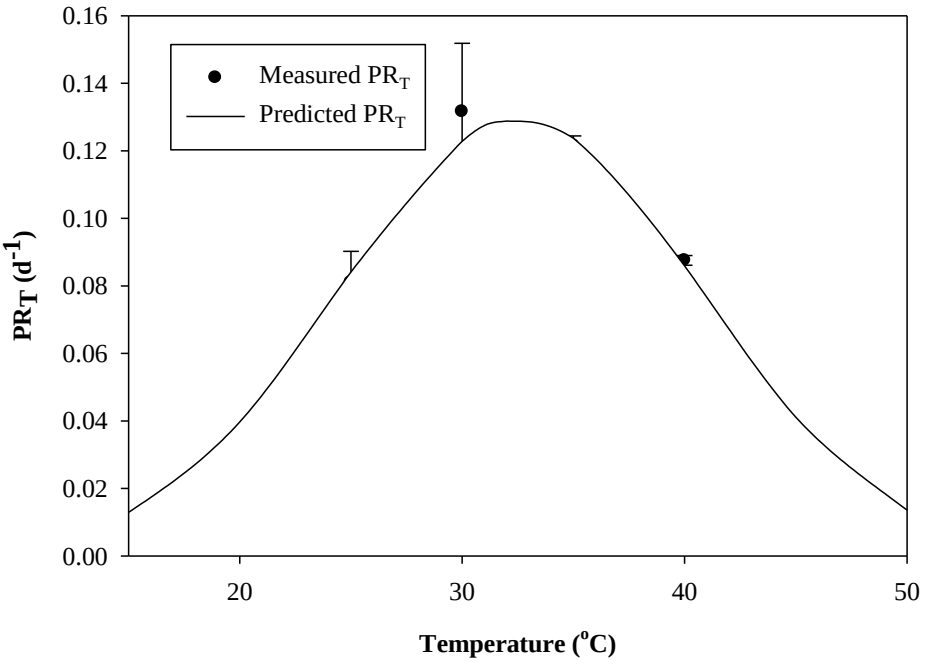

Figure 4.10. Pupal development rate (PR_T) (d^{-1}) at different temperatures and 60% RH. The measured PR_T was calculated from the data reported by Voelkel (1924), Yadav and Srivastava (2017), and Vir (1980).

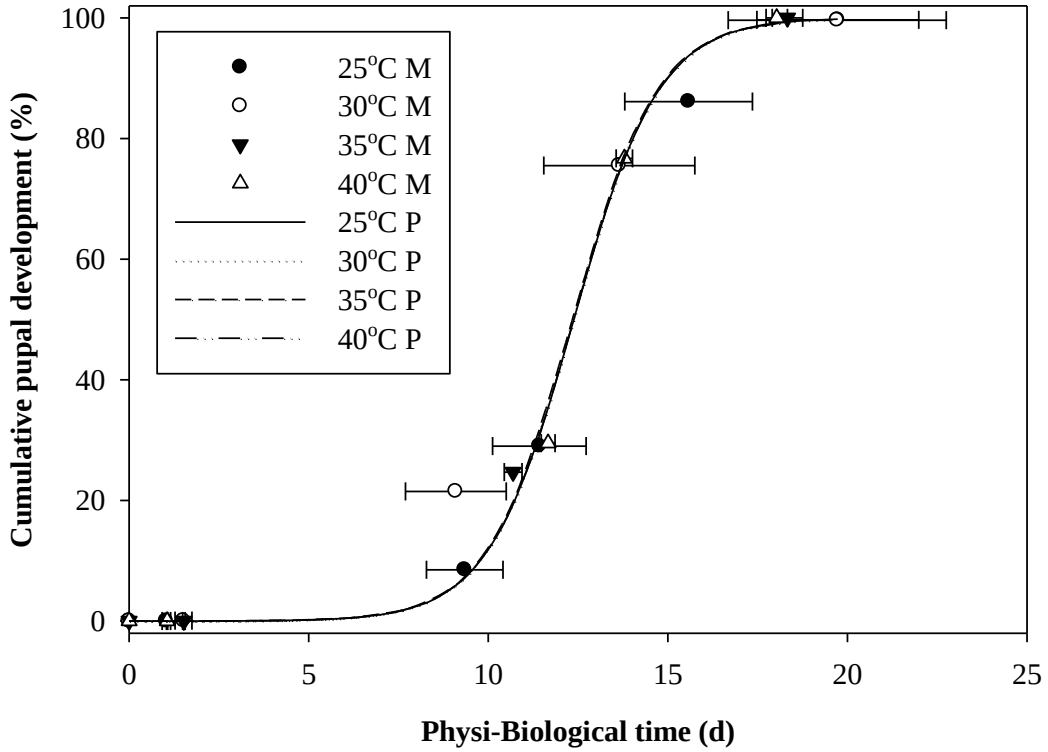

Figure 4.11. Cumulative development (%) of pupae at different temperatures and 60% RH. In the graph, M and P are measured and predicted cumulative pupal development (%). The measured cumulative mortalities were calculated from the data reported by Riaz et al. (2014).

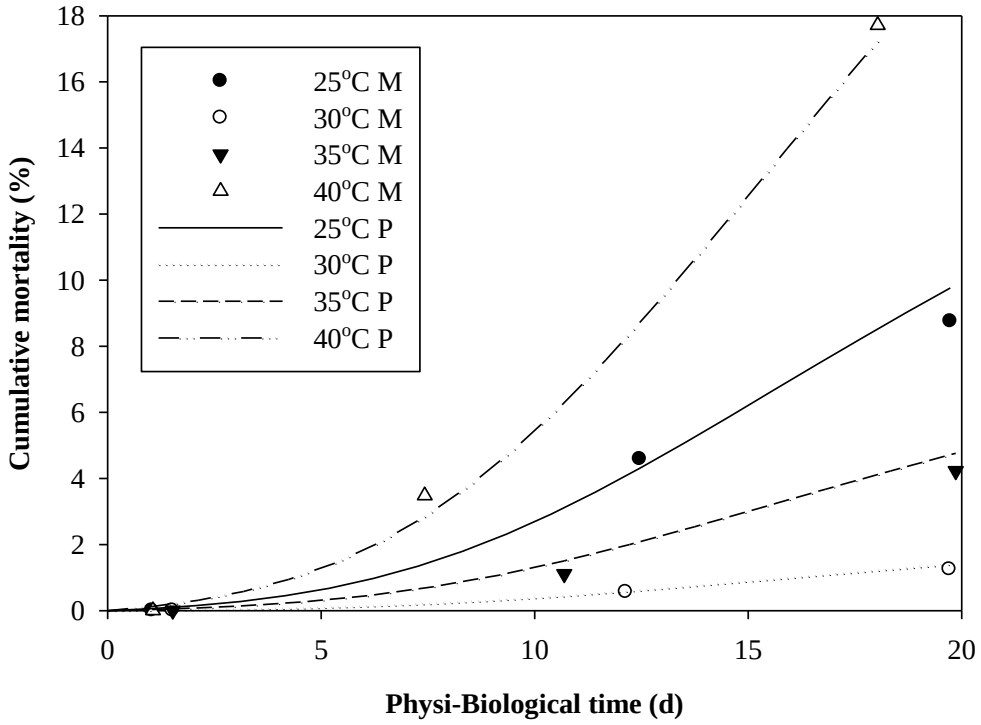

Figure 4.12. Cumulative mortality (%) of pupae at different temperatures and 60% RH. In the graph, M and P are measured and predicted cumulative mortalities, respectively. The measured mean cumulative mortalities (without SD) were reported by Saxena et al. (1992).

4.2. Simulation results

4.2.1. Simulation of population dynamics at constant temperatures

Figure 4.13 shows that the number of adults increased with an increase in time at 30°C, which resulted in the increased number of eggs and larvae. The number of non-diapausing larvae at the end of two months was higher than any other stage due to their long development time. The number of diapausing larvae was low at 30°C as the temperature is not ideal for diapause induction. The number of pupae decreased initially as the pupal development time is short and they quickly metamorphose into adults. At extreme low and high temperatures, the number of insects decreased to zero in all the stages except larva as diapause was induced at these temperatures (Fig. 4.14). The number of larvae in diapause decreased gradually with time as mortality increased. Also, it was found that mortality was higher at -20°C and 45°C than at 0°C and 15°C; therefore, the numbers started decreasing quickly at extreme temperatures.

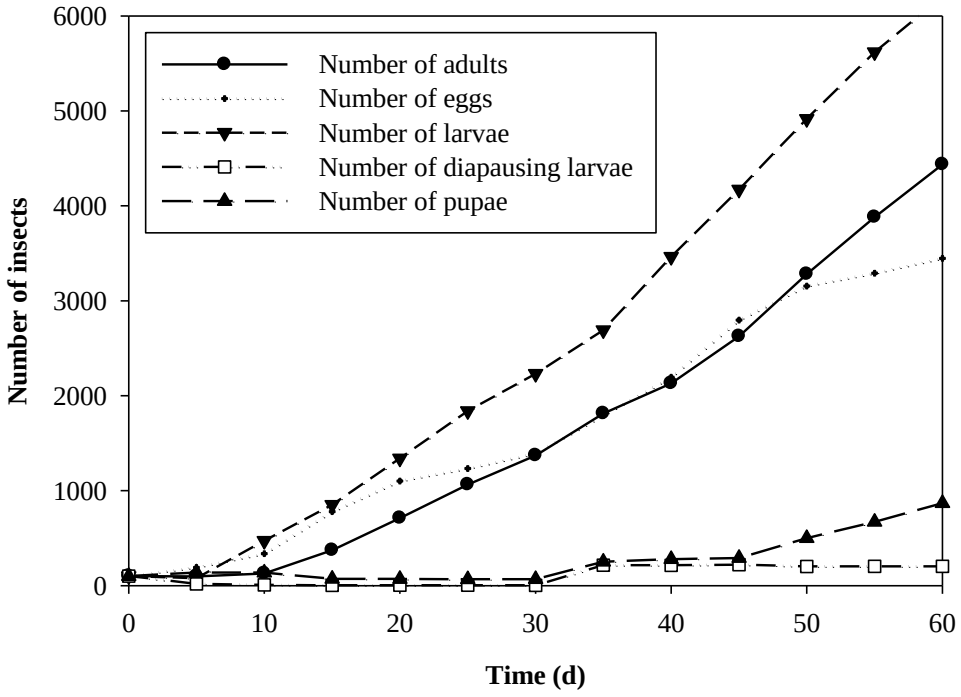

Figure 4.13. Simulation results of population dynamics at a constant temperature of 30°C, 60% RH and with excess fresh food.

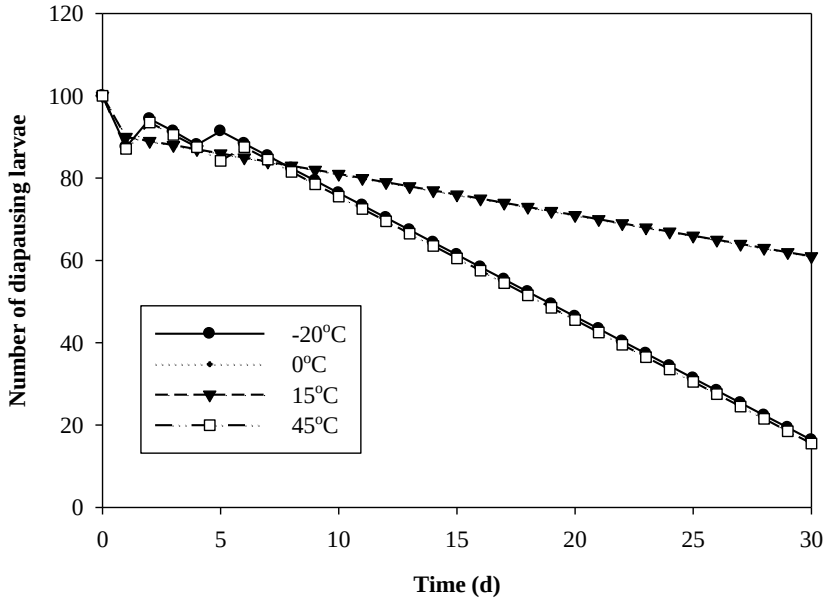

Figure 4.14. Simulation results of population dynamics at constant temperatures of -20°C, 0°C, 15°C, and 45°C and 50% RH with enough fresh food.

4.2.2. Simulation of population dynamics at constant relative humidities

The models predicted that the khapra beetle had lower rates of multiplication at lower RH. The population growth was low at 75% RH, as the total adults at the end of 30 d were around one-fifth of the population at 25% RH (Fig. 4.15). The increase in the number of eggs is higher at 25% RH than at 75% RH. The number of eggs almost reached zero at 75% RH. The number of non-diapausing larvae increased rapidly at 25% RH (Fig. 4.15). The number of diapausing larvae and pupae did not change at different RH according to the literature, hence it was adopted to the model (Hadaway, 1956). Thus, the population growth was steady from 0 to 60% RH (Simulations were conducted but not displayed in Fig. 4.15.), with the rate of development decreased at higher RH.

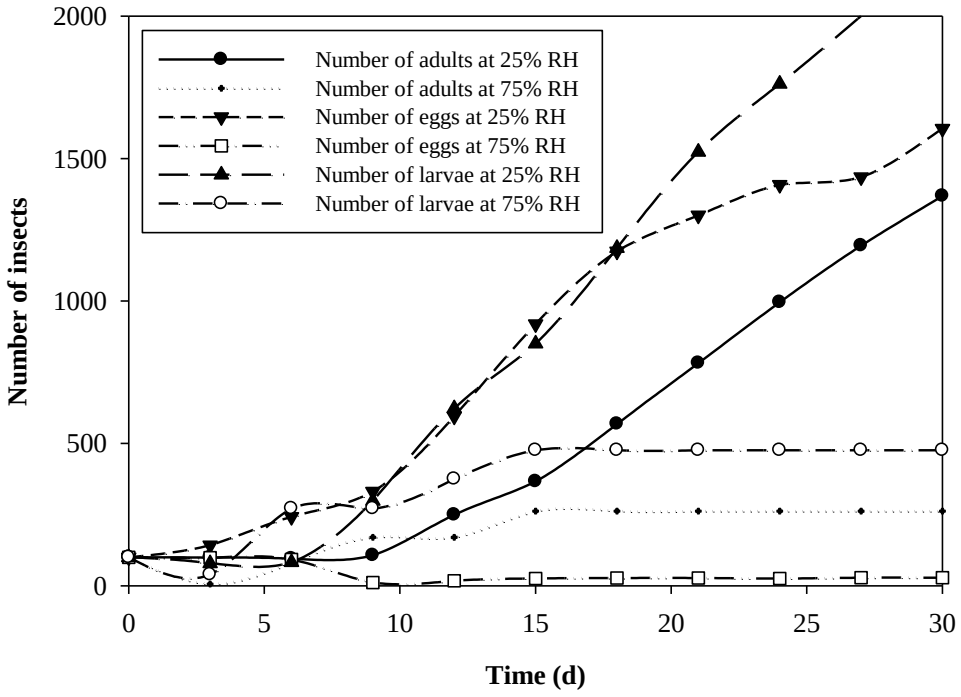

Figure 4.15. Simulation results of population dynamics at different RH with a constant temperature of 30°C and with excess fresh food.

4.2.3. Simulation of population dynamics at constant levels of food quality

The adult, egg, and pupa models did not include food quality as a variable because these stages do not feed. However, higher fresh food availability increased the population of both diapausing and non-diapausing larvae. For example, if the fresh food availability is 25%, the

growth of non-diapausing larvae did not improve after 20 d (Fig. 4.16). On the contrary, Figure 4.16 shows that diapause was induced with time at low fresh food levels. Thus, it is evident that the lack of availability of fresh food increased the number of diapausing larvae. The number of diapausing larvae was not included in the number of larvae in Figure 4.16.

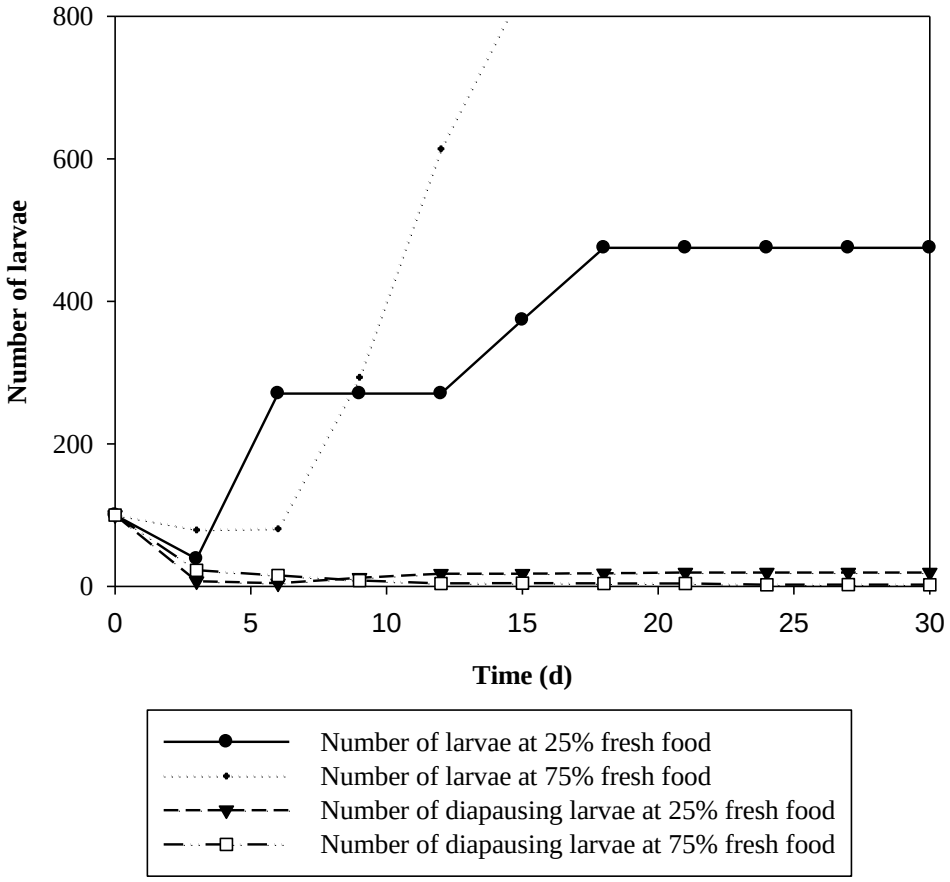

Figure 4.16. Simulation results of population dynamics larvae at a constant temperature of 30°C, 60% RH and different food qualities.

4.2.4. Simulation of population dynamics in a grain bin under Winnipeg conditions

Simulation of population dynamics at the center of the grain bin showed that the adults laid eggs during the first month of simulation when the temperature was 21°C. But all the insects died as the temperature in the center was never favourable for development and survival (Fig. 4.17). Around 90% of the larvae present initially entered diapause and survived throughout 1 yr (Fig. 4.17). However, the diapause did not terminate, and pupation did not occur as the temperature

never went above 25°C for pupation to happen. Also, the diapausing larvae survived the entire period as the temperature never went below -15°C to kill all the diapausing larvae. This is both good and bad. Good because insects did not multiply, but bad because when the grain is sold there are still live larvae in it that can infest the next structure the grain is placed in.

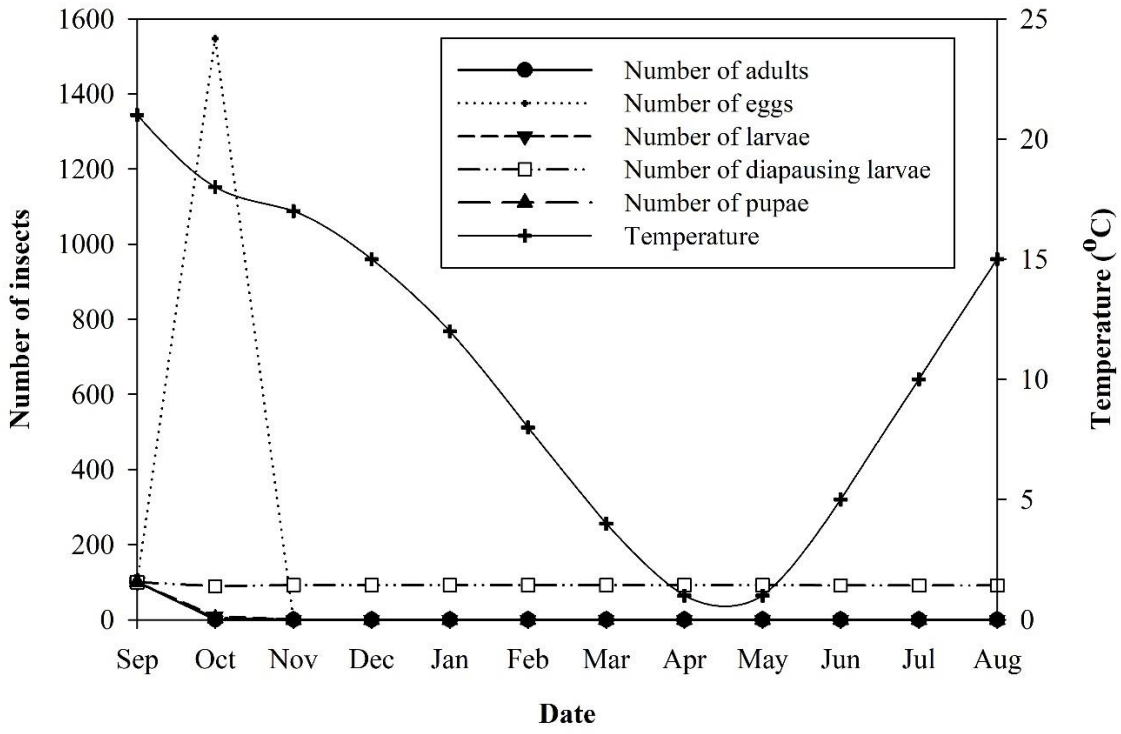

Figure 4.17. Simulation results of population dynamics of *Trogoderma granarium* in the center of a 5.56 m diameter grain bin. The grain temperature was adopted from Muir et al. (1980).

Simulation results for the condition close to the wall show that insects in all other stages except larvae reached zero immediately (Fig. 4.18). The larvae entered diapause, and the number started declining slightly over time due to mortality. The diapause was terminated, and pupation started during June when the temperatures became favourable for growth. The population multiplied rapidly over the next couple of months, and the adults began laying eggs at a high rate, thereby increasing the number of eggs. The number of non-diapausing larvae was higher than adults due to the longer lifespan. Pupae were short-lived; thus, the population of pupa was deficient. The khapra beetle survived the low temperatures because the food quality was assumed 100% fresh to simulate a big bin full of grain. Had the food quality been much lower, the

diapausing larvae may not have survived over nine months until May, when the temperatures were below 20°C (Fig. 4.14).

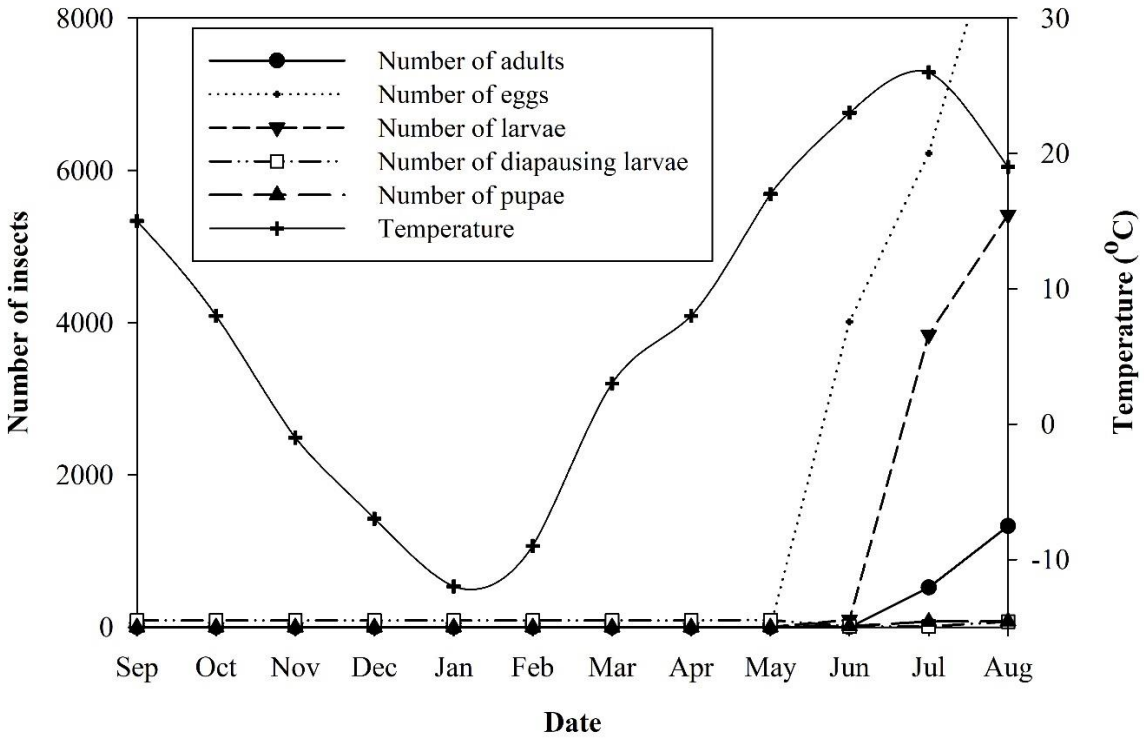

Figure 4.18. Simulation results of population dynamics of *Trogoderma granarium* in a grain bin at 5 cm from the wall. The grain temperature was adopted from Jian et al. (2005).

4.3. Discussion

Yaciuk et al. (1975) found that the temperature stays above 20°C for at least two months in at least one of the locations irrespective of the bin wall material in Winnipeg. The grain temperature peaks at 32 to 42°C during sunny autumn days in Manitoba. Therefore, the population of the khapra beetle can multiply over this period before surviving in the diapause state over the extreme winter. Yaciuk et al. (1975) simulated the temperature of grain bins in different cities in Canada and found that the temperature reached above 25°C for at least a month in a year, which is just enough for the larvae to come out of diapause and start multiplying. The developed models predicted that the khapra beetle population reached the pest status by the end of the summer, agreeing to the work published by Howe and Lindgren (1957) and Howe (1958). Also, Figure 4.18 shows that the average monthly temperature in the grain bin is greater than 27°C, which resulted

in a population explosion, acknowledging the works of Sinha and Utida (1967). In smaller bins, the temperature varies very much and would be close to the ambient temperatures; therefore, the khapra beetle has a greater chance of surviving over the summer when the temperature reaches above 30°C. But, at the same time, if the temperature of the bin is less than -20°C during winter, the diapausing larvae die quickly.

The simulation was done for conditions in the food processing facilities and warehouses. A case where the population was simulated in the elevators and premises within the processing and storage facilities with equivalent ambient temperatures. The population did not survive until summer except diapausing larvae which started developing to pupae over summer and started multiplying. This is similar to the condition in the grain bin close to the wall. Therefore, there is a greater risk of multiplication of khapra beetle in these facilities in Canada over the summertime when the temperature is ideal for growth. Another case where the room temperature is maintained below 25°C in the control rooms or office spaces in the processing facilities and warehouses, usually in the range of 18-23°C. For an initial count of 100 insects in each stage at these temperatures, did not see the multiplication in any stage except the diapausing larvae surviving for a longer period. The final case where the temperature is cooled during summer and heated during winter in the protected or insulated facilities such as feed mills, flour mills, and warehouses. Therefore, the temperatures are usually between 10 to 25°C which again did not see the multiplication of khapra beetle over time.

4.3.1. Advantages of the model

The models predicted the population dynamics of the khapra beetle under varying environmental conditions such as temperatures, RHs and food qualities each day with R^2 values predominantly over 0.9. The main reason for its high accuracy is due to the Physi-Biological method in which the heat energy, as well as the metabolism of the insect, were considered throughout the lifespan. Other published models would not predict the interaction effects between temperature and other factors very well because 1) the data used for developing the model were collected under constant temperatures and RH; 2) basic temperature-driven development model is complicated; 3) undetermined interaction effects. Therefore, the reliability of the other published development rate models is usually very low. The modelling technique used in this study was simple, flexible, and easy to approach as it did not require any probability or cumulative

distribution functions. The developed models were used to mimic the Canadian grain storage conditions and processing warehouses without conducting actual experiments. The developed algorithms can be modified easily to calculate the population for each month or hour. Additional factors such as insect density and interaction with other species could be added to the developed model with ease. The methodology used in creating this model is simpler and theoretically more accurate than the published degree-day (Subramanyam et al., 1991), nonlinear (Subramanyam and Hagstrum, 1993), distribution delay (Jian et al., 2007), simulation (Kawamoto et al., 1989; Flinn et al., 2004), cohort-based (Nachman and Gotoh, 2015), or Leslie matrix models (Longstaff, 1991). The modelling procedure was developed on the well-known same shape method and similar to the basal metabolic rate concept in the field of animal physiology. Hence, the same shape concept normalized the development time distributions under different environmental conditions using a single equation for each stage.

4.3.2. Limitations of the model

Most of the limitations of the developed models were due to the lack of published data. Mathematical modelling is a very useful tool in finding the missing data and knowledge gap in the biological system that helps in future research. Though the overall biology of the khapra beetle was well documented, the rate of development and mortality rate were not studied under different environmental conditions. The accuracy of the model was low in some cases like the egg hatching model mainly due to the very less published data. The distribution shape of the development time is not identical at extreme temperatures resulting in decreasing the accuracy of the model. Therefore, special conditions were mentioned during coding for the extreme temperatures such as above 45°C and below -20°C to predict 100% mortality on the same day. The lack of published data also resulted in the scope of verifying the model with advanced statistical methods. Same shape distribution models should be evaluated by conducting experiments in variable temperatures with small sample intervals and uniform sample size. Modelling the larval diapause was challenging as diapause can be caused by various factors or sometimes without apparent reason. Hence, a simpler approach was adopted. Studying the diapausing characteristics extensively would help in creating a more robust model. The model did not account for the number of eggs laid by the female beetles that emerged from the diapausing larvae. The model developed for the lifespan

and mortality of larvae is less accurate as the development rate of female larvae was not published at different temperatures and RH.

4.3.3. Scope of the model

Experiments should be conducted to fill the missing data gap as it would be useful in enhancing the model accuracy and understanding the biology of the beetle. Unlike most other temperature-driven models, the developed model is much simpler, easy to map, and includes other physical factors. More data on development and survival under different factors such as crowding, migration, photoperiod, interspecific competition, insecticides, broken grain, and dockage would help develop a better model for the larval diapause, which in turn help in better prediction of the entire population dynamics. The model could be adapted to other quarantine countries to predict the survival possibility in their storage conditions. Similarly, the models can be used for pest control and management in counties like India and Pakistan, where the khapra beetle is well established. Modelling population demographics under different environmental conditions could be used to study the effects of climate change. Moreover, the biology of *Trogoderma variabile* is similar to the khapra beetle; hence the model could be adopted with modifications for predicting the population growth and viability of this species. However, other *Trogoderma* species such as *T. anthrenoides*, *T. glabrum* and *T. inclusum* are quite different from the khapra beetle; therefore, the model would not be suitable. Similarly, the general algorithm can be used for developing ecological models for organisms in other species.

5. CONCLUSIONS

1) The biology and factors affecting the development and survival of the khapra beetle were reviewed.
2) Mathematical equations were developed to predict the khapra beetle's population dynamics under different environmental conditions of temperature, relative humidity, and food quality.
3) The accuracy of the developed models was validated using linear regression between predicted and published data and the calculated MSE, R^2 values.
4) Algorithms were developed to program the simulation of the population dynamics of the khapra beetle using the developed mathematical models.
5) The population dynamics were simulated under different environmental conditions such as temperature, RH, and food quality combinations using C++ programming.
6) The population dynamics were simulated for the Canadian grain storage conditions, and it was found that the larvae endured diapause over the extremely cold conditions. In contrast, the insect in other stages did not survive at these low temperatures.
7) The khapra beetle would survive in warehouses or food processing facilities with temperatures reaching ideal for growth over the summertime in Canada. But it did not survive under controlled temperatures inside the processing facilities.
8) The surviving larvae developing into pupae and adults, and they began laying eggs once the temperatures become sufficiently warm in farm grain bins.

6. RECOMMENDATIONS FOR FUTURE RESEARCH

1) Simulation results under different environmental conditions, including grain storage conditions, could be verified by conducting actual experiments.
2) The simulation could be done for other parts of the world where the khapra beetle is not established.
3) The effect of other factors such as insect density, interspecific competition, photoperiod could be studied and included in the mathematical model.
4) Factors affecting diapause induction and termination should be studied well to develop a more robust model.

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APPENDICES

Appendix A

Development time of adults of *Trogoderma granarium* at different temperatures and RH

Temperature (°C)	RH (%)	Development time (days)		Reference
15		10.20 ± 0.81		
20		16.35 ± 1.37		
25		19.62 ± 2.18		
30	60±5	18.29 ± 1.52		Riaz et al. (2014)
35		15.17 ± 2.45		
40		12.40 ± 2.92		
45		9.12 ± 1.96		
17.2		102.1±0.69		
19.9	70	54.5±0.96		Burges (2008)
22.5		27.3±1.30		
24.9		16.4±0.24 (SE)		
		Mated	Unmated	
30		10.2±0.37	25.4±1.20	
32	65±5	9.2±0.48	23.2±1.01	Yadav and Srivastava (2017)
35		7.8±0.37	19.4±1.30	
40		5.6±0.40	14.2±0.73	
		Mean	Range	
21.11		25	12-51	
26.67	-	25	6-53	Lindgren and Vincent (1955)
32.22		16	6-31	
33.89 - 35		12	4-23	
		Male	Female	
25	2	12	11	
	25	13	11	
	50	15	13	
	73	16	13	
30	2	6	5	
	25	8	6	
	50	10	8	
	73	10	8	Hadaway (1956)
35	2	4	4	
	25	6	5	
	50	6	5	
	73	6	6	
40	2	4	4	
	25	5	4	
	50	5	5	
	73	5	5	

Appendix B

Development time and mortality of the eggs of *Trogoderma granarium* at different temperatures and RH

Temperature (°C)	RH (%)	Development time (days)	Mortality	Number of eggs laid	Number of female beetles	Reference
20		25.13±1.23	48.22%	61.8		
25		13.19±1.38	5.17%	737.1		
30	60±5	8.23±2.31	4.03%	1203.6	15	Riaz et al. (2014)
35		7.15±1.92	7.53%	1084.65		
40		30.63±2.11	32.48%	259.2		
			% hatch			
20	-	4.4	0	0	-	
25	73	2.9	58	43	25	
	50	6.8	50	39	25	
	25	7.5	52	40	25	
	2	5.7	49	25	25	
30	73	3.0	58	41	25	
	50	5.0	60	41	25	
	25	4.8	53	30	25	Hadaway (1956)
	2	3.9	51	29	25	
35	73	3.6	66	44	25	
	50	3.4	75	46	25	
	25	3.4	50	29	25	
	2	3.4	55	27	25	
40	73	3.3	58	38	20	
	50	3.3	54	39	20	
	25	3.0	60	34	20	
	2	2.5	49	23	20	
27	20			26.25±4.86		
27	40			29.95±4.34		
27	60			37.20±4.76		
27	80			37.90±4.49		
27	100			26.10±5.58		Odeyemi and Hassana (1993)
		-	-		Eggs laid per female	
35	20			29.30±3.85		
35	40			36.45±3.87		
35	60			37.75±4.93		
35	80			35.20±3.59		
35	100			29.60±5.47		
17.2				No eggs laid	178	
19.9	70	-	-	2.2±0.4 (SE)	76	Burges (2008)
22.5				11.4±2.1	40	
24.9				49.8±3.2	90	

17.5 (laid @ 25°C) 20 20 (laid @ 25°C) 22.5 22.5 (laid @ 25°C) 25	70			100.0 100.0 93.4 56.4 41.0 35.8	Mean - - 23.7 15.5 15.8 10.6	Range - - 21 – 31 14 – 22 14 – 19 10 – 13	Burges (2008)
21.11 26.67 32.22 33.89 - 35	-	Mean 14 8 5 3	Range 12-15 8-9 4-6 3-3	-	Mean 65 53 93 -	Range 54-76 46-71 77-116 -	Lindgren et al. (1955)
57	-	3 min		95	-		Lindgren and Vincent (1959)
-10	-	20 d		100	-		Witches et al. (2014)

Appendix C

Development time and mortality of the larvae of *Trogoderma granarium* at different temperatures and RH

Temperature (°C)	RH (%)	Development time (days)	Mortality%	Reference
20	60±5	Not pupated	In diapause	Riaz et al. (2014)
25		35.12±1.14	21.74%	
30		27.42±1.96	11.94%	
35		24.27±1.19	7.47%	
40		Not pupated	In diapause	
30	65±5	25.00±1.00	60	Yadav and Srivastava (2017)
32		27.50±0.50	60	
35		23.00±1.35	80	
40		27.00±4.00	40	
-2	-	180	45	Mathlein (1961)
-5		90	23	
-10		30	97	
-19		15	100	
		10	100	
51	-	48 h	100	Shoab (2009)
54		12 h	100	
57		5 min	100	
60		2 min	100	
20	20	32.20±2.18	-	Odeyemi and Hassana (1993)
20	40	33.48±1.33		
20	60	27.28±3.98		
20	80	24.64±2.88		
20	100	25.04±2.73		
27	20	31.36±3.94		
27	40	27.64±4.13		
27	60	24.36±1.29		
27	80	24.08±1.09		
27	100	23.80±2.35		
35	20	23.48±1.33		
35	40	22.92±1.78		
35	60	23.00±1.91		
35	80	22.04±2.01		
35	100	23.12±1.34		
Starved larvae	-			Lindgren and Vincent (1959)
-10 to -7		36	40	
Fed larvae				
-10 to -7		36	100	
-3.89 to 8.88	--	8	0	Lindgren et al. (1955)
		12	2.5	
		16	2.5	
		20	10	

		24 28 30 51	15 47 67.5 97.5	
-10 (Acclimated) -10 -16	-	72h 25h 24h	11 73 98	Voelkel (1924) cited in Hinton (1945)
50 54 60	-	5 h 20 min 4 min	> 90 > 90 > 90	Husain and Bhasin (1921)

Development time of the larvae of *Trogoderma granarium* at different temperatures and RH

Temperature (°C)	RH (%)	Larval development time (days)				Number of larvae	% Pupated	Reference
		Male		Female				
		Mean	Range	Mean	Range			
25	2	60	55-64	68	62-72	50	10	Hadaway (1956)
	25	44	40-65	48	41-63	90	38	
	50	39	31-61	47	33-64	70	49	
	73	33	24-45	36	27-57	156	45	
30	2	28	24-39	35	26-52	112	73	
	25	27	21-60	33	23-68	127	83	
	50	24	20-51	31	25-56	157	89	
	73	22	19-34	27	21-44	120	82	
35	2	32	25-47	33	26-49	129	65	
	25	23	18-39	25	20-37	166	91	
	50	19	16-26	21	19-29	155	90	
	73	17	15-21	20	17-25	119	92	
40	2	35	29-46	38	33-45	147	61	
	25	22	17-34	24	19-33	132	79	
	50	18	15-27	19	16-29	117	86	
	73	22	17-32	24	18-38	143	85	

Probit 9 values (99.9968 % mortality) of the larvae of *Trogoderma granarium* at extreme temperatures.

Temperature (°C)	Exposure time	Reference
-20	13 (11-15)	Wilches et al. (2017)
-15	70 (62-84)	
-10	303 (271-347)	
-5	380 (339-442)	
0	778 (653-999)	
45	563 hours	Wilches et al. (2018)
50	12 hours	
55	2 hours	
60	2 hours	

Appendix D

Development time and mortality of the pupae of *Trogoderma granarium* at different temperatures

Temperature(°C)	RH (%)	Duration (Pupal period) (days)		Mortality	Reference
20		Not pupated		-	
25		12.35±1.41		8.41%	
30	60±5	6.29±1.17		2.94%	Riaz et al. (2014)
35		5.21±0.19		1.50%	
40		Not pupated		-	
		Mean	Range		
21.11		17	13-19		
26.67	-	10	7-12	-	Lindgren et al. (1955)
32.22		6	4-11		
33.89 - 35		4	3-7		
30		7.00±0.57		60	
32	65±5	8.50±2.50		60	Yadav and Srivastava
35		5.50±0.50		80	(2017)
40		6.00±0.00		40	
		Male	Female		
25		5-5.5	3		
30	-	3.5-4	2	-	Hadaway (1956)
35		3	1		
40		3	1		

Appendix E

C++ codes for the simulation of population dynamics of khapra beetle

```
#include <iostream>

#include <math.h>

#include <map>

constexpr auto PI = 3.1415926535;
using namespace std;

#define EM 30.63
#define LM 35.12
#define PM 12.35
#define AM 20
#define RH 60
#define foodQuality 100

map < int, float > adultBioMap;
map < int, float > adultBioMap2;
map < int, float > eggBioMap;
map < int, float > eggBioMap2;
map < int, float > larvaBioMap;
map < int, float > larvaBioMap2;
map < int, float > diapauseLarvaBioMap;
map < int, float > diapauseLarvaBioMap2;
map < int, float > pupaBioMap;
map < int, float > pupaBioMap2;

map < int, float > adultDayMap;
map < int, float > eggDayMap;
map < int, float > larvaDayMap;
map < int, float > diapauseLarvaDayMap;
map < int, float > pupaDayMap;

map < int, float > ::iterator itr;

void adultFunction(int currentDay, int initialAdultCount, float temperature, float previousAdultBioAge);
void eggFunction(int currentDay, int initialEggCount, float temperature, float previousEggBioAge);
void larvaFunction(int currentDay, int initialLarvaCount, float temperature, float previousLarvaBioAge);
void diapauseLarvaFunction(int currentDay, float diapauseLarvaCount, float temperature, float
        diapauseLarvaBioAge);
void pupaFunction(int currentDay, int initialPupaCount, float temperature, float previousPupaBioAge);
```

```
void processData(int currentDay, float temperature);
void printBioMaps(int currentDay);
void printDayMaps();

int main() {

    float temperature;

    float previousBioAge;
    int initialAdultCount;
    int initialEggCount;
    int initialPupaCount;
    int initialLarvaCount;
    int currentDay = 1;
    char option = 'y';

    while (option == 'y') {
        if (currentDay == 1) {

            //Getting Inputs
            cout << "\n Temperature (C) : ";
            cin >> temperature;

            cout << "\n Adult count : ";
            cin >> initialAdultCount;
            cout << "\n Egg count : ";
            cin >> initialEggCount;
            cout << "\n Larva count : ";
            cin >> initialLarvaCount;
            cout << "\n Pupa count : ";
            cin >> initialPupaCount;

            //Initial Biological age
            previousBioAge = 0.0;

            //Processing equations
            adultFunction(currentDay, initialAdultCount, temperature, previousBioAge);
            eggFunction(currentDay, initialEggCount, temperature, previousBioAge);
            larvaFunction(currentDay, initialLarvaCount, temperature, previousBioAge);
            pupaFunction(currentDay, initialPupaCount, temperature, previousBioAge);

            //Printing Maps
            printBioMaps(currentDay);
            printDayMaps();
```

```
            cout << "\n\n" << "Do you wish to continue?(y/n): ";
            cin >> option;

        }
        else if (currentDay > 1) {

            //Getting inputs
            cout << "\n Temperature (C) : ";
            cin >> temperature;


            //Processing, saving and Reteieving data
            processData(currentDay, temperature);

            //Printing maps
            printBioMaps(currentDay);
            printDayMaps();

            cout << "\n\n" << "Do you wish to continue?(y/n): ";
            cin >> option;
        }
        currentDay++;
    }
    return 0;
}

//Adult Function
void adultFunction(int currentDay, int initialAdultCount, float temperature, float previousAdultBioAge) {
    if (initialAdultCount > 0) {
        float adultRate;
        float adultMortality;
        float finalAdultCount;
        float oviPositionNumber = 0.0;
        float adultBioAge = 0.0;

        adultRate = (0.2345 - (0.0128 * temperature) + (0.00022389 * temperature * temperature)) * (1.3965
            * exp(-(0.005 * RH)));

        adultBioAge = previousAdultBioAge + (adultRate * AM);

        adultMortality = (100 / (1 + exp(-(adultBioAge - 20) / 2.9395)));

        finalAdultCount = initialAdultCount - adultMortality;
```

```
if (finalAdultCount < 0)
   finalAdultCount = 0;

try {
   adultDayMap.at(currentDay) += finalAdultCount;
}
catch (const std::exception & exc) {
   adultDayMap[currentDay] = finalAdultCount;
}
try {
   adultBioMap.at(adultBioAge) += finalAdultCount;
   if (adultBioMap.at(previousAdultBioAge) - finalAdultCount < 0) {
      adultBioMap[previousAdultBioAge] = 0;
   }
   else {
      adultBioMap.at(previousAdultBioAge) -= finalAdultCount;
   }
}
catch (const out_of_range & e) {
   adultBioMap[adultBioAge] = finalAdultCount;
   try {
      if (adultBioMap.at(previousAdultBioAge) - finalAdultCount < 0) {
         adultBioMap[previousAdultBioAge] = 0;
      }
      else {
         adultBioMap.at(previousAdultBioAge) -= finalAdultCount;
      }
   }
   catch (const out_of_range & e) {}
}
/*
   cout << "\n\n Adult";
   cout << "\n Day: " << currentDay;
   cout << "\n previousBioAge: " << previousAdultBioAge;
   cout << "\n bioage: " << adultBioAge;
   cout << "\n Adult Mortality: " << adultMortality;
   cout << "\n Adult count: " << finalAdultCount;
*/
if (adultBioAge < 25) {
   if (temperature >= 20 and temperature <= 40) {
      oviPositionNumber = (3.6 * (exp(pow((-0.5 * (temperature - 31.1956) / 5.3), 2))) * 1.0006 *
    (exp(pow((-0.5 * (RH - 61.9034) / 52), 2)) * adultBioAge));
   }
   else {
```

```
            oviPositionNumber = 0;
        }
        //cout << "\n oviPositionNumber: " << oviPositionNumber;

        if (oviPositionNumber >= 1) {
            eggBioMap[0] = oviPositionNumber;
            try {
                eggDayMap.at(currentDay) += oviPositionNumber;
            }
            catch (const std::exception & exc) {
                eggDayMap[currentDay] = oviPositionNumber;
            }
        }
    }
  }
}

//Egg Function
void eggFunction(int currentDay, int initialEggCount, float temperature, float previousEggBioAge) {
   if (initialEggCount > 0) {
      float eggRate;
      float eggHatchability;
      float finalEggCount;
      float eggMortality;
      float eggBioAge = 0.0;

      eggRate = 0.15 / (1 + (pow(((temperature - 32.2344) / 6), 2)));

      eggBioAge = previousEggBioAge + (eggRate * EM);

      if (eggBioAge < 45 and temperature > 10 and temperature < 48) {
         eggMortality = (5.1 + (-0.3491 * temperature) + (0.006 * temperature * temperature)) * (1.2486 -
          (0.004 * RH)) * eggBioAge;
      }
      else {
         eggMortality = 100;
      }
      if (eggMortality > 100) {
         eggMortality = 100;
      }

      if (eggBioAge < 45) {
         eggHatchability = (100.3890 / (1 + exp(-(eggBioAge - 30.6514) / 1.8382)));
```

```
finalEggCount = initialEggCount - eggMortality - eggHatchability;
if (finalEggCount < 0)
   finalEggCount = 0;

try {
   eggDayMap.at(currentDay) += finalEggCount;
}
catch (const std::exception & exc) {
   eggDayMap[currentDay] = finalEggCount;
}

try {
   eggBioMap.at(eggBioAge) += finalEggCount;
   if (eggBioMap.at(previousEggBioAge) - finalEggCount < 0) {
      eggBioMap[previousEggBioAge] = 0;
   }
   else {
      eggBioMap.at(previousEggBioAge) -= finalEggCount;
   }
}
catch (const std::exception & exc) {
   eggBioMap[eggBioAge] = finalEggCount;
   try {
      if (eggBioMap.at(previousEggBioAge) - finalEggCount < 0) {
         eggBioMap[previousEggBioAge] = 0;
      }
      else {
         eggBioMap.at(previousEggBioAge) -= finalEggCount;
      }
   }
   catch (const std::exception & exc) {}
}
/*
     cout << "\n\n Egg";
     cout << "\n Day: " << currentDay;
     cout << "\n previousEggBioAge: " << previousEggBioAge;
     cout << "\n eggbioAge: " << eggBioAge;
     cout << "\n Egg Hatchability: " << eggHatchability;
     cout << "\n Egg Mortality: " << eggMortality;
     cout << "\n Egg count: " << finalEggCount;
*/
if (eggHatchability >= 1) {
   larvaBioMap[0] = eggHatchability;
   try {
```

```
                larvaDayMap.at(currentDay) += eggHatchability;
            }
            catch (const std::exception & exc) {
                larvaDayMap[currentDay] = eggHatchability;
            }
        }
    }
}

//Larva Function
void larvaFunction(int currentDay, int initialLarvaCount, float temperature, float previousLarvaBioAge) {
    if (initialLarvaCount > 0) {
        float larvaRate;
        float larvaLife;
        float larvaMortality;
        float larvaBioAge = 0.0;
        float finalLarvaCount;
        float diapauseLarvaCount;

        if (temperature < 25) {
            larvaRate = 1 / (276 + (25.4533 * temperature) + (0.6 * temperature * temperature)) * (0.6349 +
             (0.4 * (1 - exp(-0.03 * RH)))) * (1.1453 * (1 - exp(-0.02 * foodQuality)));
            diapauseLarvaCount = 0.9 * initialLarvaCount;
        }
        else if (temperature >= 25 and temperature <= 40) {
            larvaRate = 0.0530 * (exp(-0.5 * (pow(((temperature - 34.6305) / 8.2), 2)))) * (0.6349 + (0.4 * (1 -
             exp(-0.03 * RH)))) * (1.1453 * (1 - exp(-0.02 * foodQuality)));
            diapauseLarvaCount = 0.1 * initialLarvaCount;
        }
        else {
            larvaRate = 1 / (55.7660 - (1.1124 * temperature)) * (0.6349 + (0.4 * (1 - exp(-0.03 * RH)))) *
             (1.1453 * (1 - exp(-0.02 * foodQuality)));
            diapauseLarvaCount = 0.9 * initialLarvaCount;
        }

        larvaBioAge = previousLarvaBioAge + (larvaRate * LM);

        if (larvaBioAge < 47) {

            if (temperature > 20 and temperature <= 40) {
                larvaLife = (100 / (1 + exp(-(larvaBioAge - 35.12) / 1.7637)));
            }
            else {
```

```
    larvaLife = 0;
}

if (larvaBioAge < 47 and temperature >= 25 and temperature <= 40) {
    larvaMortality = (5.7 + ((-0.3385) * temperature) + (0.0052 * temperature * temperature)) *
 (0.9855 + (1.0444 * exp(-0.06 * RH))) * 12.4332 * exp(-0.04 * foodQuality) * larvaBioAge;
}
else if (larvaBioAge < 47 and temperature > -23) {
    larvaMortality = 2.13 * (0.9855 + (1.0444 * exp(-0.06 * RH))) * 12.4332 * exp(-0.04 *
 foodQuality) * larvaBioAge;
}
else {
    larvaMortality = 100;
}

finalLarvaCount = initialLarvaCount - larvaMortality - larvaLife - diapauseLarvaCount;
if (finalLarvaCount < 0)
    finalLarvaCount = 0;

try {
    larvaDayMap.at(currentDay) += finalLarvaCount;
}
catch (const std::exception & exc) {
    larvaDayMap[currentDay] = finalLarvaCount;
}

try {
    larvaBioMap.at(larvaBioAge) += finalLarvaCount;
    if (larvaBioMap.at(previousLarvaBioAge) - finalLarvaCount < 0) {
        larvaBioMap[previousLarvaBioAge] = 0;
    }
    else {
        larvaBioMap.at(previousLarvaBioAge) -= finalLarvaCount;
    }
}
catch (const std::exception & exc) {
    larvaBioMap[larvaBioAge] = finalLarvaCount;
    try {
        if (larvaBioMap.at(previousLarvaBioAge) - finalLarvaCount < 0) {
            larvaBioMap[previousLarvaBioAge] = 0;
        }
        else {
            larvaBioMap.at(previousLarvaBioAge) -= finalLarvaCount;
        }
```

```
            }
            catch (const std::exception & exc) {}
        }
        /*
                cout << "\n\n Larva";
                cout << "\n Day: " << currentDay;
                cout << "\n previouslarvaBioAge: " << previousLarvaBioAge;
                cout << "\n larvabioAge: " << larvaBioAge;
                cout << "\n larva life: " << larvaLife;
                cout << "\n larva Mortality: " << larvaMortality;
                cout << "\n larva count: " << finalLarvaCount;
                cout << "\n larva rate: " << larvaRate;
        */
        if (currentDay == 1) {
            if (diapauseLarvaCount >= 1) {
                diapauseLarvaFunction(currentDay, diapauseLarvaCount, temperature, larvaBioAge);
            }
        }
        else {
            if (diapauseLarvaCount >= 1) {
                diapauseLarvaBioMap[0] = diapauseLarvaCount;
                try {
                    diapauseLarvaBioMap.at(currentDay) += diapauseLarvaCount;
                }
                catch (const std::exception & exc) {
                    diapauseLarvaDayMap[currentDay] = diapauseLarvaCount;
                }
            }
        }

        if (larvaLife >= 1) {
            pupaBioMap[0] = larvaLife;
            try {
                pupaDayMap.at(currentDay) += larvaLife;
            }
            catch (const std::exception & exc) {
                pupaDayMap[currentDay] = larvaLife;
            }
        }
    }
  }
}
```

```
void diapauseLarvaFunction(int currentDay, float diapauseLarvaCount, float temperature, float
        diapauseLarvaBioAge) {
   if (diapauseLarvaCount > 0) {
      float diapauseLarvaRate;
      float diapauseLarvaLife = 0;
      float diapauseLarvaMortality;
      float diapauseLarvalLife;
      float finalDiapauseLarvaCount;
      float larvaBioAgeInOptimalConditions;
      float larvaBioAgeInAdverseConditions;

      larvaBioAgeInAdverseConditions = diapauseLarvaBioAge;

      if (temperature >= 25 and temperature <= 40) {
         diapauseLarvaRate = 0.0530 * (exp(-0.5 * (pow(((temperature - 34.6305) / 8.2), 2)))) * (0.6349 +
          (0.4 * (1 - exp(-0.03 * RH))));
      }
      else {
         diapauseLarvaRate = 0;
      }

      larvaBioAgeInOptimalConditions = diapauseLarvaBioAge + (diapauseLarvaRate * LM);

      diapauseLarvalLife = 3.4 + (1 - exp(-0.02 * larvaBioAgeInOptimalConditions)) * (79 - 0.04 *
          larvaBioAgeInAdverseConditions);

      if (diapauseLarvaBioAge < 47 and temperature >= 25 and temperature <= 40) {
         diapauseLarvaMortality = (5.7 + ((-0.3385) * temperature) + (0.0052 * temperature * temperature))
          * (0.9855 + (1.0444 * exp(-0.06 * RH))) * diapauseLarvaBioAge;
      }
      else if (diapauseLarvaBioAge < 47 and temperature > -23) {
         diapauseLarvaMortality = 2.13 * (0.9855 + (1.0444 * exp(-0.06 * RH))) * diapauseLarvaBioAge;
      }
      else {
         diapauseLarvaMortality = 100;
      }

      finalDiapauseLarvaCount = diapauseLarvaCount - diapauseLarvaMortality - diapauseLarvalLife;
      if (finalDiapauseLarvaCount < 0)
         finalDiapauseLarvaCount = 0;

      try {
         diapauseLarvaDayMap.at(currentDay) += finalDiapauseLarvaCount;
      }
```

```
        catch (const std::exception & exc) {
            diapauseLarvaDayMap[currentDay] = finalDiapauseLarvaCount;
        }

        diapauseLarvaBioMap[diapauseLarvaBioAge] = finalDiapauseLarvaCount;

        /*
              cout << "\n\n Diapause Larva";
              cout << "\n Day: " << currentDay;
              cout << "\n previousDiapauseLarvaBioAge: " << diapauseLarvaBioAge;
              cout << "\n larvabioAge: " << diapauseLarvaBioAge;
              cout << "\n larva life: " << diapauseLarvaLife;
              cout << "\n larva Mortality: " << diapauseLarvaMortality;
              cout << "\n larva count: " << finalDiapauseLarvaCount;
              cout << "\n larva rate: " << diapauseLarvaRate;
        */
        if (diapauseLarvalLife >= 1) {
            pupaBioMap[0] = diapauseLarvalLife;
            try {
                pupaDayMap.at(currentDay) += diapauseLarvalLife;
            }
            catch (const std::exception & exc) {
                pupaDayMap[currentDay] = diapauseLarvalLife;
            }
        }
    }
}

//Pupa Function
void pupaFunction(int currentDay, int initialPupaCount, float temperature, float previousPupaBioAge) {
    if (initialPupaCount > 0) {
        float pupaRate;
        float pupaLife;
        float pupaMortality;
        float finalPupaCount;
        float pupaBioAge = 0.0;

        pupaRate = 0.1291 * (exp(-0.5 * (pow(((temperature - 32.5965) / 8.2), 2))));

        pupaBioAge = previousPupaBioAge + (pupaRate * PM);

        if (pupaBioAge < 20) {

            pupaLife = (100 / (1 + exp(-(pupaBioAge - 12.35) / 1.1758)));
```

```
if (pupaBioAge < 20 and temperature >= 25 and temperature <= 40) {
   pupaMortality = (11 + ((-0.7074) * temperature) + (0.0114 * temperature * temperature)) *
 pupaBioAge;
}
else {
   pupaMortality = 1 / pupaRate;
   if (pupaMortality > 100) {
      pupaMortality = 100;
   }
}

finalPupaCount = initialPupaCount - pupaMortality - pupaLife;
if (finalPupaCount < 0)
   finalPupaCount = 0;

try {
   pupaDayMap.at(currentDay) += finalPupaCount;
}
catch (const std::exception & exc) {
   pupaDayMap[currentDay] = finalPupaCount;
}

try {
   pupaBioMap.at(pupaBioAge) += finalPupaCount;
   if (pupaBioMap.at(previousPupaBioAge) - finalPupaCount < 0) {
      pupaBioMap[previousPupaBioAge] = 0;
   }
   else {
      pupaBioMap.at(previousPupaBioAge) -= finalPupaCount;
   }
}
catch (const std::exception & exc) {
   pupaBioMap[pupaBioAge] = finalPupaCount;
   try {
      if (pupaBioMap.at(previousPupaBioAge) - finalPupaCount < 0) {
         pupaBioMap[previousPupaBioAge] = 0;
      }
      else {
         pupaBioMap.at(previousPupaBioAge) -= finalPupaCount;
      }
   }
   catch (const std::exception & exc) {}
}
```

```
            /*
                cout << "\n\n Pupa";
                cout << "\n Day: " << currentDay;
                cout << "\n\n previouspupaBioAge: " << previousPupaBioAge;
                cout << "\n pupabioAge: " << pupaBioAge;
                cout << "\n pupa life: " << pupaLife;
                cout << "\n pupa Mortality: " << pupaMortality;
                cout << "\n pupa count: " << finalPupaCount;
            */
            if (pupaLife >= 1) {
                adultBioMap[0] = pupaLife;
                try {
                    adultDayMap.at(currentDay) += pupaLife;
                }
                catch (const std::exception & exc) {
                    adultDayMap[currentDay] = pupaLife;
                }
            }
        }
    }
}

void processData(int currentDay, float temperature) {

    for (itr = adultBioMap.begin(); itr != adultBioMap.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        adultBioMap2[age] = count;
    }
    for (itr = adultBioMap2.begin(); itr != adultBioMap2.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        adultFunction(currentDay, count, temperature, age);
    }
    for (itr = eggBioMap.begin(); itr != eggBioMap.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        eggBioMap2[age] = count;
    }
    for (itr = eggBioMap2.begin(); itr != eggBioMap2.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        eggFunction(currentDay, count, temperature, age);
    }
```

```
    for (itr = larvaBioMap.begin(); itr != larvaBioMap.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        larvaBioMap2[age] = count;
    }
    for (itr = larvaBioMap2.begin(); itr != larvaBioMap2.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        larvaFunction(currentDay, count, temperature, age);
    }

    for (itr = diapauseLarvaBioMap.begin(); itr != diapauseLarvaBioMap.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        diapauseLarvaBioMap2[age] = count;
    }
    for (itr = diapauseLarvaBioMap2.begin(); itr != diapauseLarvaBioMap2.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        diapauseLarvaFunction(currentDay, count, temperature, age);
    }

    for (itr = pupaBioMap.begin(); itr != pupaBioMap.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        pupaBioMap2[age] = count;
    }
    for (itr = pupaBioMap2.begin(); itr != pupaBioMap2.end(); itr++) {
        int age = itr->first;
        int count = itr->second;
        pupaFunction(currentDay, count, temperature, age);
    }

}

void printBioMaps(int currentDay) {
    cout << "\n\n" << "Day " << currentDay << " results:";
    cout << "\n" << "**********************************************************************";
    cout << "\n" << "BIO AGE TABLE:";

    cout << "\n\n" << "Adult BioAge:";
    for (itr = adultBioMap.begin(); itr != adultBioMap.end(); itr++) {
        cout << "\n" << itr->first << "  " << itr->second;
    }
```

```
    cout << "\n\n" << "Egg BioAge:";
    for (itr = eggBioMap.begin(); itr != eggBioMap.end(); itr++) {
        cout << "\n" << itr->first << "  " << itr->second;
    }
    cout << "\n\n" << "Larva BioAge:";
    for (itr = larvaBioMap.begin(); itr != larvaBioMap.end(); itr++) {
        cout << "\n" << itr->first << "  " << itr->second;
    }
    cout << "\n\n" << "Diapausing Larva BioAge:";
    for (itr = diapauseLarvaBioMap.begin(); itr != diapauseLarvaBioMap.end(); itr++) {
        cout << "\n" << itr->first << "  " << itr->second;
    }
    cout << "\n\n" << "Pupa BioAge:";
    for (itr = pupaBioMap.begin(); itr != pupaBioMap.end(); itr++) {
        cout << "\n" << itr->first << "  " << itr->second;
    }

    cout << "\n" << "**********************************************************************";
}

void printDayMaps() {

    cout << "\n" << "CHORONOLOGICAL TABLE:";

    cout << "\n\n" << "Adult:";
    for (itr = adultDayMap.begin(); itr != adultDayMap.end(); itr++) {
        cout << itr->first << "\n  " << itr->second;
    }

    cout << "\n\n" << "Egg:";
    for (itr = eggDayMap.begin(); itr != eggDayMap.end(); itr++) {
        cout << itr->first << "\n  " << itr->second;
    }

    cout << "\n\n" << "Larva:";
    for (itr = larvaDayMap.begin(); itr != larvaDayMap.end(); itr++) {
        cout << itr->first << "\n  " << itr->second;
    }

    cout << "\n\n" << "Diapausing Larva:";
    for (itr = diapauseLarvaDayMap.begin(); itr != diapauseLarvaDayMap.end(); itr++) {
        cout << itr->first << "\n  " << itr->second;
    }
```

```
    cout << "\n\n" << "Pupa:";
    for (itr = pupaDayMap.begin(); itr != pupaDayMap.end(); itr++) {
        cout << itr->first << "\n  " << itr->second;
    }

    cout << "\n" << "*****************************************";
}
```