POPULATION PARAMETERS OF TWO FRUIT FLY SPECIES (DIPTERA: TEPHRITIDAE) ATTACKING MANGO

BY

JUMA KWEMBEYA SALUM

A DISSERTATION SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN CROP SCIENCE OF SOKOINE UNIVERSITY OF AGRICULTURE. MOROGORO, TANZANIA.

2011

ABSTRACT

Fruit flies (Diptera: Tephritidae) are among the most notorious pests damaging fruit crops grown in Tanzania. Demographic and life history parameters of *Ceratitis cosyra* (Walker) and *Bactrocera invadens* (Drew, Tsuruta and White) reared on artificial diet were investigated at Sokoine University of Agriculture laboratory in 2010. Demographic and life history parameters of *C. cosyra* and *B. invadens* were measured in an environmental chamber at 25^0C and 30^0C with 75% RH to determine pre-adult survival and development rates, adult survival and fecundity and life history parameters such as the intrinsic rate of increase, the mean generation time and stable age distribution. The design of the experiment was split plot arranged in a Complete Randomized Design (CRD) with three replications. There were two sources of variations: Fruit fly species (being the main-factor) and temperatures (being the sub-factor). The effect of temperature and species on eggs laying and survival were tested by two-way analysis of variance (ANOVA). The Least significance difference (LSD) test was used to identify significant main effects. The analyses were performed using GenStat package. The results show that *B. invadens* had shorter egg incubation time than *C. cosyra* in all the temperatures tested**.** Larval and pupal development rates of *B. invadens* were significantly faster than those of *C. cosyra* independent of temperatures. Life expectancy of male *B. invadens* was significantly longer than that of *C. cosyra* while life expectancy of female *B. invadens* was higher than that of *C. cosyra*, however, the difference was not significant. The average net fecundity was higher for *B. invadens* than was for *C. cosyra*. Both species attained their highest intrinsic rate of increase and net reproductive rate at 30°C. Furthermore, *B. invadens* exhibited higher intrinsic rate of increase and net reproductive rate than *C. cosyra* at all the temperatures tested**.** These findings are useful for improving laboratory-rearing methods, predicting the fly's population dynamics, with a view to developing appropriate fly control and management strategies.

DECLARATION

I, Juma Kwembeya Salum, do hereby declare to the Senate of Sokoine University of Agriculture that this dissertation is the result of my own original work and it has not been submitted for a degree award in any other University.

Juma Kwembeya Salum	Date
(MSc. Candidate)	

The above declaration is confirmed

Prof. Mwatawala, M. W	Date
(Supervisor)	

Dr. Kusolwa, P. M	Date
(Supervisor)	

COPYRIGHT

ACKNOWLEDGEMENT

I humbly thank God the almighty, for enabling me to live and receive his abundant blessings, including this achievement.

I am grateful to my supervisors, Prof. M. W. Mwatawala and Dr. P. M. Kusolwa for their thoughtful and creative advice during this work. I thank them for their tireless professional guidance, and all forms of academic support given in accomplishing my studies. I am also grateful to F. J. Senkondo and R. Maganga for every form of help given to me especially, on fruit fly knowledge that they shared with me.

I am also very grateful to the District Executive Director (DED) of Manyoni District Council for granting me a study leave and for providing me with financial assistance. I am also indebted to the District Agriculture and Livestock Development Officer (DALDO), Mr. T. J. Mutagwaba for every support given to me. I also extend my thanks to Belgian Development Co-operation for their support to the fruit flies project, a collaborative project between Sokoine University of Agriculture (SUA), Morogoro, Tanzania and the Royal Museum for Central Africa. The project provided me with research materials and technical support.

I would like also to acknowledge the support and encouragement I received from my family. My wife Joyce Mziray and daughter Shamy were supportive during the entire period of my study. I thank them for their prayers and perseverance. Finally, I wish to thank my classmates, and friends who in one way or other helped me complete this study successfully.

DEDICATION

This work is dedicated to my late beloved father, Mr. Salum Juma, and my mother Mrs. P. R. Salum for taking me to school. Also this work is dedicated to my beloved wife Joyce R. Mziray and my daughter Shamy. I will always love you.

TABLE OF CONTENTS

DECLARATION--iii

COPYRIGHT---iii

ACKNOWLEDGEMENT---v

DEDICATION---vi

TABLE OF CONTENTS---vii

LIST OF TABLES---viii

LIST OF FIGURES--ix

LIST OF ABBREVIATIONS AND SYMBOLS---xi

2.7 MAJOR FRUIT FLY PEST SPECIES OF TANZANIA---xix

2.7.2 Introduced species---xix

CHAPTER SIX--37

CONCLUSION AND RECOMMENDATIONS---37

6.1 CONCLUSION--37

LIST OF TABLES

Table 1: Statistical data of mango and orange in East Africa countries and India.- xv

Table 2: The average development times (days) of immature stages of 4 species of fruit flies--13

Table 3: Population parameters of 4 species of fruit flies---------------------------------13

Table 4: Population parameters of 4 species of fruit flies---------------------------------14

Table 5: Composition of artificial diet for rearing B. invadens and C. cosyra-------18

Table 6: Definitions and formulae for various life table and demographic parameters---19

Table 7: Survival (%) of two species of fruit flies reared at two temperatures------27

Table 8: Population parameters of B. invadens and C. cosyra reared on artificial - 30

Table 9: Population parameters of B. invadens and C. cosyra reared on artificial - 31

LIST OF FIGURES

Figure 1: Marula fruit fly Ceratitis cosyra Source: Jeffrey Lotz----------------------xx

Figure 2: Natal fruit fly, Ceratitis rosa Karsch Source: CABI (2007)----------------xx

Figure 3: Bactrocera invadens (Drew, Tsuruta & White) Source: R. S. Copeland (2005)--xx

Figure 4: Melon fruit fly Bactrocera cucurbitae Coquillett Source: R. S. Copeland (2005)---xxi

Figure 5: Plastic containers for rearing fruit flies---------------------------------------16

Figure 6: Average duration of egg development time in days of B. invadens and C. cosyra at two temperature regimes--21

Figure 7: Average time (days) of larval development rates of B. invadens and C. cosyra at two temperature regimes--22

Figure 8: Average time (days) of pupal development rates of B. invadens and C. cosyra at two temperature regimes--23

Figure 9: Means of preoviposition period in days of B. invadens and C. cosyra reared at two temperatures---24

Figure 10: The daily egg production of B. invadens and C. cosyra (in days) at two temperature regimes---25

Figure 11: Survivorship curves for B. invadens and C. cosyra reared at 30 0C-----26

Figure 12: Survivorship curves for B. invadens and C. cosyra reared at 250C------26

Figure 13: Intrinsic rates of increase of B. invadens and C. cosyra at two temperatures---28

Figure 14: Net reproductive rates of B. invadens and C. cosyra at two temperature regimes ---28

Figure 15: Doubling time in days of B. invadens and C. cosyra at two temperatures29

Figure 16: Mean generation time of B. invadens and C. cosyra at two temperatures30

LIST OF APPENDICES

LIST OF ABBREVIATIONS AND SYMBOLS

CABI	Centre for Agriculture and Biosciences International
DED	District Executive Director
DALDO	District Agriculture and Livestock Development Officer
EMAN	Ecological Monitoring and Assessment Network
SIT	Sterile Insect Technique
SUA	Sokoine University of Agriculture
UK	United Kingdom
USA	United States of America
^{o}C	Degrees Celsius
e.g.	For example
IAEA	International Atomic Energy Agency
ANOVA	Analysis of Variance
USD	United State Dollar
RH	Relative Humidity
GNP	Gross National Product
ICN	Enzymatic Yeast Hydrolysate
LSD	Least Significance Difference
DT	Doubling Time
SE	Standard Error
FAO	Food and Agriculture Organization

CHAPTER ONE

INTRODUCTION

1.1 Background

Fruits and vegetables production is one of the fastest-growing agricultural sectors in Africa (Ekesi and Billah, 2005). Fruits and vegetables are very important as a source of nutrients which supplement daily dietary requirement. They form a complete, wholesome food for the grown up, those who are still growing and the infants, leading to a healthy body and mind. Fruits and vegetables are ready sources of energy with the unique capacity of guarding bodies against diseases resulting from nutrient deficiencies. Fruits can supply more than 1/3 of the requirements of calories, vitamins and minerals to mankind (Singh, 1986). Furthermore, apart from being a source of nutrients, fruits are a source of income and employment to many Tanzanian growers and traders.

Tanzania has a variety of topography and altitudes, with different climatic conditions and potential for growing different types of fruits and vegetables ranging from tropical, sub-tropical and temperate. The fruits produced in the country include orange, mango, grape, papaya, pineapple, banana, guava, lemon, tangerine, avocado, soursop, peache, plum, pear, apple, and jackfruit. Other fruit vegetables produced in the country include pumpkin, cucumber, tomato and African eggplant. Most of fruit and vegetable crops are produced by small scale farmers and are consumed locally and a very amount is left for export.

Tropical and Subtropical Regions are becoming important areas for fruit production. If export requirements can be met, there is a great potential for export of fruits from these regions to international markets. For example, it is reported by Vayssières *et al*. (2008a) that mango imports into Europe from Benin have multiplied five times over the past fourteen years, thus increasing from 42 000 tonnes in 1992 to over 210 000 tonnes in 2006. Bank of Tanzania (2008), recorded substantial increases of nontraditional exports including horticultural products which went up to USD 4.6 millions from July to September, 2007 to USD 8.3 millions in July to September, 2008.

The most challenging task in this enterprise is to have pest free fruits for export. Fruit flies (Diptera: Tephritidae) have been listed among the major pests of many fruits (CABI, 2007). The main losses that fruit flies cause include direct damage to fruits and fruit vegetables. Fruit flies compete with humans for food resources, thus create a negative impact on sustainable rural livelihoods and loss of marketing opportunities due to the imposition of strict quarantine regulations by the importing countries (Ekesi and Billah, 2005).

1.2 Problem Statement and Justification

Crop losses due to pests, in most cases, relate to the increase in pest population. High population densities of insects normally result into high crop damage. The main losses that fruit flies cause include direct damage of fruits. Fruit flies are reported to be present in all fruit growing regions of the world, where 35% of these species attack soft fruits causing losses as high as 910 millions USD (White and Elson-Harris, 1992). According to Vayssières *et al*. (2008a), in the tropical regions, mangoes are attacked by fruit flies (Diptera Tephritidae) which inflict great economic devastation in both East and West Africa. In 2003, these quarantine insects destroyed an average of 40% of the total mango crop produced yearly in Africa. The decrease in export quantities of fruits may be associated with the presence of newly invasive fruit fly which was reported shortly afterwards (Mwatawala *et al*., 2009).

In Tanzania, a number of fruit flies have been recorded (CABI, 2007); and the status of fruit flies research has also been reviewed (see Mwatawala *et al*., 2005). Recently two new species of fruit flies were introduced into the country, the first specie is *Bactrocera* *invadens* Drew Tsuruta and White which was detected in 2003 (Mwatawala *et al*., 2004), and the second is *Bactrocera latifrons* (Hendel) which was detected in 2006 (Mwatawala *et al*., 2007). The introduction of new species may result into competition of one or more species, or co-existence. Mwatawala *et al*. (2009) found that the introduced *Bactrocera* species dominate the native species in their fundamental niche. The information by Mwatawala *et al*. (2009) is based on traps catches' data in the field as well as incidence and infestation rates on fruits.

However Mwatawala *et al*. (2009) study did not establish demographic and life history parameters as related to competition. These remain unknown for *C. rosa* and partly known for *B. invadens*. The life history strategies include development rates of immature stages (i.e. egg stage duration, larval and pupal development), adult longevity, fecundity, daily mortality, pre-oviposition period, net reproductive rate, mean generation time and doubling time. Such data are currently lacking, thus this study was undertaken to determine the dominant and the key fruit fly pest of mango and hence filling knowledge gap in that regard. This information will help in formulating appropriate control and management programmes for fruit flies in orchards in Tanzania.

1.3 Objectives

1.3.1 Overall Objective

To establish inherent factors determining populations of two mango attacking fruit fly species (Diptera: Tephritidae).

1.3.2 Specific Objectives

(i) To establish life table parameters of the two fruit fly species.

(ii) To determine demographic parameters of the two fruit flies.

CHAPTER TWO

LITERATURE REVIEW

2.1 Status of fruit industry in Tanzania

2.2 Production of fruits in Tanzania

Horticulture has been identified as a potential sub-sector in which Tanzanian's can become more meaningfully engaged to increase their level of income, employment, and standard of living.

As it has been mention earlier, Tropical and Subtropical Regions are becoming important areas for fruit production. If export qualities can be met there is a great potential for export of fruits from these regions to international markets. The most challenging task in this case is to produce pest free fruits for export. According to Ashimogo and Greenhalgh (2007), most high-value horticultural products in Tanzania have experienced remarkable growth. Horticulture exports have been expanding from about USD 9 millions in 1999 to USD 14 millions in 2004. Fresh vegetable export values have risen more than fivefold in the last four years.

Mango has been produced in East Africa since the fourteenth century and it is believed to have originated from South-East Asia, but they were only initially reported in West Africa at the beginning of the nineteenth century (Vayssières *et al.,* 2008a). Mango is one of the most important fruit trees of the tropics (Mbuya *et al.,* 1994). Generally in Tanzania, the production of mango has been decreasing unlike in Kenya, but it is very low compared to major producing countries like India. On the other hand, the production of orange in Kenya has been increasing (Table 1).

Table 1: Statistical data of mango and orange in East Africa countries and India.

Country	Fruit	2005	2006	2007	2008	2009
Tanzania	Mango	360 000	400 000	220 000	300 000	100 787
Kenya		180 000	248 531	384 461	448 631	474 608
Uganda		-	-	-	-	-
India		11 829 700	12 537 900	13 501 000	13 649 400	13 557 100
Tanzania	Orange	37 000	38 000	39 000	39 000	39 000
Kenya		29 816	27 000	28 000	34 432	33 086
Uganda		-	-	-	-	-
India		3 314 000	3 437 400	4 266 900	4 860 300	5 201 350

Source: FAO, (2010)

2.3 Importance of fruits

Nutritional importance

Fruit and vegetables are important as essential building blocks of any diet. Not only are they loaded with vitamins and minerals which are essential for healthy living, but they also help in providing a balanced diet. According to Kader (2001), an increase in the intake of fruits and vegetables, benefit human health, and boosts one’s immune system, as well as building resistance to common illnesses and infections. Furthermore, fruit and vegetables can make one look better and feel great, which can lead to an all round improvement of one’s well-being. Fruits and vegetables play a significant role in human nutrition, especially as sources of vitamins (C, A, B6, thiamine, niacin, E), minerals, and dietary fiber Kader (2001).

Economic importance

Generally, fruits are economically important not only as a direct source of income to growers, but also it creates job opportunities in various processing factories and have social importance in land tenure. Fruits trees are important for providing shade in many residential areas, parks, and avenues. Furthermore, fruit export could be another source of revenue for many countries with agro-based economies like Tanzania. For example in

2006, Benin had an annual Gross National Product (GNP) of 590 USD per capita, and a GNP growth rate of 1.3% per capita, placing it among the least developed countries (Vayssières *et al.,* 2008a). However, fruit cultivation is done on a small scale, each household growing one or two trees of each species. These are mainly grown for home consumption and with a very little excess being sold in the market (Fong and Young, 1982; Mbuya *et al.,* 1994).

2.4 Constraints to fruit production

There are a number of factors that have been mentioned to affect fruit production in Tanzania. At production and marketing levels the major constraints to fruit and vegetables sector growth include poor and unspecialized extension services; poor accessibility to inputs and their high cost of production; lack of strong and effective farmer organizations, poor market information, poor rural roads leading to high costs, pests, and lack of finance. According to Mwatawala *et al.* (2006), production of high quality fruits in Tanzania is hampered by economic and developmental constraints, but also by insect pests, especially fruit flies (Diptera: Tephritidae). Fruit flies (Diptera: Tephritidae) are the most important and notorious insect pests that cause serious damage on fruit and vegetable crops in most tropical countries (White and Elson-Harris, 1992) including Tanzania.

2.5 Fruit fly insect Pests

The family Tephritidae includes about 4 000 species in 500 genera. It is one of the largest families of Diptera (the flies), and also one of the most economically important groups of insects (Ekesi and Billah, 2005). Fruit flies (Diptera: Tephritidae) are a biologically diverse family of flies whose larvae are mainly phytophagous, infesting fruits, flower heads or stems of a wide range of host plants (Copeland, *et al*., 2005) and are considered as one of the most economically important groups of insect pests worldwide (Jayanthi and

Verghese, 2008). Fruits are the worst affected crops, which include citrus, mango, apples, and some seed crops such as sunflower and safflower.

White and Elson-Harris (1992) reported the pest status, host range and distribution data for the 100 most economically important species of Tephritidae. In their assessment, they explained that the great majority of pest species of Tephritidae that attack fruits belong to the genera *Anastrepha, Ceratitis*, *Bactrocera*, *Dacus* and *Rhagoletis*. The hosts of these flies belong to a wide variety of families of plants, and include many major commercial crops.

The major pest genus found in South and Central America, West Indies and a few in the South of USA is *Anastrepha*. Some species within the genus attack a wide range of fruits. The genus *Bactrocera* is the most economically significant genus, with about 40 species considered to be important pests. Many of them are highly polyphagous. *Bactrocera* is native to Tropical Asia, Australia and South Pacific Regions, with a few species in Africa, and warm temperate areas of Europe. The genus *Ceratitis,* have about ten species which are listed as pests and are mostly restricted to Africa, except for the *Ceratitis capitata* (Wiedemann), which has spread to many tropical and subtropical parts of the world. The genus *Dacus,* is mostly found in Africa and a fair proportion in Asia, while the genus *Rhagoletis,* is found in South and Central America, Europe and North America (White and Elson- Harris, 1992).

2.6 Major fruit fly species of Afro-tropical region

Tephritids are also among the most economically important groups of insect pests in the Afrotropical Region, as they are major constraint to commercial and subsistence fruit farming in the region (Copeland *et al.*, 2005). There are about 950 species and about 150 genera of fruit fly (Tephritidae) which are known in this region and include 11 *Bactrocera* spp., 95 *Ceratitis* spp., and 195 *Dacus* spp (De Meyer *et al*., 2011).

2.7 Major fruit fly pest species of Tanzania

2.7.1 Indigenous species

According to collections made by Mwatawala *et al*. (2005) from various sources, about 50 species were found in Tanzania mainland and Zanzibar. Ten of them were of more economic importance, some of them were indigenous and the others were newly introduced. The following are the indigenous species;

- ***Ceratitis capitata*** **Wiedemann:** This is also known as the Mediterranean fruit fly. It is the most widely distributed attacking many fruits.
- ***Ceratitis cosyra*** **Walker:** the mango fruit fly or marula fruit fly is widespread species found throughout the African continent. It is known to attack mango, guava, marula and sour orange, (Figure 1).
- ***Ceratitis fasciventris*** **Bezzi:** This attacks mango, guava and coffee.
- ***Ceratitis rosa*** **Karsch:** The Natal fruit fly is a major economic pest in southern and eastern Africa. It damages mango, papaya, guava, apple and coffee, (Figure 2).

2.7.2 Introduced species

Many species mainly from the genus *Bactrocera* e.g. *Bactrocera latifrons* (Hendel), *Bactrocera cucurbitae* (Coquillett) (Figure 4) and *Bactrocera invadens* (Drew, Tsuruta and White) (Figure 3) have been introduced in Tanzania. Asian fruit fly pests of the genus *Bactrocera* are regarded as some of the most destructive insects of fruits and vegetables worldwide (White and Elson- Harris, 1992). According to Vayssières *et al.* (2008a), *B. cucurbitae* and *D. ciliatus* are the only two species which are of major economic significance especially on cucurbit crops causing heavy damages. Of these species, *B.*

invadens (Drew, Tsuruta and White) is the most destructive as it damages a wide range of fruits and it has been reported to out- compete and displace the indigenous fruit fly species (Mwatawala *et al*., 2006). As suggested by Ekesi *et al*. (2009), exploitative competition through larval scrambling for resources and interference competition through aggressive behaviors of the invader are important mechanisms contributing to the displacement of *C. cosyra* by *B. invadens* in mango agroecosystems.

Figure 1: Marula fruit fly *Ceratitis cosyra* Source: Jeffrey Lotz

Figure 2: Natal fruit fly, *Ceratitis rosa* Karsch Source: CABI (2007)

Figure 3: *Bactrocera invadens* (Drew, Tsuruta & White) Source: R. S. Copeland (2005)

Figure 4: Melon fruit fly *Bactrocera cucurbitae* Coquillett Source: R. S. Copeland (2005)

2.8 Losses due to fruit flies

The presence of fruit flies in any fruit growing region becomes an added cost in fruit production. According to White and Elson-Harris (1992), the potential losses as well as eradication costs of fruit fly pests when they are established are very high. In Madeira, there is a Medfly control programme based on the sterile insect technique (SIT), if the programme continues operating at a weekly capacity of 50 million sterile males, the average programme costs is estimated at an average of 2.7 million euros/year (IAEA, 2005).

Fruit flies cause major production constraints to horticulture. For example, out of 1.9 million tonnes of mango produced annually in Africa about 30-50% (up to 760 000 tonnes) is destroyed by fruit flies (Ekesi *et al.*, 2009). According to Mbaye *et al.* (2008), previously unknown as a pest in Senegal, the fruit flies and in particular *B. invadens* and *C. cosyra* (Diptera: Tephritidae) have seriously been threatening the fruit production. For mango, the losses are approximately 41 000 tonnes while the national production is around 100 000 tonnes. According to Vayssières *et al.* (2008a), the mango production sector suffers heavy economic losses due to the damage caused by fruit flies, which are the main menace in Benin and which considerably decreases mango yield compared with other pests. For example, the end of the crop year in 2006 as in 2007, over 75% of production in Benin was lost due to fruit flies. Unfortunately, the monetary estimates of fruit fly damage are not available for most countries (White and Elson-Harris, 1992) and this includes Tanzania.

2.9 Life history of fruit flies

The life cycle of fruit flies like many other organisms starts with the mating of adults. Ekesi and Billah (2005), present a generalized life cycle of tephritid fruit flies, in that adult fruit flies are sexually mature between 4 to 10 days after emergence and this is time when they begin to mate. Soon after mating, the female uses her sharp ovipositor to lay her eggs into the fruit by settling on the surface and piercing it to a depth of about 2-5mm where she oviposits her eggs. Eggs, which are banana-shaped, are deposited in batches of 3-8 depending on the species. Depending on the temperature conditions, the eggs hatch within 3-12 days into tiny white maggots. The maggots (larvae), the maggots cast their skin twice inside the fruit. During development and when fully grown, they measure about 7-8 mm long. By this stage the rotten fruit will probably fall to the ground. The maggots then leave the fruit and burry themselves in the soil where they change into pupae (that are enclosed in hard barrel-shaped cases called puparia). The puparia are found buried in the soil 2-5 cm beneath the host plant. Puparia can be white, brown or black and 4-12 mm long. The duration of the pupal stage can be 10 to 20 days depending on the climatic conditions. When pupation is complete, a winged fly adult emerges and crawls to the soil surface.

2.10 Development and survival of immature stages

Ekesi *et al*. (2006) did a comparative development biology of *B. invadens* maintained at 28 ± 1^{0}C, while Papadopoulos *et al.* (2002), studied the biology of a wild population of the Mediterranean fruit fly, *C. capitata* and Vargas *et al.* (2000) did a comparative demography of three Hawaiian fruit flies at alternating temperatures (Tables 2, 3 and 4). Appiah *et al*. (2009) also revealed that rainfall and temperature significantly influenced the pest population.

Although development and survival of immature stages have been well described for B. invadens in Kenya (Ekesi et al., 2006), and C. capitata in Hawaiian (Vargas et al., 2000) no detail biological data on *C. cosyra* e.g. fecundity, daily eggs, pre-oviposition and oviposition period, intrinsic rate of increase, net reproductive rate, mean generation time and longevity despite its economic importance (CABI, 2007 and De Meyer *et al*., 2011).

Table 2: The average development times (days) of immature stages of 4 species of fruit flies

Author	Vargas *et al* (2000)	Vargas *et al* (2000)	Vargas *et al* (2000)	Papadopolous *et al*. (2002)	Ekesi *et al* (2006)
Temperatures	24 ^{0}C	24 ^{0}C	24 ^{0}C	25 ^{0}C	28 ^{0}C
Stages	*B. cucurbitae*	*B. dorsalis*	*C. capitata*	*C. capitata*	*B. invadens*
Egg	1.0 ± 0.00	2.0 ± 0.00	2.0 ± 0.00	2.05 ± 0.01	1.2 ± 0.02
Larva	6.3 ± 0.13	7.7 ± 0.33	6.5 ± 0.12	17.9 ± 4.45	11.1 ± 3.12
Pupa	11.9 ± 0.07	12.4 ± 0.25	11.7 ± 0.38	10.5 ± 0.13	12.4 ± 0.15

Table 3: Population parameters of 4 species of fruit flies

Author	Vargas *et al* (2000)	Vargas *et al* (2000)	Vargas *et al* (2000)	Papadopolous *et al*. (2002)	Ekesi *et al* (2006)
Temperatures	24 ^{0}C	24 ^{0}C	24 ^{0}C	25 ^{0}C	28 ^{0}C
Parameters	*B. cucurbitae*	*B. dorsalis*	*C. capitata*	*C. capitata*	*B. invadens*
Gross fecundity	236.5 ± 57.8	1243.9 ± 226	706.2 ± 105.65	648.3	1056.8
Net fecundity	108.0 ± 21.2	467.3 ± 122.9	423.9 ± 99.7	562.4	794.6
Net fertility		12.4 ± 1.7	6.8 ± 1.2	437.2	608.1
Daily oviposition	1.1 ± 0.3			10.9	18.2

Table 4: Population parameters of 4 species of fruit flies

Author	Vargas *et al* (2000)	Vargas *et al* (2000)	Vargas *et al* (2000)	Papadopolous *et al*. (2002)	Ekesi *et al* (2006)
Temperatures	24 ^{0}C	24 ^{0}C	24 ^{0}C	25 ^{0}C	28 ^{0}C
Parameters	*B. cucurbitae*	*B. dorsalis*	*C. capitata*	*C. capitata*	*B. invadens*
R	0.053 ± 0.008	0.065 ± 0.005	0.12 ± 0.004	0.08	0.113
Ro	42.1 ± 8.19	169.9 ± 41.2	178 ± 34.9	65	273
DT	14 ± 2.1	11 ± 1.02	5.8 ± 0.16	9	6.16
T	72.7 ± 7.7	78.2 ± 3.7	42.9 ± 0.67	53	30.7

r = intrinsic rate, Ro = net reproductive rate, DT = doubling time, and T = mean generation time.

Duyck and Quilici (2002) presented the survival and development of *C. capitata, C. rosa* and the Mascarenes fruit fly, *Ceratitis catoirii* Guérin-Mèneville. These species were compared at five constant temperatures ranging from 15 to 35°C. Durations of the immature stages of *C. capitata*, *C. rosa* and *C. catoirii* ranged from 14.5–63.8, 18.8–65.7 and 16.8–65.8 days, respectively, at 30–15°C. Species differed mainly during the larval stages and ovarian maturation period, with smaller differences in the egg stage. *Ceratitis rosa* appeared to be better adapted to low temperatures than the two other species. However, detailed biology of *C. cosyra* is not very well known e.g. fecundity, daily eggs, longevity but it is considered to be quite similar to that of *C. capitata* in biology and survive capacity (CABI, 2007 and De Meyer *et al*., 2011).

Liu and Ye (2009) revealed that an increase in the temperature of the rearing chamber from 18° to 36° C resulted in faster development of eggs, larvae, and pupae of *Bactrocera correcta* (Bezzi) ranging from 66.75 to 26.5 hours. Similarly, *B. cucurbitae* and *D. ciliatus,* which were exposed to different temperature regimes of between 15° and 30° C under laboratory conditions, completed their total development from egg to adult ranging from 44.2 days to 13.2 days and 86.3 days to 16.4 days respectively (Vayssières *et al.*, 2008b), In another study conducted by Duyck and Quilici (2002), discovered that the developmental time of *C. capitata* from egg to adult decreased rapidly with an increase in temperature from 64 to 16 days, between 15 and 30°C. Kasap, and Alten (2006), observed that, the fecundity and longevity of the insects were both highly variable, depending on the temperature.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Establishment of fruit fly colonies

Colonies of adult fruit flies were established from field infested fruits of mango *Mangifera indica* L., soursop *Annona muricata* L., guava *Psidium guajava* L., and Tropica almond *Terminalia catappa* L., collected from SUA Horticulture Unit, and Morogoro town centre. These fruits were collected and brought to the rearing unit in the laboratory and put in the rearing plastic containers containing a thin layer of sand at the bottom for pupation. Containers were checked every day for puparia and adult flies that emerged. Upon emergence, the adult fruit flies were collected and identified using standard key presented by White and Elson-Harris (1992) and held in plastic containers covered with fine mesh (Figure 5). Adults were fed simultaneously with enzymatic yeast hydrolysate (ICN Biomedical) and sucrose in a ratio of 1:3 and water was supplied in Petri dishes in different plastic containers for each species. Fruit flies were reared at room temperatures following protocols used by Vayssières *et al.* (2008b).

Figure 5: Plastic containers for rearing fruit flies

3.2 Determination of life table parameters

Egg stage duration

Eggs of *B. invadens* and *C. cosyra* were collected using mango (a single fruit each) placed for 3 to 6 hours into stock fly colonies. The duration of the egg stage was established by using samples of 100 eggs collected randomly with a camel hair brush and placed on a moist filter paper in a Petri dish at 25 and 30^0C with 75% RH maintained in an environmental growth chamber. Eggs were placed in the environmental growth chamber for 20 hours and then the hatching of the eggs was determined after every 12 hours using a microscope.

Larval and pupal development

Fifty newly emerged larvae from the lots of eggs above were gently introduced using fine camel's hair brush onto the 50 g of specific artificial larval diet (Table 5) in a Petri dish for each species. Changes on larval stages were observed twice per day. The time needed for 50% of individuals to develop to a particular stage (third larval instars) was noted at 25, and 30^0C with 75% RH. Larval instars were differentiated by their size, body surface sculpturing, and color according to White and Elson-Harris (1992). By the end of the third larval instars, mature larvae were allowed to leave the Petri dish to pupate in the sand in plastic container. Pupae were collected by sifting the sand and counted. They were transferred to a plastic container covered with fine a mesh. At the end of the pupae stage, the number of newly emerged adults was recorded twice a day. The design of the experiment was split plot arranged in a Complete Randomized Design (CRD) with three replications. There were two sources of variations: Fruit fly species (being the main-factor) and temperatures (being the sub-factor). The effect of temperature and species on eggs laying and survival were tested by two-way analysis of variance (ANOVA). The

Least significance difference (LSD) test was used to identify significant main effects. The analyses were performed using GenStat package.

Table 5: Composition of artificial diet for rearing *B. invadens* and *C. cosyra*

Ingredients	**Quantity in the diet (%)**	**Quantity per 200 ml diet**
Carrot powder	24.2	48.4g
Sugar	16.2	32.4g
Brewer's yeast	8.1	16.2g
Citric acid	0.6	1.2g
Methyl p-hydroxybenzoate	0.2	0.4g
Distilled water	50.7	101.4ml
Total	**100**	**200ml**

Source: Ekesi (2006).

3.3 Adult demographic parameters

Adult life history traits were assessed using 15 pairs of newly emerged adult of each species isolated in individual plastic container covered with fine a mesh placed at 25 and 30^{0}C for each fly species. Adults were fed with enzymatic yeast hydrolysate (ICN Biomedicals) and sugar in a ratio of 1:3. A single ball of wrapped artificial larval diet (Table 5 above) and mango were placed in plastic containers each containing *B. invadens* and *C. cosyra* daily to monitor egg laying. The wrapping of the diet and skin of the fruit were punctured using an entomological pin to facilitate oviposition. Eggs on the wrapping of the diet and skin of the fruit were gently removed as previously described, counted by using binocular microscope and the daily mortality of flies was recorded. The design of the experiment was split plot arranged in a Complete Randomized Design (CRD) with three replications. There were two sources of variations: Fruit fly species (being the main-factor) and temperatures (being the sub-factor). The effect of temperature and species on eggs laying and survival were tested by two-way analysis of variance (ANOVA). The Least significance difference (LSD) test was used to identify significant main effects. The analyses were performed using GenStat package. Standard life table parameters among the different species and treatments were calculated from daily records of mortality of immature stages, fecundity, and fertility of pairs of adults. Life table and demographic parameters were estimated following symbols, formula and definition described by Carey (1993) (Table 6).

3.4 Population parameters

Population parameters such as intrinsic rate, net reproductive rate, doubling time and mean generation time were simply using parameters symbols, formulae, and definitions as presented in Table 6.

Table 6: Definitions and formulae for various life table and demographic parameters

Parameter	**Definition**	**Formula**
X	Age interval in days	
l_x	Proportion of females surviving to start of the age interval	
m_x	Number of female egg laid by average female at age x	
M_x	Total number of eggs (males and female) laid by female at age x	
Preoviposition period	Amount of time prior to eggs being laid	
Gross fecundity rate	Theoretical natality rate during lifetime of female	$\sum_{x=\alpha}^{\beta} M_x$
Net fecundity rate	Number eggs the average newly eclosed female will lay during her lifetime	$\sum_{x=\alpha}^{\beta} l_x M_x$
Daily reproduction	Avg. no. of eggs produced per day in terms of entire female life-span	$\sum_{x=\alpha}^{\beta} M_x/(\omega-\varepsilon)$
Female longevity	Life-span of female	e_0
Male longevity	Life-span of male	e_0
Net reproductive rate (R_o)	Per generation contribution of newborn females to the next generation	$\sum_{x=\alpha}^{\beta} l_x m_x$
Intrinsic rate (*r*)	Rate of natural increase in a closed population	$1=\sum_{x=\alpha}^{\beta} e^{-rx} lxmx$
Mean generation time (T)	Time required for a newborn female to replace herself R_o-fold	$(\log_e R_o)/r$
Doubling time (DT)	Time required for the population to increase twofold	$(\log_e{}^2)/r$

Definitions and formula adopted from Carey 1993.

CHAPTER FOUR

RESULTS

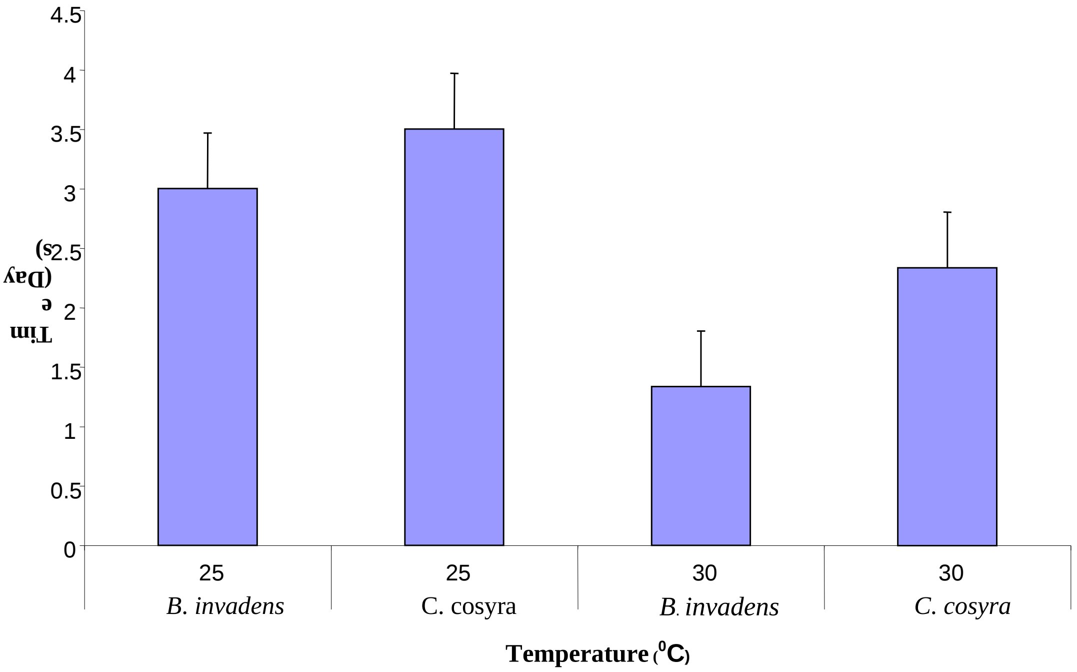
4.1 Life table parameters

Life table parameters of *B. invadens* and *C. cosyra* reared on artificial diet which address one of the specific objectives of this study are reported. These parameters include egg stage duration, larval and pupal development rates, preoviposition period, net fecundity rate and daily mortality. This study also reports the demographic (population) parameters of two fruit fly species which is a second objective of this study. In general, this study provides new information on immature stage development and adult demographic parameters of *C. cosyra* which have never been reported, despite its economic importance. These findings are presented and discussed in the following sub-sections.

4.2 Egg stage duration, larval and pupal development of the two species

Egg stage duration

The egg stage duration varied significantly between both species (F = 44.51; df = 1; P = 0.001) and with temperature (F = 89.88; df = 1; P = 0.001) (Figure 7). The egg stage duration of both species was markedly shorter at 30^0C. The invasive *B. invadens* exhibited a significantly shorter egg development period than the *C. cosyra* for all temperatures tested.

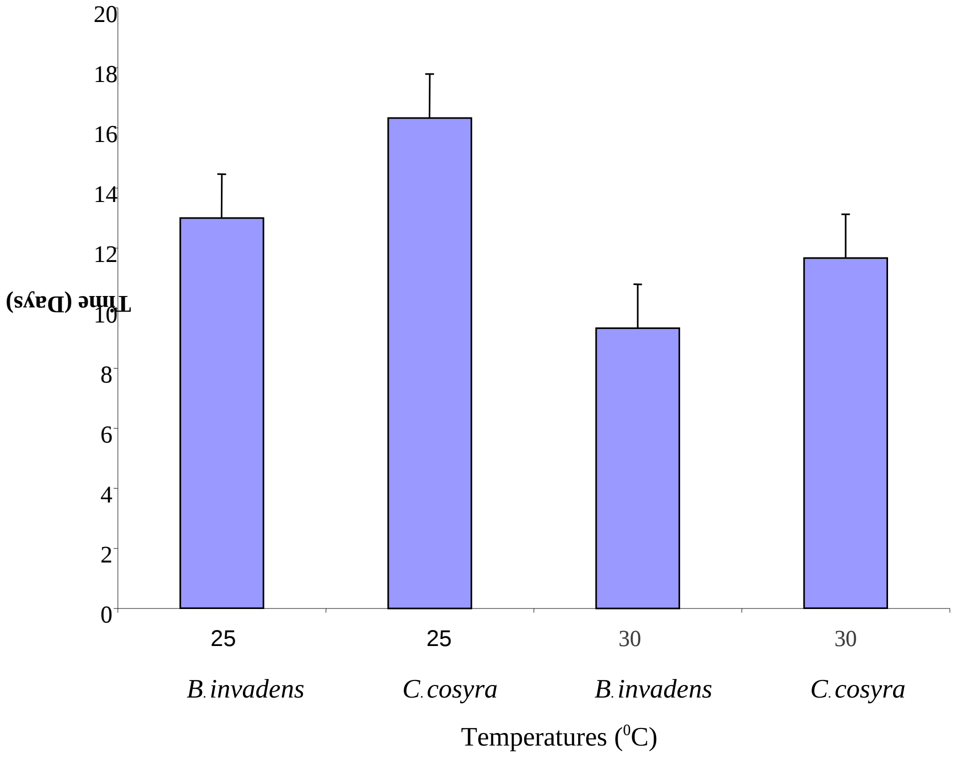


SE 2.01, LSD (0.05) 6.44 and CV 10%

Figure 6: Average duration of egg development time in days of *B. invadens* and *C. cosyra* at two temperature regimes

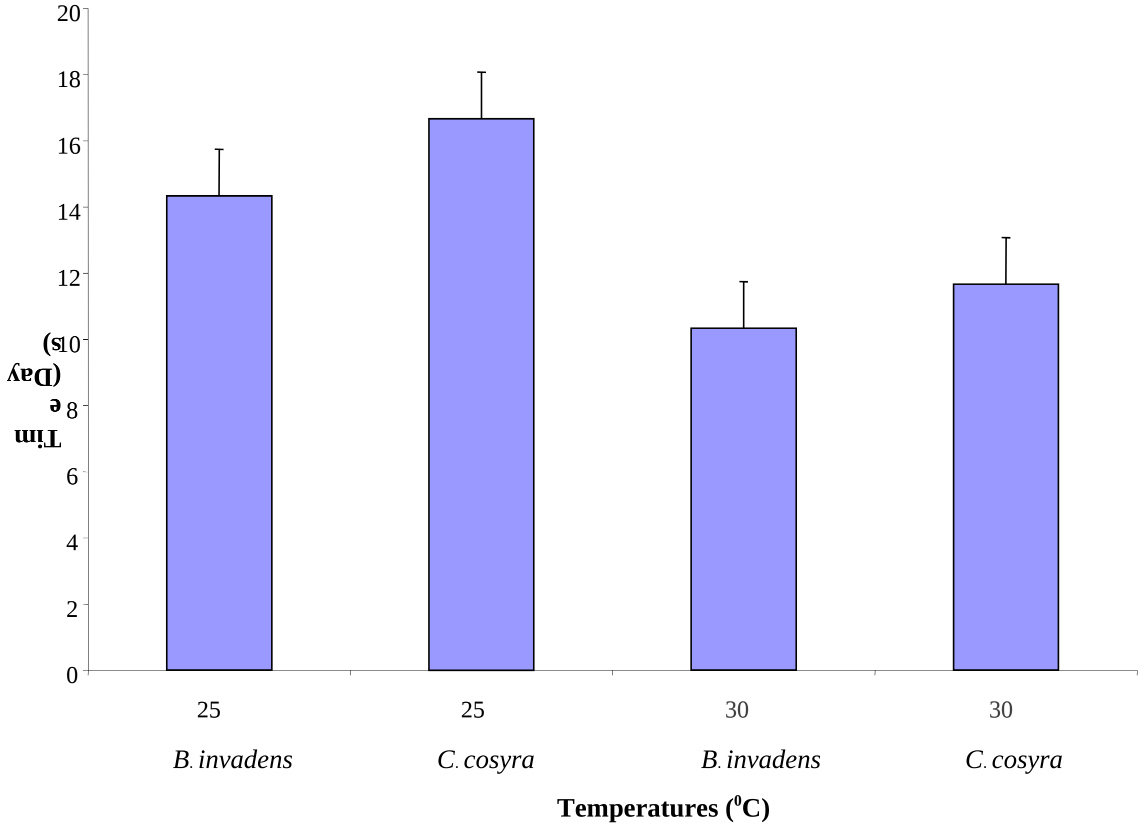
Larval and pupal development

The larval developmental time varied significantly among species (F = 42.88; df = 1; P = 0.001) and temperature (F = 76.24; df = 1; P = 0.001) (Figure 7). The pupal developmental time also varied significantly with species (F = 26.56; df = 1; P = 0.001) and temperature (F = 160.02; df = 1; P = 0.001) (Figure 8). The larval and pupal development times of *B. invadens* were shorter than those of *C. cosyra* for all temperatures tested. The average developmental time of larval and pupal for *B. invadens* at 30^{0}C was 9.3 d and 10.3 d respectively while it took 13.0 d and 14.3 d at 25^{0}C. Furthermore, the developmental time of larval and pupal for *C. cosyra* at 30^{0}C was 12.0 d and 11.7 d respectively while at 25^{0}C it took 16.3 d and 16.7 d. The total development time of immature stages of *B. invadens* and *C. cosyra* seems to decrease as the temperature increases and ranged from 29.7 days to 20.7 days and 35.9 days to 25.7 days from 25 to 30°C respectively.



SE 0.324, LSD (0.05) 1.036 and CV 6.3%

Figure 7: Average time (days) of larval development rates of *B. invadens* and *C. cosyra* at two temperature regimes



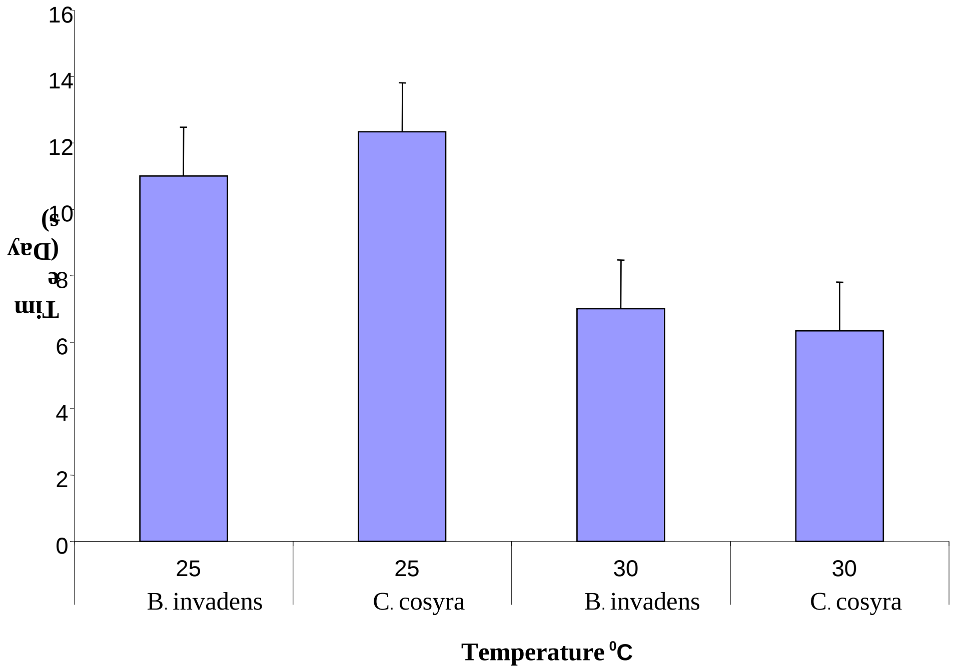
SE 0.252, LSD (0.05) 0.805 and CV 4.7%

Figure 8: Average time (days) of pupal development rates of *B. invadens* and *C. cosyra* at two temperature regimes

4.3 The pre-oviposition period, gross fecundity, net fecundity, daily egg production per female per day and longevity

The pre-oviposition period

Pre-oviposition period varied significantly different between temperatures (F = 41.33; df = 1; P = 0.001). The average pre-oviposition period at 25^{0}C was 11.0 and 12.3 days for *B. invadens* and *C. cosyra* respectively (Figure. 9). At 30^{0}C the mean pre-ovipositional period was 7.0 days for *B. invadens* and 6.3 days for *C. cosyra*. No significant differences were observed for pre-oviposition period (in days) between the two fruit fly species (P > 0.05) (Figure 9).



SE 0.55 LSD (0.05) , 1.759 and CV 14.7 %

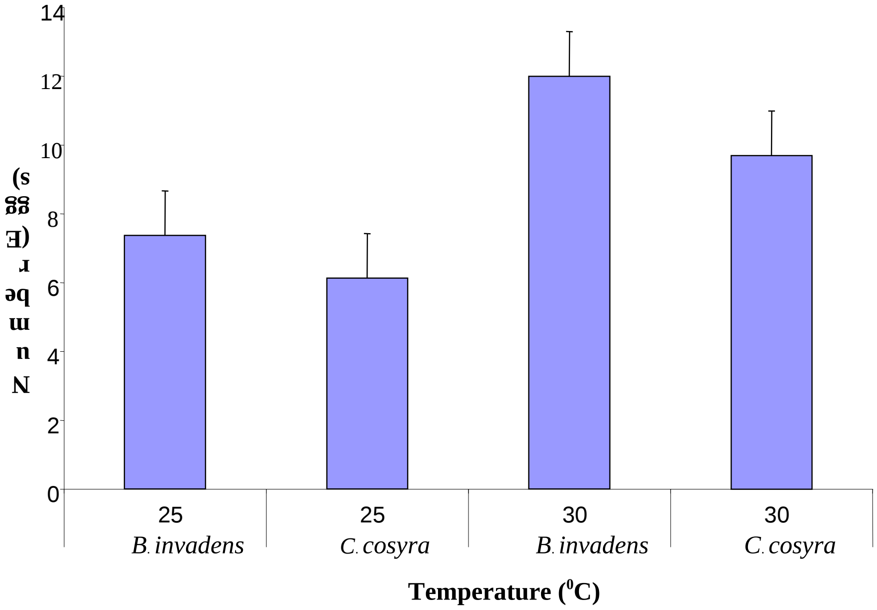
Figure 9: Means of preoviposition period in days of *B. invadens* and *C. cosyra* reared at two temperatures

Gross fecundity and net fecundity

The average gross fecundity at 25^{0}C for *B. invadens* was 577.6 eggs (Appendix 1) and 499.1 eggs for *C. cosyra* (Appendix 2). At 30^{0}C the average gross fecundity was 969.6 eggs for *B. invadens* (Appendix 7) and 768.4 eggs for *C. cosyra* (Appendix 8). The average net fecundity rate at 25^{0}C for *B. invadens* was 371.8 (Appendix 1) and 294.5 for *C. cosyra* (Appendix 2). At 30^{0}C, the average net fecundity was 544.5 for *B. invadens* (Appendix 7) and 316.4 for *C. cosyra* (Appendix 8).

Daily egg production per female per day

Numbers of eggs laid were significantly different between species (F = 33.95; df = 1; P = 0.001) and temperatures (F = 95.86; df = 1; P = 0.001). Highest numbers of eggs production per female per day for all species were laid at 30 ^{0}C (Figure 10).



SE 0.296 LSD (0.05), 0.946and CV 8.6%

Figure 10: The daily egg production of *B. invadens* and *C. cosyra* (in days) at two temperature regimes

Longevity

Life expectancy at pupal eclosion varied significantly among species for males (F = 23.41; df = 1; P = 0.001), but not significantly between temperatures (F = 8.37; df = 1; P = 0.001). In female life expectancy at pupal eclosion was 63.5 days for *B. invadens* and 58.6 days for *C. cosyra* at 25 ^{0}C (Appendices 3 and 4), and 37.5 days for *C. cosyra* while *B. invadens* was 50.5 days at 30 ^{0}C (Appendices 5 and 6 respectively) but were not significantly difference. Survivorship curves for both species are presented in Figures 11 and 12. Generally *B. invadens* had much higher survivorship compared to the *C. cosyra* in both temperatures (Figures 11 and 12).

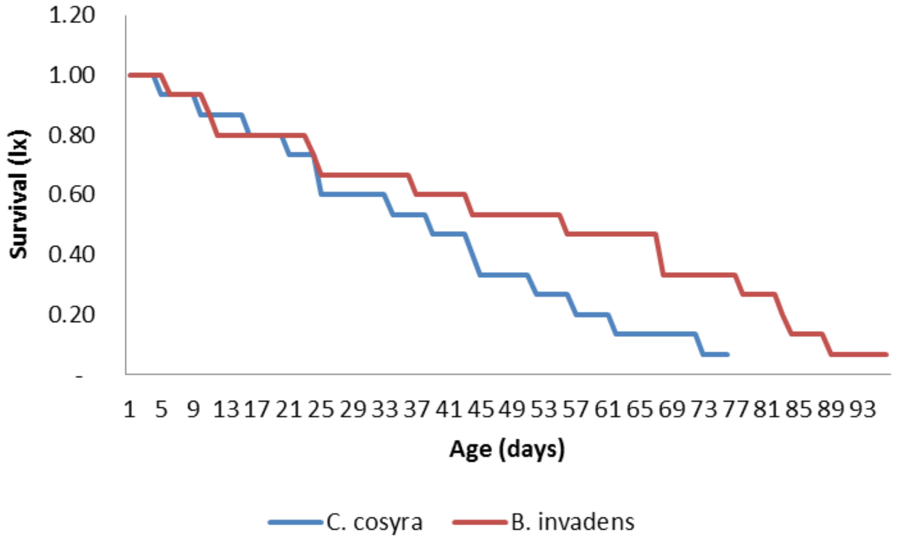


Figure 11: Survivorship curves for *B. invadens* and *C. cosyra* reared at 30 ^{0}C

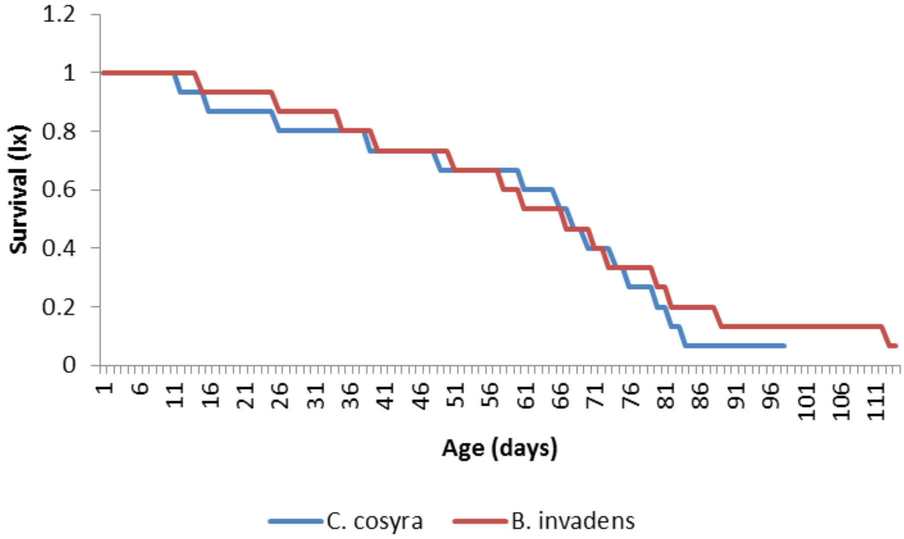


Figure 12: Survivorship curves for *B. invadens* and *C. cosyra* reared at 25^{0}C

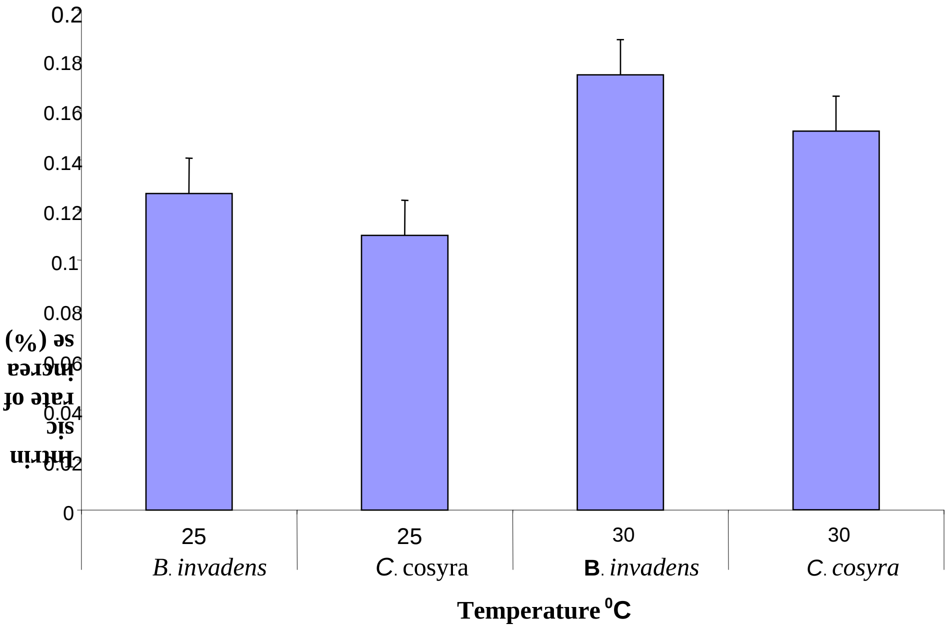
Table 7: Survival (%) of two species of fruit flies reared at two temperatures

Species	Temperature (^{0}C)	Eggs	Larvae	Puparia	Egg to adult
B. invadens	25	82.7	77.3	50.6	38.7
C. cosyra	25	85	77.3	43.2	33.3
B. invadens	30	90.7	81.3	64.3	52
C. cosyra	30	92.3	75.3	72.6	54.7

4.4 Demographic parameters

4.4.1 Intrinsic rate of increasing

Population parameters of *B. invadens* and *C. cosyra* are summarized in Tables 8 and 9. The intrinsic rate of increasing varied significantly with temperature (F = 189.84; df = 1; P = 0.001) and species (F = 37.11; df = 1; P = 0.001) (Figure 13). Both species exhibited their highest intrinsic rate of increase at 30^{0}C and low at 25^{0}C with *B. invadens* demonstrating the highest rate in all temperatures tested.

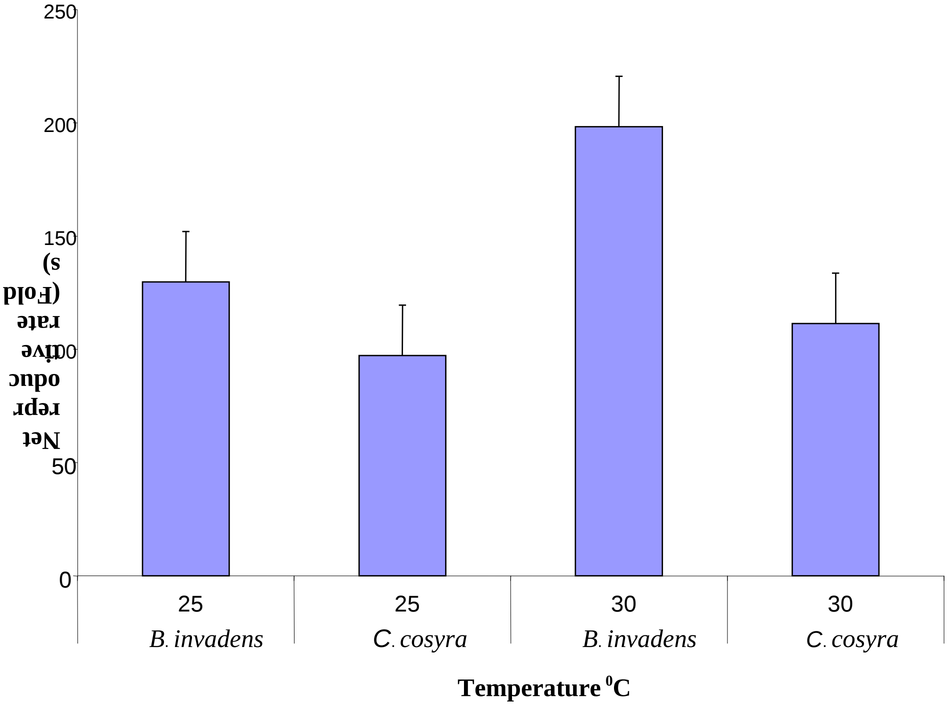


SE 0.0824 LSD (0.05) ,0.00731 and CV 4.0%

Figure 13: Intrinsic rates of increase of *B. invadens* and *C. cosyra* at two temperatures

4.4.2 Net reproductive rate

In the current study, net reproductive rate varied significantly with species (F = 28.69; df = 1; P = 0.001) and but not with temperatures (Figure 14). At 25^{0}C the average net reproductive rate of *B. invadens* was 130.5 (Table 8, Appendix 1) and 96.6 for *C. cosyra* (Table 8, Appendix 2). At 30^{0}C, the average net reproductive rate was 196.1 for *B. invadens* (Table 9; Appendix 7) and 107.5 for *C. cosyra* (Table 9; Appendix 8).



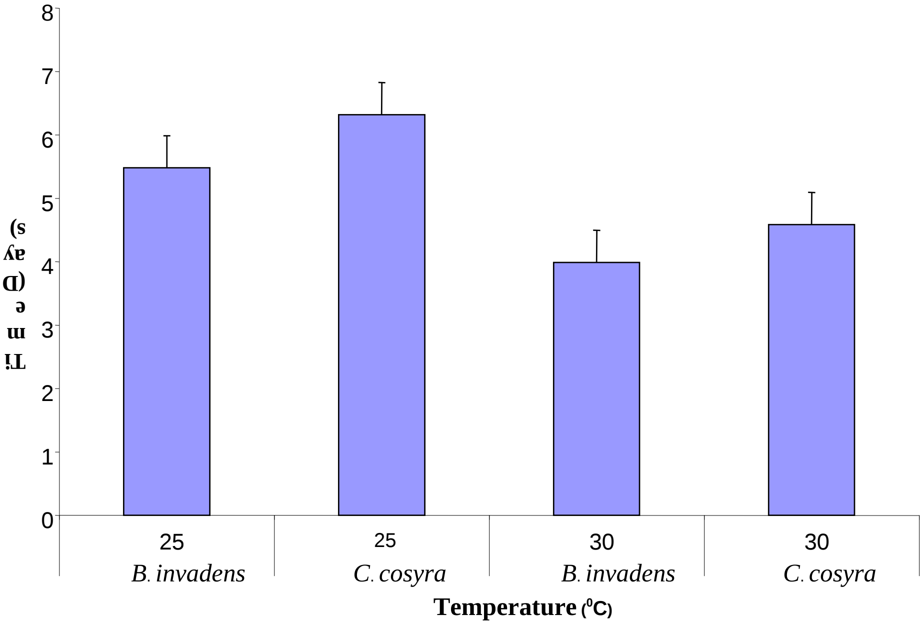
SE 7.88 LSD (0.05), 25.21 and CV 14.4 %

Figure 14: Net reproductive rates of *B. invadens* and *C. cosyra* at two temperature regimes

4.4.3 Doubling time

Doubling time (DT) varied significantly with temperature (F = 191.53; df = 1; P = 0.001) and species (F = 37.88; df = 1; P = 0.001) (Figure 15). The average DT at 25^{0}C was 5.5 days for *B. invadens* (Table 8; Appendix 1) and 6.3 days for *C. cosyra* (Table 8; Appendix

2). At 30^0C, the DT was 3.9 days for *B. invadens* (Table 9; Appendix 7) and 4.5 days for *C. cosyra* (Appendix 8).

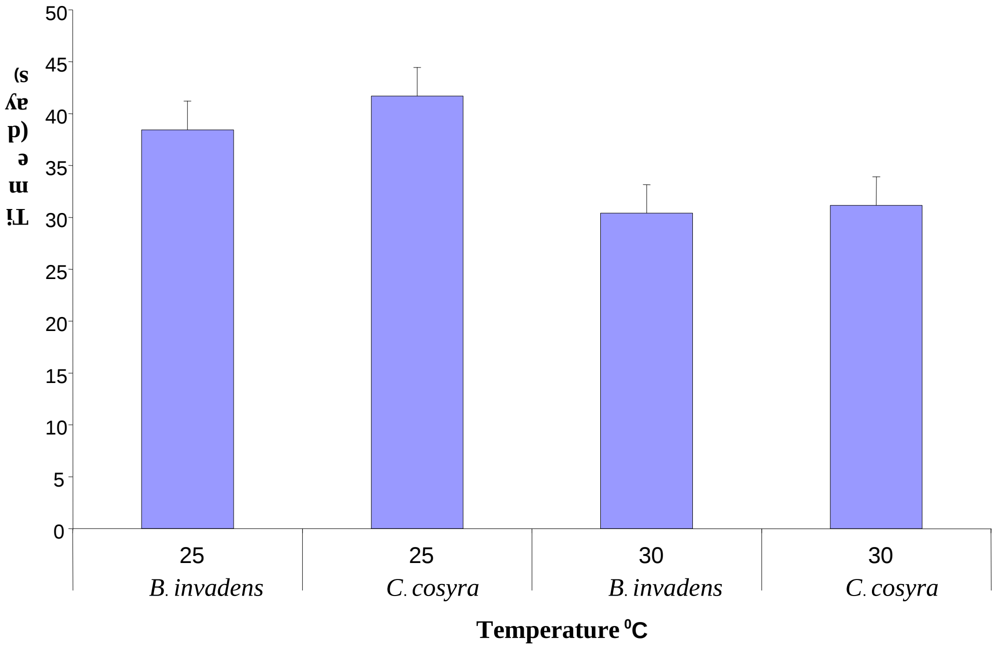


SE 0.0824 LSD (0.05), 0.2638 and CV 4.0 %

Figure 15: Doubling time in days of *B. invadens* and *C. cosyra* at two temperatures

4.4.4 Mean generation time

The mean generation times varied significantly with temperatures, but were not between the two species (Figure 16). The average mean generation time at 25^0C was 38.4 days for *B. invadens* (Table 8, Appendix 1) and 41.7 days for *C. cosyra* (Appendix 2). At 30^0C the average mean generation time were 30.4 days for *B. invadens* (Table 9, Appendix 7) and 31.2 days for *C. cosyra* (Appendix 8). The mean generation times decrease as the temperature increases from 25 to 30^0C.



SE 0.744 LSD (0.05), 2.379 and CV 5.1 %

Figure 16: Mean generation time of *B. invadens* and *C. cosyra* at two temperatures

Table 8: Population parameters of *B. invadens* and *C. cosyra* reared on artificial diet at 25 ^{0}C

General trait/parameters	Formula	Value at 25 ^{0}C	
Rates		*B. invadens*	*C.cosyra*
Net reproductive rate (Ro)	$\sum_{x=\alpha}^{\beta} lxmx$	130.5	96.6
Intrinsic rate of increasing (r)	Ln(Ro)/T	0.128	0.109
Finite rate of increasing (λ)	e^r	1.135	1.116
Times			
Doubling time (DT)	Ln(2)/r	6.3	5.4
Mean generation time (T)	$\sum_{x=\alpha}^{\beta} xlxmx \sum_{x=\alpha}^{\beta} lxmx$	38.08	41.77

α = Age at the start of reproduction; β = age at the end of reproduction; w = maximum age; Lx = fraction per capita lived between age x and x + 1; mx = hxmx/2, the number of female eggs laid by average female at age x.

Table 9: Population parameters of *B. invadens* and *C. cosyra* reared on artificial diet at 30 ^{0}C

General trait/parameters	Formula	Value at 30 ^{0}C	
Rates		*B. invadens*	*C.cosyra*
Net reproductive rate (Ro)	$\sum_{x=\alpha}^{\beta} lxmx$	196.1	107.5
Intrinsic rate of increasing (r)	Ln(Ro)/T	0.174	0.154
Finite rate of increasing (λ)	e^r	1.19	1.16
Times			
Doubling time (DT)	Ln(2)/r	3.98	4.51
Mean generation time (T)	$\sum_{x=\alpha}^{\beta} xlxmx / \sum_{x=\alpha}^{\beta} lxmx$	30.34	30.4

α = Age at the start of reproduction; β = age at the end of reproduction; w = maximum age; Lx = fraction per capita lived between age x and x + 1; mx = hxmx/2, the number of female eggs laid by average female at age x.

CHAPTER FIVE

DISCUSSION

5.1 Egg stage duration, larval and pupal development of the two species

5.1.1 Egg stage duration

The average duration of egg development was 1.08 and 2.0 days for *B. invadens* and *C. cosyra* at 30^0C, while was 2.3 and 2.9 days at 25^0C respectively. It was found in several studies that temperature, an important factor on development of fruit flies, also influences the survival of immature stages. Liu and Ye (2009) observed that the rate of egg stage duration of *B. correcta* increased rapidly with increasing temperature between 24^0C and 30^0C. According to Duyck and Quilici (2002), developmental time of *C. capitata* from egg to adult increased rapidly with decreasing temperature between 30 and 15°C, from 16 to 64 days. Similarly, *Bactrocera cucurbitae* (Coquillett) and *Dacus ciliatus* Loew, which was exposed to different temperature regimes between 20° and 30° C under laboratory conditions, completed its total development from egg to adult faster as temperature increased (Vayssières *et al*., 2008b). In the case of simultaneous laying of eggs of two Dacini species, the competitive advantage of the melon fly can be explained by its shorter egg incubation period and its shorter duration of immature stages, regardless of temperature Vayssières *et al*. (2008b). These results concur with these findings when egg stage duration of *B. invadens* and *C. cosyra* are compared.

5.1.2 Larval and pupal development

In the previous studies, larval and pupal development of *B. correcta* reared on artificial diet at 24^0C took 12.0 days and 11.2 days respectively while at 30^0C larval and pupal development took 8.2 days and 7.4 days respectively (Liu and Ye, 2009). Vargas *et al*. (2000) reported larval and pupal development for *B. dorsalis* at $29{:}18^0$C (Maximum and minimum temperatures) to be 7.3 days and 12.2 days respectively and that of *C. capitata* to be 6.7 days and 11. 4 days respectively. Larval and pupal development for *B. invadens* reared on artificial diet at 28^{0}C was 11.0 days and 12.0 days respectively (Ekesi *et al.*, 2006). The differences between the current study and the results of the previous studies on *Bactrocera* species can come from the rearing conditions mainly temperature.

It is obvious that temperature has an important role on the developmental rates of all immature stages as well as an effect on the adult survival. In the current study, among the examined temperatures, the longest development time was observed at the lowest temperature (25°C), while the fastest development occurred at the highest temperature (30°C) and a reduction in development time of immature stages was observed as temperature increased. This study of the relationship of development time and survival at different constant temperatures may contribute towards improving small scale laboratory rearing of the *B. invadens* and *C. cosyra* fruit flies. The results should also be useful in optimizing the rearing conditions in the laboratory that are necessary for biological studies and control methods such as releases of parasitoids for biocontrol of releases of sterile flies for eradication programmes.

5.2 The pre-oviposition period, gross fecundity, net fecundity, daily egg production per female per day and longevity

5.2.1 The pre-oviposition period

The mean pre-oviposition period varied significantly at different temperatures. According to the study conducted by Ekesi *et al*. (2006), the mean pre-oviposition period for *B. invadens* reared at 28^{0}C was 7.1 days and in the study by Vayssières *et al*. (2008b), the mean pre-oviposition period for *B. cucurbitae* at 25^{0}C was 10.9 days. These results for the pre-oviposition period are generally in line with the data from the current study. The shortest pre-oviposition time was detected in females at 30° C. This suggests that increasing temperature might be one of the limiting factors on populations that might create bottlenecks, as a possible explanation for the variation in time.

5.2.2 Gross fecundity and net fecundity

Gross fecundity of both two species reported in this study are lower than those reported for *B. invadens* reared at 28^0C by Ekesi *et al*. (2006), but higher than those reported by Vargas *et al*. (2000) for *B. cucurbitae* reared at 24^0C and at $29{:}18^0$C. The lower fecundities of *B. invadens* and *C. cosyra* recorded in this study may be a result of the egging device to which *C. cosyra* are not adapted. However, the ranges of fecundities in this study are to some extent in agreement with those of Vargas *et al*. (2000) reported for *B. cucurbitae, B. dorsalis* and *C. capitata.*

5.2.3 Daily egg production per female per day

The invasive *B. invadens* showed higher fecundity than *C. cosyra*. In this study the result suggest that a higher fecundity rate of *B. invadens* at 30^0C is related to a higher number of eggs produced by the female per day coupled with their longer egg producing period in their life. Daily eggs production per female reported in this study were also consistent with the results in the previous studies for other species reported by Vargas *et al.* (2000) whereby the eggs of *C. capitata* at $29{:}18^0$C and 24^0C per female per day were reported to be 11.2 eggs and 6.8 eggs respectively while for *B. cucurbitae* at 25^0C, 7.0 eggs were reported (Vayssières *et al*., 2008b). This is a crucial comparative advantage when adults of both species are exploiting the same host in the same locality.

5.2.4 Longevity

Longevity is reflected in the net reproductive rate of *B. invadens* being higher in all temperature tested and greater expectation of life. The survivorship and life expectancy reported in this study are lower than those reported by Vargas *et al.* (2000); Ekesi *et al*, (2006); and Vayssières *et al*. (2008b) but are more or similar to that reported by Papadopolous *et al.* (2002). This difference may possibly be resulting from temperature and species.

5.3 Population parameters

Population parameters are important in the measurement of population growth capacity. These parameters include intrinsic rate of increase, net reproductive rate, doubling time and mean generation time and discussed in the following sub-sections.

5.3.1 Intrinsic rate of increasing

Previous studies conducted by Vayssières *et al*. (2008b) observed similar results of intrinsic rate of increase for *B. cucurbitae* and for *C. capitata* reared at 25^0C and 24^0C respectively (Vargas *et al*., 2000). The intrinsic rate of increase is described as a desirable trait in exploring for new environment Ekesi *et al.* (2006). In this study, *B. invadens* had higher intrinsic rate of increase, indicating a daily increase of 12.8% and 17.4% at 25 and 30^0C respectively while *C. cosyra* had daily increase of 10.9% and 15.4% at 25 and 30^0C respectively and thus gives *B. invadens* an important advantage for interspecific competition.

5.3.2 Net reproductive rate

The net reproductive rate of *B. invadens* and *C. cosyra* was 130.5 and 96.6 at 25^0C respectively while at 30^0C was 196.1 for *B. invadens* and 107.5 for *C. cosyra.* In previous studies conducted by Papadopolous *et al.* (2002) found that the net reproductive rate of *C. capitata* at 25^0C was 64.7. *B. cucurbitae,* at 24:24^0C was 42.1 and 62.8 at 29:18^0C, while for *B. dorsalis* the net reproductive rate was 169.9 at 24:24^0C and 197.3 at 29:18^0C (Vargas *et al.*, 2000). In the study conducted by Ekesi *et al*. (2006) the net reproductive rate at 28^{0}C were 273.0. This disagreement between the results obtained here and those from other studies could be a result of different origin of the fly's species and temperature.

5.3.3 Doubling time

At 25 and 30^{0}C the population of *B. invadens* was estimated to double in 5.5 and 3.9 days respectively while for *C. cosyra* it was 6.3 and 4.5 days respectively. These results are comparable with the results reported by Vayssières *et al*. (2008b) which on *B. cucurbitae* whose population was estimated to double in 5.3 at 25^{0}C while for *B. invadens* DT was 6.16 days at 28^{0}C (Ekesi *et al*., 2006).

5.3.4 Mean generation time

The present results showed that the reproductive rate (R_0) and the intrinsic rate of increase (r) values increased with increasing temperature from 25 to 30° C, in contrast, the mean generation time of the cohorts declined with increasing temperature. The reduction in the mean generation time (T) at higher temperatures may be a result of a reduction in the development times of immature stages and in the average age of reproduction of the females. The result in this study is similar to the one in the study conducted by Ekesi *et al*. (2006) for *B. invadens* and Vargas *et al.* (2000) for *C. capitata* reared at 28^{0}C and 24:24^{0}C respectively.

CHAPTER SIX

CONCLUSION AND RECOMMENDATIONS

6.1 Conclusion

The overall objective of this study was to establish inherent factors determining population of two mango attacking fruit fly species. Development rates of immature stages were studied. The life table and population parameters of the adult were also determined. Many field records show that *Bactrocera species* are best adapted to exploit and to compete with other species in the same ecological niche. According to the demographic results of this study, *B. invadens* seems to perform better than *C. cosyra* for all immature growth stages and adult parameters tested.

It has been observed that, a similar pattern of temperature dependence of developmental time in colony reared *B. invadens* and *C. cosyra*; an increase in the temperature of the rearing chamber from 25° to 30° C resulted in faster development of eggs, larvae, and pupae. The data presented here provides life table and demographic parameters of the *B. invadens* and *C. cosyra*. Generally, *B. invadens* had a shorter egg incubation period and a shorter duration of immature stages, shorter pre-oviposiyion period, and great gross and net fecundity irrespective of temperature. This is a crucial comparative advantage when adults of both species are exploiting the same host in the same locality. Furthermore, *B. invadens* had high intrinsic rate of increasing in all temperatures tested which has been suggested as an important index for identification of tephritid fruit fly populations with good attributes for mass rearing and to develop population growth models.

This suggests that demographic and life history parameters of *B. invadens* obtained in this study give an advantage to out-competing the native *C. cosyra*, and most likely the other native fruit fly species.

6.2 Recommendations

The current study has generated the data that are pre-requisite before analyzing more complex ecological relations. The current study provides the necessary information on demographic parameters which can be combined with the results of other studies on trapping and population fluctuations, and be used in the construction of computer simulation models of fruit fly population dynamics that will enable better monitoring and management of the key fruit fly pest.

Findings from the study support the recommendation that more attention should be paid to develop management measures to control *B. invadens.* The fly possess traits that include, high mobility and dispersive powers, high reproductive rates, and extreme polyphagy, members of the *B. dorsalis* complex of fruit flies are generally recognized as being among the most destructive insects of fruits and vegetables worldwide, and they rank high on quarantine lists around the world.

Similar research works to establish life table and demographic parameters of the two fruit fly species to semi-natural and natural field experiments to obtain more applied results in field conditions are recommended.

REFERENCES

Appiah, E. F., Afreh-Nuamah, K and Obeng-Ofori, D (2009). Abundance and distribution of the Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae), in Late Valencia citrus orchards in Ghana. *International Journal of Tropical Insect Science.*29(1):11-16.

Ashimogo, G and Greenhalgh, P (2007). *Regoverning Markets. Small-scale producers in modern agrifood markets*. Swedish International Development Cooperation Agency (SIDA). 2 pp.

Bank of Tanzania, (2008). *Economic bulletin for the quarter ending September*, 2008. Vol. XL No. 3. 14 Pp. [http://www.bot-tz.org/publications/quarterly Economic Bulletins/QEB_Sep-2008.pdf] Site visited on 12/February/ 2010.

CABI, (2007). *Crop protection compendium*. Commonwealth Bureau of Agriculture International, Wallington, UK. A CD ROM.

Carey, J. R. (1993)**.** Applied demography for biologists, with special emphasis on insects. Oxford University Press, New York. 211. 206 pp.

Copeland, R. S., Okeka, W., Freidberg, A., Merz, B., White, I. M., De Meyer, M and Luke, Q. (2005). Fruit flies (Diptera; Tephritidae) of Kakamega Forest, Kenya. *Journal of East African Natural History* 94(2): 247 - 278.

De Meyer, M, Mohamed, S and White, I. M. (2011). Invasive Fruit Fly Pests in Africa. A diagnostic tool and information reference for the four Asian species of fruit fly (Dptera: Tephritidae) that have become accidentally established as pest in Africa, including the Indian Ocean Island. *Entomology Section, Royal Museum for Central Africa, Tervuren, Belgium*. [http://www.africamuseum.be/fruitfly/AfroAsia.htm] Site visited on 7/4/2011.

Duyck, P. F. and Quilici, S. (2002). Survival and development of different life stages of three *Ceratitis* spp. (Diptera: Tephritidae) reared at five constant temperatures. *Bulletin of Entomological Research* 92: 461 – 469.

Ekesi, S and Billah, M. K. (Eds) (2005). *A field guide to the management of economically important Tephritid fruit flies in Africa*. ICIPE, Nairobi, Kenya. 12 pp.

Ekesi, S. (2006). Mass rearing technology for *Bactrocera invadens* and several Ceratitis species in Africa. Paper presented at: *The 7th international symposium of fruit fly of Economic importance and 6th meeting of the working group on Fruity fly of western Hemisphere*. 10 - 25 September 2006, Salvador, Brazil. 430 pp.

Ekesi, S. Nderitu P.W. and Rwomushana I. (2006) Field infestation, life history and demographic parameters of the fruit fly *Bactrocera invadens* (Diptera: Tephritidae) in Africa. *Bulletin of Entomological Research* 96: 379 – 386.

Ekesi, S., Billah, M. K., Nderitu P. W., Lux S. A and Rwomushana I. (2009). Evidence for competitive displacement of *Ceratitis cosyra* by the invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) on mango and mechanisms contributing to the displacement. *Journal of Economic Entomology* 102(3): 981 – 991.

FAO, (2010). FAOStat. Food and Agriculture Organization. Rome, Italy. [www.faostat.com.] site visited on 20/03/2011.

Fong, C. H. and Young, H. S. (1982). *Malaysian fruits in colour*. Tropical Press SDN, BHD, Kuala Lumpur. 19 pp.

IAEA (2005). *Environmental benefit of medfly Sterile Insect Technique in Madeira and their inclusion in a cost-benefit analysis*. International Atomic Energy Agency, Vienna, Austria 2005. [http://www-pub.iaea.org/MTCD/publications/PDF/TE_1475_web.pdf] Site visited on 8/2/2010

Kader, A. (2001). Importance of Fruits, Nuts, and Vegetables in Human Nutrition and Health, Department of Pomology, UC Davis. 4 pp. [http://ezinearticles.com/?The-Importance-Of-Fruit-AndVegetables &id=879213] Site visited on 8/2/2010.

Kasap, O. E and Alten, B. (2006). Comparative demography of the sand fly *Phlebotomus papatasi* (Diptera: Psychodidae) at constant temperatures. *Journal of Vector Ecology* 31 (2): 378 – 385.

Liu, X. and Ye, H. (2009). Effect of temperature on development and survival of *Bactrocera correcta* (Diptera: Tephritidae**).** *Scientific Research and Essay* 4 (5): 467 - 472.

Mbaye N, Elhadji O. D, and Gilles D. (2008). Population dynamics and on-farm fruit fly integrated pest management in mango orchards in the natural area of Niayes in Senegal. *Pest Management in Horticultural Ecosystem* 14 (1): 1 - 8.

Mbuya, L.P., Msanga. H.P., Ruffo, C.K., Ann B. and Bo T. (1994). *Useful Trees and shrubs for Tanzania. Identification, Propagation and Management for Agricultural and Pastoral Communities.* Regional Soil Conservation Unit (RSCU) Nairobi, Kenya. 320 pp.

Mwatawala, M.W., White, I.M., Maerere, A.P., Senkondo, F.J. & De Meyer, M. (2004). A new invasive *Bactrocera* species (Diptera: Tephritidae) in Tanzania. *African Entomology* 12: 154 – 158.

Mwatawala, M.W., Senkondo, F.J. Maerere, A.P., & De Meyer, M. (2005) Current status of and future needs for fruit fly research in Tanzania. *International Pest Control* 45 (4): 184 - 187.

Mwatawala, M.W., De Meyer, M., Makundi, R. H and Maerere A. P. (2006). Biodiversity of fruit flies (Diptera, Tephritidae) in orchards in different agro-ecological zones of the Morogoro region, Tanzania. *Fruits* 61: 321-332.

Mwatawala, M.W., De Meyer, M., White, I.M., Maerere, A. & Makundi, R.H. (2007) Detection of the Solanum fruit fly, Bactrocera latifrons (Hendel) in Tanzania (Diptera., Tephritidae). *Journal of Applied Entomology* 131: 501–503.

Mwatawala, M.W., De Meyer, M., R.H. Makundi & A.P. Maerere, (2009). An Overview of *Bactrocera* (Diptera: Tephritidae) Invasions and Their Speculated Dominancy over Native Fruit Fly Species in Tanzania. *Journal of Entomology* 6 (1): 18 – 27.

Papadopoulos, N. T., Katsoyannos, B.I and Carey, J.R. (2002). Demographic Parameters of the Mediterranean fruit fly (Diptera: Tephritidae) reared in Apple. *Annals of the Entomological Society of America* 95 (5): 564 - 569.

Singh, A. (1986). *Fruit physiology and production*. Second revised edition. Kalyani Publishers, New Delhi-Ludhiana 23 pp.

Vargas. R. I., Walsh, W. A., Kanehisa, D., Stark, J. D., and Nishida, T. (2000). Comparative Demography of Three Hawaiian Fruit Flies (Diptera: Tephritidae) at alternating Temperatures. *Annals of the Entomological Society of America* 93 (1): 75 – 81.

Vayssières, J.F., Korie, S., Coulibaly, O., Temple, L.**,** Boueyi1**,** S. L. (2008a). The mango tree in central and northern Benin: cultivar inventory, yield assessment, infested stages and loss due to fruit flies (Diptera Tephritidae). *Fruit* 63: 335 – 348.

Vayssières, J.F., Carel Y., Coubes, M. and Duyck P. F (2008b). Development of immature stages and comparative demography of two cucurbit-attacking fruit flies in Reunion Island: *Bactrocera cucurbitae* and *Dacus ciliatus* (Diptera Tephritidae). *Environmental. Entomology*. 37(2): 307 – 314.

White, I. M., and M. M. Elson-Harris. 1992**.** *Fruit flies of economic importance: their identification and bionomics.* CAB International, Wallingford, United Kingdom. 601 pp.

APPENDICES

Appendix 1: Population parameters of *B. invadens* at 25 ^{0}C

Age	Proportion of original cohort surviving to each stage	Number offsprings in a stage	No of offsprings per individual in a stage	No of offsprings per original individual in each stage		Net Reproductive Rate R_o (Replacement rate)		Cohort generation time T_c	Intrinsic rate of natural increase	
x	**l_x**	**F_x**	**m_x**	**$l_x m_x$**	**hx**	**$\sum l_x m_x$**	**$x l_x m_x$**	**$\underline{\sum x l_x m_x}$**	**$r = LnR_o/T_c$**	**DT**
	$l_x = N_x/N_0$		**F_x/N_x**		**C**			**$\sum l_x m_x$**		
1										
2										
3										
4										
5										
6										
7										
8										
9										
10	1.00	34.33	2.29	2.29	0.17	0.20	1.96			
11	1.00	105.00	7.00	7.00	0.53	1.85	20.40			
12	1.00	95.00	6.33	6.33	0.74	2.35	28.18			
13	1.00	95.52	6.37	6.37	0.80	2.54	32.99			
14	1.00	87.33	5.82	5.82	0.87	2.53	35.46			
15	0.93	95.30	6.81	6.35	0.87	2.75	41.29			
16	0.93	87.61	6.26	5.84	0.90	2.62	41.88			
17	0.93	99.40	7.10	6.63	0.87	2.89	49.14			
18	0.93	97.55	6.97	6.50	0.94	3.07	55.21			
19	0.93	106.43	7.60	7.10	0.84	2.97	56.35			
20	0.93	99.40	7.10	6.63	0.85	2.82	56.40			
21	0.93	109.19	7.80	7.28	0.84	3.07	64.57			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	**l_x**	**F_x**	**m_x**	**l_xm_x**	**hx**	**$\sum l_xm_x$**	**xl_xm_x**	**$\underline{\sum xl_xm_x}$**	**$r=LnR_o/T_c$**	**DT**
	$l_x = N_x/N_0$		**F_x/N_x**		**C**			**$\sum l_xm_x$**		
22	0.93	104.64	7.47	6.98	0.89	3.12	68.66			
23	0.93	94.61	6.76	6.31	0.86	2.73	62.69			
24	0.93	101.68	7.26	6.78	0.87	2.96	71.06			
25	0.93	99.65	7.12	6.64	0.83	2.76	69.09			
26	0.87	98.70	7.59	6.58	0.80	2.63	68.42			
27	0.87	102.83	7.91	6.86	0.79	2.71	73.09			
28	0.87	98.21	7.55	6.55	0.86	2.82	79.09			
29	0.87	90.67	6.97	6.04	0.88	2.67	77.49			
30	0.87	89.76	6.90	5.98	0.84	2.50	74.97			
31	0.87	91.82	7.06	6.12	0.81	2.48	77.03			
32	0.87	99.45	7.65	6.63	0.85	2.81	89.95			
33	0.87	105.00	8.08	7.00	0.81	2.83	93.38			
34	0.87	117.79	9.06	7.85	0.80	3.14	106.77			
35	0.80	109.00	9.08	7.27	0.77	2.82	98.54			
36	0.80	107.67	8.97	7.18	0.80	2.87	103.45			
37	0.80	102.33	8.53	6.82	0.71	2.41	89.30			
38	0.80	103.33	8.61	6.89	0.72	2.46	93.61			
39	0.80	90.67	7.56	6.04	0.71	2.14	83.33			
40	0.73	82.00	7.45	5.47	0.70	1.90	76.18			
41	0.73	85.67	7.79	5.71	0.65	1.86	76.41			
42	0.73	84.33	7.67	5.62	0.67	1.90	79.60			
43	0.73	80.00	7.27	5.33	0.67	1.77	76.26			
44	0.73	88.95	8.09	5.93	0.62	1.84	80.89			
45	0.73	83.67	7.61	5.58	0.63	1.77	79.52			
46	0.73	79.33	7.21	5.29	0.60	1.59	73.04			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\underline{\sum xl_xm_x}$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**C**			$\sum l_xm_x$		
47	0.73	72.67	6.61	4.84	0.59	1.43	67.27			
48	0.73	78.00	7.09	5.20	0.57	1.49	71.71			
49	0.73	78.67	7.15	5.24	0.54	1.43	70.02			
50	0.73	75.33	6.85	5.02	0.57	1.42	71.17			
51	0.67	66.00	6.60	4.40	0.59	1.30	66.05			
52	0.67	64.33	6.43	4.29	0.61	1.30	67.83			
53	0.67	76.33	7.63	5.09	0.58	1.48	78.41			
54	0.67	64.00	6.40	4.27	0.59	1.26	67.87			
55	0.67	67.67	6.77	4.51	0.54	1.22	67.13			
56	0.67	70.00	7.00	4.67	0.57	1.33	74.47			
57	0.67	68.33	6.83	4.56	0.69	1.56	89.03			
58	0.60	58.00	6.44	3.87	0.68	1.32	76.47			
59	0.60	61.00	6.78	4.07	0.64	1.30	76.80			
60	0.60	60.33	6.70	4.02	0.58	1.17	70.42			
61	0.53	67.67	8.46	4.51	0.57	1.28	77.84			
62	0.53	57.33	7.17	3.82	0.60	1.15	71.40			
63	0.53	54.00	6.75	3.60	0.63	1.13	71.02			
64	0.53	58.67	7.33	3.91	0.62	1.21	77.41			
65	0.53	55.33	6.92	3.69	0.57	1.05	68.13			
66	0.53	57.00	7.13	3.80	0.54	1.03	68.01			
67	0.47	52.67	7.52	3.51	0.56	0.98	65.57			
68	0.47	52.00	7.43	3.47	0.45	0.77	52.66			
69	0.47	47.33	6.76	3.16	0.52	0.81	56.22			
70	0.47	47.67	6.81	3.18	0.55	0.88	61.41			
71	0.40	47.00	7.83	3.13	0.56	0.88	62.14			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\underline{\sum xl_xm_x}$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**C**			$\sum l_xm_x$		
72	0.40	49.00	8.17	3.27	0.57	0.93	66.98			
73	0.33	37.67	7.53	2.51	0.61	0.77	56.11			
74	0.33	39.33	7.87	2.62	0.64	0.84	61.80			
75	0.33	34.00	6.80	2.27	0.62	0.70	52.67			
76	0.33	37.00	7.40	2.47	0.61	0.76	57.39			
77	0.33	32.67	6.53	2.18	0.57	0.62	47.48			
78	0.33	35.33	7.07	2.36	0.53	0.63	49.00			
79	0.33	33.33	6.67	2.22	0.61	0.67	53.11			
80	0.27	28.00	7.00	1.87	0.56	0.53	42.08			
81	0.27	27.00	6.75	1.80	0.53	0.48	38.64			
82	0.20	24.67	8.22	1.64	0.59	0.48	39.72			
83	0.20	21.67	7.22	1.44	0.54	0.39	32.32			
84	0.20	20.67	6.89	1.38	0.37	0.25	21.23			
85	0.20	18.67	6.22	1.24	0.54	0.34	28.65			
86	0.20	17.33	5.78	1.16	0.45	0.26	22.35			
87	0.20	15.33	5.11	1.02	0.32	0.16	14.01			
88	0.20	12.33	4.11	0.82	0.36	0.15	13.03			
89	0.13	7.33	3.67	0.49	0.32	0.08	6.88			
90	0.13	8.33	4.17	0.56	0.29	0.08	7.22			
91	0.13	4.00	2.00	0.27	0.14	0.02	1.69			
92	0.13	4.67	2.33	0.31	0.19	0.03	2.73			
93	0.13	4.33	2.17	0.29	0.15	0.02	2.07			
94	0.13	3.67	1.83	0.24	0.18	0.02	2.09			
95	0.13									
96	0.13									

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	**l_x**	**F_x**	**m_x**	**$l_x m_x$**	**hx**	**$\sum l_x m_x$**	**$x l_x m_x$**	**$\underline{\sum x l_x m_x}$**	**$r = LnR_o/T_c$**	**DT**
	$l_x = N_x/N_0$		**F_x/N_x**		**C**			**$\sum l_x m_x$**		
97	0.13									
98	0.13									
99	0.13									
100	0.13									
101	0.13									
102	0.13									
103	0.13									
104	0.13									
105	0.13									
106	0.13									
107	0.13									
108	0.13									
109	0.13									
110	0.13									
111	0.13									
112	0.13									
113	0.07									
114	0.07									
115	**55.07**		**577.58**	**371.83**	**53.16**	**130.54**	**4,971.38**	**38.08**	**0.128**	**5.42**

Appendix 2: Population parameters of *C. cosyra* at 25 ^{0}C

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\underline{\sum xl_xm_x}$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**C**			$\sum l_xm_x$		
1										
2										
3										
4										
5										
6										
7										
8										
9										
10										
11										
12	0.93	22.33	1.60	1.49	0.39	0.29	3.51			
13	0.93	27.33	1.95	1.82	0.40	0.37	4.79			
14	0.93	31.00	2.21	2.07	0.71	0.73	10.26			
15	0.93	31.68	2.26	2.11	0.79	0.83	12.47			
16	0.87	41.67	3.21	2.78	0.85	1.18	18.81			
17	0.87	56.67	4.36	3.78	0.88	1.67	28.41			
18	0.87	59.67	4.59	3.98	0.91	1.82	32.76			
19	0.87	68.65	5.28	4.58	0.89	2.04	38.69			
20	0.87	71.67	5.51	4.78	0.90	2.15	43.10			
21	0.87	69.33	5.33	4.62	0.91	2.10	44.01			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	**l_x**	**F_x**	**m_x**	**$l_x m_x$**	**hx**	**$\sum l_x m_x$**	**$x l_x m_x$**	**$\underline{\sum x l_x m_x}$**	**$r = LnR_o/T_c$**	**DT**
	$l_x = N_x/N_0$		**F_x/N_x**		**C**			**$\sum l_x m_x$**		
22	0.87	66.34	5.10	4.42	0.89	1.97	43.38			
23	0.87	74.33	5.72	4.96	0.85	2.10	48.40			
24	0.87	72.33	5.56	4.82	0.88	2.13	51.14			
25	0.87	75.67	5.82	5.04	0.85	2.15	53.85			
26	0.80	77.33	6.44	5.16	0.90	2.32	60.33			
27	0.80	77.00	6.42	5.13	0.83	2.14	57.84			
28	0.80	76.67	6.39	5.11	0.86	2.19	61.38			
29	0.80	75.00	6.25	5.00	0.88	2.20	63.86			
30	0.80	79.67	6.64	5.31	0.83	2.21	66.26			
31	0.80	84.00	7.00	5.60	0.81	2.25	69.88			
32	0.80	79.33	6.61	5.29	0.84	2.21	70.71			
33	0.80	71.33	5.94	4.76	0.85	2.03	67.06			
34	0.80	69.00	5.75	4.60	0.81	1.86	63.35			
35	0.80	68.00	5.67	4.53	0.78	1.77	62.08			
36	0.80	71.33	5.94	4.76	0.79	1.87	67.35			
37	0.80	72.00	6.00	4.80	0.75	1.79	66.18			
38	0.80	71.33	5.94	4.76	0.75	1.78	67.61			
39	0.73	73.67	6.70	4.91	0.70	1.73	67.49			
40	0.73	65.32	5.94	4.35	0.72	1.57	62.90			
41	0.73	72.33	6.58	4.82	0.62	1.50	61.68			
42	0.73	73.33	6.67	4.89	0.65	1.59	66.82			
43	0.73	77.98	7.09	5.20	0.56	1.46	62.98			
44	0.73	74.99	6.82	5.00	0.62	1.54	67.93			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	**l_x**	**F_x**	**m_x**	**l_xm_x**	**hx**	**$\sum l_xm_x$**	**xl_xm_x**	**$\sum xl_xm_x$**	**$r=LnR_o/T_c$**	**DT**
	$l_x = N_x/N_0$		**F_x/N_x**		**C**			**$\sum l_xm_x$**		
45	0.73	70.00	6.36	4.67	0.60	1.40	63.10			
46	0.73	72.33	6.58	4.82	0.63	1.52	69.91			
47	0.73	64.33	5.85	4.29	0.61	1.31	61.60			
48	0.73	65.67	5.97	4.38	0.60	1.31	62.87			
49	0.67	65.67	6.57	4.38	0.60	1.30	63.93			
50	0.67	65.67	6.57	4.38	0.61	1.33	66.26			
51	0.67	64.67	6.47	4.31	0.57	1.22	62.18			
52	0.67	64.67	6.47	4.31	0.63	1.35	70.15			
53	0.67	66.01	6.60	4.40	0.57	1.26	66.98			
54	0.67	77.00	7.70	5.13	0.51	1.31	70.53			
55	0.67	70.00	7.00	4.67	0.52	1.21	66.50			
56	0.67	63.00	6.30	4.20	0.50	1.04	58.48			
57	0.67	57.00	5.70	3.80	0.54	1.03	58.83			
58	0.67	62.00	6.20	4.13	0.51	1.05	61.14			
59	0.67	60.67	6.07	4.04	0.52	1.04	61.55			
60	0.67	53.00	5.30	3.53	0.57	1.01	60.34			
61	0.60	62.32	6.92	4.15	0.55	1.15	70.00			
62	0.60	62.00	6.89	4.13	0.54	1.11	68.95			
63	0.60	63.00	7.00	4.20	0.52	1.10	69.31			
64	0.60	57.67	6.41	3.84	0.60	1.16	74.29			
65	0.60	67.35	7.48	4.49	0.54	1.22	79.07			
66	0.53	60.33	7.54	4.02	0.50	1.00	65.96			
67	0.53	56.33	7.04	3.76	0.56	1.06	70.79			

Age	Proportion of original cohort surviving to each stage	Number offsprings in a stage	No of offsprings per individual in a stage	No of offsprings per original individual in each stage		Net Reproductive Rate R_o (Replacement rate)		Cohort generation time T_c	Intrinsic rate of natural increase	
x	$\mathbf{l_x}$	$\mathbf{F_x}$	$\mathbf{m_x}$	$\mathbf{l_x m_x}$	**hx**	$\sum \mathbf{l_x m_x}$	$\mathbf{x l_x m_x}$	$\frac{\sum \mathbf{x l_x m_x}}{\sum \mathbf{l_x m_x}}$	$\mathbf{r = Ln R_o / T_c}$	**DT**
	$\mathbf{l_x = N_x/N_0}$		$\mathbf{F_x/N_x}$		**C**					
68	0.47	55.33	7.90	3.69	0.56	1.03	70.06			
69	0.47	61.00	8.71	4.07	0.53	1.08	74.35			
70	0.40	59.67	9.94	3.98	0.52	1.04	72.53			
71	0.40	54.68	9.11	3.65	0.53	0.96	68.27			
72	0.40	59.33	9.89	3.96	0.52	1.03	74.14			
73	0.40	58.66	9.78	3.91	0.50	0.97	70.89			
74	0.33	60.67	12.13	4.04	0.52	1.06	78.50			
75	0.33	65.35	13.07	4.36	0.49	1.08	80.80			
76	0.27	54.67	13.67	3.64	0.55	1.00	76.35			
77	0.27	54.00	13.50	3.60	0.46	0.83	63.89			
78	0.27	43.67	10.92	2.91	0.31	0.45	34.95			
79	0.27	41.00	10.25	2.73	0.29	0.40	31.74			
80	0.20	39.33	13.11	2.62	0.26	0.35	27.74			
81	0.20	24.00	8.00	1.60	0.15	0.12	9.90			
82	0.13	18.67	9.33	1.24	0.11	0.07	5.77			
83	0.13	19.00	9.50	1.27	0.12	0.07	6.15			
84	0.07									
85	0.07									
86	0.07									
87	0.07									
88	0.07									
89	0.07									
90	0.07									

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	**l_x**	**F_x**	**m_x**	**l_xm_x**	**hx**	**$\sum l_xm_x$**	**xl_xm_x**	**$\sum xl_xm_x$**	**$r=LnR_o/T_c$**	**DT**
	$l_x = N_x/N_0$		**F_x/N_x**		**C**			**$\sum l_xm_x$**		
91	0.07									
92	0.07									
93	0.07									
94	0.07									
95	0.07									
96	0.07									
97	0.07									
98	0.07									
99										
100	**48.13**		**499.10**	**294.54**	**45.00**	**96.62**	**4,036.03**	**41.77**	**0.109**	**6.335**

Appendix 3: Life history parameters of *B. invadens* at 25 ^{0}C

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	N_x	l_x	d_x	q_x	$Lx = \underline{l_x + l_{x+1}}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
1	15	1.00	-	-	15.00	**953.00**	**63.53**
2	15	1.00	-	-	15.00		
3	15	1.00	-	-	15.00		
4	15	1.00	-	-	15.00		
5	15	1.00	-	-	15.00		
6	15	1.00	-	-	15.00		
7	15	1.00	-	-	15.00		
8	15	1.00	-	-	15.00		
9	15	1.00	-	-	15.00		
10	15	1.00	-	-	15.00		
11	15	1.00	-	-	15.00		
12	15	1.00	-	-	15.00		
13	15	1.00	-	-	15.00		
14	15	1.00	0.07	0.07	14.50		
15	14	0.93	-	-	14.00		
16	14	0.93	-	-	14.00		
17	14	0.93	-	-	14.00		
18	14	0.93	-	-	14.00		
19	14	0.93	-	-	14.00		
20	14	0.93	-	-	14.00		
21	14	0.93	-	-	14.00		
22	14	0.93	-	-	14.00		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	**N_x**	**l_x**	**d_x**	**q_x**	**$Lx = \underline{l_x + l_{x+1}}$**	**T_x**	**e_x**
		$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
23	14	0.93	-	-	14.00		
24	14	0.93	-	-	14.00		
25	14	0.93	0.07	0.07	13.50		
26	13	0.87	-	-	13.00		
27	13	0.87	-	-	13.00		
28	13	0.87	-	-	13.00		
29	13	0.87	-	-	13.00		
30	13	0.87	-	-	13.00		
31	13	0.87	-	-	13.00		
32	13	0.87	-	-	13.00		
33	13	0.87	-	-	13.00		
34	13	0.87	0.07	0.08	12.50		
35	12	0.80	-	-	12.00		
36	12	0.80	-	-	12.00		
37	12	0.80	-	-	12.00		
38	12	0.80	-	-	12.00		
39	12	0.80	0.07	0.08	11.50		
40	11	0.73	-	-	11.00		
41	11	0.73	-	-	11.00		
42	11	0.73	-	-	11.00		
43	11	0.73	-	-	11.00		
44	11	0.73	-	-	11.00		
45	11	0.73	-	-	11.00		
46	11	0.73	-	-	11.00		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	N_x	l_x	d_x	q_x	$Lx = \underline{l_x + l_{x+1}}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
47	11	0.73	-	-	11.00		
48	11	0.73	-	-	11.00		
49	11	0.73	-	-	11.00		
50	11	0.73	0.07	0.09	10.50		
51	10	0.67	-	-	10.00		
52	10	0.67	-	-	10.00		
53	10	0.67	-	-	10.00		
54	10	0.67	-	-	10.00		
55	10	0.67	-	-	10.00		
56	10	0.67	-	-	10.00		
57	10	0.67	0.07	0.10	9.50		
58	9	0.60	-	-	9.00		
59	9	0.60	-	-	9.00		
60	9	0.60	0.07	0.11	8.50		
61	8	0.53	-	-	8.00		
62	8	0.53	-	-	8.00		
63	8	0.53	-	-	8.00		
64	8	0.53	-	-	8.00		
65	8	0.53	-	-	8.00		
66	8	0.53	0.07	0.13	7.50		
67	7	0.47	-	-	7.00		
68	7	0.47	-	-	7.00		
69	7	0.47	-	-	7.00		
70	7	0.47	0.07	0.14	6.50		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	N_x	l_x	d_x	q_x	$Lx = \underline{l_x + l_{x+1}}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
71	6	0.40	-	-	6.00		
72	6	0.40	0.07	0.17	5.50		
73	5	0.33	-	-	5.00		
74	5	0.33	-	-	5.00		
75	5	0.33	-	-	5.00		
76	5	0.33	-	-	5.00		
77	5	0.33	-	-	5.00		
78	5	0.33	-	-	5.00		
79	5	0.33	0.07	0.20	4.50		
80	4	0.27	-	-	4.00		
81	4	0.27	0.07	0.25	3.50		
82	3	0.20	-	-	3.00		
83	3	0.20	-	-	3.00		
84	3	0.20	-	-	3.00		
85	3	0.20	-	-	3.00		
86	3	0.20	-	-	3.00		
87	3	0.20	-	-	3.00		
88	3	0.20	0.07	0.33	2.50		
89	2	0.13	-	-	2.00		
90	2	0.13	-	-	2.00		
91	2	0.13	-	-	2.00		
92	2	0.13	-	-	2.00		
93	2	0.13	-	-	2.00		
94	2	0.13	-	-	2.00		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	N_x	l_x	d_x	q_x	$Lx = \underline{l_x + l_{x+1}}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
95	2	0.13	-	-	2.00		
96	2	0.13	-	-	2.00		
97	2	0.13	-	-	2.00		
98	2	0.13	-	-	2.00		
99	2	0.13	-	-	2.00		
100	2	0.13	-	-	2.00		
101	2	0.13	-	-	2.00		
102	2	0.13	-	-	2.00		
103	2	0.13	-	-	2.00		
104	2	0.13	-	-	2.00		
105	2	0.13	-	-	2.00		
106	2	0.13	-	-	2.00		
107	2	0.13	-	-	2.00		
108	2	0.13	-	-	2.00		
109	2	0.13	-	-	2.00		
110	2	0.13	-	-	2.00		
111	2	0.13	-	-	2.00		
112	2	0.13	0.07	0.50	1.50		
113	1	0.07	-	-	1.00		
114	1	0.07					
115		**64.07**					

Appendix 4: Life history parameters of *C. cosyra* at 25 ^{0}C

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	**N_x**	**l_x**	**d_x**	**q_x**	**$Lx = \underline{l_x + l_{x+1}}$**	**T_x**	**e_x**
		$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
1	15	1.00	-	-	15.00	**879**	**58.6**
2	15	1.00	-	-	15.00		
3	15	1.00	-	-	15.00		
4	15	1.00	-	-	15.00		
5	15	1.00	-	-	15.00		
6	15	1.00	-	-	15.00		
7	15	1.00	-	-	15.00		
8	15	1.00	-	-	15.00		
9	15	1.00	-	-	15.00		
10	15	1.00	-	-	15.00		
11	15	1.00	0.07	0.07	14.50		
12	14	0.93	-	-	14.00		
13	14	0.93	-	-	14.00		
14	14	0.93	-	-	14.00		
15	14	0.93	0.07	0.07	13.50		
16	13	0.87	-	-	13.00		
17	13	0.87	-	-	13.00		
18	13	0.87	-	-	13.00		
19	13	0.87	-	-	13.00		
20	13	0.87	-	-	13.00		
21	13	0.87	-	-	13.00		
22	13	0.87	-	-	13.00		
23	13	0.87	-	-	13.00		

Age	Number of individuals in a stage	Proportion of original cohort surviving to each stage	Proportion of original cohort dying at each stage	Mortality rate	Average proportion alive alive at each stage	Total number of individuals living at age x and beyond	The probability of living e number of years at a given age
x	N_x	l_x	d_x	q_x	Lx = $l_x + l_{x+1}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
24	13	0.87	-	-	13.00		
25	13	0.87	0.07	0.08	12.50		
26	12	0.80	-	-	12.00		
27	12	0.80	-	-	12.00		
28	12	0.80	-	-	12.00		
29	12	0.80	-	-	12.00		
30	12	0.80	-	-	12.00		
31	12	0.80	-	-	12.00		
32	12	0.80	-	-	12.00		
33	12	0.80	-	-	12.00		
34	12	0.80	-	-	12.00		
35	12	0.80	-	-	12.00		
36	12	0.80	-	-	12.00		
37	12	0.80	-	-	12.00		
38	12	0.80	0.07	0.08	11.50		
39	11	0.73	-	-	11.00		
40	11	0.73	-	-	11.00		
41	11	0.73	-	-	11.00		
42	11	0.73	-	-	11.00		
43	11	0.73	-	-	11.00		
44	11	0.73	-	-	11.00		
45	11	0.73	-	-	11.00		
46	11	0.73	-	-	11.00		
47	11	0.73	-	-	11.00		
48	11	0.73	0.07	0.09	10.50		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	**N_x**	**l_x**	**d_x**	**q_x**	**$Lx = \underline{l_x + l_{x+1}}$**	**T_x**	**e_x**
		$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
49	10	0.67	-	-	10.00		
50	10	0.67	-	-	10.00		
51	10	0.67	-	-	10.00		
52	10	0.67	-	-	10.00		
53	10	0.67	-	-	10.00		
54	10	0.67	-	-	10.00		
55	10	0.67	-	-	10.00		
56	10	0.67	-	-	10.00		
57	10	0.67	-	-	10.00		
58	10	0.67	-	-	10.00		
59	10	0.67	-	-	10.00		
60	10	0.67	0.07	0.10	9.50		
61	9	0.60	-	-	9.00		
62	9	0.60	-	-	9.00		
63	9	0.60	-	-	9.00		
64	9	0.60	-	-	9.00		
65	9	0.60	0.07	0.11	8.50		
66	8	0.53	-	-	8.00		
67	8	0.53	0.07	0.13	7.50		
68	7	0.47	-	-	7.00		
69	7	0.47	0.07	0.14	6.50		
70	6	0.40	-	-	6.00		
71	6	0.40	-	-	6.00		
72	6	0.40	-	-	6.00		
73	6	0.40	0.07	0.17	5.50		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	N_x	l_x	d_x	q_x	$Lx = \underline{l_x + l_{x+1}}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
74	5	0.33	-	-	5.00		
75	5	0.33	0.07	0.20	4.50		
76	4	0.27	-	-	4.00		
77	4	0.27	-	-	4.00		
78	4	0.27	-	-	4.00		
79	4	0.27	0.07	0.25	3.50		
80	3	0.20	-	-	3.00		
81	3	0.20	0.07	0.33	2.50		
82	2	0.13	-	-	2.00		
83	2	0.13	0.07	0.50	1.50		
84	1	0.07	-	-	1.00		
85	1	0.07	-	-	1.00		
86	1	0.07	-	-	1.00		
87	1	0.07	-	-	1.00		
88	1	0.07	-	-	1.00		
89	1	0.07	-	-	1.00		
90	1	0.07	-	-	1.00		
91	1	0.07	-	-	1.00		
92	1	0.07	-	-	1.00		
93	1	0.07	-	-	1.00		
94	1	0.07	-	-	1.00		
95	1	0.07	-	-	1.00		
96	1	0.07	-	-	1.00		
97	1	0.07	-	-	1.00		
98	1	0.07					

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	**N_x**	**l_x**	**d_x**	**q_x**	**$Lx = \underline{l_x + l_{x+1}}$**	**T_x**	**e_x**
		$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
99							
100		**59.13**					

Appendix 5: Life history parameters of *C. cosyra* at 30 ^{0}C

Number of individuals in a stage	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
N_x	**l_x**	**d_x**	**q_x**	**$Lx = \underline{N_x + N_{x+1}}$**	**T_x**	**e_x**
	$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
15	1.00	-	-	15.00	**562.00**	**37.47**
15	1.00	-	-	15.00		
15	1.00	-	-	15.00		
15	1.00	0.07	0.07	14.50		
14	0.93	-	-	14.00		
14	0.93	-	-	14.00		
14	0.93	-	-	14.00		
14	0.93	-	-	14.00		
14	0.93	0.07	0.07	13.50		
13	0.87	-	-	13.00		
13	0.87	-	-	13.00		

Number of individuals in a stage	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
N_x	**l_x**	**d_x**	**q_x**	**$L_x = \underline{N_x + N_{x+1}}$**	**T_x**	**e_x**
	$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
13	0.87	-	-	13.00		
13	0.87	-	-	13.00		
13	0.87	-	-	13.00		
13	0.87	0.07	0.08	12.50		
12	0.80	-	-	12.00		
12	0.80	-	-	12.00		
12	0.80	-	-	12.00		
12	0.80	-	-	12.00		
12	0.80	0.07	0.08	11.50		
11	0.73	-	-	11.00		
11	0.73	-	-	11.00		
11	0.73	-	-	11.00		
11	0.73	0.13	0.18	10.00		
9	0.60	-	-	9.00		
9	0.60	-	-	9.00		
9	0.60	-	-	9.00		
9	0.60	-	-	9.00		
9	0.60	-	-	9.00		
9	0.60	-	-	9.00		
9	0.60	-	-	9.00		
9	0.60	-	-	9.00		
9	0.60	0.07	0.11	8.50		
8	0.53	-	-	8.00		
8	0.53	-	-	8.00		
8	0.53	-	-	8.00		
8	0.53	-	-	8.00		

Number of individuals in a stage	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
N_x	**l_x**	**d_x**	**q_x**	**Lx = $\underline{N_x + N_{x+1}}$**	**T_x**	**e_x**
	$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
8	0.53	0.07	0.13	7.50		
7	0.47	-	-	7.00		
7	0.47	-	-	7.00		
7	0.47	-	-	7.00		
7	0.47	-	-	7.00		
7	0.47	0.07	0.14	6.50		
6	0.40	0.07	0.17	5.50		
5	0.33	-	-	5.00		
5	0.33	-	-	5.00		
5	0.33	-	-	5.00		
5	0.33	-	-	5.00		
5	0.33	-	-	5.00		
5	0.33	-	-	5.00		
5	0.33	0.07	0.20	4.50		
4	0.27	-	-	4.00		
4	0.27	-	-	4.00		
4	0.27	-	-	4.00		
4	0.27	-	-	4.00		
4	0.27	0.07	0.25	3.50		
3	0.20	-	-	3.00		
3	0.20	-	-	3.00		
3	0.20	-	-	3.00		
3	0.20	-	-	3.00		
3	0.20	0.07	0.33	2.50		
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		

Number of individuals in a stage	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
N_x	**l_x**	**d_x**	**q_x**	**$Lx = \underline{N_x + N_{x+1}}$**	**T_x**	**e_x**
	$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		
2	0.13	-	-	2.00		
2	0.13	0.07	0.50	1.50		
1	0.07	-	-	1.00		
1	0.07	-	-	1.00		
1	0.07	-	-	1.00		
1	0.07					
	38.00					

Appendix 6: Life history parameters of *B. invadens* at 30 ^{0}C

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	N_x	l_x	d_x	q_x	$Lx = \underline{N_x + N_{x+1}}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
1	15	1.00	-	-	15.00	**757.00**	**50.47**
2	15	1.00	-	-	15.00		
3	15	1.00	0.07	0.07	14.50		
4	14	0.93	-	-	14.00		
5	14	0.93	-	-	14.00		
6	14	0.93	-	-	14.00		
7	14	0.93	-	-	14.00		
8	14	0.93	-	-	14.00		
9	14	0.93	-	-	14.00		
10	14	0.93	0.07	0.07	13.50		
11	13	0.87	0.07	0.08	12.50		
12	12	0.80	-	-	12.00		
13	12	0.80	-	-	12.00		
14	12	0.80	-	-	12.00		
15	12	0.80	-	-	12.00		
16	12	0.80	-	-	12.00		
17	12	0.80	-	-	12.00		
18	12	0.80	-	-	12.00		
19	12	0.80	-	-	12.00		
20	12	0.80	-	-	12.00		
21	12	0.80	-	-	12.00		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	N_x	l_x	d_x	q_x	Lx = $\underline{N_x + N_{x+1}}$	T_x	e_x
		$l_x = N_x/N_0$	$d_x = l_x - l_{x+1}$	$q_x = d_x/l_x$	2	$T_x = \sum L_x$	T_x/l_x
22	12	0.80	-	-	12.00		
23	12	0.80	0.07	0.08	11.50		
24	11	0.73	0.07	0.09	10.50		
25	10	0.67	-	-	10.00		
26	10	0.67	-	-	10.00		
27	10	0.67	-	-	10.00		
28	10	0.67	-	-	10.00		
29	10	0.67	-	-	10.00		
30	10	0.67	-	-	10.00		
31	10	0.67	-	-	10.00		
32	10	0.67	-	-	10.00		
33	10	0.67	-	-	10.00		
34	10	0.67	-	-	10.00		
35	10	0.67	-	-	10.00		
36	10	0.67	0.07	0.10	9.50		
37	9	0.60	-	-	9.00		
38	9	0.60	-	-	9.00		
39	9	0.60	-	-	9.00		
40	9	0.60	-	-	9.00		
41	9	0.60	-	-	9.00		
42	9	0.60	-	-	9.00		
43	9	0.60	0.07	0.11	8.50		
44	8	0.53	-	-	8.00		
45	8	0.53	-	-	8.00		
46	8	0.53	-	-	8.00		

Age	Number of individuals in a stage	Proportion of original cohort surviving to each stage	Proportion of original cohort dying at each stage	Mortality rate	Average proportion alive at each stage	Total number of individuals living at age x and beyond	The probability of living e number of years at a given age
x	**N_x**	**l_x**	**d_x**	**q_x**	**$Lx = \underline{N_x + N_{x+1}}$**	**T_x**	**e_x**
		$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
47	8	0.53	-	-	8.00		
48	8	0.53	-	-	8.00		
49	8	0.53	-	-	8.00		
50	8	0.53	-	-	8.00		
51	8	0.53	-	-	8.00		
52	8	0.53	-	-	8.00		
53	8	0.53	-	-	8.00		
54	8	0.53	-	-	8.00		
55	8	0.53	0.07	0.13	7.50		
56	7	0.47	-	-	7.00		
57	7	0.47	-	-	7.00		
58	7	0.47	-	-	7.00		
59	7	0.47	-	-	7.00		
60	7	0.47	-	-	7.00		
61	7	0.47	-	-	7.00		
62	7	0.47	-	-	7.00		
63	7	0.47	-	-	7.00		
64	7	0.47	-	-	7.00		
65	7	0.47	-	-	7.00		
66	7	0.47	-	-	7.00		
67	7	0.47	0.13	0.29	6.00		
68	5	0.33	-	-	5.00		
69	5	0.33	-	-	5.00		
70	5	0.33	-	-	5.00		
71	5	0.33	-	-	5.00		

Age	**Number of individuals in a stage**	**Proportion of original cohort surviving to each stage**	**Proportion of original cohort dying at each stage**	**Mortality rate**	**Average proportion alive at each stage**	**Total number of individuals living at age x and beyond**	**The probability of living e number of years at a given age**
x	**N_x**	**l_x**	**d_x**	**q_x**	**Lx = $\underline{N_x + N_{x+1}}$**	**T_x**	**e_x**
		$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
72	5	0.33	-	-	5.00		
73	5	0.33	-	-	5.00		
74	5	0.33	-	-	5.00		
75	5	0.33	-	-	5.00		
76	5	0.33	-	-	5.00		
77	5	0.33	0.07	0.20	4.50		
78	4	0.27	-	-	4.00		
79	4	0.27	-	-	4.00		
80	4	0.27	-	-	4.00		
81	4	0.27	-	-	4.00		
82	4	0.27	0.07	0.25	3.50		
83	3	0.20	0.07	0.33	2.50		
84	2	0.13	-	-	2.00		
85	2	0.13	-	-	2.00		
86	2	0.13	-	-	2.00		
87	2	0.13	-	-	2.00		
88	2	0.13	0.07	0.50	1.50		
89	1	0.07	-	-	1.00		
90	1	0.07	-	-	1.00		
91	1	0.07	-	-	1.00		
92	1	0.07	-	-	1.00		
93	1	0.07	-	-	1.00		
94	1	0.07	-	-	1.00		
95	1	0.07	-	-	1.00		
96	1	0.07					

Age	Number of individuals in a stage	Proportion of original cohort surviving to each stage	Proportion of original cohort dying at each stage	Mortality rate	Average proportion alive at each stage	Total number of individuals living at age x and beyond	The probability of living e number of years at a given age
x	**N_x**	**l_x**	**d_x**	**q_x**	**Lx = $\underline{N_x + N_{x+1}}$**	**T_x**	**e_x**
		$l_x = N_x/N_0$	**$d_x = l_x - l_{x+1}$**	**$q_x = d_x/l_x$**	**2**	**$T_x = \sum L_x$**	**T_x/l_x**
		51.00			**757.00**		

Appendix 7: Population parameters of *B. invadens* at 30 ^{0}C

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\frac{\sum xl_xm_x}{\sum l_xm_x}$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**B**					
1								**30.34**	**0.174**	**3.98**
2										
3										
4										
5										
6	0.93	41.33	2.95	2.76	0.23	0.32	1.93			
7	0.93	84.33	6.02	5.62	0.54	1.50	10.53			
8	0.93	126.67	9.05	8.44	0.83	3.49	27.95			
9	0.93	190.33	13.60	12.69	0.87	5.52	49.64			
10	0.93	193.67	13.83	12.91	0.88	5.71	57.06			
11	0.87	202.33	15.56	13.49	0.92	6.18	67.98			
12	0.80	202.00	16.83	13.47	0.92	6.20	74.35			
13	0.80	199.33	16.61	13.29	0.92	6.14	79.87			
14	0.80	199.00	16.58	13.27	0.92	6.10	85.38			
15	0.80	188.67	15.72	12.58	0.94	5.90	88.55			
16	0.80	179.67	14.97	11.98	0.93	5.59	89.46			
17	0.80	189.67	15.81	12.64	0.93	5.89	100.14			
18	0.80	183.00	15.25	12.20	0.91	5.58	100.37			
19	0.80	179.67	14.97	11.98	0.91	5.47	103.91			
20	0.80	189.67	15.81	12.64	0.88	5.56	111.20			
21	0.80	183.67	15.31	12.24	0.87	5.35	112.34			
22	0.80	181.00	15.08	12.07	0.88	5.33	117.35			
23	0.80	177.67	14.81	11.84	0.87	5.18	119.11			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\sum xl_xm_x$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**B**			$\sum l_xm_x$		
24	0.73	186.67	16.97	12.44	0.82	5.08	122.00			
25	0.67	176.33	17.63	11.76	0.83	4.85	121.28			
26	0.67	168.33	16.83	11.22	0.82	4.60	119.71			
27	0.67	163.67	16.37	10.91	0.78	4.24	114.44			
28	0.67	167.67	16.77	11.18	0.77	4.30	120.47			
29	0.67	157.67	15.77	10.51	0.77	4.05	117.46			
30	0.67	160.33	16.03	10.69	0.74	3.96	118.72			
31	0.67	137.33	13.73	9.16	0.72	3.30	102.18			
32	0.67	134.33	13.43	8.96	0.70	3.11	99.60			
33	0.67	135.00	13.50	9.00	0.66	2.96	97.52			
34	0.67	122.33	12.23	8.16	0.66	2.69	91.40			
35	0.67	118.33	11.83	7.89	0.64	2.51	87.97			
36	0.67	121.33	12.13	8.09	0.65	2.64	94.98			
37	0.60	112.33	12.48	7.49	0.64	2.40	88.88			
38	0.60	100.00	11.11	6.67	0.66	2.20	83.69			
39	0.60	95.67	10.63	6.38	0.64	2.03	79.11			
40	0.60	86.00	9.56	5.73	0.64	1.82	72.92			
41	0.60	88.00	9.78	5.87	0.59	1.74	71.51			
42	0.60	87.33	9.70	5.82	0.63	1.83	76.97			
43	0.60	87.67	9.74	5.84	0.56	1.63	69.91			
44	0.53	83.33	10.42	5.56	0.61	1.71	75.11			
45	0.53	80.33	10.04	5.36	0.57	1.52	68.52			
46	0.53	79.00	9.88	5.27	0.58	1.52	69.81			
47	0.53	81.67	10.21	5.44	0.56	1.52	71.39			
48	0.53	74.33	9.29	4.96	0.60	1.50	71.79			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\sum xl_xm_x$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**B**			$\sum l_xm_x$		
49	0.53	74.67	9.33	4.98	0.62	1.54	75.62			
50	0.53	75.33	9.42	5.02	0.59	1.48	73.98			
51	0.53	72.00	9.00	4.80	0.56	1.34	68.57			
52	0.53	71.67	8.96	4.78	0.57	1.37	71.02			
53	0.53	74.33	9.29	4.96	0.62	1.53	81.31			
54	0.53	64.67	8.08	4.31	0.58	1.25	67.41			
55	0.53	71.67	8.96	4.78	0.62	1.49	82.12			
56	0.47	63.00	9.00	4.20	0.62	1.30	72.62			
57	0.47	65.00	9.29	4.33	0.57	1.24	70.90			
58	0.47	66.00	9.43	4.40	0.56	1.24	71.79			
59	0.47	62.33	8.90	4.16	0.57	1.19	70.42			
60	0.47	63.33	9.05	4.22	0.55	1.16	69.52			
61	0.47	71.00	10.14	4.73	0.54	1.27	77.37			
62	0.47	62.67	8.95	4.18	0.52	1.09	67.72			
63	0.47	61.00	8.71	4.07	0.52	1.05	66.32			
64	0.47	59.33	8.48	3.96	0.52	1.03	65.74			
65	0.47	59.67	8.52	3.98	0.54	1.08	70.14			
66	0.47	58.33	8.33	3.89	0.45	0.87	57.25			
67	0.47	61.33	8.76	4.09	0.47	0.97	64.69			
68	0.33	53.67	10.73	3.58	0.52	0.94	63.76			
69	0.33	53.67	10.73	3.58	0.52	0.92	63.75			
70	0.33	53.00	10.60	3.53	0.47	0.84	58.58			
71	0.33	57.00	11.40	3.80	0.48	0.92	65.34			
72	0.33	45.67	9.13	3.04	0.46	0.70	50.71			
73	0.33	46.33	9.27	3.09	0.46	0.72	52.35			

Age	Proportion of original cohort surviving to each stage	Number offsprings in a stage	No of offsprings per individual in a stage	No of offsprings per original individual in each stage		Net Reproductive Rate R_o (Replacement rate)		Cohort generation time T_c	Intrinsic rate of natural increase	
x	l_x	F_x	m_x	$l_x m_x$	hx	$\sum l_x m_x$	$x l_x m_x$	$\sum x l_x m_x$	$r = LnR_o/T_c$	DT
	$l_x = N_x/N_0$		F_x/N_x		B			$\sum l_x m_x$		
74	0.33	47.33	9.47	3.16	0.43	0.68	50.13			
75	0.33	46.00	9.20	3.07	0.47	0.71	53.62			
76	0.33	45.67	9.13	3.04	0.47	0.71	53.99			
77	0.33	44.00	8.80	2.93	0.44	0.64	49.40			
78	0.27	38.67	9.67	2.58	0.46	0.60	46.73			
79	0.27	35.00	8.75	2.33	0.52	0.61	48.30			
80	0.27	35.00	8.75	2.33	0.51	0.59	47.54			
81	0.27	34.33	8.58	2.29	0.43	0.49	39.96			
82	0.27	33.00	8.25	2.20	0.45	0.49	40.16			
83	0.20	18.00	6.00	1.20	0.30	0.18	14.71			
84	0.13	18.33	9.17	1.22	0.33	0.20	16.74			
85	0.13	16.00	8.00	1.07	0.26	0.14	11.78			
86	0.13	15.67	7.83	1.04	0.28	0.15	12.75			
87	0.13	17.67	8.83	1.18	0.32	0.19	16.15			
88	0.13	14.33	7.17	0.96	0.34	0.16	14.23			
89	0.07	9.67	9.67	0.64	0.35	0.11	9.93			
90	0.07	11.00	11.00	0.73	0.32	0.12	10.50			
91	0.07	6.33	6.33	0.42	0.14	0.03	2.70			
92	0.07	4.67	4.67	0.31	0.12	0.02	1.70			
93	0.07	6.00	6.00	0.40	0.15	0.03	2.76			
94	0.07	3.33	3.33	0.22	0.13	0.01	1.39			
95	0.07	1.67	1.67	0.11	0.20	0.01	1.06			
96	0.07	2.00	2.00	0.13	0.17	0.01	1.07			
	46.13		**969.58**	**544.47**	**53.08**	**196.14**	**5,950.82**			

Appendix 8: Population parameters of *C. cosyra* at 30 ^{0}C

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\underline{\sum xl_xm_x}$	$r = LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**C**			$\sum l_xm_x$		
1								**30.42**	**0.154**	**4.51**
2										
3										
4										
5	0.93	6.67	0.48	0.44	0.22	0.05	0.24			
6	0.93	17.32	1.24	1.15	0.53	0.30	1.82			
7	0.93	19.35	1.38	1.29	0.62	0.40	2.80			
8	0.93	24.00	1.71	1.60	0.80	0.64	5.12			
9	0.93	31.01	2.21	2.07	0.86	0.89	8.03			
10	0.87	31.33	2.41	2.09	0.92	0.97	9.66			
11	0.87	45.33	3.49	3.02	0.93	1.40	15.39			
12	0.87	75.67	5.82	5.04	0.94	2.36	28.38			
13	0.87	105.57	8.12	7.04	0.92	3.25	42.21			
14	0.87	111.63	8.59	7.44	0.92	3.40	47.67			
15	0.87	115.99	8.92	7.73	0.92	3.56	53.37			
16	0.80	123.17	10.26	8.21	0.90	3.71	59.35			
17	0.80	118.85	9.90	7.92	0.92	3.63	61.65			
18	0.80	120.70	10.06	8.05	0.93	3.74	67.36			
19	0.80	121.10	10.09	8.07	0.91	3.69	70.14			
20	0.80	124.84	10.40	8.32	0.89	3.70	73.90			
21	0.73	117.14	10.65	7.81	0.87	3.39	71.09			
22	0.73	110.61	10.06	7.37	0.90	3.30	72.66			
23	0.73	106.52	9.68	7.10	0.85	3.03	69.71			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\sum xl_xm_x$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**C**			$\sum l_xm_x$		
24	0.73	96.67	8.79	6.44	0.81	2.62	62.78			
25	0.60	87.33	9.70	5.82	0.89	2.60	65.02			
26	0.60	87.32	9.70	5.82	0.82	2.38	61.93			
27	0.60	95.18	10.58	6.35	0.75	2.39	64.55			
28	0.60	78.67	8.74	5.24	0.79	2.07	58.02			
29	0.60	76.33	8.48	5.09	0.79	2.01	58.24			
30	0.60	75.00	8.33	5.00	0.70	1.75	52.42			
31	0.60	81.33	9.04	5.42	0.69	1.88	58.15			
32	0.60	83.00	9.22	5.53	0.67	1.84	58.99			
33	0.60	79.00	8.78	5.27	0.61	1.61	53.25			
34	0.53	72.67	9.08	4.84	0.65	1.57	53.45			
35	0.53	83.00	10.38	5.53	0.63	1.73	60.56			
36	0.53	81.14	10.14	5.41	0.65	1.75	62.98			
37	0.53	83.11	10.39	5.54	0.63	1.73	64.08			
38	0.53	85.35	10.67	5.69	0.58	1.64	62.40			
39	0.47	85.67	12.24	5.71	0.59	1.69	66.07			
40	0.47	83.67	11.95	5.58	0.61	1.70	67.97			
41	0.47	83.85	11.98	5.59	0.60	1.68	69.08			
42	0.47	89.92	12.85	5.99	0.54	1.61	67.73			
43	0.47	85.01	12.14	5.67	0.54	1.52	65.51			
44	0.40	82.67	13.78	5.51	0.59	1.61	71.06			
45	0.33	79.33	15.87	5.29	0.54	1.42	63.76			
46	0.33	88.67	17.73	5.91	0.53	1.56	71.59			
47	0.33	97.00	19.40	6.47	0.48	1.57	73.63			
48	0.33	84.67	16.93	5.64	0.51	1.44	69.36			

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	l_x	F_x	m_x	l_xm_x	**hx**	$\sum l_xm_x$	xl_xm_x	$\underline{\sum xl_xm_x}$	$r=LnR_o/T_c$	**DT**
	$l_x = N_x/N_0$		F_x/N_x		**C**			$\sum l_xm_x$		
49	0.33	82.34	16.47	5.49	0.58	1.58	77.60			
50	0.33	79.33	15.87	5.29	0.57	1.50	74.75			
51	0.33	78.65	15.73	5.24	0.61	1.61	82.05			
52	0.27	75.00	18.75	5.00	0.58	1.45	75.56			
53	0.27	87.64	21.91	5.84	0.53	1.55	82.13			
54	0.27	87.00	21.75	5.80	0.56	1.61	87.04			
55	0.27	53.33	13.33	3.56	0.43	0.77	42.49			
56	0.27	50.00	12.50	3.33	0.42	0.70	38.94			
57	0.20	48.35	16.12	3.22	0.40	0.64	36.74			
58	0.20	50.33	16.78	3.36	0.37	0.63	36.48			
59	0.20	51.67	17.22	3.44	0.36	0.63	37.03			
60	0.20	46.33	15.44	3.09	0.36	0.56	33.55			
61	0.20	44.35	14.78	2.96	0.37	0.54	33.14			
62	0.13	41.00	20.50	2.73	0.39	0.53	33.04			
63	0.13	36.67	18.33	2.44	0.43	0.53	33.36			
64	0.13	41.00	20.50	2.73	0.32	0.44	28.06			
65	0.13	58.43	29.21	3.90	0.29	0.56	36.54			
66	0.13	45.32	22.66	3.02	0.29	0.43	28.44			
67	0.13	32.00	16.00	2.13	0.32	0.34	22.82			
68	0.13	24.33	12.17	1.62	0.13	0.10	7.05			
69	0.13									
70	0.13									
71	0.13									
72	0.13									
73	0.07									

Age	**Proportion of original cohort surviving to each stage**	**Number offsprings in a stage**	**No of offsprings per individual in a stage**	**No of offsprings per original individual in each stage**		**Net Reproductive Rate R_o (Replacement rate)**		**Cohort generation time T_c**	**Intrinsic rate of natural increase**	
x	**l_x**	**F_x**	**m_x**	**$l_x m_x$**	**hx**	**$\sum l_x m_x$**	**$x l_x m_x$**	**$\underline{\sum x l_x m_x}$**	**$r = LnR_o/T_c$**	**DT**
	$l_x = N_x/N_0$		**F_x/N_x**		**C**			**$\sum l_x m_x$**		
74	0.07									
75	0.07									
76	0.07									
	34.00		**768.40**	**316.36**	**40.22**	**107.51**	**3,269.89**			