Biodiversity of fruit fly *Bactrocera* spp. (Diptera: Tephritdae) in peninsular Thailand and population ecology of some species on guava *Psidium guajava* L.

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ABSTRACT

The biodiversity of fruit fly *Bactrocera* spp. and the population ecology of two key factors species of these genera were carried out in peninsular Thailand on guava *Psidium guajava* (L.) during April 2011 and March 2013 at twelve sampling sites. The objectives of the research were to (1) elucidate and identify *Bactrocera* spp. infesting plants in the family myrtaceae, (2) determine the seasonality of *B. carambolae* and *B. papayae* on guava and, (3) construct cohort life tables of *B. carambolae* and *B. papayae*. Fruit fly specimens were collected from the field with the aid of (1) Steiner trap (Thailand modification) baited with a mixture of para-pheromone (methyl eugenol Benzene,1,2,-dimethoxy-4-(2-propenyl) and pyrethriod (Changzhou Kangmei Chemical Industry, China) at the rate of 62.5 ml pyrethroid / 1,000 ml methyl eugenol, and (2) Ball trap AR934 (ISCA modified McPhail trap USA) baited with food substance (Torula yeast). Fruits were also sampled from *P. guajava* and other fruit bearing trees to the radius of approximately 1,500 meters. Adult flies were maintained in the laboratory at 25 ± 1^{o}C, 75 ± 5% relative humidity (RH) and photoperiod of L12:D12 for life history strategy study.

The sum of 226,658 specimens of 33 species belonging to two genera; *Bactrocera* and *Dacus* were collected from the field across southern Thailand during the biodiversity study. Sampling of fruit flies was conducted in four provinces with Steiner and Ball traps, respectively. One commercial guava orchard located in agro-forested area was selected at each province. Each of the trap was replicated twice on the orchards and it surroundings. From this study, the genus *Bactrocera* had the highest number of 31 species of which 8 species were common to all sites among which *B. papayae* and *B. carambolae* were the most abundant, hence, key factor species occurring in large numbers across southern Thailand. From the *Bactrocera*

spp., 14, including a taxon (*B.* sp1) were new records in this region and were found to be localized occurring mostly at provinces adjacent to peninsular Malaysia. The biodiversity pattern was analyzed for richness, evenness and similarity of sites and two associations were elucidated viz; (1) provinces adjacent to peninsular Malaysia were the richest in species, and (2) provinces towards the hinterland were less rich in species number. Similarity of sites also followed the aforementioned groupings. The most probable reasons for the differential biodiversity patterns could be link to the cross infestation from neighbouring countries, forest type, vegetation cover, availability of host plants and the average weather conditions prevailing at each province.

Seasonality of the key factor species; *B. carambolae* and *B. papayae* was studied for 53 consecutive weeks in guava orchards and surrounding environments in southern Thailand. The fruit flies were collected by using Steiner traps baited with methyl eugenol as an attractant only. Guava fruits were sampled and categorized into three developmental stages as ripe, mature and immature with the aid of fruit firmness tester. Both species were trapped in the field throughout the season and exhibited distinct patterns of seasonal occurrence with two population peaks, August-September and May for *B. papayae* and protracted irregular pattern of occurrence for *B. carambolae*. The density was almost always greater for *B. papayae* than for *B. carambolae* at all the study sites. The population density was affected to some extent by the interaction of temperature, rainfall and relative humidity. The fruit sampling revealed that both fruit fly species emerged in large numbers from ripe guava fruits than for any other of the developmental stages. High fecundity, gregariousness, ability to colonise and invade new environment could be responsible for large population occurrence of *B. papayae*.

The life history strategy of the pre-imaginal stages of *B. carambolae* and *B. papayae* were compared at six constant temperatures of 15, 20, 25, 27, 30 and 35^{o}C, 70±5 RH and at photoperiod of L12:D12. The objective was to determine the effect of temperature on the developmental stages for optimizing rearing and to understand their geographical pattern of occurrence. A strong and positive linear relationship was observed between temperature and developmental rate of immature

stages of *B. carambolae*, correlation coefficient (R^2) = 0.99, 0.95 and 0.99 for egg, larva and pupa, respectively. Similarly, a strong and positive linear relationship was observed between temperature and developmental rate of *B. papayae*, R^2 = 0.98, 0.91 and 0.99 for egg, larva and pupa, respectively. *B. carambolae* was found to exhibit high threshold temperature and consequently, high degree days when compared to *B. papayae*. A temperature summation model was used to estimate lower threshold temperature and thermal constant. The lowest threshold temperatures for *B. carambolae* and *B. papayae* were 12.4, 11.2 and 11.6°C; and 12.1, 10.5 and 10.9°C for eggs, larvae and pupa, respectively. The thermal constants for total development of *B. carambolae* and *B. papayae* were 371.4 and 330.1 degree-days respectively. *B. papayae* was significantly faster in development and higher in survival, and appeared to be better adapted to low temperatures than *B. carambolae* as it exhibited lowest threshold temperatures at all immature stages. The observed differences in response to various temperatures revealed to some extent the impact of temperature on their distribution in peninsular Thailand and other parts of the world.

The discrepancies observed in hatching time between the eggs of both species at specific constant temperature, led to the examination of the latter by using Olympus microscope with inbuilt ocular micrometer for morphometric study, Olympus DP72 Universal Camera microscope to capture the image of the eggs and Scanning Electron Microscope (SEM) was used for the detailed morphological studies. None of the eggs of the studied species had conspicuous respiratory appendage. The eggs are similar in gross morphology, tapering towards the anterior and posterior poles. Presence of papilla, mycropyle and aeropyles are peculiar to both species but with some variations. The papilla and mycropyle with clumsy woolly structure was common to *B. carambolae*. But the aeropyles on the chorion of *B. papayae* were numerous and in variable diameters. The diagnostic characters to differentiate between these two species include the chorion ornamentation, location of aeropyles and rim of chorion.

Life table of *B. carambolae* and *B. papayae* were compared at constant temperatures of 20, 25, 27 and 30 ± 1°C, 70 ± 5% relative humidity (RH) and photoperiod of L12:D12. The “intermediate optimum temperature” fall in the range of

25-27^{o}C. Fly populations declined rapidly towards extreme temperatures (cold or hotness). All population and reproductive parameters analysed revealed that *B. papayae* survived better than *B. carambolae*. Male flies of both species were also found to live longer and had high life expectancy than their female cohort members.

The study suggested that *B. papayae* can invade and colonise a new area faster than other species in this region. This may be the reason behind it more prevalence and abundance in field over other *Bactrocera* spp. Therefore, *B. carambolae* and *B. papayae* should be considered as notorious pests that could threaten the growth of horticultural industry and have an immense impact on the fruit fly fauna in southern Thailand.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

General introduction

Biodiversity describes the variety of all forms of life, from genes to species, through to the broad scale of ecosystems (Faith, 2007). Biodiversity, or the variety of living things that exist, is fundamental to the existence of life on Earth, and the importance of it cannot be underestimated. It is not only the variety of living organisms on our planet, but also the interdependence of all these living things. It thus creates and maintains ecological systems; the most recognizable of which are Earth's biomes, which can be divided into the broad categories of Forests, Tundra, Aquatic, Grasslands, and Deserts. The biodiversity to the south of the equator is much more extravagant than to the North. Furthermore, Australasian biodiversity displays biogeographic patterns uniting the southern continents (Craston, 2009).

All multicellular species on Earth are insects (May, 1986), and yet explanations for terrestrial biodiversity are largely based on birds, large mammals and plants. Studies of insect diversity by Novotny *et al*. (2007) and Dyer *et al*. (2007) help to redress this imbalance to some extent, and provide an improved understanding of the distribution of global diversity. Some 80–95% of insect species are yet to be collected, named and described, most of them living in the tropics. Even for the 850,000 plus species that have been named, we know little about how they are distributed or what they feed on (Stork, 1999). Recent advances in understanding insect communities in tropical forests (Lewinsohn and Novotny, 2005; Novotny and Basset, 2005) have contributed little to our knowledge of large-scale patterns of insect diversity, because incomplete taxonomic knowledge of many tropical species hinders the mapping of their distribution records (Novotny and Weiblen, 2005). This impedes an understanding of global biodiversity patterns and explains why tropical insects are underrepresented in conservation biology. Hence, huge knowledge vacuum in insect biodiversity and ecology exist. Biodiversity apart from serving as a pointer to conservation also offers great potential for managing insect pests. It provides

resistance genes and anti-insect compounds; a huge range of predatory and parasitic natural enemies of pests; and community ecology-level effects operating at the local and landscape scales to check pest build-up.

Asia is ranked very high among the world's regions with respect to biodiversity and productivity; however, the region has undergone rapid economic growth. The biodiversity of Asian forests plays an important role not only for the people and countries of Asia, but also for the rest of the world (Nakashizuka, 2004). Southeast Asia contains some of the highest complexity of biodiversity, and also consists of many kinds of different habitats such as coral reef, mangrove, tropical forest etc. (Whitmore, 1975; Turner *et al*., 2001).

Thailand, with land area of 513,115 sq km, is one of the southeast Asian countries which lie between the northern Indochinese and southern Sundaic biogeographical regions which are separated by Isthmus of Kra (Cobert and Hill, 1992). To the south of the Isthmus of Kra is the southern peninsula which terminates at the Kangar-Pattani. The southern peninsula presents unique distribution patterns of zoogeography and phytogeography and is referred to as paninsular Thailand (Wikramanayake *et al*., 2002; Hughes *et al*., 2003). The tropical rainforests of peninsular Thailand are rich in biological diversity. They are essential bio-resources for human survival and wellbeing in terms of food, medicines, clothing and housing (Baimai and Brockelman, 1998). In this part of the globe, plant species, especially orchids, have been well studied, with 80% of the estimated flora already identified, but only 20% of the estimated 87,500 indigenous animal species have been identified, of which almost 50% are insects. The only general representation of insects is in a private museum, there is need to remedies the situation by boosting up the former reference collections of the country's insects.

Amongst the numerous insects species abound in peninsular Thailand are the fruit flies belonging to various families. Approximately 10% of the fruit fly families are serious pests distributed around the world in temperate, subtropical and tropical areas (Christenson and Foote, 1960; Weems and Heppner, 1999). The family Tephritidae especially the sub-family Dacinae were great threat to fruits, vegetables and flowers. Among the more than 4,400 species known worldwide (Norrbom, 2004), nearly 200 are considered pests. The genus *Bactrocera* is of worldwide recognition

for its destructive impact on agriculture. Besides causing billions of dollars in direct losses to a wide variety of fruit, vegetable and flower crops, they limit the development of agriculture in many countries because of the strict trade quarantines imposed to prevent their spread (Carey and Dowell, 1989; Carroll *et al.*, 2004). Most are polyphagous species and some are multivoltine (White and Elson-Harris, 1992). Dacine fruit flies of the *Bactrocera* (Diptera: Tephritidae) are arguably the most serious pests of fruits and vegetables throughout Asia and the Pacific. Among the serious pest species, several are indigenous to Thailand and Peninsular Malaysia. Species natives to these countries include several of the *Bactrocera dorsalis* complex, including *Bactrocera dorsalis* sensu stricto (Hendel), *B. carambolae* and *B. papayae* (Drew and Hancock) and the cucurbit feeders *B. cucurbitae* (Coquillet) and *B. tau* (Walker) (Clarke *et al*., 2001). *B. carambolae* and *B. papayae* are formally of the *B. dorsalis* complex (Drew and Hancock, 1994). These two species have been found to be well distributed in southern Thailand affecting different kinds of fruits and vegetables. Fruit flies are attracted to host plants when fruit is developing. Different fruit fly species have different host ranges. Fruit flies feed and breed around their host plants and lay eggs in the ripening fruit (Drew and Romig, 1997). When the larvae or maggots emerge they feed off the ripening fruit. This can cause fruit to drop prior to harvest, or if harvested, the resultant damage makes the fruit unsaleable.

The production of fruits and vegetables in Thailand generate important sources of income. These crops represent an important part of the gastronomic culture for Thai people (Victor, 2009). A constantly growing population, rising of incomes and urbanization levels increase the demand for fruits and vegetables. To fill the gap of this demand, better farming strategies are necessary. The presences of pests such as fruit flies constitute an obstacle in their production. These fruit flies are considered a very destructive group of insects that cause enormous economic losses in agriculture, especially in a wide variety of fruits, vegetables and flowers (Diamantidis *et al*., 2008). In cucumber (*Cucumis sativus* L.) and bitter gourd (*Momordica charantia* L.) field infestation problems caused by *B. cucurbitae* are very common in Thailand (Ramadan and Messing, 2003). The last named represents one of the most popular vegetables from the cucurbit family in this region. The cost of losses due to infestation of fruit flies can be surprisingly high; there are examples where losses

have been up to 100% in cucurbit species, caused by Melon fly *B. cucurbitae* (Dhillon *et al*., 2005). Crop losses in mango (12-60%), guava (40-90%) and papaya (12-60%) have also been recorded by Allwood and LeBlanc (1997).

This study focused on the biodiversity of the Genus *Bactrocera* on the guava family (Myrtaceae). It also verified the ecology and the life history of two sympatric sibling species of the *B. dorsalis* complex (*B. carambolae* and *B. papayae*). Most of the species in this genus were indigenous to Thailand and peninsular Malaysia (Drew and Hancock, 1994; Clarke *et al*., 2001).

Rationales

The family Myrtaceae, is the family of one of the most consumed fruits family in Thailand and the most popular fruit of this family is the Guava *Psidium guajava* L. There are several species of fruit flies in the genus *Bactrocera* in peninsular Thailand which are of economic importance to fruit production. Their menace on guava is great which call for a scrutiny of this genus in order to identify those members that infest or in close association with the guava family. Fruit flies biodiversity have not been sufficiently studied on members of this family. Therefore, the biodiversity of fruit flies on the family is paramount at this juncture.

B. carambolae and *B. papayae* are sympatric sibling species and polyphagous members of the *B. dorsalis* complex. This complex is large and the complex members are well distributed in Asia. *B. carambolae* and *B. papayae* have been found to co-subsist on a family member of myrtaceae (*P. guajava*) in the preliminary study of this research. Study of these flies was not sufficient enough to vividly conclude on their ecological status on *P. guajava* as there was no such study in text before now. Hence, comprehensive enquiry is needed to elucidate the knowledge about the behaviours of the complex members in their environments and on their host plants. Some of the major studies carried out on Tephritidae in Thailand are about the host plants records for fruit flies (Allwood *et al*., 1999), survey of opine parasitoid of fruit flies (Chinajariyawong *et al*., 2000), seasonal abundance and host use patterns of some species, which was a generalized survey and done without any statistical framework on ground (Clarke *et al*., 2001), efficacy of protein bait sprays in controlling fruit flies (Chinajariyawong *et al*., 2003). Sexual and oviposition

behaviour have been studied on some species of fruit flies in other parts of the globe. Daily activity patterns have been studied less intensively and among the continents Asia has very few of such studies (Aluja and Norrbom, 2000). Daily activity studies in fruit flies where behavioural factors like locomotion and feeding have been carried out (Miyatake, 1997) and some observations related to this topic are mentioned by Christenson and Fotte (1960). Diurnal activity of *B. dorsalis* and *B cucurbitae* under field conditions has been investigated in Thailand (Victor, 2009). Few ecological studies have dealt concurrently with multiple species within the *B. dorsalis* complex and thus the known ecology of the complex is actually the ecology of a few selected species (Clarke *et al.*, 2005). Such ecological studies have been carried out on two species; *B. cucurbitae* and *B. dorsalis* (Jang, 1997; Kuba *et al*., 1982; Kuba *et al*., 1984; Smith, 1989). The population ecology and life history strategies of *B. carambolae* and *B. papayae* fruit flies is yet to be study in this part of Thailand.

Research Questions:

From the above justifications the following questions are deduced to be answered by the study:

1. What are the *Bactrocera* species of fruit fly associated with the family Myrtaceae?
2. How does the seasonal abundance and distribution patterns of *B. carambolae* and *B. papayae* differs?
3. What are the differences between the life table of *B. carambolae* and *B. papayae*?

Hypothesis:

The following hypothesis are set for the study;

1. There are several *Bactrocera* species of fruit fly associated with the plants in the family myrtaceae.
2. Seasonal abundance and distribution patterns of *B. carambolae* and *B. papayae* do not differ.
3. The life table of *B. carambolae* and *B. papayae* do not vary.

Objectives:

1. To elucidate and identify *Bactrocera* spp. infesting plants in the family myrtaceae.
2. To determine the seasonality of *B. carambolae* and *B. papayae* on guava.
3. To construct cohort life tables of *B. carambolae* and *B. papayae.*

Literature review

Historical background of peninsular Thailand

Peninsular Thailand is located on the Malay peninsula, with land area of 70,713 sq km, bounded to the north by Kra Isthmus as the narrowest part of the peninsular (Corbet and Hill, 1992; Metcalfe, 1996). The western part has steeper coasts, while on the east side, river plains dominate. The largest river of the south is the Tapi in Surat Thani, which together with the Phum Duang in Surat Thani drains more than 8,000 sq km, more than 10% of the total area of southern Thailand. Smaller rivers include the Pattani, Saiburi, Krabi and the Trang. The biggest lake of the south is the Songkhla Lake (1,040 sq km altogether) and the largest artificial lake is the Chiao Lan (Ratchaprapha dam) with 165 sq km within the Khao Sok national park in Surat Thani. Running through the middle of the peninsula are several mountain chains. The highest elevation is at the Khao Luang (1,835m high) in the Nakhon Si Thammarat Province. Ranging from the Kra Isthmus till the Phuket Island is the Phuket chain, which connects to the Tanao Si Mountain Range further north. Almost parallel to the Phuket chain but 100 km to the east is the Nakhon Si Thammarat or Banthat chain, which begins with the Samui island Ko Pha Ngan Ko Tao in Surat Thani and ends at the Malaysian border at the Ko Ta Ru Tao archipelago (Collins *et al*., 1991; Lekagul and Round, 1991). Thailand is one of the tropical countries teeming with diverse flora. But southern Thailand is predominantly rainforest zone.

Classifications of fruit fly

Tephritidae is one of two fly families referred to as "fruit flies", the other family being Drosophilidae. Tephritidae does not include the biological model organisms of the genus *Drosophila* (in the family Drosophilidae), which is often called the "common fruit fly". There are nearly 5,000 described species of tephritid fruit fly, categorized in almost 500 genera. Description, recategorization, and genetic analysis are constantly changing the taxonomy of this family. To distinguish them from the Drosophilidae, the Tephritidae are sometimes called peacock flies, in reference to their elaborate and colorful markings (Norrbom, 2004).

Kingdom: Animalia

Phylum: Arthropoda

Class: Insecta

Order: Diptera

Section: Schizopora

Subsection: Acalyptratae

Super family: Tephritoidea

(McAlphine, 1989)

Family: Tephritidae

(Newman, 1834)

Sub-family:

Blepharoneurinae

Dacinae

Phytalmiinae

Tachiniscinae

Tephritinae

Trypetinae

Biology of fruit fly

Fruit flies go through four development stages; eggs, larvae (three larval instars), pupae and adult (White and Elson-Harris, 1992). The adult female fly lays eggs in batches in groups of 4 – 5 under the skin of fruits with a needle like ovipositor (egg-laying tube at tip of abdomen). While puncturing the fruit, the fly pushes bacteria from the skin into the flesh. These bacteria cause fruit decay, which results in a substrate in which the larvae feed (Drew and Lloyd, 1989; Fletcher, 1987). The role of these bacteria are complex and not yet fully understood, and many authors regard their role as symbiotic although that is doubted by others (Drew and Lloyd, 1989; Girolami, 1983; Howard, 1989). Eggs hatch in 1 – 2 days under tropical conditions (24 – 27^{o}C, 70% RH) (Sauers-Muller, 1991) to produce larvae that feed on the fruits flesh, causing more decay and, in some cases, premature fruit fall. The larva grows in size by shedding its skin twice, defining three larval stages (instars). The larvae develop in the fruit for approximately 6 – 9 days (Sauers-Muller, 1991). When

fully grown, the larva escapes from the fruit, drops on the ground, burrows into the soil or organic matter for a short distance and its skin thickens and hardens to form a shell called a puparium, inside which the larva transforms itself into the adult (White and Elson-Harris, 1992; Andrew and Anthony, 2006; Frías *et al*., 2006; Daniel *et al*., 2009).

Some flower associated species complete the first instar emerging from the egg (White and Clement, 1987) and most flower feeding Tephritidae pupariate within the host tissues (Christenson and Foote, 1960). The melon fly is known to have develop from the stem of both cucurbits and tomato (Carey and Dowell, 1989; Syed, 1971). The larvae of some Trypetinae develop in leaf mines, e.g the celery fly, *Euleia heraclei* (L), and many Ceratitini (subtribe Gastrozonina) develop in bamboo shoots. Some species have more unusual larval habitats, namely some Acanthonevrini and Phytalmiini in dead wood, and the larvae of *Euphranta toxoneura* (Leow) develop in the leaf gall of a sawfly (White and Elson-Harris, 1992).

After 10 – 14 days, the adult fly emerges from the puparium and digs its way out of the soil or organic matter. Different puparium periods of 8 – 10 days have been observed for *B. carambolae* (Malavasi *et al*., 1998). Sauers-Muller (1993) observed that the majority of adult emergence was in the morning hours, between 9 am and 12 noon. Shortly after females emerge, they search for a protein meal to mature eggs. Studies have shown that plant surface bacteria are very important source of nutrients for the female flies (Drew, 1989; Drew and Lloyd, 1989; Lloyd, 1991). During this phase, flies may disperse quite large distances in search of protein sources. Females mate within 7 – 10 days of emergence and are ready to lay eggs when these have become mature. *B. papayae* was found to mate earlier than *B. carambolae*. Mating for *B. carambolae* began 2 weeks after emergence which start around 1800 hrs at a light intensity of approximately 300 lux, at about 30 minutes before darkness (McLnnis *et al*., 1994).

In the laboratory, working at different temperature ranges, Brèvault and Quilici (2000) recorded 13.29, 5.25, 3.42, 2.50 and 2.71 days for egg development, 23, 11, 8, 5 and 5 days for larva development, 40, 25, 14, 11 and 0 days for pupa development at 15, 20, 25, 30 and 35^{o}C, respectively for *Neoceratitis cyanescens* (Bezzi). No adult emergence at 35^{o}C. Similarly, Duyck and Quilici (2002)

reported the range of 7-8, 3-4, 2-3, 1-2 days for egg development, 21-23, 8-11, 6-10, and 5-9 days for larva development, 35-36, 16-17, 10-12 and 8-9 days for pupa development at 15, 20, 25 and 30^{o}C, respectively for *Ceratitis* spp. No development was recorded at 35^{o}C for all the developmental stages. Study on *Bactrocera zonata* (Saunders) revealed 10.16, 3.46, 2.04, 1.42 and 1.54 days for egg development, 30, 10, 5, 4 and 4 days for larva development, 53, 20, 10, 8 and 8 days for pupa development at 15, 20, 25, 30 and 35^{o}C (Duyck *et al*., 2004). In Kenya, Rwomushan *et al*. (2008) worked on *Bactrocera invadens* (Drew, Tsuruta and White) and reported 5.71, 2.88, 1.69, 1.41 and 1.24 days for egg development, 35.95, 14.99, 9.48, 7.85 and 6.64 for larva development, 34.08, 13.59, 10.02, 8.50 and 0 days for pupa development at 15, 20, 25, 30 and 35^{o}C, respectively. No adult emergence was observed at 35^{o}C for the pupa stage. In *Bactrocera oleae* (Gmelin) an approximate of 11.4, 4.3, 2.7 and 2.1 days for egg development, 32.8, 14.1, 10.5 and 5.0 days for larva development, 29.2, 12.4, 8.2 and 0 days for pupa development at 16, 22, 27 and 35^{o}C, respectively were recorded. No emergence of adult at 35^{0}C (Genc and Nation, 2008). In the same trend, Liu and Ye (2009) worked on *Bactrocera correcta* (Bezzi) and reported 66.75, 41.50, 28.50, 26.50 and 26.75 for egg development, 17.59, 12.05, 8.28, 7.56 and 7.96 days for larva development, 18.47, 11.24, 7.45, 7.00 and 6.76 for pupa development at 18, 24, 30, 33 and 36^{o}C respectively.

There are different life history strategies associated with fruit flies depending on their locations. Temperate species with a narrow host range, such as *Rhagoletis* spp., are usually univoltine, that is, they only have one generation per year. However, tropical pest species of *Anastrepha*, *Bactrocera*, *Ceratitis* and *Dacus* are typically multivoltine, that is, they have several generations per year (Fletcher, 1989; Zwölfer, 1983).

Biodiversity of fruit flies in the Australasian regions

The Tephritids family are found in all the world regions except the Antarctica. Each of the major pest genera have a limited natural distribution around the world. The Tropical Asia, including Indonesia to the west of Irian Jaya, the Ryukyu Island of Japan and China south of the Yangtze River, forms the Oriental region. About 160 genera are known from this region, including about 180 *Bactrocera*

spp. and about 30 genera of *Dacus* spp. Kapoor *et al*., (1980) presented a key to the Indian genera, and monographic works cover all the species known from Thailand and the Philippines (Hardy, 1973; 1974). The Indonesian Tephritids fauna has also been described in a series of paper by Hardy (1988) and Ibrahim and Ibrahim (1990). The work of Hardy (1977) catalogued the oriental tephritids fauna as available in southern China.

Australasian region comprises of Australia and New Guinea while New Zealand and Pacific Islands form the Oceanic region. About 130 genera are found in these regions, including about 270 *Bactrocera* spp., *Ceratitis capitata* and 27 *Dacus* spp. Drew (1989) revised the Dacini and provide a useful guide which was reprinted in the work of Ibrahim and Ibrahim (1990). Europe, temperate Asia, the Middle East and North Africa form the Palaeartic region. Here, about 140 genera are known, including 13 *Bactrocera* spp., *C. capitata*, 5 *Dacus* spp. and 22 *Rhagoletis* spp. Rohdendorf (1961) provided a key to most of the *Rhagoletis* spp. and many of the *Bactrocera* and *Dacus* spp. were included in Itô (1983-5).

Recently, Drew and Hancock (1994) studied the *B. dorsalis* complex in Asia and elucidated fourteen of this complex to be distributed in Thailand. These species were; *B. arecae* (Hardy and Adachi), *B. carambolae* (Drew and Hancock), *B. dorsalis* (Hendel), *B. irvingiae* (Drew and Hancock), *B. kanchanaburi* (Drew and Hancock), *B. melastomatos* (Drew and Hancock), *B. osbeckiae* (Drew and Hancock), *B. papayae* (Drew and Hancock), *B. propingua* (Hardy and Adachi), *B. pyrifoliae* (Drew and Hancock), *B. raiensis* (Drew and Hancock), *B. thailandica* (Drew and Hancock), *B. unimacula* (Drew and Hancock) and *B. verbascifoliae* (Drew and Hancock). Further work by Drew and Romig (2007) had revealed the occurrence of *B. zonata* (Saunders), *B. diversa* (Coquillett), *B. correcta* (Bezzi) and *B. cucurbitae* (Coquillett) in Thailand. While *B. gombokensis* (Drew and Hancock) in Peninsular Malaysia. Their study also confirmed *B. diaphora* (Hendel), *B. scutellatan* (Hendel), *B. scutellaris* (Bezzi), *B. tau* (Walker) and *Daucus longicornis* (Wiedemann) to be widely spread in Southeast Asia. Bamboo shoot fruit flies were also studied in Southern Thailand and sixteen species have been reported (Permkam, 1995; 2005; Permkam *et al*., 1997). The sixteen species were members of two distinct subfamilies; Ceratitinae and Trephritinae of the family Tephritidae. Hardy (1973) conducted an

extensive study of the fruit flies in the family Tephritidae in Thailand and bordering countries. His work treated 211 species of which about half of these total were described as new records.

Ecology of fruit fly

The early stages of development of insect assemblages, based on initial colonization of new ground, are an intriguing source of ecological knowledge (New, 2008). The ecosystem is dynamic with species varying over space and time and the environment is understood to provide the selective forces in natural selection. In a community, plant susceptibility to insects depends on the phenological synchrony between both. In turn, a suitable plant for the development of an insect population can often escape herbivory because the insect seasonality does not coincide with the plant susceptible stage (Messina and Jones, 1990).

Field under fallowing from agriculture leads to change in plant diversity and the composition change in predictable ways (Corbet, 1995; Tscharnike and Greiler, 1995). It is less well known how animal communities respond to these changes (Sieman *et al*., 1999; Raghu *et al*., 2000). Correlative studies have generally supported the hypothesis that changes in arthropod herbivore diversity are driven by changes in vegetation (Steffan-Dewenter and Tscharnike, 1997). Because each plant species may represent one or more resources for herbivores, theory predicts, correlative and experimental studies have found that increasing plant diversity increases herbivore diversity (Sieman *et al*., 1997). Herbivore may be sensitive not only to plant taxonomic diversity, but also to plant architectural or height diversity (Brown, 1991) or plant productivity (Rosenzweig and Abramsky, 1993; Sieman 1998) which are likely to correlate with plant diversity and field successional age (Corbet, 1995; Tscharnike and Greiler, 1995). The importance of these different factors can be assessed by testing the dependence of both arthropod diversity and abundances of individual species on different vegetation characteristics.

Changes in the physical and biotic environments during succession constrain the type of species that dominate different stages of succession (Tilman, 1990). Conversely, changes in the type of arthropods that characterize different stages of succession may indicate the environmental constraints and organismal tradeoffs

that are important in determining arthropod successional dynamics. Because body size is correlated with many important organismal characteristics including dispersal ability and metabolic and digestive efficiencies (Peter, 1983; Brown, 1995) that likely influence the degree of diet specialization (Brown *et al*., 1993; Brown, 1995), changes in body size of arthropods during succession may be a powerful indicator of changing environmental constraints (Sieman *et al*., 1999).

Knowledge about fruit fly species and their respective seasonality related to host plant phenology is crucial to understand the population dynamics of these insects (Souza-Filho, 2009). Fruit flies require food, mates, oviposition sites and refugiae as essential resources (Prokopy *et al*., 1994). Foraging for these resources in several species of fruit flies is a dynamic process (Hendrichs *et al*., 1991; Aluja & Birke, 1993; Aluja and Prokopy, 1993). Individual flies have been tracked moving between habitats on a daily cycle due to feeding, mating and egg laying requirements. Flies have also been observed to adjust their foraging behavior in response to the changes in the spatial, temporal and seasonal distribution of food resources (Hendrichs *et al*., 1991). The spatio-temporal dispersion patterns of a fruit fly population throughout the landscape can be interpreted as a reflection of the summary of foraging behaviour of individual adult flies. Ecological theory requires that organisms differs in their use of shared, limiting resources if they are to coexist. Specialization reduces interspecific competition and facilitates species coexistence by partitioning niche space (Dyer *et al*., 2007). Intergeneric polyphagy does occur and has been reported by some researchers (Copeland *et al*. 2002, 2006; Mwatawala *et al*. 2006a). This could lead to displacement and niche differentiation in tephritid flies and this occur in hierarchical order and that no reversal displacement was recorded before (Duyck *et al*. 2004) and complete exclusion does not occur (Duyck *et al*., 2004; Vayssières *et al*., 2005). Daily activities of flies consist of resting, feeding, lek formation, mating, and egg laying (Hendrichs and Hendrichs, 1990; Hendrichs *et al*., 1991; Warburg and Yuval, 1997). In most cases flies tend to perform all of these activities within a restricted space, composed principally of ripe and unripe host fruit trees, in which they can obtain enough nutrients, shelter and egg-laying hosts (Hendrichs & Hendrichs, 1990; Warburg and Yuval 1997). Thus, dispersion of flies to other places is minimal as long as habitat conditions are appropriate (Fletcher, 1989,

Hendrichs & Hendrichs, 1990; Prokopy *et al*., 1994). On the other hand, when habitat conditions deteriorate flies will emigrate and disperse in search of more favourable habitats (Fletcher, 1989).

Host availability has been shown to have an impact on seasonal abundance of fruit flies in early studies (Tora Vueti *et al*., 1997; Mwatawala *et al*., 2006b), but climatic variables such as temperature, rainfall and relative humidity seasonal variations play vital role (Birch, 1957; Amice and sales 1997; Vayssières *et al*., 2005; Mwatawala *et al*., 2006b; Muthuthantri *et al*., 2010) in determining fruit fly population. Vayssières *et al*. (2005) reported that the population of *B. invadens* increases with rise in temperature and rainfall. Rainfall can affect plant phenology and nutrient quality for insects (Pedigo and Zeiss, 1996) and is among the factors causing the rapid increase of various *Bactrocera* species (Amice and Sales, 1997).

Distribution of *B. carambolae* and *B. papayae* in Asia

As reported by Drew and Hancock (1994), *B. carambolae* are found in southern Thailand, peninsular Malaysia, Singapore, Borneo, Indonesia, Andaman Island (India). It was introduced to Surinam and French Guiana (First recorded in Surinam in 1975).

The *B. papayae* are native to and widespread in southeast Asia (Thailand, peninsular Malaysia, east Malaysia, Singapore, Indonesia and Kalimantan) (Drew and Hancock, 1994). It invaded Papua New Guinea from Asia through Irian Jaya in 1992. For a long time, it had been only trapped in the Western and West Sepik Provinces, but was later detected in Port Moresby (May, 1986), Morobe Province (September, 1998), and the Highlands (Eastern Highlands, Simbu, Western Highlands) (November, 1998). It is present in most provinces of mainland Papua New Guinea, but not yet in the Island Provinces. It was detected in Cairns (Northern Queensland, Australia) in October 1995, but may have established about two years earlier (Allwood and LeBlanc, 1997). It has been eradicated from Queensland by implementing an eradication programme using male annihilation and protein bait spraying, that cost AUD 35 million (Fay *et al*., 1997).

Host of *B. carambolae* and *B. papayae*

B. carambolae infest a wide range of commercial and endemic rainforest fruits (Drew and Hancock, 1994). Contrarily, Vijaysegaran *et al.* (1991) stated in their findings that *B. carambolae* tends to predominate in orchards and urban areas and it is rarely if ever found in undisturbed rainforests. White and Elson-Harris (1992) stated that *B. carambolae* is not a pest of banana. In Surinam, the principal hosts are *Averrhoa carambola* (Oxalidaceae) and *Syzygium samaragense* (*S. javanica*) (Myrtaceae); secondary hosts are *Malpighia punicifolia* (Malpighiaceae), *Mangifera indica* (Anacardiaceae) and *Psidium guajava* (Myrtaceae). Several other species received incidental infestation (Aluja *et al*., 1987; Sauers-Muller, 1991; Caroline *et al*., 2008).

B. papayae is *a* polyphagous species and major pest recorded in Asia from 193 host species, in 114 genera and 50 families (Allwood *et al*.,1999). It was bred from 35 host species in Australia (Hancock *et al*., 2000) and caused considerable damage to fruits and coffee berries. There are presently not enough data available to establish a comprehensive host list for some regions, but it has been occasionally bred from carambola, cashew, papaya, pomelo, mango and guava. No infestations of coffee berries have been observed or reported so far in Papua New Guinea, even though *B. papayae* is commonly trapped in the Highlands.

Allwood *et al.* (1999), Drew and Hancock (1994), Ranganath and Veenakumari (1995) and Yong (1994) had worked extensively on the host plant records for fruit flies (Diptera: Tephritidae) in Southeast Asia. Their work revealed that both *B. carambolae* and *B. papayae* are polyphagous species of tephritids flies found in Southeast Asia. Their work lead to the summary of host plants for *B. carambolae and B. papayae* in this region (Table 1).

Table 1. Host plants of *B. carambolae* and *B. papayae*.

SN	Plant family	Species of plant	Number of samples from which fly species have been reared	
			B. papayae	*B. carambolae*
1	Alangiaceae	*Alangium griffithii*	-	1
1	Amaryllidacae	*Crinum asiaticum*	1	-
2	Anacardiacae	*Anacardium occidentale*	68	-
		Bouea macrophylla	1	-
		Bouea oppositifolia	5	2
		Holigarna kurzii	3	-
		Mangifera caesia	3	-
		Mangifera caloneura	2	-
		Mangifera foetida	19	-
		Mangifera griffithii	1	-
		Mangifera indica	74	7
		Mangifera laurina	2	-
		Mangifera odorata	3	-
		Mangifera pajang	2	-
		Spondias cytherea	19	-
3	Annonacae	*Annona glabra*	1	-
		Annona monstana	7	2
		Annona muricata	19	(**)
		Annona reticulate	3	-
		Annona squamosa	16	-
		Artabotys siamensis	38	-
		Desmos chinensis	2	-
		Spondias cytherea	2	-
		Rollinia pulchrinervis	3	1
		Uvaria grandiflora	5	1
4	Apocynacae	*Carissa carandas*	8	-
		Thevetia peruviana	13	(**)
		Willughbeia cochinchinensis	1	-
5	Arecaceae	*Areca catechu*	2	-
		Arenga pinnata	**(*)(**)**	**(**)**
		Arenga westerhoutii	2	-
		Borassus flabellifer	2	-
		Caryota mitis	1	-

		Veitchia merrillii	1	-
6	Boraginaceae	*Cordia dentate*	1	-
		Ehretia microphylla	1	-
7	Burseraceae	*Canarium sp.*	1	-
8	Cactaceae	*Pereskia grandiflora*	1	-
9	Caricaceae	*Carica papaya*	129	-
10	Clusiaceae	*Calophyllum inophyllum*	4	-
		Garcinia atroviridis	1	1
		Garcinia cowa	-	3
		Garcinia dulcis	7	-
		Garcinia griffithii	1	1
		Garcinia hombroniana	12	-
		Garcinia mangostana	3	1
		Garcinia parvifolia	2	-
		Garcinia prairiana	1	-
		Mammea siamensis	3	-
11	Combretaceae	*Terminalia catappa*	266	16
		Terminalia citrina	1	-
		Terminalia manii	-	(a)
		Terminalia procera	-	(a)
12	Cucurbitaceae	*Coccina grandis*	12	-
		Cucumis sativus	2	-
		Gymnopetalum integrifolium	1	-
		Momordica charantia	5	-
13	Dilleniaceaeareolata	*Dillenia obovata*	2	-
14	Ebenaceae	*Diospyros areolata*	1	-
		Diospyros diepenhorstii	2	-
		Diospyros blancoi	3	-
		Diospyros melabarica	7	-
		Diospyros philippensis	5	-
15	Elaeocarpaceae	*Muntingia calabura*	17	-
16	Euphorbiaceae	*Antidesma ghaesembilla*	1	-
		Baccaurea motleyana	2	-
		Breynia reclinata	2	-
		Drypetes longifelia	-	(a)
		Excoecaria agallocha	2	-
		Glochidion litorrale	1	-

		Sapium baccatum	1	-
		Sapium indicum	1	-
		Sauropus androgynus	6	-
16	Fagaceae	*Castanopsis sp.*	1	-
17	Flacourtiaceae	*Dovyalis hebecarpa*	1	-
		Flacourtia rukam	2	-
18	Flagellariaceae	*Hanguana malayana*	1	-
19	Lauraceae	*Lindera oxyphylla*	1	-
		Lisea glutinosa	1	-
		Persea americana	1	2
20	Lecythidaceae	*Careya sphaerica*	1	-
21	Leguminosae	*Adenathera pavonina*	1	-
		Parkia speciosa	1	-
		Phaseolus vulgaris	1	-
22	Loganiaceae	*Fagraea ceilanica*	2	5
23	Malphiaceae	*Malphigia emarginata*	11	-
24	Meliaceae	*Aglaia domestica*	5	-
		Aglaia dookoo	6	3
		Azadirachta excelsa	6	-
		Lansium dommesticum	3	1
		Sandoricum koetjape	65	2
25	Menispermaceae	*Fbraurea tinctoria*	1	-
26	Meraceae	*Artocarpus altilis*	17	1
		Artocarpus comeziana	-	(a)
		Artocarpus elastic	3	1
		Artocarpus heterophyllus	13	6
		Artocarpus integer	14	4
		Artocarpus lakoocha	4	3
		Artocarpus odoratissimus	1	1
		Artocarpus rigidus var asperulus	13	1
		Artocarpus sericicarpus	2	-
		Ficus benjamini	2	-
		Ficus chartaceae	1	-
		Ficus concatian	1	-
		Ficus eligodon	1	1
		Ficus grossularioides	-	1
		Ficus hispida	4	1

		Ficus microcarpa	1	-
		Ficus obpyramidiata	1	-
		Ficus paefolia	-	1
		Ficus religiosa	1	-
		Morus alba	3	-
		Morus nigra	1	-
		Streblus asper	1	-
27	Musaceae	*Musa acuminate*	2	-
		Musa balbisiana	2	-
		Musa paradisiacal	161	-
28	Myristicaceae	*Horsfieldia subglobosa*	1	-
		Knema angustifolia	-	1
		Knema globularia	34	-
		Knema missionis	1	-
29	Myrsinaceae	*Ardisia crenata*	1	-
30	Myrtaceae	*Eugenia formosana*	1	-
		Eugenia longiflora	1	-
		Eugenia mitchelii	1	-
		Eugenia pseudosubtilis	2	-
		Eugenia uniflora	**(**)**	**(**)**
		Psidium cattleianum	2	2
		Psidium guajava	567	179
		Rhodomyrtus tomentosa	5	1
		Syzygium aqueum	12	15
		Syzygium grande	5	2
		Syzygium jambos	10	6
		Syzygium malaccense	26	17
		Syzygium samarangense	162	39
31	Oleaceae	*Linociera parkinsoni*	2	-
	Olacaceae	*Ochanostachys amentosa*	-	2
32	Oxalidaceae	*Averrhoa bilimbi*	4	5
		Averrhoa carambola	289	139
33	Passifloraceae	*Passiflora edulis*	31	-
		Passiflora foetida	9	-
		Passiflora quadrangularis	1	-
	Polygalaceae	*Xanthophyllum amoenum*	-	1
34	Punicaceae	*Punica granatum*	1	1

35	Rhamnaceae	*Ziziphus jujube*	2	1
		Ziziphus mauritiana	120	-
		Ziziphus oenoplia	5	1
36	Rhizophoraceae	*Pellacalyx saccardianus*	-	1
		Rhizophora sp.	1	1
37	Rosaceae	*Eriobotrya japonica*	1	-
		Prunus persica	1	-
38	Rubiaceae	*Anthocephalus chinensis*	30	-
		Coffea canephora	1	-
		Ixora javanica	5	-
		Ixora macrothyrsa	2	-
		Morinda citrifolia	4	-
		Morinda coreia	1	-
		Morinda elliptica	2	-
		Morinda umbellate	1	-
		Nauclea orientalis	7	-
		Ochreinauclea maingayi	2	-
39	Rutaceae	*Citrofortunella mitis*	20	1
		Citrus aurantifolia	9	1
		Citrus grandis	15	-
		Citrus hystrix	8	-
		Citrus limon	4	2
		Citrus madurensis	**(**)**	**(**)**
		Citrus paradise	**(**)**	**(**)**
		Citrus reticulate	18	1
		Citrus sinensis	1	-
		Clausena lansium	1	-
		Fortunella margarita	**(**)**	**(**)**
		Fortunella polyandia	**(**)**	**(**)**
		Glycosmis pentaphylla	2	-
		Murraya paniculata	21	-
		Paramignya andamanica	-	(a)
		Triphasia trifolia	**(**)**	**(**)**
		Tetractomia majus	-	1
40	Sapindaceae	*Lepisanthes alata*	**(**)**	**(**)**
		Lepisanthes rubiginosa	2	-
		Nephelium eriopetalum	1	-

		Nephelium lappaceum	20	-
41	Sapotaceae	*Chrysophyllum cainito*	9	1
		Manilkara zapota	89	16
		Manilkara littoralis	-	(a)
		Mimusops elengi	7	(a)
		Palaquium maingayi	1	-
		Planchonella longipetiolatum	-	(a)
		Pouteria caimito	1	-
		Pouteria compechiana	-	1
42	Simaroubaceae	*Irvingia malayana*	1	1
43	Solanaceae	*Capsicum annum*	19	1
		Lycopersicon esculentum	1	1
		Physalis minima	2	-
		Solanum aculeatissimum	18	-
		Solanum ferox	1	1
		Solanum granuloso-leprosum	6	-
		Solanum incanum	1	-
		Solanum melongena	7	-
		Solanum stramonifolium	5	-
		Solanum torvum	10	-
44	Sterculiaceae	*Theobrama cacao*	1	-
	Symplocaceae	*Symplocos cochinchinensis*	-	1
45	Tiliaceae	*Grewia paniculata*	2	-
46	Ulmaceae	*Celtis tetranda*	4	-
47	Verbenceae	*Callicarpa longifolia*	1	-
		Gmelina elliptica	2	-
		Gmelina philippensis	5	-
		Premna serratifolia	1	-
48	Vitaceae	*Cissus repens*	1	-
49	Zingiberaceae	*Alpinia mutica*	2	-

All plant names followed by numbers in column were observed by Allwood *et al*. (1999)

(*)Observed by Drew and Hancock (1994)

(**)Observed by Yong (1994)

Damage and economic loss caused by fruit flies to crops

Fruit flies are attracted to host plants when fruit is developing. Different fruit fly species have different host ranges. Fruit infestation is influenced by its degree of maturation during the fruit fly oviposition period (Messina and Jones, 1990). Foraging differences can be observed, as fruit flies make incursions into fruits of a certain developmental stage (Diaz and Vásquez, 1993). As a suitable host is located the female fruit flies insert their ovipositor into the fruit's soft skin which scars the fruit surface. They lay their eggs under the soft skin in both mature and green fruits (Hollingsworth and Allwood, 2000). The egg hatch and larva feeds inside the fruit causing the fruit to rot (Dhillon *et al*., 2005). However, larvae that feed and develop within the fruit cause the most damage. Larvae tunnel throughout the fruit as they feed and grow. They also introduce bacteria and fungi which cause infested fruit to quickly turn putrescent and fall to the ground prematurely (Christenson and Foote, 1960; Fletcher,1987).

Typically, the pest status of a fruit fly species is reported in terms of the percentage of a fruit crop infested by the fly. In some fruits, losses can be very high. Tobin (1990) reports losses close to 100% in carambola and guava plants in Malaysia and Allwood and LeBlanc (1997) report losses of 60% in cumquat, 89%–97% in chilli, papaya (12-60%), guava (40-90%) and 20%–25% in mangoes across seven Pacific Island countries. Dhillon *et al*. (2005) reported 100% in cucurbit species, caused by Melon fly *B. cucurbitae*.

Eradication costs can be significant. For example, the Queensland papaya fruit fly eradication program cost close to U$33m by the planned completion date in 1999 (QDPI, 1998). Mediterranean and Oriental fruit fly incursions in the USA have occurred since 1980 and have been eradicated at a total cost of US$350m (Armstrong and Jang, 1997).

Management and control of fruit fly

Many management and control strategies have been employed in the control of fruit flies over several decades. This management and control strategies include the use of chemicals, biological control, farm sanitation, male sterile techniques, transgenic based embryo-specific lethality system, quarantine, host plant

resistance, monitoring and control with parapheromones lure/cue-lure traps (Dhillon *et al*., 2005). Chemical control is widely used among farmers (Victor 2009). Several chemical compounds have been tested and used for the control of fruit flies in different part of the globe based on the occurrence and species available. On melon fly control, for example, Bhatnagar and Yadava (1992) reported malathion (0.5%) to be more effective than carbaryl (0.2%) and quinalphos (0.2%) on bottle gourd, sponge gourd, and ridge gourd. The application of molasses + malathion (Limithion 50 EC) and water in the ratio of 1: 0.1: 100 provides good control of melon fly. Application of either 0.05% fenthion or 0.1% carbaryl at 50% appearance of male flowers, and again at 3 days after fertilization is helpful in reducing the melon fly damage (Srinivasan, 1991). Gupta and Verma (1982) reported that fenitrothion (0.025%) in combination with protein hydrolysate (0.25%) reduced fruit fly damage to 8.7 % as compared to 43.3 % damage in untreated control.

Gallo (2007), stated that the use of insecticides as the only way to control pests in fruits and vegetables causes environmental pollution and hygenic problems that represent a risk for people and animals. In the last four decades the use of synthetic pesticides such as organophosphate and carbamate in an extensive way has led to the development of insecticide resistance in a number of pest species (Casida and Quistad, 1998; Claudianos *et al.*, 1999; Hsu and Feng, 2006) and in Thailand residues of organophosphate and organochlorine and other compounds have been detected in soil, water and crops (Thapinta and Hudak, 2000). Pest-free or low pest density zones are being advocated worldwide for fruit export with minimal or zero quarantine restrictions (FAO, 2006). The use of more ecologically friendly methods are desired to make fruits and vegetables suitable for exportation and safe for human consumption.

Introduction of parasitoids to infested fields has given good results in management of fruit flies. The use of biological control to control fruit flies started already in 1902 (Wharton, 1989). There are examples where reductions of infestation have been nearly 95% as the experiment in Hawaii showed when larvae parasitoids belonging to the families Eulophidae, Braconidae and Chalcididae were introduced (Allwood *et al*., 2001). *Psyttalia fletcheri* (Hymenoptera: Braconidae) is one of the parasitoids that had showed a high parasitism degree in *B. cucurbitae*, *Fopius*

arisanus (Sonan) is other promising parasitoid tested in Hawaii to control *B. latifrons* (Bokonon-Gatan *et al*., 2007).

Chinajariyawong *et al*. (2000) surveyed opiine parasitoids of fruit flies in Thailand and Malaysia. Table 2 below is the summary of the parasitoids they identified for *B. Papayae* and *B. carambolae*.

Table 2. Parasitoids of *B. carambolae* and *B. papayae*.

SN	Parasitoid
1	*Diachsmimorpha longicaudata*
2	*Fopius arisanus*
3	*Fopius vandenboschi*
4	*Psyttalia incise*
5	*Psyttalia makii*
6	*Psyttalia* sp. *nr fletcheri*
7	*Psyttalia* sp. *nr. Makii*

The use of sterile insect technique (SIT) is also a common practice nowadays, this has been employed in the area wide management of fruit flies in some parts of the world. This method requires a great amount of sterile flies which should be in same proportions to the number of the wild flies but also an appropriate rearing of flies that carry many of the genetic characteristics presented in the population that will be controlled (Itô *et al*., 2003).

The production of crop varieties that are less attractive for fruit flies has shown good effects. There are some chilli varieties that are classified as non-hosts for fruit flies in Fiji islands. In Thailand, there are some fruit crops that are not susceptible to fruit fly attacks (Allwood *et al*., 2001).

Bagging is a kind of exclusion. A single fruit or a cluster or even a whole tree can be covered by a bag. The bags prevent fruit flies from infesting the fruits. Often the bag is made of paper, but also cloth can be a material resistant enough. In Thailand, this method is used in particular in mango orchards (Allwood *et al*., 2001). Even plant leaves can be an appropriate material for bagging fruits (e.g. banana) (Victor, 2009).

Weather and its impacts on insects

Insects are cold-blooded organisms; the temperature of their bodies is approximately the same as that of the environment. Therefore, temperature is probably the single most important environmental factor influencing insect behaviour, distribution, development, survival, and reproduction (Sei-woong, 2008). Insect life stage predictions are most often calculated using accumulated degree days from a base temperature and biofix point. Some researchers believe that the effect of temperature on insects largely overwhelms the effects of other environmental factors (Brévault and Quilici, 2000; Bale *et al*., 2002). It has been estimated that with a $2^{o}C$ temperature increase, insects might experience one to five additional life cycles per season (Yamamura and Kiritani 1998). The work of Fletcher (1989) and confirmed by Brévault *et al*. (2008) working on relationship between temperature, development and survival of different life stages of tomato fruit fly, *Neoceratitis cyanescens* revealed that temperature-development rate relationships are linear and, therefore, a constant number of heat units above this threshold is needed to complete development. Other researchers have found that moisture and CO_2 effects on insects can be potentially important considerations in a global climate change setting (Hamilton *et al*., 2005; Coviella and Trumble 1999; Hunter, 2001).

Temperature may change gender ratios of some pest species such as thrips (Lewis, 1997) potentially affecting reproduction rates. Insects that spend important parts of their life histories in the soil may be more gradually affected by temperature changes than those that are above ground simply because soil provides an insulating medium that will tend to buffer temperature changes more than the air (Bale *et al*., 2002).

Some insects are sensitive to precipitation and are killed or removed from crops by heavy rains (Reiners and Petzoldt, 2005). One would expect the predicted more frequent and intense precipitation events forecasted with climate change to negatively impact these insects. Other insects such as pea aphids are not tolerant of drought (Mcvean and Dixon, 2001). As with temperature, precipitation changes can impact insect pest predators, parasites, and diseases resulting in a complex dynamic. Fungal pathogens of insects are favoured by high humidity and

their incidence would be increased by climate changes that lengthen periods of high humidity and reduced by those that result in drier conditions.

Existing studies suggest that direct effects of temperature are likely to be larger and more important than any other factor. Direct effects of temperature rise on insects may be greater in the Polar Regions than in temperate or tropical zones, reflecting the more severe environmental conditions, the tighter constraints and the prediction of much larger proportional temperature rises in these areas (Bale *et al*., 2002; Convey and Block 1996; Hodkinson *et al.*, 1998; Vernon *et al*., 1998). Tephritid distribution and abundance are notably dependent on several abiotic factors (e.g., temperature, relative humidity, and rainfall) and several biotic factors (e.g., host plants and natural enemies) (Vayssièeres *et al*., 2008).

In conclusion, for insect herbivores, the ability to complete their life cycle represents a successful adaptation to both their host plant and to the climatic environment in which they are found. Climate can act directly on an insect either as a mortality factor or by determining the rate of growth and development (Bale *et al*., 2002).

Life tables

The life table is one of the most important tools in demographic and gerontological research because it is used to characterize the mortality and survival properties of cohorts and to quantify the actuarial rate of aging (Müller *et al*., 2004). The historical application of classical life table methods in aging science has been largely restricted to the use of mortality data from either humans or experimental animals maintained in the laboratory, or to life tables based on capture–recapture methods to assess aging in wild populations (Udevitz and Ballachey, 1998). Life table identity reveals a mathematical relationship between the distribution of deaths in the marked cohort and the age structure of the original population. Individuals in the captured and marked sample are assumed to have remaining lifetimes similar to those in the wild (Müller *et al*., 2004). In fruit-infesting fruit flies (Tephritidae), as well as several other categories of insects that include important agricultural pests, the only age class that can be recognized with certainty is that of very young adults, which do not yet have mature oocytes or sperm (Fletcher *et al*., 1978; Kendra *et al*., 2006).

In polyphagous insects, life history traits mainly depend on host plant range. Substantial longevity, high fecundity and larval competition are the major traits of polyphagous tephritidae while species with a restricted host range generally exhibit a lower longevity and fecundity as well as mechanism to avoid larval competition (Brévault *et al*., 2008).

Temperature may induce changes in life-cycle duration (rate of development), voltinism, population density, size, genetic composition, extent of host plant exploitation as well as local and geographical distribution linked to colonization and extinction. These effects are likely to be greatest in above-ground herbivores, exposed to the full variability of micro- and macroclimate, while soil-dwelling species experience thermal regimes that are buffered by the denser soil environment. Many species are limited in their distribution by summer heat availability rather than the lethal effect of extreme temperatures (Bale *et al*., 2002). Host plant and insect herbivore synchrony may also limit both the possible range of host plant species exploited and the actual plant tissues utilized. The psyllid *Cochlearia groenlandica* (L.) expands its range of willow (Salix) host-plant species from one to four along a latitudinal gradient as the demands of temporal synchrony lessen as the thermal environment becomes more benign (Hodkinson, 1997).

Traps and traping of fruit flies

The McPhail trap was the first device to be used with protein baits (McPhail, 1939). Steiner traps were developed in 1957 (Steiner *et al*., 1952) and Jackson traps in 1971 for Trimedlure (TML) (Harris *et al*., 1971). These traps are currently used in various countries for fruit fly surveys in support of control activities and eradication campaigns. The combination of a McPhail trap with a protein attractant, Jackson trap with TML, and the Steiner trap with ME or cuelure (CUE), has remained unchanged for several decades. After years of validating trapping technology through coordinated research programmes, the Joint Division FAO/IAEA proposes the use of proven technologies in improving trap sensitivity in area-wide fruit fly control programmes (IAEA, 1996 and IAEA, 1998). These proven technologies include the use of synthetic food lures such as female attractants that can be used for several species of *Anastrepha*, *Bactrocera* and *Ceratitis*. Several traps

have also been manufactured, these are properly described in IAEA (2003). Several experts have used various traps in fruit flies research in various part of the world based on the species of fruit flies available and the objectives of the research. Some traps were simulated which were also found effective (Victor, 2009).

CHAPTER 2

BIODIVERSITY OF FRUIT FLY

Introduction

The production of fruits and vegetables in Thailand generate important sources of income. These crops provide required nutritional essentials for the populace. The importance of horticultural sector was noticed by the government and subsequently it development was included in the National, Social and Economic Development Plan since 1981 (Plan V) (Subhadrabandhu and Wongwanich, 1996). Due to increase in population and urbanization levels, there is also increase in the demand for fruits and vegetables. For several tropical fruits, the production is mainly by smallholder producers largely intended for local consumption in the rapidly expanding local-urban green market (*Thalad kaset*). However, reliable markets for fruits can be secured only when a country is able to produce high quality fruits free from pests and diseases. Production of high quality fruits and vegetables worldwide is hampered by insect pests, especially fruit fly (Diptera: Tephritidae) (Mwatawala *et al*. 2006a).

The Tephritid flies especially those in the sub-family Dacinae are well distributed in south-east Asian countries. Apart from the clearly distinct few species of this subfamily, it is known that a complex of sibling species exists in this region and much of these complex members are of serious economic importance to agriculture because of damage caused to commercial fruits and vegetables. The damage, if uncontrolled, may result in a total loss of the crop in question (Yong *et al*., 2010). The cost of losses due to infestation of fruit flies can be surprisingly high, there are examples where losses have been up to 100% in cucurbit species, caused by melon fly (*Bactrocera cucurbitae*) (Dhillon *et al*., 2005). Crop losses in mango (12-60%), guava (40-90%) and papaya (12-60%) have also been recorded by Allwood and Leblanc (1997). Species in the *B. dorsalis* complex are certainly the most significant fruit fly pest species in south-east Asia (Drew and Hancock, 1994). Korneyev (1999) revised the family tephritidae and proposed two distinct genera, *Bactrocera* and *Dacus*, for the tribe Dacini (Sub-family Dacinae). *Bactrocera* is a large genus

consisting of 629 described species out of 880 in the tribe Dacini (Drew, 2004), and contains most of the fruit fly pests in the tropical and subtropical countries.

Thailand fauna is rich in biodiversity, but few diversity studies were known to be carried out on the tephritid flies. Examples of such studies include the pioneer survey study by Hardy (1973) of the fauna of Thailand and neighboring countries which treated 211 species of fruit flies. Half of which were described as new, and brings up to date the knowledge of these flies for Thailand, Cambodia, Laos, Vietnam, Malaya and Tenasserim and lower Burma. The species were arranged in 4 subfamilies, 13 tribes, 69 genera (13 were new) and 7 subgenera. Most recent study was the identification of the *B. dorsalis* complex of fruit flies in Asia (Drew and Hancock, 1994). This study identified 75 members of this complex of which 14 were found to be prevalence in Thailand. Except for the extensive survey carried out on fruit flies of bamboo shoot (Permkam, 1995, 2005; Permkam *et al*., 1997), most other pronounced studies were on biology and ecological studies (Jang, 1997; Kuba and Koyama, 1982, Kuba *et al*., 1984; Smith, 1989; Clarke *et al*. 2001). Most studies available were general with reference to host plants. Therefore, the scope of this present work was limited to the plant family Myrtaceae and specifically *P. guajava* as it is one of the fruits cultivated in southern Thailand.

The family Myrtaceae, is the family of one of the most consumed fruits family in Thailand and the most popular fruit of this family is the *P. guajava*. Fruit flies biodiversity have not been sufficiently studied on many members of this family. Therefore, this research aimed at identifying those fruit flies that subsist in guava orchards and it surrounding environments. The alpha and beta diversity at different site were presented. These biodiversity studies would enhance pest advisors with the ideas about what fruit flies were localize and or prevalence and how to develop friendly ecological control schemes for this pests.

Materials and Methods

Study site

The study was conducted from March 2012 to March 2013. Four provinces were selected for sample collections; these were Narathiwat (Ban Bala, 6^{o}50'00''N and 101^{o}49'00.11''E), Songkhla (Ban Koyai, 7^{o}00'52.98''N and 100^{o}27'35.18''E), Trang (Khuan Mao, 7^{o}58'12''N and 99^{o}37'48''E) and Surat Thani (Ban Thakham, 9^{o}5'2.65''N and 99^{o}13'33.59''E) (Figure 1).

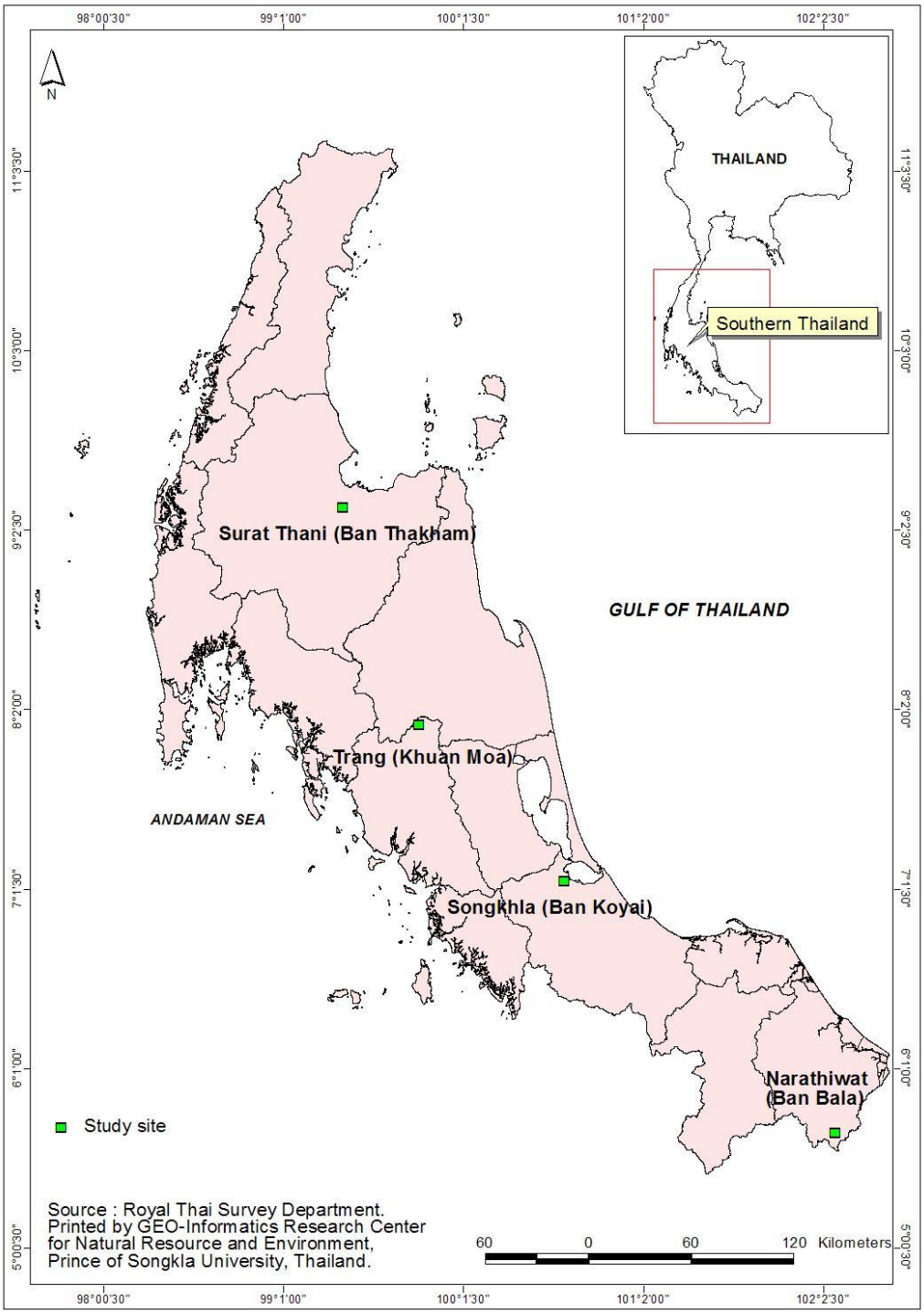


Figure 1. Location of agro-forested sites studied in southern Thailand for fruit fly biodiversity.

The sample collections were based specifically in guava orchards and their surrounding environments. Guava orchards were selected because guava fruits were the most cultivated and consumed among the fruit plants in the family Myrtaceae in southern Thailand. Also documentation of the fruit flies on these fruits before now was scanty. Furthermore, preliminary survey of this study revealed some *Bactrocera* spp. to be in close association with the guava fruits. Commercial orchards were chosen and were mainly located within agro-forested areas of which most vegetation were extended rubber plantations except for the few vegetable garden and fruit orchards that were patchy spot among the rubber plantations. Apart from the great distances among the sites, also were different geographical features and physical factors which distinctly distinguished each site. Vegetables, wild and economic fruits available at each site were observed, but their inventory and identification was outside the scope of this research.

Characteristics of the biodiversity study sites

The orchards at Ban Koyai / Ban Phru (4.45ha) and Khuan Mao (3.23ha) sites were located in extensive rubber plantation. But the Ban Bala (1.21ha) site was surrounded by forest comprising of different vegetation. Ban Thakham (2.42ha) site was located in an extensive palm plantation. Other economic fruits which occur within the range of the study sites were similar, these include; jackfruit (*Artocarpus heterophyllus* Lam.), rose apple (*Syzygium samarangense* Merrill & Perry), banana (*Musa* spp. L.), mango (*Mangifera indica* L.), pawpaw (*Carica papaya* L.), citrus (*Citrus sinensis* L.), rambutan (*Nephelium lappaceum* L.), mangosteen (*Garcinia mangostana* L.), sapodilla (*Manilkara zapota* L.), star fruit (*Averrhoa carambola* L.), santol (*Sandoricum koetjape* Merr.), bitter bean (*Parkia speciosa* Hassk.), durian (*Durio zibethinus* L.), tamarind (*Tamarindus indica* L.), coconut (*Cocos nucifera* L.), palmyra palm (*Borassus flabellifer* L.), palm (*Livistona speciosa* Kurz.), langsat (*Lansium domesticum* Corrêa.) and malabar almond (*Terminalia catappa* L.). The vegetables and legumes that were sited were; cucumber (*Cucumis sativus* L.), chilli pepper (*Capsicum annum* L.), eggplant (*Solanum melongena* L.) and lentils (*Vigna unguiculata* Verdc.). Roots and tubers found were; sweet potato

(*Ipomoea batatas* Lam.) and cassava (*Manihot. esculenta* Crantz.). The economic grasses were; sugar cane (*Saccharum officinarum* L.), rice (*Oryza sativa* L.) and bamboo (*Bambusa arundinacea* Willd.).

Trap and trapping

Consecutive trapping of fruit flies was conducted for a year. The focus was on fruit infesting species of the genus *Bactrocera* and most significantly the *B. dorsalis* complex members.

Two types of trap were implored for this research; Steiner trap (Steiner *et al*., 1952) (Thailand modification) (Figure 2) and Ball trap AR934 (ISCA modified McPhail trap USA) (Figure 3). Methyl eugenol (Benzene,1,2,-dimethoxy-4-(2-propenyl) (Thailand) and torula yeast (ISCA, USA) were the two attractants used. For the Steiner trap, methyl eugenol was mixed with Pyrethriod (Changzhou Kangmei Chemical Industry, China) at the rate of 63ml pyrethroid / 1000ml methyl eugenol, 1ml of the mixture was used to impreginate cotton wool placed in the trap. The Ball trap AR934 was baited with torula yeast pellets dissolved in water (3 pellets to 1½ litres) as recommended by ISCA Technologies USA. Methyl eugenol is relatively specific and was used to attract the members of the genus *Bactrocera* and mostly the *B. dorsalis* complex members. The torula yeast is less specific and was used to attract other fruit flies.

At each site two replicates of each type of traps were set up in orchard and around the orchard (2 Steiner traps and 2 Ball traps) given a total of four traps each in and around the orchards. In guava orchards, the traps were hung and suspended between the ranged of 1.3 - 1.5m height. But 1.5 - 2.3m height was maintained around the guava orchards where traps were hung on bamboo trunk, rubber, sapodilla, and biter bean trees. Traps were inspected and trapped flies were collected once a week in Songkhla province and all baits were changed every month. Flies were collected at other sites once in a month and baits replaced accordingly. Traps were rotated anticlockwise after each clearance.

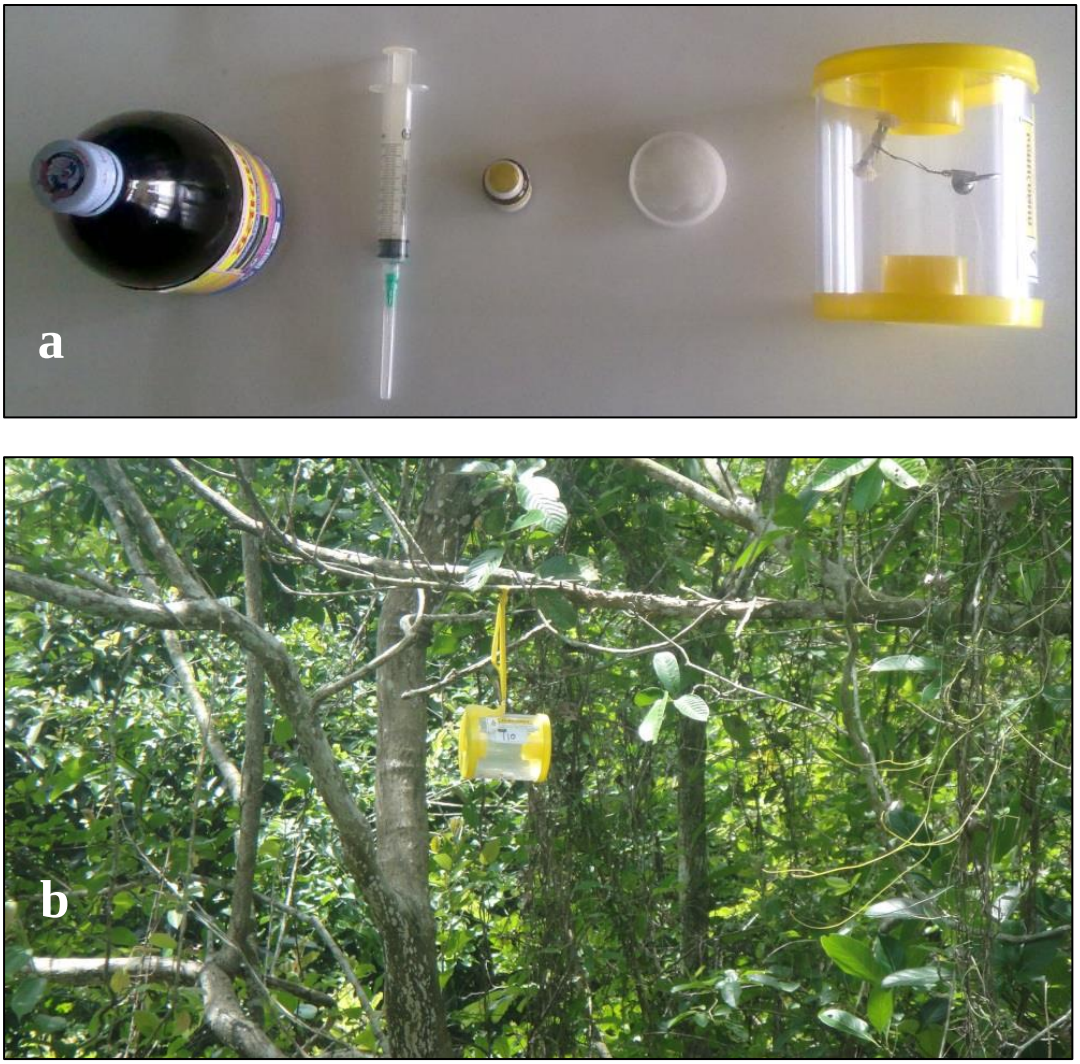


Figure 2. Steiner trap (a) loading of trap (b) trap hanged in the field.

Figure 3. Ball trap (a) ball trap and torula yeast (b) trap hanged in the field.

Identification

The sampled specimens were sorted on the basis of morphological characters detailed by Hardy (1973, 1974) and White and Elson-Harris (1992) for genus *Bactrocera* and Drew and Lloyd (1989) and Drew and Hancock (1994) for *B. dorsalis* complex members with the aid of stereo microscope. Further confirmations were done by Assoc. Prof. Dr. Surakrai Permkam of the Faculty of Natural Resourses, Prince of Songkla University, Hat Yai. Voucher specimens were kept at the Entomology Research Unit of the Department of Biology and Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University, Hat Yai, Thailand.

Morphological characters used in identification of the species

General characters for Tephritidae and tribe Dacini

The listed characters adopted here were extracted from the key detailed in the work of White and Elson-Harries (1992) and Drew and Hancock (1994).

1. Vein Sc abruptly bent forward at nearly 90^0, weakened beyond the bend and ending at subcostal break; dorsal side of vein R_1 with setulae. Wing usually patterned by coloured bands. Wing cell cu*p* with an acute extension.

   …….TEPHRITIDAE

2. Cell cu*p* very narrow and it extension very long. The flagellomere (3^{rd} segment of antenna) is at least 3 times as long as broad. Wing pattern usually confined to a costal band and an anal streak.

   …….BACTROCERA and DACUS

3. Abdomen with all tergites separate.

   …….BACTROCERA

4. Abdomen with all tergites fused into a single plate, at most with smooth transverse lines marking the boundaries of each segment.

   …….DACUS

Characters for each Bactrocera species

5. Postpronotal lobes without well-developed setae. Aberrant individuals with a fine seta on each lobe do occur. Scutum with both lateral and medial yellow

strpes (vittae). Scutellum not bilobed, usually with 2 marginal setae (apical pair), rarely 4. Abdomen terga III in male with pectin.

…….*B. tau*

6. Wing with cross vein dm-cu covered by an infuscate area which is separate from other parts of the wing patterns. Wing with a costal band expanded into an apical spot and varies in length (4 - 7mm).

   …….*B. tau*

7. Scutum predominantly black with lateral yellow stripes (vittae); with facial spot, anterior supra alar setae, prescullar acrostichial setae, 2 scutellar setae. Abdomen varies in colour.

   ……*B. umbrosa*

8. Wing with a pattern made of three cross bands, each of which extends across the whole length of the wing, from costal band to hind margin. Wing length ranged from 5.5 – 8.1mm.

   ……*B. umbrosa*

9. Face with tranverse dark markings adjacent to the antennal furrows which usually join to form a line across the lower facial margin. Scutum predominantly black with lateral yellow stripes; with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae.

   ……*B. correcta*

10. Wing without a complete costal band; area of cell br immediately above cell bm without any microtrichia and with variable lengths (4.3 – 6.0 mm).

    ……*B. correcta*

11. Postpronotal lobe with anterior third largely black, posterior 2/3 largely yellow. Scutum with lateral yellow stripes; with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae. Characteristic wing pattern which varies in length (5 – 6 mm). Scutellum often with a triangular black mark. Male with pectin on tergite III.

    …….*B. albistrigata*

12. Thorax and abdomen pale orange-brown to red-brown. Scutum with lateral yellow stripes; with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae. Wing length varies (5.2 – 6.1).

    ……*B. zonata*

13. Facial spot present. Scutum predominantly black with lateral yellow stripes; with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae. Wing length varies (4.5 – 6.1 mm). Costal band distinctly expanded near the apex of cell R2+3 to form a spot which extends below vein R4+5. Abdomen predominantly red-brown; usually without any black markings, but sometimes with an indistinct T-shaped mark on tergite III-V and male with pectin on tergite III.

    ……*B. latifrons*

14. An orange to black species with facial spot; scutum with lateral yellow stripes; with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae. A typical dacine wing pattern which varies in length (4.9 – 6.7 mm). Abdominal tergites III-V without a distinct black T-shaped mark. Poorly defined narrow dark medial stripe and narrow dark markings across the base of tergite III forming a poorly defined T-shaped mark present in some individuals.

    ……..*B. musae*

15. Face of male entirely yellow without any markings (female has a brown or black line across the mouth opening). Scutum predominantly black with lateral and medial yellow stripes; with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae, rarely 4 in male. Wing length varies (4.8 – 5.9 mm). Abdominal tergite III of male without pectin.

    ……..*B. diversa*

16. Face of both sexes with a black line across mouth opening. Abdominal terga III of male with pectin. Scutum predominantly black with both lateral and medial yellow stripes; with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae. Wing with costal band expanded into an apical spot; length varies (4.4 – 6.5 mm).

    ……..*B. caudata*

17. Predominantly orange-brown species with facial spot. Wing with crossvein dm-cu covered by an infuscate area which is separate from other parts of the wing pattern. Scutellum with anterior supra alar setae, prescullar acrostichal setae, 2 scutellar setae, rarely 4. Scutum with both lateral and medial yellow stripes. Wing with characteristic pattern; length varies (4.2 – 7.1 mm). Tergite III of male with pectin.

    ……...*B. cucurbitae*

    Characters for B. dorsalis complex members

    Key 18 – 22 are common to all complex members.

18. Orbital setae black; 1 s.or, 2 i.or; lunule fuscous. Ocellar triangle black.
19. Scutum black except brown behind lateral postsutural vittae. Setae; *sc.* 2; *prsc.* 2; *ia*. 1; *p.sa.* 1; *a.sa.* 1; *mpl.* 1; *npl.* 2; *scp.* 4.
20. Lateral postsutural vittae parallel sided (narrow to broad) or sub parallel and broad
21. Lateral postsutural vittae narrowing distinctly posteriorly to end at or before intra alar setae
22. Presence of pectin on male abdominal tergum III. A pair of oval orange-brown shining spots on tergum V
23. Large dark spot on outer apical surfaces of for femora only. Abdominal terga III-V with a very narrow medial longitudinal fuscous line; narrow dark markings on anterolateral corners of terga IV and V. Narrow fuscous costal band confluent with R2+3 and ending between extremities of R4+5 and M, narrow fuscous and anal streak ending before wing margin; no dense aggregation of microtrichial around A1 + CuA2

    ……...*B. kandiensis*

24. Large dark spot on outer apical surfaces of for femora only. Abdominal terga III-V with a broader medial longitudinal dark bands. Very narrow fuscous costal band confluent with R2+3 and ending beyong extremity of R4+5; narrow fuscous anal streak contained within lobe of posterior cubital cell; dense aggregation of microtrichial around A1 + CuA2.

    ……...*B. caryeae*

25. Small dark spots on outer apical surfaces of fore femora and inner apical surface of mid and hind femora. Abdominal terga III-V orange-brown except for a narrow transverse black band across anterior margin of targum III, a moderately broad medial longitudinal black band over all three terga and anterolateral corners of terga IV and V black. Narrow dark fuscous costal band confluent with R2+3 and widening uniformly across apex of R4+5, narrow fuscous and anal streak ending before wing margin; dense aggregation of microtrichial around A1 + CuA2. Wing length 7.0 mm.

    ……..*B. malaysiensis*

26. Pleural area immediately below postpronotal lobe brown to fuscous. Abdominal terga III-V orange-brown except for a narrow transverse black band across anterior margin of targum III widening to cover lateral margins, anterolateral corner of tergum IV dark fuscous to black and anterolateral corner of tergum V dark fuscous, a medial longitudinal black band of medium width covering all three terga. Narrow fuscous costal band confluent with R2+3 and continuing narrowly around costal margin to end between extremities of R4+5 and M. Narrow fuscous anal streak ending before wing margin, no dense aggregation of microtrichial around A1 + CuA2. Wing length 6.2 mm.

    ……..*B. papayae*

27. Femora entirely fulvous except for a small oval dark fuscous spot on outer apical surfaces of fore femora, fore and mid tibiae fuscous and hind tibiae dark fuscous. Abdominal anterolateral corners of terga IV and V dark fuscous to black and a very broad medial longitudinal black band over all three targa. Narrow fuscous costal band confluent with R2+3 and continuing narrowly around costal margin to end between extremities of R4+5 and M. Narrow fuscous anal streak ending before wing margin, no dense aggregation of microtrichial around A1 + CuA2. Wing length 7.2 mm.

    ……..*B. neopropingua*

28. Femora entirely fulvous or with a small pale fuscous spot on outer apical surfaces of fore femora; fore and hind tibiae dark fuscous but mid tibiae dark

fuscous basally and fulvous apically. Abdominal terga III-V with a narrow medial longitudinal black band with two broad lateral longitudinal dark fuscous to black bands over all three terga which join over anterior margin of tergum III. Narrow fuscous costal band confluent with R2+3 and with a very slightly swelling around apex of R4+5, Narrow fuscous anal streak ending well before wing margin, no dense aggregation of microtrichial around A1 + CuA2. Wing length 5.5 mm.

…….*B. raiensis*

29. Femora entirely fulvous in male or with small dark fuscous spot on outer apical surfaces of fore femora in females, fore tibiae dark fuscous, mid tibiae fuscous basally and fulvous apically, hind tibiae dark fuscous to black, tarsi fulvous; mid tibiae each with an apical black spur. Abdominal terga III-V with triangular shaped dark anterolateral markings. Narrow fuscous costal band confluent with R2+3 and ending in a very slight swelling just beyond extremity of the vein, narrow pale fuscous anal streak ending before wing margin, no dense aggregation of microtrichial around A1 + CuA2. Wing length 5.0 mm.

    …….*B. irvingiae*

30. Femora fulvous with black on outer apical ½ of fore femora and small black areas on innenr apical surfaces of mid and hind femora, all tibiae dark fuscous, tarsi fulvous; mid tibiae each with an apical black spur. Abdominal terga III-V with black band across anterior margin of tergum III which extend laterally to cover 2/3 of tergum, anterolateral corners of terga IV and V dark fuscous, a moderately broad medial longitudinal black band over all three terga. Costal band broadening slightly beyond apex of R2+3 to end between extremities of R4+5 and M, narrow fuscous anal streak ending at wing margin, dense aggregation of microtrichial around A1 + CuA2. Wing length 5.5 mm.

    …….*B. lombokensis*

31. Femora with apical ¾ of fore, apical 1/3 mid and apical 2/5 hind shining black; tibiae all dark fuscous to black; facial spot very large. Terga III-V with a broad transverse black band across anterior ½ of tergum III and a broad

medial and two broad lateral longitudinal black bands over all three terga. Narrow fuscous costal band just overlapping R2+3 and ending between extremities of R4+5 and M1+2 with very slight expansion across apex of R4+5, narrow fuscous anal streak ending at wing margin; dense aggregation of microtrichial around A1 + CuA2. Wing length 6.1 mm.

…….*B. atrifemur*

32. Dark spots on outer surfaces of fore and inter surfaces of mid and hind femora; tibiae pale fuscous. Narrow transverse black band across anterior margin of tergum III and expanding to cover lateral margin, anterolateral corners of terga IV and V dark fuscous, a medial longitudinal black band over terga III-V or terga III and IV. Narrow dark fuscous costal band just overlapping R2+3 as a pale fuscous pattern and expanding slightly across apex of R4+5, narrow fuscous anal streak ending at wing margin; dense aggregation of microtrichial around A1 + CuA2. Wing length 6.7 mm.

……..*B. bimaculata*

33. Dark spots on outer apical surfaces of fore and mid femora. Abdominal rectangular black marking in anterolateral corner of tergum IV and a triangular dark fuscous to black marking anterolaterally in tergum V. Narrow fuscous costal band almost reaching R2+3 (paler below R2+3) and widening as it crosses apex of R4+5, narrow fuscous anal streak ending before wing margin, no dense aggregation of microtrichial around A1 + CuA2. Wing length 6.8 mm.

……..*B. quasipropinqua*

34. Hind legs missing in type; femora fulvous with dark fuscous spots on outer apical surfaces of fore and inner apical surfaces of mid and hind femora, fore tibiae fuscous, mid tibiae fulvous tending fuscous basally, hind tibiae dark fuscous, tarsi fulvous; mid tibiae each with an apical spur. Tergum II with an oval black spot centrally and narrow black lateral margins. Costal band overlapping R2+3 and widening across apex of R4+5; narrow fuscous anal streak ending before wing margin, no dense aggregation of microtrichial

around A1 + CuA2. Wing length 7.6 mm. lateral postsutural vittae ending before intra alar setae.

…….....*B. holtmanni*

Data analysis

Alpha diversity (species richness or within habitat) and Beta diversity (differentiation diversity or between habitats diversity) at the different locations and on guava orchards and around the guava orchards were analyzed and compared to determine which site is more in species or diverse. Qualitative Sorenson similarity index were calculated to determine extent of similarity among sites by using the formulae described by Magurran (2004).

$$QS = 2C / A + B$$

Where; QS = Quotient of similarity (0-1), C = Number of species shared by the two sites and A + B = Sum of species in site A and B.

The traps were also compared by pooling the data for each trap type together. Only the presence and absence data are used, since the differences in attractiveness of the different lures used do not allow the use of quantitative data. Mean number of individuals / traps / week was also determined by dividing total catches by the length of sampling and by the number of traps deployed, respectively. The formula thus was used;

$$F.T.D = F / (TxD)$$

Where; F = Total number of flies, T = Number of serviced traps and, D = average number of days traps were exposed in the field.

Shannon Wiener index, evenness and fishers alpha were also calculated for appropriate comparisons. Analysis was conducted on DIVERSITY software.

Results

Alpha diversity

Species composition and abundance

The sum of 226,658 fly specimens was collected during the field sampling period of one year at all sites. From the total specimens collected, 75.6973% and 22.7735% represents *B. papayae* and *B. carambolae*, respectively (Table 1.). These two species constituted 98.4708%. Others species represent very low percentage of 1.5292%. The Ban Koyai site revealed the highest species number of 30. The Ban Bala present 19 species, while 10 species each were observed at Khuan Mao and Ban Bakham sites. The total species number for all sites was 31 species (APPENDIX A. 1-31). All the species collected so far belong majorly to the genus *Bactrocera* and two species from the genus *Dacus* (APPENDIX A. 32-33). Among the 31 species of *Bactrocera* collected at all sites, 20 species belong to the *Bactrocera dorsalis* complex (*) and 11 species were other *Bactrocera*. Out of the 31 species, 8 were common to all sites, these were; *B. albistrigata*, *B. carambolae*, *B. cucurbitae*, *B. irvingiae*, *B. osbeckiae*, *B. papayae*, *B. propingua*, *B. umbrosa*. But *B. kinabalu* was only found at Ban Bala and likewise, *B.* sp1 was common to Ban Koyai site only.

Table 1. Species and population trapped among the four sites in southern Thailand.

Species	Narathiwat	Songkhla	Trang	Surat thani
B. albistrigata	2	10	1	1
*B. atrifemur**	0	5	0	0
*B. bimaculata**	0	27	0	0
*B. caramabolae**	3091	38552	7196	2778
*B. caryae**	0	3	0	0
B. caudatus	3	349	0	0
B. correcta	5	204	0	0
B. cucurbitae	2	16	7	2
B. diversa	8	460	0	0
*B. floresiae**	1	5	0	0
*B. holtimanni**	10	43	0	0
*B. irvingiae**	7	66	23	10
*B. kandiensis**	0	3	0	0
*B. kinabalu**	1	0	0	0
B. latifrons	1	8	1	0
*B. lombokensis**	4	15	0	0
*B. malaysiensis**	2	24	0	0
*B. melastomatos**	0	17	0	0
B. musae	0	5	2	2
*B. neocognata**	0	3	0	0
*B. neopropingua**	0	2	0	0
*B. osbeckiae**	13	78	33	21
*B. papayae**	7936	132596	20034	11005
*B. philippinensis**	0	32	0	0
*B. propingua**	2	7	2	1
*B. quasipropingua**	0	8	0	0
*B. raiensis**	1	2	0	0
B. tau	1	6	0	1
B. umbrosa	3	1569	253	13
B. zonata	0	60	0	0
B. Sp1	0	1	0	0
Total individual / site	11093	174176	27552	13834
Species richness / site	19	30	10	10
Shannon-Wiener index	0.64094	0.52582	0.64362	0.53063
Evenness	0.18665	0.15312	0.18743	0.15452
Fishers Alpha	2.3074	4.0803	1.4075	1.3673
Mean of individuals / traps / week	28.89	453.58	71.75	36.03

**B. dorsalis* complex members

Apart from the *Dacus* spp. which is not within the scope of this present work, thirteen new records were observed all belonging to the *B. dorsalis* complex previously revised by Drew and Hancock (1994). Except for a taxon tagged *B.* sp1 whose identity is still unclear, all other *Bactrocera* have been previously identified and described by other tephritid scientists. The total number of flies collected belonging to the new records was 188 specimens from the four sites. Out of this, *B. holtimanni* was the highest with 28.1915%, followed by *B. philippinensis* with 17.0213% and *B. bimaculata* 14.3617% (Table 2).

Table 2. New records of *B. dorsalis* complex in southern Thailand.

Species	Narathiwat	Songkhla	Trang	Surat thani
B. atrifemur	0	5	0	0
B. bimaculata	0	27	0	0
B. caryae	0	3	0	0
B. floresiae	1	5	0	0
B. holtimanni	10	43	0	0
B. kandiensis	0	3	0	0
B. kinabalu	1	0	0	0
B. lombokensis	4	15	0	0
B. malaysiensis	2	24	0	0
B. neocognata	0	3	0	0
B. neopropingua	0	2	0	0
B. philippinensis	0	32	0	0
B. quasipropingua	0	8	0	0
B. Sp1	0	1	0	0
Total	18	171	0	0
Species richness	5	13	0	0

Only the sites in Narathiwat and Songkhla provinces were found to have shared these new records in the order of 5 and 13 species, respectively. Only four species among the new records were common to both sites, these were; *B. floresiae, B. holtimanni, B. lombokensis* and *B. malaysiensis*.

In general, 14 species were trapped on guava orchards (Table 3), these were as follow; *B. albistrigata, B. carambolae, B. caudata, B. correcta, B. cucurbitae, B. diversa, B. holtimanni, B. latifrons, B. irvingiae, B. papayae, B. philippinensis, B. tau, B. umbrosa,* and *B. zonata.* But 22 species were trapped from around the guava orchards. This phenomena of less species on guava orchards and lot around the guava orchards was common to all sites.

Table 3. Population of *Bactrocera* species caught on and around guava orchards.

Species	NtGO	NtAGO	SoGO	SoAGO	TrGO	TrAGO	SuGO	SuAGO
B. albistrigata	0	2	10	0	1	0	0	1
*B. atrifemur**	0	0	0	5	0	0	0	0
*B. bimaculata**	0	0	0	27	0	0	0	0
*B. caramabolae**	1098	1993	8197	30355	2630	4566	1069	1709
*B. caryae**	0	0	0	3	0	0	0	0
B. caudata	3	0	349	0	0	0	0	0
B. correcta	5	0	204	0	0	0	0	0
B. cucurbitae	2	0	16	0	7	0	2	0
B. diversa	8	0	460	0	0	0	0	0
*B. floresiae**	0	1	0	5	0	0	0	0
*B. holtimanni**	0	10	23	20	0	0	0	0
*B. irvingiae**	0	7	22	44	0	23	0	10
*B. kandiensis**	0	0	0	3	0	0	0	0
*B. kinabalu**	0	1	0	0	0	0	0	0
B. latifrons	1	0	8	0	1	0	0	0
*B. lombokensis**	0	4	0	15	0	0	0	0
*B. malaysiensis**	0	2	0	24	0	0	0	0
*B. melastomatos**	0	0	0	17	0	0	0	0
B. musae	0	0	0	5	0	2	0	2
*B. neocognata**	0	0	0	3	0	0	0	0
*B. neopropingua**	0	0	0	2	0	0	0	0
*B. osbeckiae**	0	13	0	78	0	33	0	21
*B. papayae**	2957	4979	49634	82962	8643	11391	3787	7218

Species	**NtGO**	**NtAG**	**SoGO**	**SoAG**	**TrGO**	**TrAG**	**SuGO**	**SuAG**
*B. philippinensis**	0	0	19	13	0	0	0	0
*B. propingua**	0	2	0	7	0	2	0	1
*B. quasipropingua**	0	0	0	8	0	0	0	0
*B. raiensis**	0	1	0	2	0	0	0	0
B. tau	1	0	6	0	0	0	1	0
B. umbrosa	2	1	100	1469	33	220	4	9
B. zonata	0	0	60	0	0	0	0	0
B. Sp 1	0	0	0	1	0	0	0	0
Total Individual / site	4077	7016	59108	115068	11315	16237	4863	8971
Species richness	9	13	14	22	6	7	5	8
Shannon Wiener index	0.62358	0.64508	0.54053	0.8149	0.56817	0.68782	0.53856	0.52339
Evenness	0.18159	0.18785	0.1574	0.2373	0.16545	0.2003	0.15683	0.15242
Fishers Alpha	1.1337	1.5966	0.59893	2.8049	0.78441	0.88849	0.47715	0.67914
Mean of individuals / traps/ week	10.62	18.27	153.93	299.66	29.47	42.28	12.66	23.36

**B. dorsalis* complex members

NtGO: Narathiwat Guava Orchard, NtAG: Narathiwat Around Guava Orchard, SoGO: Songkhla Guava Orchard,

SoAG: Songkhla Around Guava Orchard, TrGO: Trang Guava Orchard, TrAG: Trang Around Guava Orchard,

SuGO: Surat Thani Guava Orchard and, SuAG: Surat Thani Around Guava Orchard

Beta diversity

Qualitative Sorenson Similarity Index (QS) for this study (Table 4) revealed high similarity between Trang and Surathani sites. Also high similarity was observed between Narathiwat and Songkhla sites. Except for low similarity observed between Narathiwat and Trang sites, all other comparisons revealed medium similarities.

Table 4. Diversity indices of the fruit fly species at different agro-forested location in southern Thailand.

Site	Trang	Surathani	Narathiwat
Songkhla	0.500	0.500	0.735
Trang	-	0.900	0.462
Surathani	-	-	0.513

QS Indices

Attractant response

Methyl eugenol and torula yeast were they two para-pheromones used as attractants for this study. Though methyl eugenol was known for its specificity and limited species attraction, but it was revealed from this study that it attracted more species of *Bactrocera* fruit flies than the torula yeast which has broad spectrum of attracting more species (Table 5). This scenario was more pronounced in Narathiwat and Songkhla where 19 and 26 species were attracted by methyl eugenol and 3 and 7 species were attracted by torula yeast, respectively. Methyl eugenol attracted mostly the *B. dorsalis* complex members while torula yeast attracted more of the cucurbit species (*B. cucurbitae*, *B. caudatus*, *B. tau* etc) and very few individuals of *B. carambolae* and *B. papayae* as well as other *Dacus* species and some bamboo shoot genus outside the scope of this study.

Table 5. Response of fruit fly species to attractants.

Species	NT/ME	NT/TY	SG/ME	SG/TY	TR/ME	TR/TY	ST/ME	ST/TY
B. albistrigata	2	0	0	10	0	1	1	0
B. atrifemur	0	0	5	0	0	0	0	0
B. bimaculata	0	0	27	0	0	0	0	0
B. caramabolae	2526	565	20999	17553	6797	399	2290	488
B. caryae	0	0	3	0	0	0	0	0
B. caudatus	3	0	224	125	0	0	0	0
B. correcta	5	0	204	0	0	0	0	0
B. cucurbitae	2	0	0	16	0	7	0	2
B. diversa	8	0	460	0	0	0	0	0
B. floresiae	1	0	5	0	0	0	0	0
B. holtimanni	10	0	43	0	0	0	0	0
B. irvingiae	7	0	66	0	23	0	10	0
B. kandiensis	0	0	3	0	0	0	0	0
B. kinabalu	1	0	0	0	0	0	0	0
B. latifrons	1	0	0	8	0	1	0	0
B. lombokensis	4	0	15	0	0	0	0	0
B. malaysiensis	2	0	24	0	0	0	0	0
B. melastomatos	0	0	17	0	0	0	0	0
B. musae	0	0	5	0	2	0	2	0
B. neocognata	0	0	3	0	0	0	0	0
B. neopropingua	0	0	2	0	0	0	0	0
B. osbeckiae	13	0	78	0	33	0	21	0
B. papayae	7053	883	89071	43525	16100	3934	9592	1413
B. philippinensis	0	0	32	0	0	0	0	0
B. propingua	2	0	7	0	2	0	1	0
B. quasipropingua	0	0	8	0	0	0	0	0
B. raiensis	1	0	2	0	0	0	0	0
B. tau	0	1	0	6	0	0	0	1
B. umbrosa	3	0	1569	0	237	16	11	2
B. zonata	0	0	60	0	0	0	0	0
B. Sp1	0	0	1	0	0	0	0	0
Total	9644	1449	112933	61243	23194	4358	11928	1906
Species richness	18	3	26	7	7	6	8	5
Mean of individuals / trap/ week	25.11	3.77	294.1	159.49	60.4	11.35	31.06	4.96

*ME=Methyl eugenol, TY=Torula yeast, NT=Narathiwat, SG=Songkhla and ST=Surathani

Discussion

Alpha diversity

The *Bactrocera* Macquart contains over 500 described species of fruit flies. It is the most predominant genus of fruit fly in the Asia and Pacific regions (Drew, 1989; 2004). Within this genus, the *B. dorsalis* complex contained 75 species which is a monophyletic group of species of relatively recent evolutionary origin (Kroch *et al*., 2012). From the present study, eight species were found to be common to all sites of which five of them belong to the *B. dorsalis* complex. *B. carambolae* and *B. papayae* were found to be the most abundant and predominating at all agro-forested locations in southern Thailand. Though classified as sympatric sibling species, but their relatedness was recently distinguished (Boykin *et al*., 2013). These species were reported by several researchers (Drew and Hancock, 1994; Clarke *et al*., 2001) to have predominated over other species assuming a notorious status posing high threat to fleshy fruits. Although the two species were prevalence at all locations, *B. papayae* was more predominating and abundant at all locations. The occurrence of these two species can be attributed to having wide range of host plants among wild and cultivated species. This was evidenced from some tephritid workers (Drew and Hancock, 1994; Yong, 1994; Ranganath and Veenakumari, 1995; Allwood *et al*., 1999) whose works had resulted into 75 and 193 hosts for *B. carambolae* and *B. papayae*, respectively. Other members of the *B. dorsalis* complex common to all sites were *B.irvingiae*, *B. osbeckiae* and *B. propingua*. The remaining fifteen were recorded in 1 – 3 location(s). These were relatively less in number, may be due to fewer available hosts, less colonization ability and their phytophagous status (Diaz-Fleischer *et al*., 1999; Aluja and Mangan, 2008). *B. umbrosa* was common to all locations and it was the third most abundant species after *B. carambolae* and *B. papayae*. It was not surprising to record this species at all locations as it is not a pest of guava. But it got attracted to methyl eugenol (White and Elson-Harris, 1992), also their hosts (Bread fruit and jack fruit) are widely cultivated at all locations. Though in less number, *B. albistrigata* were also recorded at all locations within guava orchards only as they have affinity for fruit plants in the family Myrtaceae and rarely respond to methyl

eugenol. *B. cucurbitae* was also common to all locations. This is an oligophagous species recorded on cucurbitae, there occurrence on guava orchards was due to the presence of their hosts (cucumber, bitter guards etc) on and around the orchards.

Other species trapped at 1 - 3 locations of significant pest status were *B. diversa*, *B. caudatus* and *B. correcta*. Apart from the first two species which have their host range among the cucurbitae plants, *B. correcta* has been reported to be pest of guava. *B. diversa* though not a pest of guava, but have been reported to form winter swarms and congregate at the underside of guava leaves (Batra, 1964). The three species were trapped only from guava orchards inter-planted with the plants from cucurbitae family.

The other species found were usually present in very low numbers, often represented by 1-5 specimens (e.g, *B. atrifemur*, *B. caryae*, *B. floresiae*, *B. kandiensis*, *B. kinabalu*, *B. neocognata*, *B. neopropingua*, *B. raiensis* and *B.* sp1). All of them were trapped among the guava orchard surrounding vegetation. These species might be of low economic importance due to fewer hosts and or newly introduced to such areas.

The new records were fourteen species of which thirteen belong to the *B. dorsalis* complex and *B.* sp1 which could not be described due to it representation by single specimen. These species were very few in numbers of individuals trapped. All of them except *B.* sp1 were found to be introduced from adjacent countries. This phenomenon is similar to the report of Chua (2002) that South East Asia (Thailand, Penisular Malaysia, Indonesia and Borneo Island consisting of East Malaysia, Brunei Darussalam, and Kalimantan) appears to share many fruit fly species. Hence cross infestation is common to most of these countries. But there are some species too from as far as India and Sri Lanka (*B. caryae* and *B. kandiensis*) and Philippine (*B. neopropingua, B. philippinensis* and *B. quasipropingua*) which were found in southern Thailand in this present study.

Songkhla site (Ban Koyai / Ban Phru) was the most diverse with reference to species richness and available hosts. Thirty species were observed. Related to this site is the Ban Bala in Narathiwat which recorded 19 species. This site is rich in wild and some economically important host fruits. The Trang (Khuan Mao)

and Surathani (Ban Thakham) sites were not different in the number of species recorded and less diverse compared to the other two sites mentioned before. This may be due to the fact that, these sites were relatively less in density of host plants. Therefore, species richness and abundance is directly proportional to hosts availability.

Beta Diversity

High fauna similarities existed between the sites in Trang and Surathani, and between Narathiwat and Songkhla. Other similarity comparisons fall in low-medium status. This was most likely caused by the different range of fruits at each agro-forested location and most significantly the impact of weather such as temperature, rainfall and relative humidity. The Ban Koyai agro-forest location in Songkhla had 30 species and the richest in species, richer than Ban Bala in Narathiwat by 12 species and richer than Khuan Mao in Trang and Ban Thakham in Surathani by 21 species. Out of the 14 new records of species, 13 were observed at Ban Koyai and 5 at Ban Bala agro-forest locations. Khuan Mao and Ban Thakham agro-forest location had none. The disparity may be due to weekly sampling at Ban Koyai compared to monthly sampling at other locations. The distribution of species therefore, should be referenced with caution until more intensive sampling is carried out in other areas. It is also worth mentioning that Ban Koyai and Ban Bala present a more conducive environment for fruit fly to thrive. These agro-forest locations, apart from heavy rubber plant cover which present a cool environment and subsequently moderate temperature; there are several varieties of fruit producing plants coupled with reasonable distance between guava orchard and human settlement. But Khuan Mao and Ban Thakham agro-forest locations do not have such vegetation covers and are relatively close to human settlement. Out of the 8 common species, *B. carambolae* and *B. papayae* were the most abundant in reasonable number above economic threshold. These notorious species have significantly dominated over other species causing damages to fleshy fruits in southern Thailand.

Attractants response

The attractants correspond to published records for different species. Methyl eugenol is known to be very potent and attract some species of the genus *Bactrocera* especially the *B. dorsalis* complex members (Drew and Hancock, 1994). The *B. carambolae* and *B. papayae* have been long known to respond immensely to methyl eugenol. Hence, it is not surprising having them in large number at all locations. The torula yeast is known to attract fly from sub-family of tephritidae (Blepharoneurinae, Dacinae, Phytalmiinae, Tachiniscinae, Tephritinae and Trypetinae). But because the scope of this present work is limited to dacinae (genus *Bactrocera*) makes it less potent. Furthermore, torula yeast is actually an attractant that do not operate as para-pheromones but as food substances required for proper development of eggs (attract mostly female and any male attracted are accidental). Hence, more general than the specific parapheromones attractants. There captures reflect more the proportional presence of different fruit flies in particular environment. Also the radius of attraction is less compared to para-pheromones and therefore presents better the fruit fly fauna immediately surrounding trap location, rather than a wide area as common to para-pheromones.

The Steiner traps captured large number of flies from all locations than the ball traps. But most cucurbit feeders (*B. cucurbitae*, *B. caudatus, B. tau* and *B. latifrons*) and *B. carambolae* and *B. papayae* were captured by the ball traps because the responded significantly to torula yeast than methyl eugenol. Accidental trapping was rarely recorded, only for a *B. latifrons* and some *B. cucurbitae* that were found in methyl eugenol trap which is very uncommon. However, this does not reflect a true parapheromone response.

Impact of *B. carambolae* and *B. papayae* on other fruit fly diversity

The present work revealed 31 species of the genus *Bactrocera* to be present in southern Thailand of which 14 were new records. Therefore, 17 species were present before now attacking fleshy fruits in this region. The relative abundance of other species seems to be affected by the presence of *B. carambolae* and *B. papayae*. It seems as if this two notorious species are outcompeting and displacing

many other species. This phenomenon has also been observed with *B. invadens* in Kenya (Mwatawala *et al.*, 2006b) and *B. tryoni* in Australia (Raghu *et al*., 2000). The two species have been found to co-subsist on guava fruits which lead to intergeneric competition (Duyck *et al*., 2004) that might have limited other species (*B. correcta*) to other hosts. The abiotic factors at various environments may be well adapted to by these species as they subsist very well over a wide range of temperature. Other factor could be the nature of various agro-forest locations and their life history strategies. It seems the *B. papayae* multiply rapidly and subsequently developed the ability to colonise new areas faster than other species. Conclusively, *B. carambolae* and *B. papayae* should be considered as a serious pest that could threaten the growth of horticultural industry and have an immense impact on the fruit fly fauna of southern Thailand.

CHAPTER 3

POPULATION ECOLOGY OF *B. CARAMBOLAE* AND *B. PAPAYAE*

Introduction

Guava is one of the most common fruits in Thailand, appearing at all stalls and markets. It is an important source of income and also represents an important part of gastronomic culture for Thai people. The fruit is produced via small-scale farming and sometimes at the subsistence level. It is found intercropped among rubber plantations surrounded by little or no forest and sometimes grown side-by-side or intercropped with other major economic fruits such as rambutan (*Nephelium lappaceum* L.), durian (*Durio zibethinus* L.), jackfruit (*Artocarpus heterophyllus* Lam.), rose apple (*Syzygium samarangense* Merrill & Perry) and mangosteen (*Garcinia mangostana* L.).

Infestation by fruit flies (Diptera: Tephritidae) leads to economic losses for smallholder farmers as well as a reduced source of essential dietary components to the population (Mwatawala *et al*., 2009). Infestation leads to losses of up to 12–60% in mango, 40–90% in guava and 12–60% in papaya (Allwood and Leblanc, 1997). The preferred fruit developmental stage of female flies has been studied. Liquido *et al*. (1995) reported the mature stage of the Sharwil avocado to be more heavily infested by the Oriental fruit fly, *Bactrocera dorsalis* (Hendel). In contrast, Vayssières *et al*., (2005) reported that an increase in the population of *B. invadens* (Drew and Hancock) appeared to be directly linked to the ripening of different mango cultivars. In peninsular Thailand, the damage to fleshy fruits is caused primarily by a limited number of highly polyphagous species, mostly *B. dorsalis* complex members and few other *Bactrocera* species. Most prominent of these polyphagous species are *B. carambolae, B. papayae* and the cucurbit feeders *B. cucurbitae, B. umbrosa*, *B. correcta* and *B. tau* (Clarke *et al*., 2001). Of these, *B. carambolae* and *B. papayae* are classified as highly polyphagous species and are prevalent in peninsular Thailand and Malaysia (Drew and Hancock 1994; Clarke *et al*., 2001). Their polyphagous status has been confirmed by the total number of hosts

from which they were reared. In this region, 76 and 193 host species have been reported for *B. carambolae* and *B. papayae*, respectively. Amongst the listed hosts, guava, which is one of the most-consumed fruits in this region, was found to have yielded a significantly higher population of these flies compared to any other sampled host (Allwood *et al*., 1999; Clarke *et al*., 2001). Although both species have been reported to be prevalent in most Asian countries, *B. carambolae* has also been reported from French Guiana and Brazil. Before its eradication, *B. papayae* was also reported from northern Australia near Cairns (Drew and Romig, 1997; Pike and Corcoran, 1998). Both species have been found to be limited to tropical regions of the world, which is an indication of their adaptation to a tropical climate rather than any other type of climate, as evidenced from their occurrence pattern. Furthermore, one of their complex members was first reported in Kenya (Lux *et al*., 2003) but has spread to several African countries (Drew *et al*., 2005). Therefore, with their wide host range and tolerance for tropical climate conditions, these species could be highly invasive and notorious if accidentally introduced to other tropical regions.

A recent study by Abuja *et al*. (2012) revealed that both local (temperature and rainfall) and global climate variations have been reported to be responsible for the detected differences among fruit fly species and locations. Similarly, Bale *et al*. (2002) stated that temperature is the dominant abiotic factor that directly affects the development, survival, range and abundance of herbivorous insects. Tephritid distribution and abundance are notably dependent on several abiotic factors (e.g., temperature, relative humidity, and rainfall) and several biotic factors (e.g., host plants and natural enemies) (Vayssières *et al*., 2008).

There are few ecological studies on fruit flies in Thailand, and Clarke *et al*. (2001) covered seven species of *Bactrocera* in Thailand and peninsular Malaysia with no consideration of specific fruits and with little or no statistical application, hypothesis or experimental design in mind. The seasonality, distribution and abundance of other fruit fly species have been studied in other parts of the world (Vargas *et al*., 1983, 1989, 1990; Harris *et al*., 1986; Raghu *et al*., 2000; Mwatawala *et al*., 2006b; Esculdero-Colomar *et al*., 2008). In peninsular Thailand, guava is available in all seasons, highly consumed and suffers a high rate of infestation from fruit flies. Therefore, it is pertinent to study the ecology of fruit flies for this important

fruit. This paper presents the first results of trapping these flies in guava orchards and surrounding areas in peninsular Thailand. The aim of this study was to compare the seasonal abundance and pattern of distribution of *B. carambolae* and *B. papayae* in guava orchards and their surroundings and to determine the most suitable guava developmental stage for their development and survival. All of this was aimed towards generating the specific information necessary for the development of suitable control measures to reduce the damage caused by these notorious pests.

Materials and methods

Study areas

This study was carried out in Songkhla province of Southern Thailand which lies within latitude 7° 2' 56.7779"N and longitude 100° 28' 11.8945"E. This province is situated in the tropical rainforest. The rainfall distribution pattern was unimodal and covers 8 months (May-December). From the prevailing weather factors for the study period, relative humidity ranged from 63.75 – 89.00% and temperature ranged from 24.55 – 30.38^{o}C for the period of the study, respectively. Four guava orchards were selected from two environments (Agro-forested areas and town). The agro-forest study sites were Ban Koyai (BK) and Ban Phru (BP) rural settlement areas. While town study sites were Hat Yai Nai (HN) and Prince of Songkla University (PSU), Hat Yai campus, respectively (Figure 1).

Orchards size ranged from 0.2 – 0.8 hectares. Apart from the PSU orchard that was planted with local cultivar of guava, other sites were solely improved cultivar. No chemical were used at all the sites against fruit flies except fruit bagging which was common in all orchards planted with improved guava cultivar. The Agro-forested sites were within extended rubber (*Hevea brasiliensis* Arg.) plantations. But other fruits bearing plants to the radius of 3 km from the orchards were observed. The town orchards were also screened for other fruit bearing plants to the distance of 200 m. Common fruit bearing plants to all sites were; *A. heterophyllus*, *S. samarangense*, banana (*Musa* spp. L.), bitter bean (*Parkia speciosa* Hassk.), satol (*Sandoricum koetjape* Merr.), mango (*Mangifera indica* L.) and papaya (*Carica papaya* L.). Other fruit plants common to agro-forested sites were sapodilla (*Manilkara zapota* L.), Citrus (*Citrus sinensis* L.), Star fruit (*Averrhoa carambola* L.), *N. lappaceum*, *D. zibethinus*, *G. mangostana* and Langsat (*Lansium domesticum* Corrêa.). Malabar almond (*Terminalia catappa* L.) was only common to town orchards.

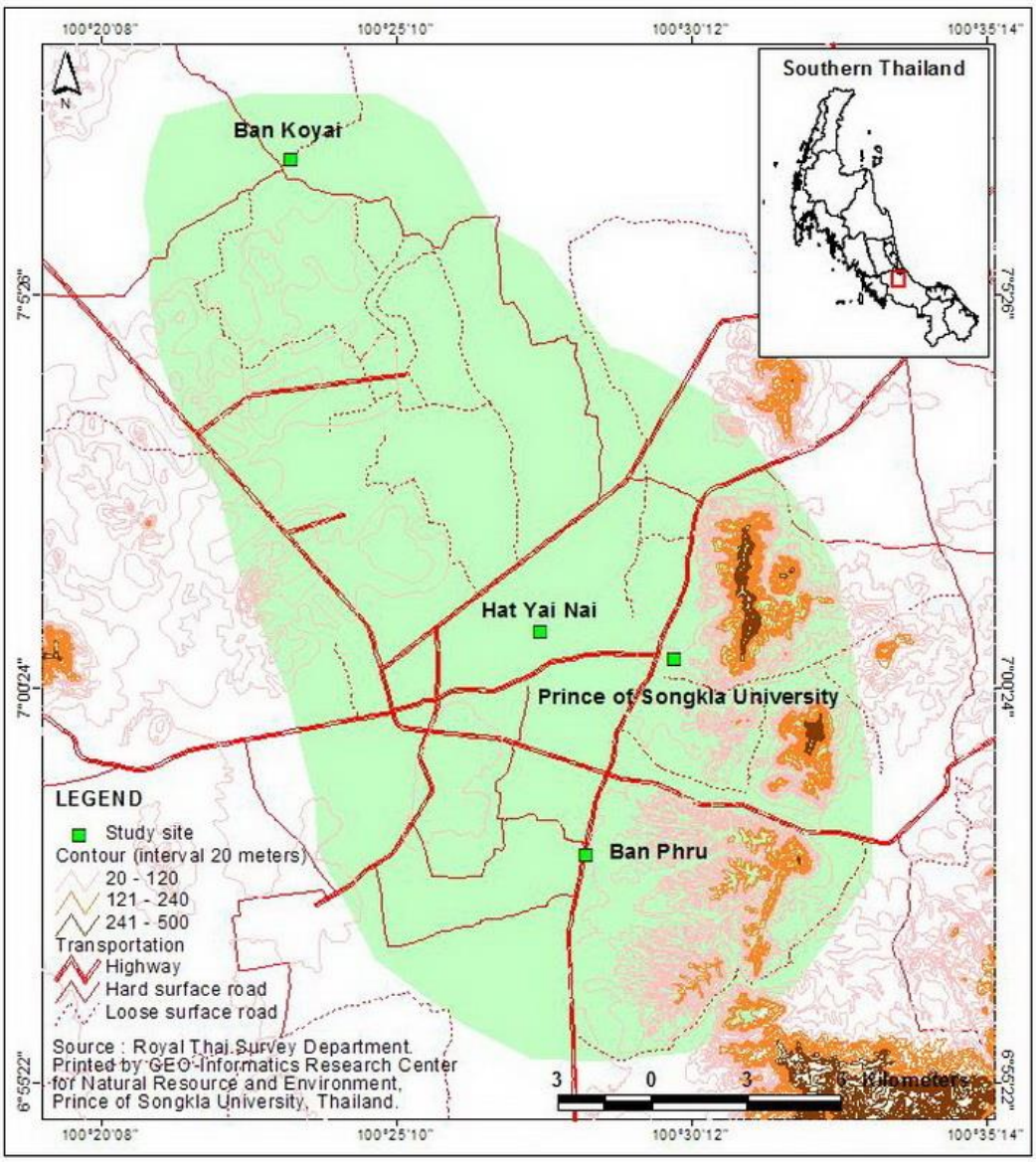


Figure 1. Locations of the study sites for the ecology of *B. carambolae* and *B. papayae*

Trap and trapping

Trapping was conducted for the period of 53 weeks consecutively. The trapping was focused emphatically on *B. carambolae* and *B. papayae* which were the major fruit infesting species. Steiner traps was used for fly trapping. Male of the species studied have been found to largely respond to a parapheromone, methyl eugenol (Benzene, 1,2,-dimethoxy-4-(2-propenyl) (Drew & Hancock, 1994). Therefore, the combination of Steiner trap and methyl eugenol was a suitable trapping method for these species. The adult male fly were trapped and killed solely with the mixture of methyl eugenol and pyrethriod (Changzhou Kangmei Chemical Industry, China) at the rate of 62.5 ml pyrethroid / 1000 ml Methyl Eugenol. One millilitre of the mixture was used to impreginate lid of 4.5 diameter packed with cotton wool.

Six Steiner traps were set up on each of the agro-forested guava orchards and six around each orchard. Three Steiner traps each were set up within town orchards, respectively. The radius of attraction of traps at all guava orchards ranged from 20 – 25 m. Traps were also set up at the radius of 500 – 1,500 m around the guava orchards at the agro-forested sites only. At each orchard, traps were hung permanently on guava trees. But around the agro-forested orchards, traps were set on rubber trees, sapodilla trees, banana trunk, bamboo trunk and bitter beans tree. The Steiner traps were suspended between the ranged of 1.3 - 1.5 m height in the guava orchards and 1.5 - 2.3 m height around the guava orchards depending on the height of vegetation that abound at each setting point. Traps were rotated anticlockwise at each inspection day. Fruit fly samples were collected from the traps on a weekly (7 days) basis at all sites. The lure + insecticide were recharged every 21 days and the cotton wools were changed at every 42 days (6 weeks).

Guava fruit sampling

Fruit sampling followed the method of Copeland *et al*. (2002), as described below. Guava fruits were sampled systematically from the trees on a monthly basis at all study sites. Sites were divided into homogeneous subgroups, and simple random sampling method was used to sample fruits within each subgroup (Papadiopoulos *et al*., 2003). A total of 20–50 guava fruits per month were sampled directly from the guava trees at each site. All sampled fruits were packed in a

Styrofoam box according to site of collection and transported to the laboratory. Fruits were then washed, dried and weighed, and maturity stages (ripe, mature and immature) were determined immediately by observing the fruits' colour (greenish = immature, green – brown = mature, and brown – yellow = ripe), size in diameters (2-4 cm = immature, >4-7 cm = mature, and >7cm = ripe) and hardness, was ascertained by exerting pressure with the fingers (very hard = immature, hard – relatively soft and not breakable under pressure from finger = mature, and soft, easily broken under finger pressure = ripe). Finally, the classifications were standardised with a digital fruit firmness tester (Penetrometer, Agriculture Solution LLC, Strong ME, USA) with an 11.1 mm plunger tip, and the results were recorded as kilogram-force (kgf). These were categorised as ripe when hardness was < 8.5±0.45 kgf, mature from 8.5-10.5±0.87 kgf and immature when hardness >10.5±0.55 kgf.

Other fruits sampling

Other fruits were picked randomly as available around the orchards. Fruits sampled include; rose apple, carambola fruit, sapodilla, mango, banana, pawpaw, satol and malabar almond. The fruiting season for species of plant present at different orchard sites were recorded based on observations performed during trapping periods in order to be able to relate the results of the trapping programme to the availability and phenology of the fruiting plants.

Treatment of Sampled fruits

All fruits were washed and dried. Each fruit was weighed and placed individually in Plexiglass boxes of 20 cm × 15 cm × 7 cm covered at the bottom with sterilised sawdust with a thickness of 1 cm. A hole with a diameter of 8.4 cm was cut into the lid of each box and screened with netting materials to provide ventilation. Rearing conditions were maintained at 25 ± 1°C, 75 ± 5% relative humidity (RH) and a photoperiod of L12:D12.

The boxes were checked after 7 days of culturing by sifting the sawdust to collect any pupated larvae. After 10 days, the fruit in each box was also cut open to ascertain that there were no more larvae left within the reared fruits. Collected pupae were then transferred into a Plexiglass box of 10 cm × 7.5 cm × 5.5 cm lined

with tissue paper until emergence. All pupae emerging from the fruit culture were kept until the adults emerged either as fruit fly or parasitoids. These adults were knockdown with the aid of ethyl acetate (Merck Chemicals, Darmstadt, Germany) and observed under stereo microscope for identification into species. All records of emerging fruit fly and their parasitoids were kept accordingly.

Records of fruit weight, number of pupae and emerged flies were made for every fruit stage. Fruit that had suffered any type of physical damage, possessed exit holes or appeared diseased was excluded from the rearing experiment.

Identification

Samples were identified on the basis of morphological characters detailed by Drew and Hancock (1994), Iwahashi (1999) and Iwaizumi (2004) with the aid of stereo microscope. The morphological characters were; presence or absence of black markings on the femur of each pairs of legs, black marking on the targite IV of abdomen and costal band width and depth around wing vein R_{2+3}. Further confirmations were done by Assoc. Prof. Dr. Surakrai Permkam of the Faculty of Natural Resourses, Prince of Songkla University, Hat Yai. Voucher specimens were deposited at the Entomology Research Unit of the Department of Biology, Prince of Songkla University, Hat Yai.

Data analysis

The data analysed for this period were from the cultured guava fruits, weather information and insect counts. Because the fruit samples were of varying sizes, quantitative data were expressed as infestation indices following Cowley *et al*. (1992) and Mwatawala *et al*. (2006b), with the number of pupae expressed per weight of fruits (unit of 1 kg). Percentages of adult emergence per guava developmental stage for each sampling site was compared between species within the guava orchards using paired t-test statistics, and damage to the sampled guava trees observed in the field was expressed as percentage ranges with the formula thus;

(NSF – HF) / NSF x 100.

Where; NSF = Number of Sampled Fruits,

HF = Healthy Fruits.

Weather information (temperature, rainfall and relative humidity) was collated on a daily basis, then summarised into weekly and monthly data. The average number of flies caught per week for 53 weeks for each species and site was used to determine the relationships between the fly capture rate and weather variables (temperature (Tem), rainfall (R/fall) and relative humidity (RH)) by using linear and multiple regression analysis, respectively.

Adult fly populations resulting from field monitoring were only compared intraspecifically as the species does respond to methyl eugenol differently. The means of the data generated for *B. carambolae* and *B. papayae* were computed by dividing the corresponding data for each species by the number of traps employed per site. These were pooled into three groups as follows: (1) urban orchards, (2) agro-forest orchards, and (3) surroundings of agro-forest orchards, respectively. Each species was then compared intraspecifically based on the pooled data and site regrouping.

All trapped *B. carambolae and B. papayae* counts were averaged per trap and per week and month separately for every studied site to compute the seasonality curves. Additionally, emerged flies from each guava developmental stage were counted. All fly counts were transformed using a log transformation (log[x+1]) to satisfy the assumption of homogeneity of variances. Standard ANOVA was then used to compare fly abundance intraspecifically and interspecifically. The Student-Newman-Keuls (SNK) test was adopted to compare means ($p<0.05$) (Sigmaplot 11.0).

Results

Seasonal abundance of *B. carambolae* and *B. papayae*

The total number of *B. carambolae* and *B. papayae* trapped in town and agro-forested sites were summarised in Table I.

Table 1. Total number of fruit fly trapped at four guava growing areas.

Environment	Trapping site	No of traps	*B. carambolae* male	*B. carambolae* female	*B. papayae* male	*B. papayae* female	Other tephritids
Urban	PSU	3	4,039	13	14,798	14	815
	Hat Yai Nai	3	2,544	24	17,284	42	895
Agro-forest	Ban Koyai						
	1. Guava orchard	6	2,643	14	11,254	49	162
	2. Around guava orchard	6	10,297	18	49,672	62	846
	Ban Phru						
	1. Guava orchard	6	3,407	4	14,666	22	284
	2. Around guava orchard	6	5,219	0	22,257	8	582

From table 1, the mean population of males of *B. carambolae* and *B. papayae* trapped in agro-forest and urban sites over 53 consecutive weeks were deduced and summarised in table 2 according to site of collections.

Table 2. Mean (±SD) of fruit fly per trap over the period of a year

			B. carambolae	*B. papayae*
Environment	Trapping site	No of traps	Male	Male
Urban	PSU	3	1346.33 ± 22.74**aB**	4932.67 ± 72.31**bA**
	Hat Yai Nai	3	848.00 ± 13.31**bB**	5762.33 ± 94.63**aA**
Agro-forest	Ban Koyai			
	1. Guava Orchard	6	440.50 ± 7.99**bB**	1875.67 ± 38.82**bA**
	2. Around Guava Orchard	6	1715.50 ± 41.46**aB**	8278.67 ± 157.08**aA**
	Ban Phru			
	1. Guava Orchard	6	567.83 ± 10.16**bB**	2444.33 ± 43.47**bA**
	2. Around Guava Orchard	6	869.83 ± 17.13**aB**	3709.50 ± 55.37**aA**

*Figures followed by different small letters in the same column for each species and site are significantly different while all figures followed by different capital letters in the same row for both species and site are significantly different ($p<0.005$) [APPENDIX B. 1-14]

At the urban sites comparisons among orchards and the each species revealed that *B. carambolae* population was significantly more at PSU than for those observed at HN ($F = 14.265$, d.f. = 23, $p < 0.001$). But *B. papayae* population was significantly more at HN than for those observed at PSU ($F = 19.144$, d.f. = 23, $p < 0.001$). Comparison between species revealed that *B. papayae* was significantly more in population than *B. carambolae* at the urban sites ($F = 30.663$, d.f. = 23, $p < 0.001$, for HN and $F = 25.633$, d.f. = 23, $p < 0.001$, for PSU, respectively) (Table 2).

Comparison within each agro-forest site revealed that *B. carambolae* trapped around the orchards were significantly more than those trapped on the orchards ($F = 9.641$, d.f .= 23, $p < 0.001$, for BK and $F = 6.238$, d.f .= 23, $p < 0.001$, for BP, respectively). Similarly, *B. papayae* had a similar trend of significantly more population around the orchards than on the orchards ($F = 22.334$, d.f. = 23, $p < 0.001$, for BK and $F = 8.787$, d.f. = 23, $p < 0.001$, for BP, respectively). The comparisons between *B. carambolae* and *B. papayae* at the BK agro-forest revealed that *B. papayae* was significantly more than *B. carambolae* both on the orchard and around the orchard ($F = 21.893$, d.f. = 23, $p < 0.001$on the orchard and $F = 21.529$, d.f. = 23, $p < 0.001$ around the orchard, respectively). Similarly, *B. papayae* was significantly more than *B. carambolae* on the orchard and around the orchard at BP ($F = 15.423$, d.f. = 23, $p < 0.001$ on the orchard and $F = 11.127$, d.f. = 23, $p < 0.001$ around the orchard, respectively) (Table 2).

The means of the data generated for *B. carambolae* and *B. papayae* were computed by dividing each corresponding data for each species by the number of traps employed. These were pooled into three as thus; urban orchards, agro-forest orchards and surroundings of agro-forest, respectively. Each species was then compared based on the pooled data and site regrouping accordingly. *B. carambolae* trapped in urban orchards and around agro-forest orchards were significantly more than those trapped on agro-forest orchards, but no significant difference was observed between urban orchards and surroundings of agro-forest orchards ($F = 12.405$, d.f. = 2, $p < 0.001$). Similarly, *B. papayae* trapped in urban orchards and around agro-forest orchards were significantly more than those trapped on agro-forest orchards, but no significant difference was observed between urban orchards and surroundings of agro-forest orchards ($F = 18.908$, d.f. = 2, $p < 0.001$). Comparison between the mean

populations of the two species revealed that *B. papayae* was significantly more in population than *B. carambolae* for the period of the study (paired t-test $p<0.005$).
At all study sites *B. papayae* population was larger than *B. carambolae* population. The agro-forest sites revealed that flies population was large around the orchards compared to a small population observed on the orchards. This may be due to flies returning to the nearby vegetation to roost after oviposition and feeding at the orchards. That could also be why the mean population of these fly was high for the urban orchards as there were no much vegetation nearby for them to roost on.

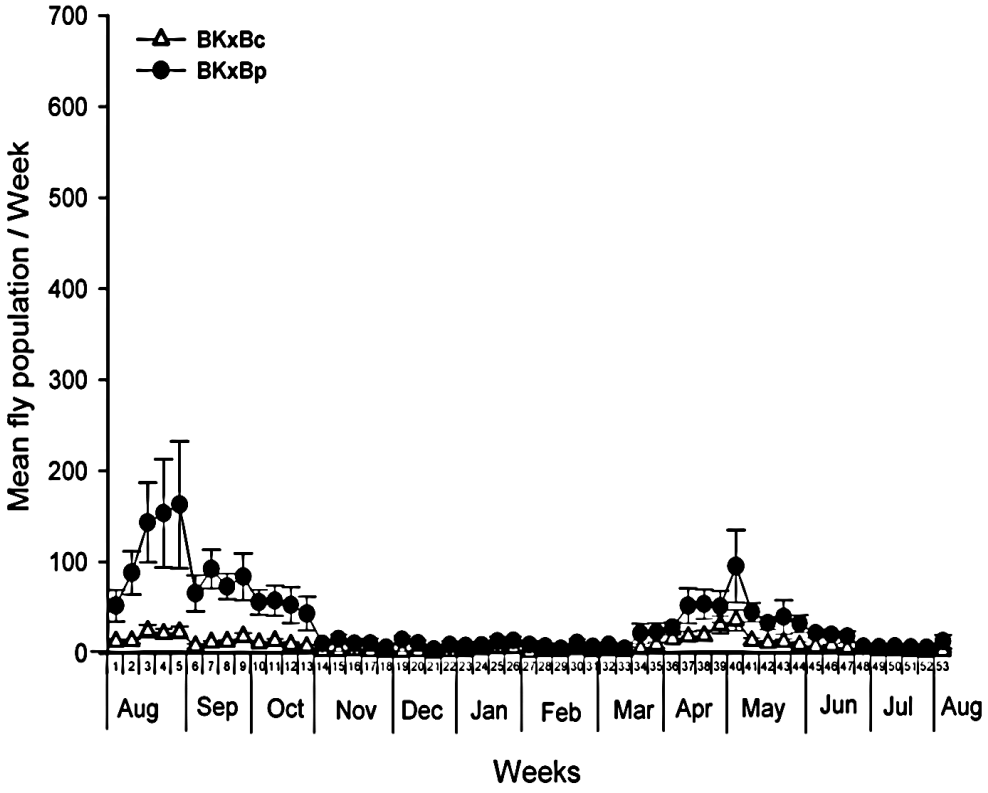
Flies abundance was also determined by comparing the population recovered from guava fruit rearing experiment. *B. papayae* was significantly more than *B. carambolae* at all sites (paired t-test $p<0.05$). Intraspecific comparison revealed that both flies were more significantly abundant at PSU than any other sites, but no significant difference were observed among other sites ($F = 3.583$, d.f. = 3, $p=0.02$, for *B. carambolae* and $F = 2.861$, d.f. = 3, $p=0.04$, for *B. papayae*). Pooled population of each species from the two environments (Agro-forest and urban) revealed no significant difference intraspecifically (paired t-test $p=0.52$ for *B. carambolae* and paired t-test $p=0.45$ for *B. papayae*).

Seasonal fluctuation of fly population

Consecutive trapping at all study sites on weekly basis for 53 weeks provided the seasonal abundance and distribution patterns for a full year cycle. Figures 2, 3, 4 and 5 depict the mean population of *B. carambolae* and *B. papayae* trapped per week and their corresponding temperature and rainfall for all sites. As a result of trap theft and flooding, the weekly records for weeks 23 and 24 at Ban Phru guava orchard were not available. Similarly, at Prince of Songkla University weeks 1 – 5 records of fly trapped were impaired. All trapping records were complete for other sites. The number of trapped flies fluctuated considerably, *B. carambolae* and *B. papayae* were available on and around the guava orchards at all sites throughout the year. This was confirmed by the weekly trapping programme for the year (Figures 2, 3, 4 and 5). Catches of both flies were recorded in all weeks, with *B. papayae* having larger number of individuals caught and *B. carambolae* had smaller number of individuals concurrently. This scenario was common to all sites.

Common pattern of abundance and distribution were observed on and around the guava orchards for all sites. It was observed that at each peak period, the density of *B. papayae* was always greater than that of *B. carambolae.* The first peak period was observed to fall in the range of weeks 1 – 9 (August – September) and then gradually declined from week 10 (October) through to week 34 (March). The second peak period falls in the range of weeks 35 – 45 (April – May) and further declined from weeks 45 – 53 (Figures 2. a1 – a2, 3. a3 - a4, 4. a5 and, 5. a6). This revealed a bimodal peak pattern of population distribution with the first peak corresponding with the months of August – September and second peak in the month of May. *B. carambolae* population though very low in density, but tend to follow the same pattern of distribution as was observed for *B. papayae*. All peaks periods corresponded with increase in temperature. But contrary was the case with rainfall data (Figures 2. b1, 3. b2, 4. b3 and, 5. b4).

a1


BKxBc
BKxBp
Mean fly population / Week
0
100
200
300
400
500
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700
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Sep
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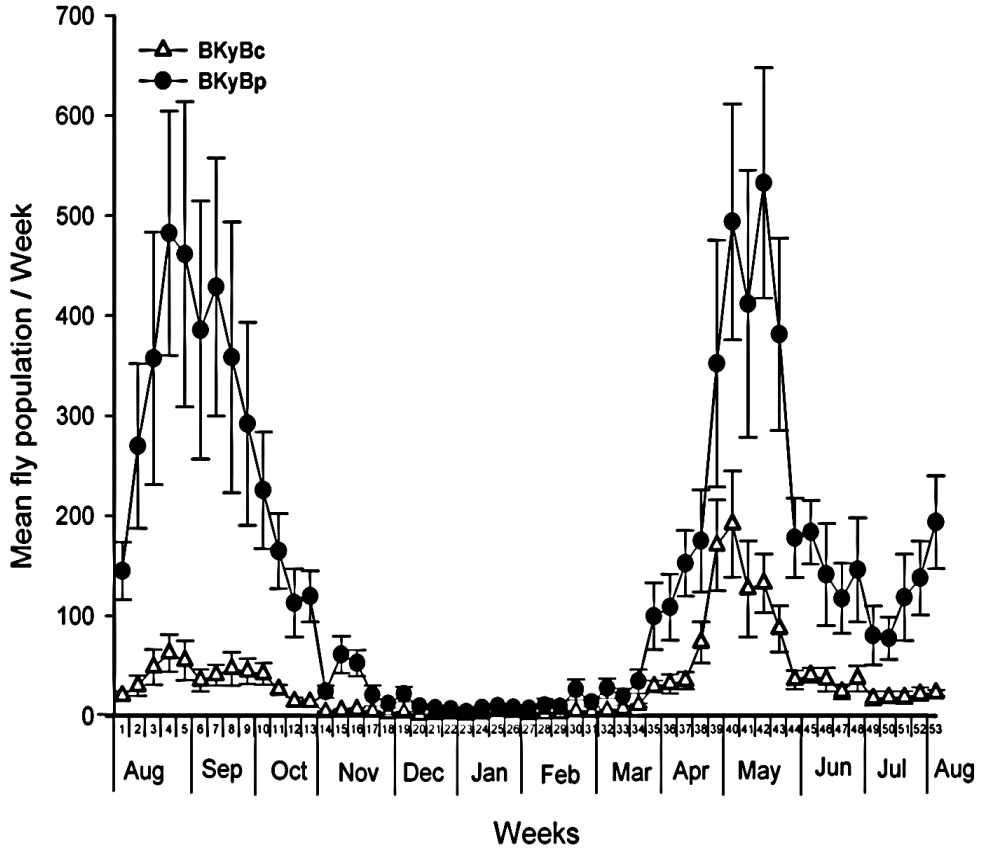
Weeks

a2


BKyBc
BKyBp
Mean fly population / Week
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100
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300
400
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700
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Weeks

b1

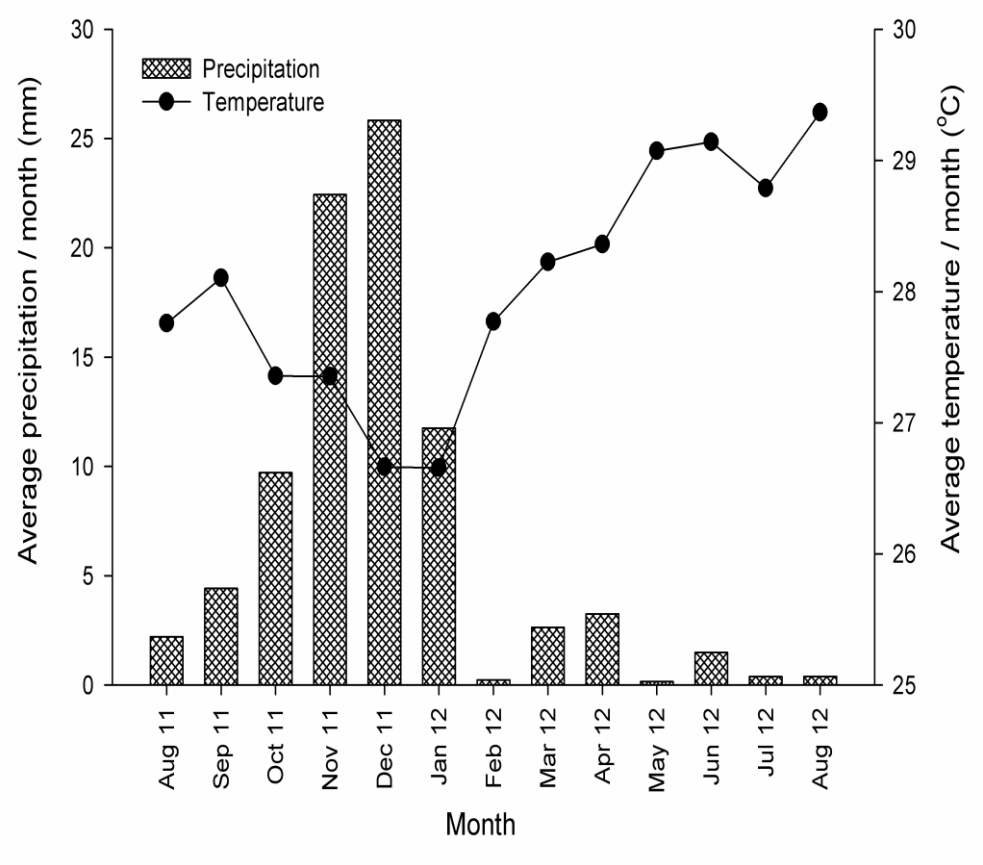
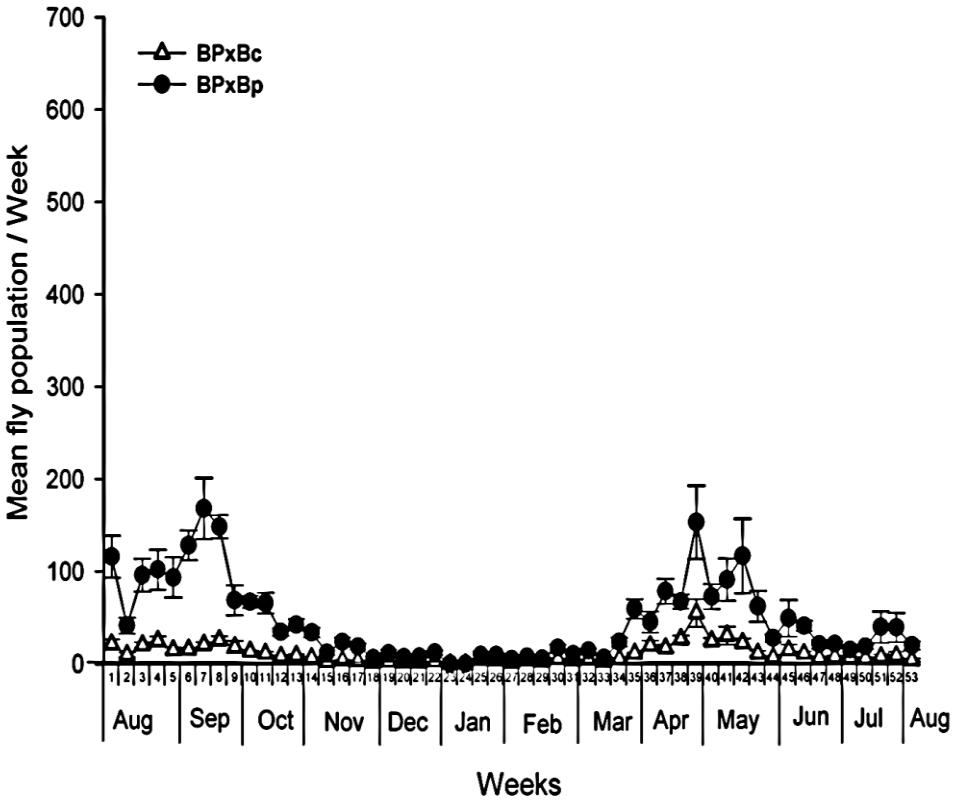


Figure 2. Weekly and monthly distributions of fruit fly at agro-forested area: (a1) Ban Koyai guava orchard; BKxBc: Ban Koyai guava orchard *B. carambolae* and BKxBp: Ban Koyai guava orchard *B. papayae*, (a2) Around Ban Koyai; BKyBc: Around Ban Koyai guava orchard *B. carambolae* and BKyBp Around Ban Koyai *B. papayae.* Symbols represents means of fly population trapped per week (± SE; n=6). (b1) Prevailing weather condition: temperature (line graph) and rainfall (bar graph).

a3


BPxBc
BPxBp
Mean fly population / Week
0
100
200
300
400
500
600
700
Aug
Sep
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Nov
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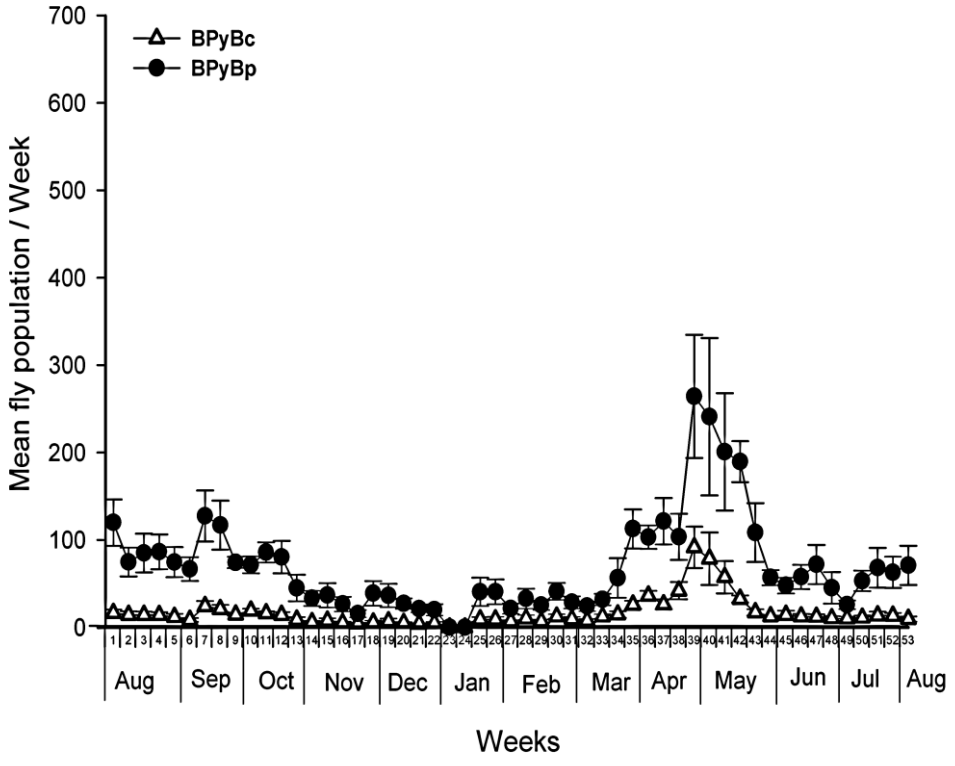
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Weeks

a4


BPyBc
BPyBp
Mean fly population / Week
0
100
200
300
400
500
600
700
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Weeks

b2

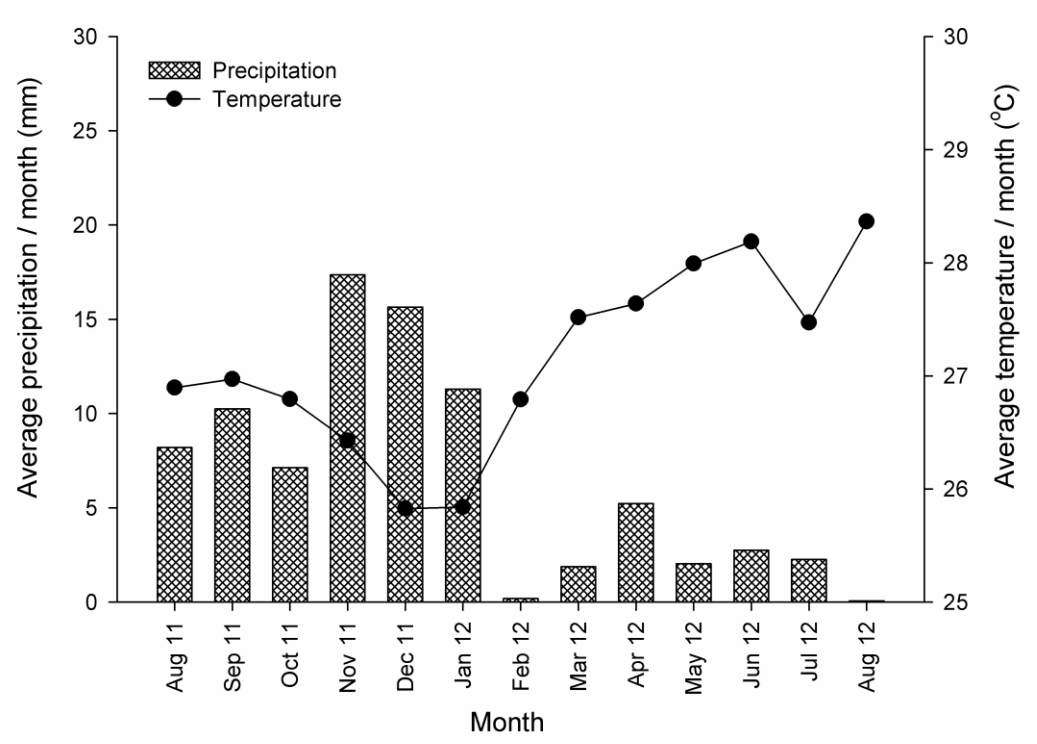
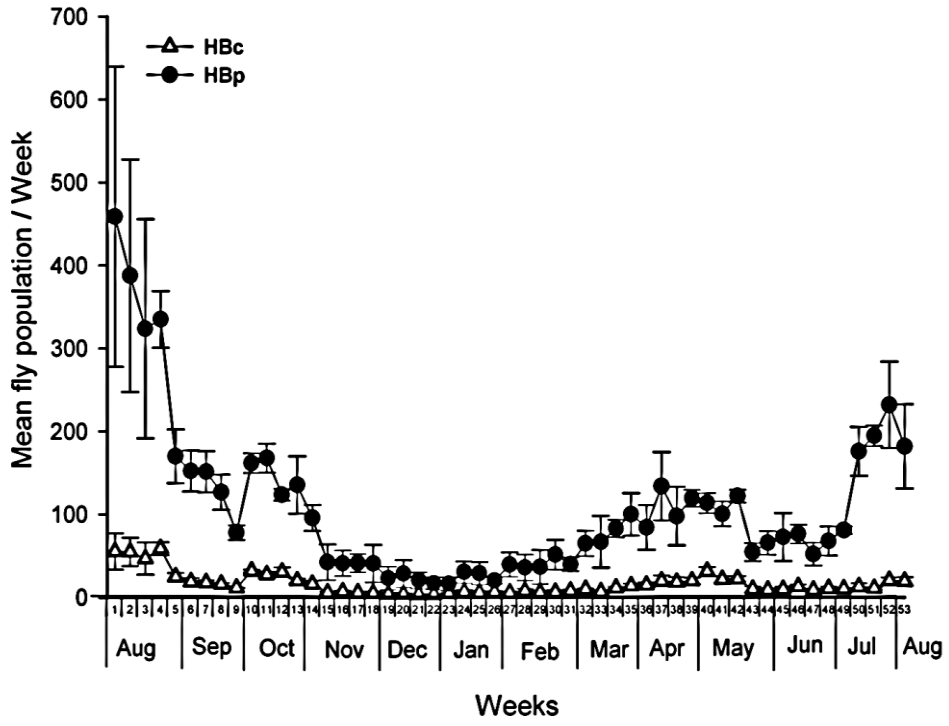


Figure 3. Weekly and monthly distributions of fruit fly at agro-forested area: (a3) Ban Phru; BPxBc: Ban Phru guava *B. carambolae* and Ban Phru guava orchard *B. papayae* and (a4) Around Ban Phru; BPyBc: Around Ban Phru guava orchard *B. carambolae* and BPyBp: Around Ban Phru guava orchard *B. papayae*. Symbols represents means of fly population trapped per week (± SE; n=6). (b2) Prevailing weather condition: temperature (line graph) and rainfall (bar graph).

a5



b3

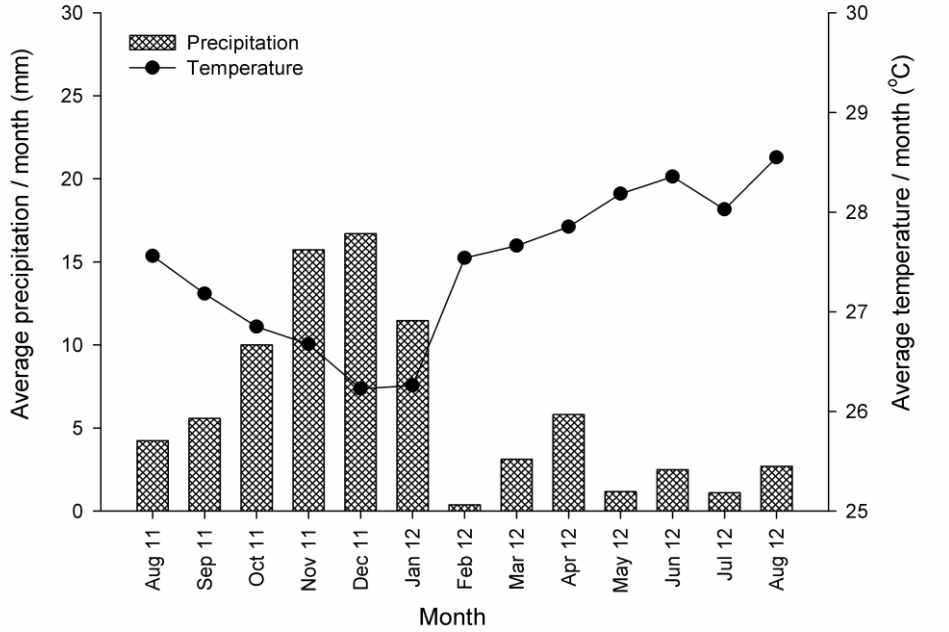
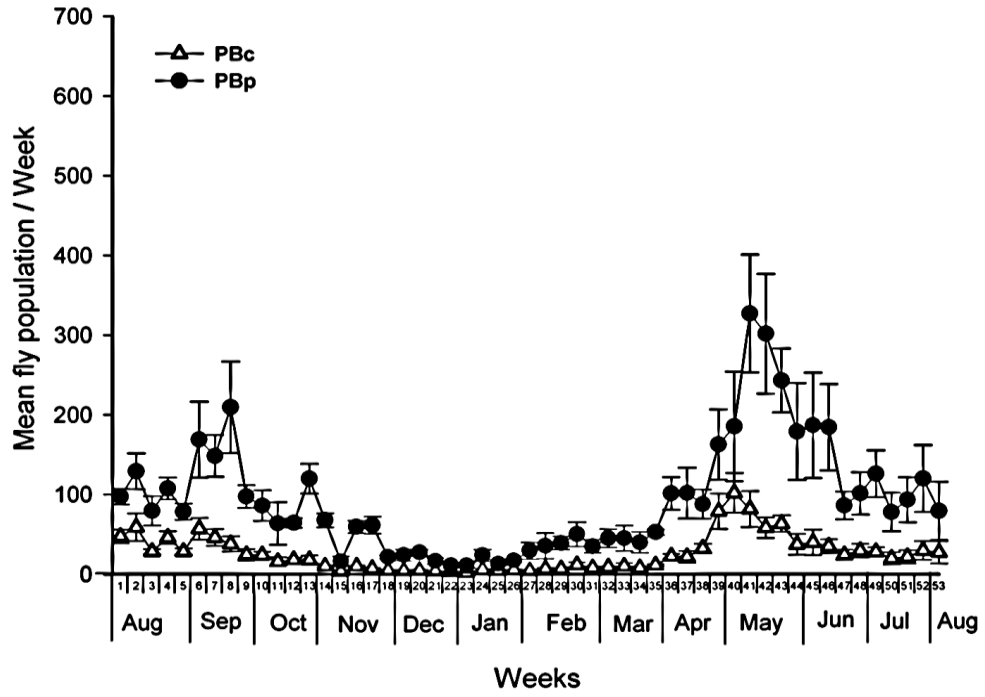


Figure 4. Weekly and monthly distributions of fruit fly in guava orchards located within human settlement area: (a5) Hat Yai Nai guava orchard; HBc: Hat Yai Nai *B. carambolae* and HBp: Hat Yai Nai *B. papayae*. Symbols represents means of fly population trapped per week (± SE; n=3). (b3) Prevailing weather condition: temperature (line graph) and rainfall (bar graph).

a6



b4

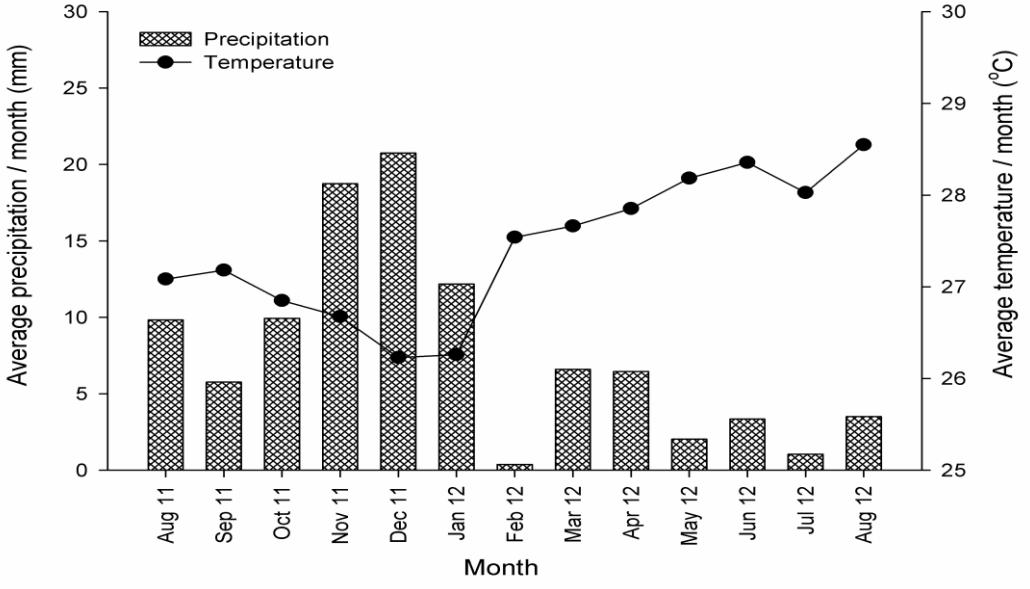


Figure 5. Weekly and monthly distributions of fruit fly in guava orchards located within human settlement areas: (a6) Prince of Songkla University guava orchard; PBc: PSU *B. carambolae* and PBp: PSU *B. papayae*. Symbols represents means of fly population trapped per week (± SE; n=3). (b4) Prevailing weather condition: temperature (line graph) and rainfall (bar graph).

Fly population fluctuation and weather information

The relationship between fly (*B. carambolae* and *B. papayae*) caught and weather variables (temperature, rainfall and relative humidity) were determined with the aid of multiple linear regression and linear regression analysis (Table 3). These were found to be inconsistent throughout the sampling sites. Significant correlation between fly caught and weather variables were detected for *B. carambolae* trapped on and around guava orchards at agro-forested areas. Significant correlation was also observed for *B. carambolae* trapped at Prince of Songkla Univeristy. Only *B. papayae* trapped around guava orchard at Ban Phru and at Prince of Songkla University revealed significant correlations, all others were not significantly correlated.

Table 3. Results of multiple linear regression analysis for the relationship between weekly *B. carambolae* and *B. papayae* trapped at three weather variables (weekly averages of temperature, rainfall and relative humidity) at two different environments in Southern Thailand.

Environment	Site	Farm	Species	week	R^2	F	P	LRC		
								Tem	R/fall	RH
Agro-forested areas	Ban Koyai	GO	BKxBc	52	0.41	3.19*	0.032	0.17	0.30	0.31
			BKxBp	52	0.37	2.47ns	0.073	0.01	0.24	0.15
		AGO	BKyBc	52	0.39	2.89*	0.044	0.34	0.29	0.37
			BKyBp	52	0.38	2.73ns	0.054	0.29	0.34	0.33
	Ban Phru	GO	BPxBc	52	0.40	3.08*	0.036	0.33	0.22	0.38
			BPxBp	52	0.30	1.59ns	0.204	0.29	0.12	0.27
		AGO	BPyBc	52	0.45	4.15*	0.011	0.30	0.27	0.41
			BPyBp	52	0.47	4.37*	0.009	0.37	0.28	0.42
Human Settlement areas	HYN	GO	HBc	52	0.27	1.23ns	0.309	0.16	0.25	0.09
			HBp	52	0.35	2.29ns	0.090	0.29	0.29	0.20
	PSU	GO	PBc	52	0.57	7.53**	<0.001	0.51	0.29	0.29
			PBp	52	0.65	11.42**	<0.001	0.53	0.38	0.26

ns=not significant; *=significant at $p<0.05$; **=significant at $p<0.001$. HYN: Hat Yai Nai; PSU: Prince of Songkla University; GO: Guava Orchard; AGO: Around Guava Orchard; BKx: Ban Koyai guava Orchard; Bky: Around Ban Koyai Guava Orchard; BPx Ban Phru Guava Orchard; BPy: Around BanPhru Guava Orchard; H: Hat Yai Nai Guava Orchard; P: Prince of Songkla University Guava Orchard; Bc: *B. carambolae*; Bp: *B. papayae*, R^2: Multiple Regression coefficient; LRC: Linear Regression Coefficient.

Linear regression analysis revealed that temperature was clearly the most important variable at Prince of Songkla University guava orchard as it revealed strong correlation for the two species. *B. papayae* trapped on guava orchard at Ban Koyai depicted no correlation with temperature. Except for this anomaly, small to medium correlations were observed between fly trapped and other weather variables at all sites (Table 3).

Impact of guava fruit developmental stages on fly population

Improved guava trees produced fruits all year round during the sampling period. But local varieties abound at Prince of Songkla University and fruit production peaks fell between April – May and with a decline in production from June - July and an extended peak from August – September (Figure 6). Other months were relatively guava off-season for this site. A total of 481, 369, 327 and 236 fruits were sampled at Ban Koyai, Ban Phru, Hat Yai Nai and Prince of Songkla University, respectively. The breakdowns of total number of guava fruits sampled per developmental stage were presented in Table 4.

Table 4. Total number of guava fruits sampled at various orchards based on developmental stages

Fruit	Site	B K				B P				H N				PSU			
dev. stage	Species	No of fruit	Inf. fruit (%)	pupae / kg	% fly em.	No of fruit	Inf. fruit (%)	pupae / kg	% fly em.	No of fruit	Inf. fruit (%)	pupae / kg	% fly em.	No of fruit	Inf. fruit (%)	pupae / kg	% fly em.
Ripe	*B. carambolae*	188	173(92.02)	12.77	25.15b	140	131(93.53)	13.96	19.61b	125	107(85.60)	16.2	21.7b	106	103(97.17)	20.18	24.95b
	B. papayae				74.77a				80.39a				78.3a				75.05a
Mature	*B. carambolae*	149	102(68.46)	6.75	26.84b	118	84(71.19)	8.49	34.74b	89	59(66.29)	6.49	30.49b	59	45(76.27)	9.75	36.63b
	B. papayae				73.16a				65.26a				69.02a				63.37a
Immature	*B. carambolae*	144	46(31.94)	3.84	24.76b	111	22(19.82)	1.42	34.95b	113	26(23.01)	1.1	37.84b	71	15(21.13)	0.75	35.48b
	B. papayae				75.23a				65.05a				62.16a				64.52a

BK: Ban Koyai, BP: Ban Phru, HN: Hat Yai Nai and PSU: Prince of Songkla University

Inf.: infested fruits (% of infested fruits), % fly em.: percentage of fly emergent

* Each sampling site has four columns; first column shows numbers of guava fruit sampled per developmental stage, second column shows the number of infested fruits (% of infested fruits), third column shows pupae per kilogram of fruit, and fourth column shows % fly emergence, respectively.

* All adult fly emergence percentages per specific guava developmental stage in the same column followed by different letters are significantly different (t-test $p<0.05$).

B. papayae was significantly more than *B. carambolae* in population density from the result of fruit rearing for all stages of guava fruits (t-test $p<0.05$). Guava fruit cultured from Prince of Songkla University support more fly population than any other orchard. It was also evidenced that riped guava fruit was the most favoured by flies (Figure 6). The percentage damage observed on orchards ranged between 15-40% for improved cultivar orchards and 60-90% for the local cultivar orchard.

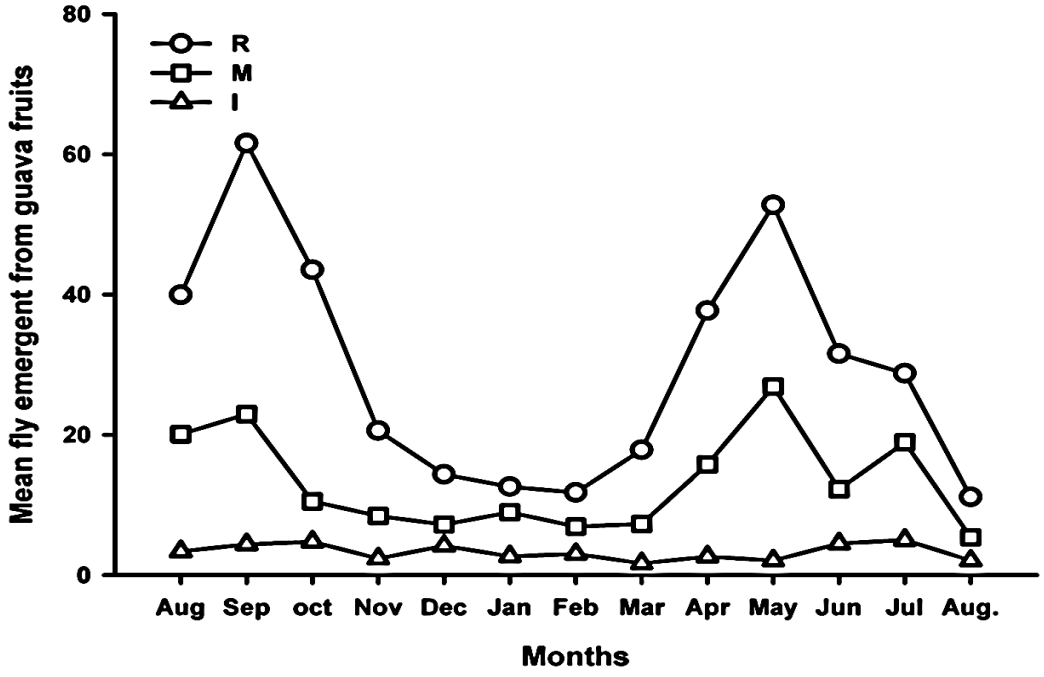


Figure 6. Mean population of *B. carambolae* and *B. papayae* emergent from guava fruits classified into 3 developmental stages; Ripe (R), Mature (M) and Immature (I).

Vegetation assessment

Vegetation assessment revealed that agro-forested sites had the greatest number of *B. carambolae* and *B. papayae* cultivated host plants which were sited within the vicinity of the trapping sites. The host plants were seen cultivated as monoculture, mixed culture and or scattered among rubber trees which form the major plantation that possessed wider area of Southern Thailand. At the human settlement guava orchards, other host plants than guava were few occurring as an individual or group of < 5 individual plants growing among the buildings surrounding the guava orchards. Wild fruit bearing shrubs were not easily accessible as most were cleared for agricultural purposes. The lists of plants available at all sites during this research were itemized under the site descriptions. The most available host plants were represented based on their fruiting phenology in figure 7.

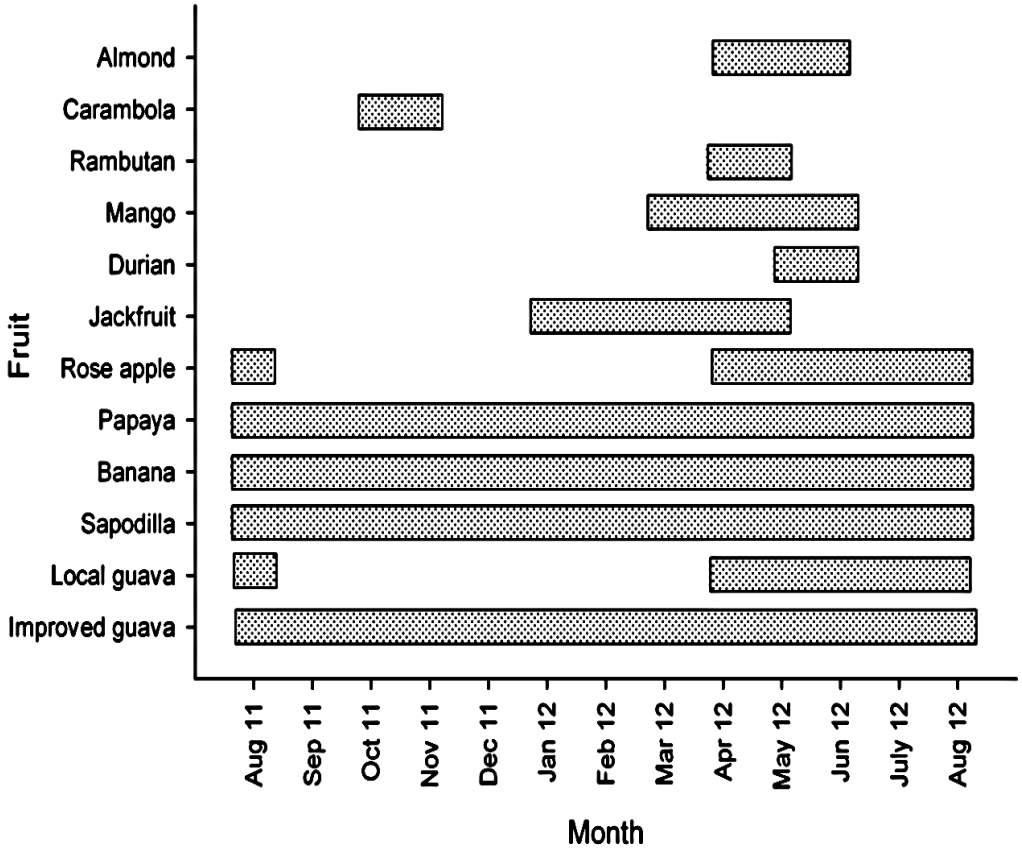


Figure 7. Fruiting phenology of major host plants of *B. carambolae* and *B. papayae* in Southern Thailand

The fruiting phenology was found to synchronize with the fly abundance period and exert pressure on population distribution pattern. Hence, fly population were observed to be more at fruiting periods. Fruits that were sampled during the course of this study other than guava were listed in Table 5.

Table 5. Positive rearing results for fruits infested by *B. carambolae* and *B. papayae*

			Average fly / kg	
Host Scientific name	**Common name**	**Total (+ve fruits)**	***B. carambolae***	***B. papayae***
Averrhoa carambolae L.	Star fruit	5 (5)	5.1	11.12
Syzygium malaccense L.	Rose apple	56 (48)	8.55	23.62
Tamarindus indica L.	Tamarind	10 (0)	0	0
Manilkara zapota L.	Sapodilla	57 (13)	1.8	5.77
Nephelium lappaceum L.	Rambutan	13 (3)	0.78	1.95
Sandoricum Koetjape Mer	Santol	5 (2)	0	3.31
Musa spp. L.	Banana	10 (7)	0	13.32
Carica papaya L.	Pawpaw	5 (2)	1.05	2.36
Mangifera indica L.	Mango	15 (5)	1.02	2.58
Terminalia catappa L.	Malabar almond	25 (11)	2.77	5.82

*+ve fruits: Total number of fruits that were positive for *B. carambolae* and *B. papayae* rearing

Discussion

Seasonality of *B. carambolae* and *B. papayae*

Consecutive field monitoring and guava fruits sampling for a year, revealed fluctuated abundance and distribution patterns for *B. carambolae* and *B. papayae* on and around guava orchards. Both species were trapped in the field throughout the season and exhibited very similar patterns of seasonal occurrence with marked two density peaks, August-September and May. The density at each peak period was almost always greater for *B. papayae* than for *B. carambolae* at all the study sites. Hence, bimodal distribution structure was common to all sites. Contrary to these findings, an earlier survey study by Clarke *et al*. (2001) in Thailand and peninsular Malaysia reported a unimodal population pattern for *B. papayae* in Thailand, with the peak late in the monsoon season (August/September). However, the present findings agreed with the report of those authors that *B. carambolae* exhibits no repeatable patterns of distribution and abundance. The observed disparity could be due to differences in frequency of trap clearance and trapping sites. Other seasonality studies of tephritids have revealed unimodal and bimodal patterns depending on the study locations. Vargas *et al*. (1983) studied *D. dorsalis* in Hawaii (Kauai) in a tropical climate and reported a unimodal population peak. Raghu *et al*. (2000) observed the same unimodal trend in southeast Queensland in a sub-tropical climate. On the other hand, a bimodal pattern was revealed by Mwatawala *et al*. (2006b), who worked on *B. invadens* in Kenya in a tropical climate and Muthuthantri *et al*. (2010), who studied *B. tryoni* in Queensland in a sub-tropical climate, recorded both unimodal and bimodal population patterns at different sites. The population density at a given time depends on the prevailing weather conditions, location, available hosts and species studied.

At all study sites, the *B. papayae* population was larger than the *B. carambolae* population. The agro-forest sites revealed that the fly populations were large outside of the orchards compared to the smaller populations observed within the orchards. High trap catches were expected in host areas; however the high trap captures at the surrounding of the orchards were unexpected. This may be due to flies returning to nearby vegetation to roost after oviposition and feeding in the orchards (Vargas *et al*., 1983, 1989, 1990) and or to obtain food and shelter (Hendrichs and Hendrichs, 1990, Souza-Filho *et al*., 2009). Furthermore, Vargas *et al*. (1989) reported high

numbers of *Dacus dorsalis* (Hendel) consistently outside crop production areas. That could also be the reason why the mean populations of these flies were high for the urban orchards, as there was not much vegetation nearby for them to roost on (McQuate and Vargas, 2007). Hence, fly population build-up in guava orchards and subsequently spread to other agricultural areas. This finding support earlier studies (Newell and Haramoto, 1968; Vargas et al. 1983) and further suggest that guava serve as a reservoir from which flies moves into other cultivated areas.

Seasonality fluctuations in population could also be linked to host availability. Several other hosts of these flies were available in their respective seasons at the study sites, most significantly in large numbers at the agro-forest sites. Previous studies have revealed that host availability has a positive impact on the seasonal abundance of fruit flies (Tora Vueti *et al*., 1997; Mwatawala *et al*., 2006b). *B. carambolae* and *B. papayae* are polyphagous species, and their hosts' fruiting seasons span from April–September. Therefore, the variable fruit availability from the flies' assorted hosts could be responsible for the flies' occurrence in these periods and likely helped to maintain these species in areas where the orchards were located (Souza-Filho *et al*., 2009). Though a fly might be polyphagous, there is still a primary host that it prefers most. Allwood *et al*. (1999) have recovered larger numbers of *B. carambolae* and *B. papayae* from guava fruits than from any other sampled host. Similarly, guava has been reported to have presented the greatest tephritid species diversity, confirming its condition of host with the highest number of fruit fly species in Brazil (Malavasi *et al*., 1980). Furthermore, Newell and Haramoto (1968) reported that fruit fly population develops in guava, *P. guajuva*, and that population cycles are determined primarily by guava fruiting. Similarly, Vargas *et al*. (1983) worked on *D. dorsalis* and reported that peak captures of this fly coincided with fruiting of *P. cattlelanum* and *P. guajava*. Related to this apparent preference, increases in the population of *B. invadens* have been reported to be directly linked to the ripening of different mango cultivars (Vayssieres *et al*., 2005; Mwatawala *et al*., 2006b). In the same vein, host availability and abundance have been reported to be partly responsible for population fluctuations in *Bactrocera* species and other fruit flies (Drew and Hopper, 1983; Vargas *et al*., 1990; Leblac and Allwood, 1997; Tora Vueti *et al*., 1997; Katsoyannos *et al*., 1998) and in other genus of fruit flies (Harris *et al*., 1993; Segura *et al*., 2004).

On a global scale, seasonal temperatures and rainfall patterns constitute the major factors that determined the distribution of organisms in space (Bateman, 1972; Bale *et al*., 2002). The role of temperature as a determinant of abundance in Tephritids, as in all poikilothermic animals, is mediated either directly or indirectly through its effects on rates of development, mortality, and fecundity (Bateman, 1972). During dry season in peninsular Thailand, rainfall becomes critical, therefore *B. carambolae* and *B. papayae* survival depends on relative humidity and temperature. Dry atmospheres and high temperatures were particularly detrimental to survival of fly. Mature larva and newly emerged adults are most susceptible to desiccation resulting in great reduction in number of adults that comes into being and indirectly reduced emigration to other areas (Bateman, 1972). This may suggest why fly population fluctuate greatly even when hosts were available. From the present study, it was evidently sufficient to conclude that vagaries of weather also play an indispensable role in seasonal abundance of *B. carambolae* and *B. papayae*. The interactions of weather factors (temperature, rainfall and relative humidity) exert great pressure on population of *B. carambolae*. Generally, temperature, rainfall and relative humidity distinctly determined the population growth of *B. carambolae* and *B. papayae*. This finding was similar to the report of other tephritids fly workers who confirmed that temperature and rainfall (Amice and Sales, 1997; Vayssières *et al*., 2005; Mwatawala *et al*., 2006; Muthuthantri *et al*., 2010) and relative humidity (Muthuthantri *et al*., 2010) were the primary determinant of fruit fly population.

Impact of guava developmental stages on *B. carambolae* and *B. papayae*

In tephritid fruit flies, as in many other families of phytophagous insects, both chemical and visual stimuli from plants play a significant role in guiding adults to sites where essential resource can be found (Fletcher and Prokopy, 1991; Bernays and Chapman, 1994). More specifically when seeking oviposition sites after arrival on host plants, female of many frugivorous tephritid species respond positively to the visual and in some cases to the chemical properties of fruit (Katsoyannos, 1989; Fletcher and Prokopy, 1991). Hue, silhouette, contrast with the background, form, and size are used by both sexes of *Rhagoletis pomonella* (Walsh) and probably by other species to detect host plants (Prokopy and Owen, 1983). Once they arrive in the host plant habitat, visual

characteristics are the main or sole stimuli guiding host fruit detection (Aluja and Prokopy, 1993). On the other hand, Aluja and Prokopy (1992, 1993) showed that when fruits are not visible or scarce, fruit odour may interact with visual cues throughout the searching process. Fein *et al.* (1982) identified seven volatile esters that triggered the upwind flight of *R. pomonella* towards the host fruit.

The rearing experiment revealed that both fruit fly species exhibited a stronger preference for riped guava than for guava at any other developmental stages. More *B. carambolae* and *B. papayae* individuals were recovered from ripe guava than from the other developmental stages. Both flies co-infest guava fruits, as revealed by the rearing experiment, which is evidence of niche overlap (Duyck *et al*., 2004). This finding confirms the reports of other researchers (Copeland *et al*. 2002, 2006; Mwatawala *et al*. 2006b; Papachristos and Papadopoulos, 2009) that co-occurrence of fruit fly species and intergeneric polyphagy on host fruits do occur. It was revealed in this study that the local cultivar of guava yielded more fruit flies than the improved cultivar. This might be due to the local cultivar's aromatic nature (strong smell) and its genetic closeness to the guava's wild natives. This agreed with Vargas *et al*. (1983) whose studies revealed high recovery of *D. dorsalis* pupae per kg from *P. cattleinum* and *P. guajava.* The genetic modifications to the improved cultivar, such as little or no smell, a rough surface, the hardness and thickness of the mesocarp etc., may be responsible for the lower rate of fly infestation. Notwithstanding, the number of emergent larvae was always greater for *B. papayae* than for *B. carambolae*. This suggests some type of interspecific interaction, which might be responsible for the great disparity observed in the fly densities. Such interactions could consist of competition for limited resources, displacement and/or niche differentiation (Duyck *et al*. 2004). *B. carambolae* and *B. papayae* both have an intermediate body size and exhibit mixed traits of r-k strategy. Their reproductive patterns and the required developmental periods of their immature stages may be useful characteristics for predicting the differences observed in their population fluctuations. *B. papayae* is faster than *B. carambolae* in completing its immature stages (Danjuma *et al*. 2013).

Fruit fly population fluctuated despite the availability of the improved guava hosts throughout the study period. But the mechanisms behind decline in population and infestation rate as the fruiting season progresses are insufficiently

known (Mwatawala *et al*., 2009). Therefore, the observed patterns need to be confirmed through continuous sampling over successive years prior to any control programme.

Agro-forest and human settlement orchards

Due to increase in population and high demand for food, the anthropogenic activities of man had adverse effect on the environment. Agricultural activities and urbanization has altered the rainforest in peninsular Thailand and this has reduced the landscape into mere mosaic rainforest. These alterations have impact on the abundance and distribution of many insect species. However, how these alterations impact insects, whether negatively, neutrally and or positively are not always clear (Raghu *et al*., 2000). Fruit fly trapped in town orchards were greater than those trapped at the agro-forested orchards. *B. carambolae* tends to predominate in orchard and urban areas (Vijaysegaran and Shamsudin, 1991). But *B. papayae* were trapped in rainforest areas that were relatively close to urban areas (Meat *et al*., 2008). Hence, they are tolerance of both urban and fairly forest habitat. Raghu *et al*. (2000) worked with *B. tryoni* and had a similar trend. Courtice and Drew (1984) presumed that suburbia was now the major breeding habitat of tephritid flies. Conclusively, the transformation of rainforest into suburbia and cultivation of tamed hosts enhanced the abundance and distribution of *B. carambolae* and *B. papayae.*

The findings presented in this study have important implications for both research and pest management. Because the studied species belong to the *B. dorsalis* complex, which encompasses several world quarantine pests, this study would be pertinent for further studies of other complex members. It will also be a useful reference in the development of suitable control measures against these notorious flies. *B. carambolae* and *B. papayae* are expected to occur around commercial farm and residential areas where cultivated host plants may be found and in native vegetation where their hosts abound. Therefore, similar vegetation among peninsular Thailand agro forest areas may be expected to have similar *B. carambolae* and *B. dorsalis* seasonality. Such distribution and abundance information is important in formulating eradication strategies. *B. papayae* was formerly eradicated from Cairns, Australia (Meat *et al*., 2008). Both species responded greatly to methyl eugenol, hence control could be achieved through male annihilation technique where this parapheromone combined with insecticide in traps are placed on the field throughout the infested areas. Sterile

insect technique may also be useful as both flies could be bred in large number in a short period (Danjuma *et al*., 2013). Destruction of flies host plants in agro forest areas will reduce roosting sites and consequently limit the possibility of re-infestation. Population fluctuation information by habitat revealed the time of the year when populations of these fruit flies are lowest and mass trapping will be most appropriate at this period. Information gathered from fruit experiment would be necessary in planning sustainable cultural control methods. Such as fruit bagging, farm cleaning and appropriate disposal of discarded fruits.

CHAPTER 4

LIFE HISTORY STRATEGIES OF PRE-IMAGINAL STAGES OF *B. CARAMBOLAE* AND *B. PAPAYAE*

Introduction

The genus *Bactrocera* is of worldwide recognition for its destructive impact on agriculture. Besides causing billions of dollars in direct losses to a wide variety of fruit, vegetable and flower crops (e.g., citrus, apple, mango, sunflower), hence, limit the development of agriculture in many countries due to reduction in farm income and leads to overuse of pesticides. Growers and governments face rising costs as they attempt to meet demands for food. Therefore, pest free or low pest density zones are being advocated worldwide for fruit export with minimal or zero quarantine restrictions (Carroll *et al*., 2004; FAO, 2006). The damage, if uncontrolled, may result in a total loss of the crop in question (Yong *et al*., 2010). The genus *Bactrocera* is known to be largely endemic to Asia and the pacific. Among the serious pest species, several are indigenous to peninsular Thailand and Malaysia. Species native to these countries include several of the *B. dorsalis* complex, including *B. dorsalis* sensu stricto, *B. carambolae* and *B. papayae* and the cucurbit feeders *B. cucurbitae* and *B. tau* (Clarke *et al*., 2001).

B. carambolae and *B. papayae* are members of the *B. dorsalis* complex (Drew and Hancock, 1994). These two species have been found to be well distributed in Southern Thailand affecting different kinds of fruits and vegetables. Drew and Hancock (1994), Ranganath and Veenakumari (1995), Allwood *et al*. (1999), and Sauers-Muller (2005) had worked extensively on the host plant records for fruit flies (Diptera: Tephritidae) in Southeast Asia. Their work revealed that *B. carambolae* and *B. papayae* are polyphagous species of tephritids flies found in Southeast Asia. They reported 76 and 193 host species for *B. carambolae* and *B. papayae* in this region, respectively. Amongst the listed hosts revealed, guava was found to be more infested compared to any other host listed.

Guava is one of the most common fruits ubiquitous; appearing at all stalls and markets in Thailand. It is an important source of income and also represents an important part of the gastronomic culture for Thai people (Victor, 2009). The fruit is produced under small scale farming and sometimes at subsistence level. For several tropical fruits, the production is mainly by smallholder producers largely intended for local consumption in the rapidly expanding local-urban green market (Lux, 1999). Occurrence of high population of fruit fly species leads to economic losses for the smallholder farmers, as well as a reduced source of essential dietary components especially vitamins and minerals to local and urban population (Mwatawala *et al*., 2006b). *B. carambolae* and *B. papayae* have been found to co-infest the guava fruit causing enormous economic loss in peninsular Thailand, even more serious than the *B. correcta* which has been recognised as it major pest.

Tephritid distribution and abundance are notably dependent on several abiotic factors (e.g., temperature, relative humidity, and rainfall) and several biotic factors (e.g., host plants and natural enemies) (Vayssières *et al*., 2008). This study focussed on the effect of temperature on the pre-imaginal developmental stages of *B. carambolae* and *B. papayae*. Either working in the laboratory or on the field, some scientists have elucidated that temperature is the main abiotic factor affecting survival and development of many tephritid species (Fletcher, 1987; Vargas *et al*., 1997; Brévault and Quilici, 2000; Duyck and Quilici, 2002; Rwomushana *et al*., 2008; Vayssières *et al*., 2008; Liu and Ye, 2009). Two fundamental thermal parameters that expresses how the rate of development of ectotherms depends on temperature are the lower threshold temperature for development (T_{min}: temperature below which no measurable development takes place) and the thermal constant K (number of degree days (DD) above temperature T_{min} for completion of development) (Higley *et al*., 1986; Rwomushana *et al*., 2008). There is no published report on the effect of these important variables on *B. carambolae* and *B. papayae*. Therefore, this study aimed at establishing and comparing the effect of six constant temperatures on the development and survival of immature stages of these flies. The study will also test and reveal how the flies survive on the food from their host plant (*Psidium guajava*). Because this species are reported to cohabitate on guava fruits in the field, hence, they exhibit niche overlap via fruit (Duyck *et al*., 2008).

The results from this study will be useful in optimizing rearing procedures and to understand and predict *B. carambolae* and *B. papayae* occurrence, geographical distribution pattern and abundance in peninsular Thailand and other part of the globe where they occur. It would also help in the development of better ecological management strategies for these flies.

Materials and methods

Insect culture

This study was conducted on the third filial generation, F_3 laboratory reared fruit fly. The population was initially generated in 2011 from infested guava fruits sampled from guava orchards in southern part of Thailand (latitude 7° 2' 56.7779"N and longitude 100° 28' 11.8945"E). The fruit fly colonies were reared and maintained at the Entomology Research Unit of the Department of Biology, Prince of Songkla University, Hat Yai, Thailand. Rearing conditions were maintained at 25 ± 1^{o}C, 75 ± 5% relative humidity (RH) and Photoperiod of L12:D12.

Larva food

The larval food was simulated from that used at the National Biological Control Research Centre (NBCRC), Prince of Songkla University, Hat Yai. Uninfested guava fruits and fresh maize cobs were obtained from the fresh market and properly washed with water. Guava fruit weighed 150g was cut into smaller pieces for easy blending. Similarly, 150g of the dehusked fresh maize were also weighed and grinded with the aid of a blending machine (Philips HR2021, China) of fine particle size ≤ 2.5 micrometres, likewise 30g of toilet tissue paper (Tesco Lotus Ltd, Thailand) were soaked in water and grinded with the aid of a blender. The guava, maize and tissue paper were blended properly and yeast extract (Bacton Dickson and company, Le Pont de Claix, France), sugar, HCl and sodium benzoate were added in the required proportion accordingly (Table 1).

Table 1. Components of larval diet

Ingredient	Quantity
Guava fruit	150g
Maize	150g
Absorbent (Tissue paper)	30g
Yeast extract	30g
Sugar	30g
Sodium benzoate	0.8g
HCl	1.6ml
Water	300ml

Egg collection

Eggs were collected from *B. carambolae* and *B. papayae* stock colony with the aid of an artificial egg-laying device offered to the 200 females of both flies maintained separately in 27 × 27 × 27cm cages. The egg-laying device consisted of a plastic yellow ball SR2003 (SR Toy Ltd, Thailand) which was cut into two equal halves to produce a dome-like structure (Figure 1). Each dome was pierced with an entomological pin (4cm long and 0.3 mm in diameters) to make 150 tiny pores on each dome. Each dome was placed in a petri dish of 9 cm diameter lined with a black coloured Whatman 9.0 cm filter paper (W & R Balston Ltd, England). Before the domes were place in petri dishes, they were spray with water to simulate the surface of fruits in order to facilitate oviposition (Unpublished). Eggs were collected within 4 hours of setting with the aid of a camel brush onto the black background. These eggs were carefully observed through a stereo microscope and counted.

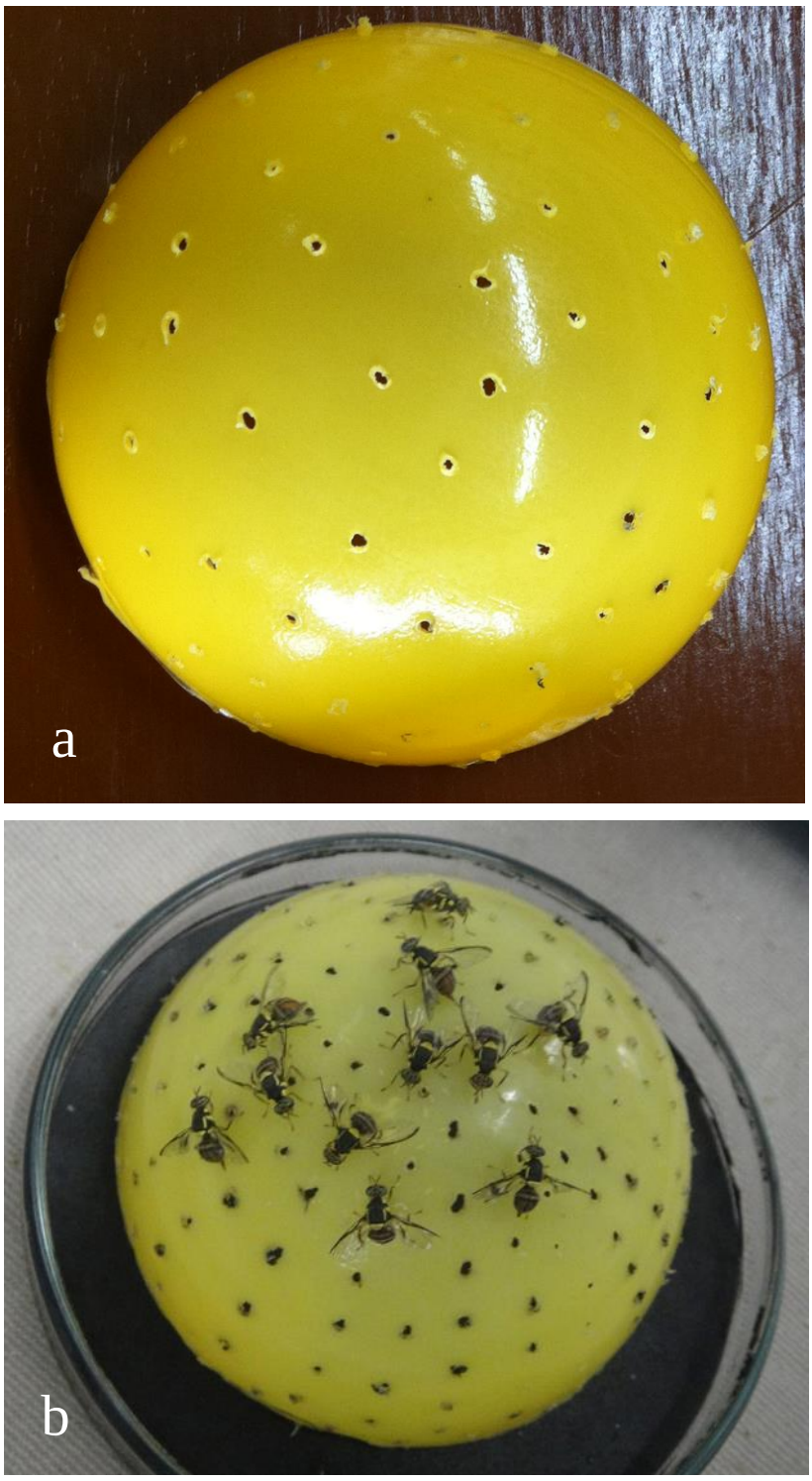


Figure 1. Egg collecting device (a) plastic yellow ball cut into halves (b) female flies laying eggs on the device.

Egg culture

Some 50g of guava diet were placed into cleaned petri dishes. The surface of the diet was covered with 3cm diameter single layer of toilet tissue paper. Fifty eggs of each species were counted with the aid of a stereo microscope. These were carefully arranged in a line on the tissue paper and placed at the center of each diet in the petri dishes and then individually placed into rectangular rearing containers (Plexiglas boxes of 20cm × 15cm × 7cm) which were covered with a dark cut-to-fit cardboard paper. The lids of the boxes were cut at the centre to the diameter of 8.4 cm and screened with netting materials to provide ventilation. The petri dishes were immediately transferred to thermostatically controlled environmental chambers (Contherm phytotron climate simulator, New Zealand) set and maintained at six constant temperatures of 15, 20, 25, 27, 30 and 35^{o}C (1±^{o}C), 70 ± 5% RH and Photoperiod of L12:D12 respectively. Egg hatchability was determined by observing the eggs at 3-hourly intervals under a stereo microscope.

Larva Stage

After the eggs had hatched, the dark cut-to-fit cardboard papers around the Plexiglas boxes were then removed. The bottoms of the Plexiglas boxes (20cm × 15cm × 7cm) were lined with sterilised sawdust to the thickness of 1cm to enhance pupation. The Plexiglas boxes were then maintained at the various constant experimental temperatures in the thermostatically controlled environmental chambers until the matured third instars larvae jumped (by curling into a 'U'-shape and then rapidly straightening) out of the diet from the petri dishes onto the sawdust for pupation. The boxes were checked for pupae after 6 days and pupa were separated from the sawdust 6-hourly by sifting.

Pupa stage

The resulting pupae from the culture were transferred into 10cm × 7.5cm × 5.5cm Plexiglas box lined with tissue paper. The pupae were maintained at the same six constant temperatures until emergence. All developmental tests for the immature stages were replicated five times for each constant temperatures and each was tested three times (5 × 3 = 15).

Data Recording

The mortality, duration and developmental rate of different stages were recorded. Developmental duration was estimated from the median time when 50% of the stages were transformed from egg hatching, larva metamorphose into pupa and adult eclosion from pupa. Stage specific survival rates were determined as a proportion of individuals alive at the end of each stage in relation to the initial starting number. The final numbers of emerged adults were calculated as the product of survival rates in the different stages from egg to adult.

Temperature summation model

The developmental time of individual life stages (time necessary for 50% of individuals to complete a given stage) was determined for six constant temperatures. The developmental rate (100/developmental time) was plotted against temperature (Brévault and Quilici, 2000; Rwomushana *et al*., 2008). This approach was based on the assumption that above some lower threshold for development, temperature-development rate relationships are linear and, therefore, a constant number of heat units (joules) above this threshold are needed to complete development (Arnold, 1959; Fletcher, 1989). Regression analysis was used to estimate lower development thresholds *t* (defined as the temperature below which there is no measurable development) for egg, larva and pupa (Liu *et al*., 1995; Liu and Meng, 1999). The *t* was determined by extrapolation of the regression line back to the x-axis or by the formula;

$$R(T) \text{ or } 1/D = a + bT.$$

Where; R is the rate of development, *D* is the duration of development (in days) of a particular stage at temperature *T*, while *a* and *b* are the regression parameters (Wagner *et al*., 1984; Liu and Ye, 2009; Jalali *et al*., 2010).

The thermal constant *K* (the degree days above the lower threshold required to complete development) was calculated from the regression equation using the relationship;

$$K = n\,(T - t).$$

Where; *K*; thermal constant, n; duration of development (days), T; average temperature of the period (^{o}C) and, *t*; threshold temperature (^{o}C) (Pruess, 1983, Vargas *et al*., 1996; Brévault and Quilici, 2000; Rwomushana *et al*., 2008).

The range of variation in developmental time for each immature stage was determined by using the formula: r.v. = max. developmental time – min. developmental time. The coefficient of variation was thus calculated for as c.v. = 100 x r.v./developmental time for each stage (Brévault and Quilici, 2000; Rwomushana *et al*., 2008).

Data analysis

A linear regression model was used to establish the relationship between temperature and developmental rate. Developmental time data and survival rate percentages were transformed by using In(x+1) and Log_{10} respectively. The data were checked for normality by using Shapiro-wilk test and Student's t-test was used for the analysis to compare development and survival for each stage between the two species at each temperature. Considering various replicates as multiple observations at each temperature, Developmental time (days) and adult eclosion were also submitted to one way Analysis of variance (ANOVA). Student-Newman-Keuls (SNK) was adopted to compared the means accordingly ($P<0.05$). All statistical analyses were performed by using Sigmaplot version 11.0 statistical package (Sigmaplot, 2008).

Results

Relationship between temperature and developmental rate for *B. carambolae* and *B. papayae*

Linear regression model was used to establish the relationship between temperature and developmental rate of immature stages of *B. carambolae* and *B. papayae* over the range of 15 – 30°C (Figures 2 and 3).

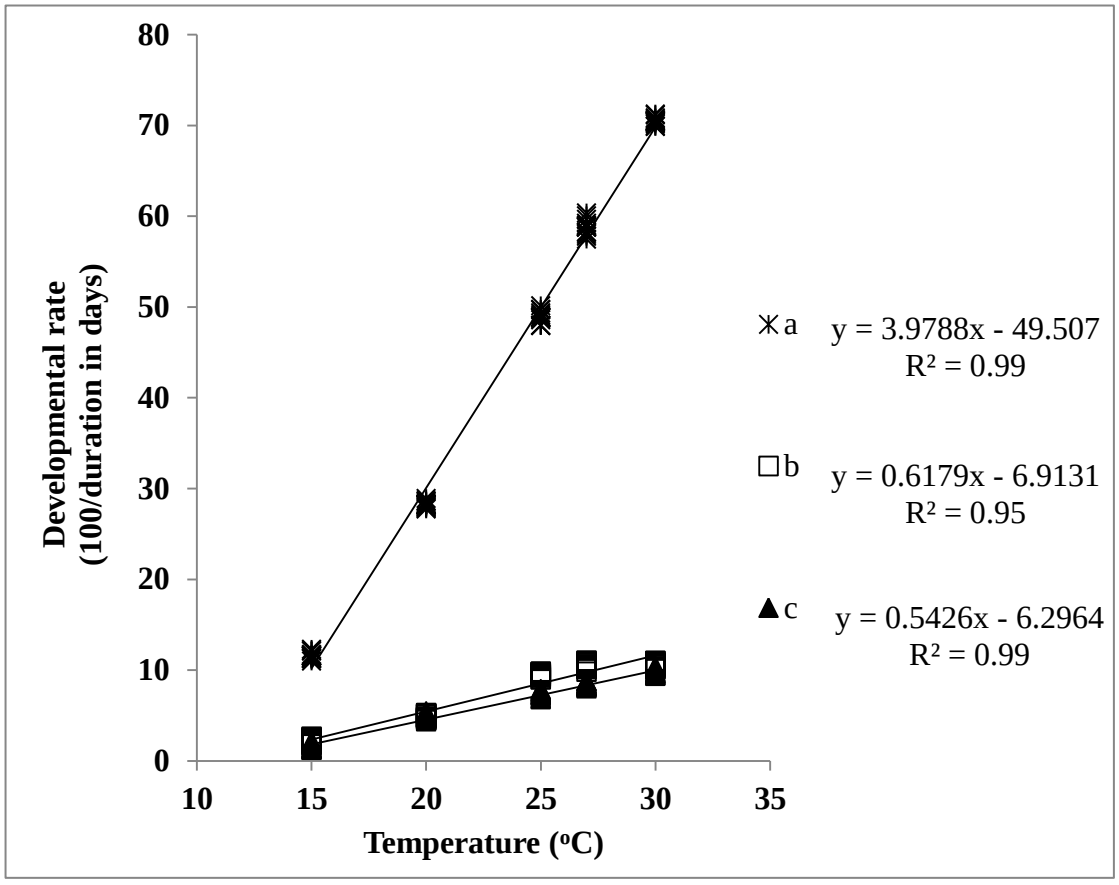


Figure 2. Effect of constant temperature on developmental rate (100/duration in days) of different life stages of *B. carambolae*: (a) Egg; (b) Larva; (c) Pupa.

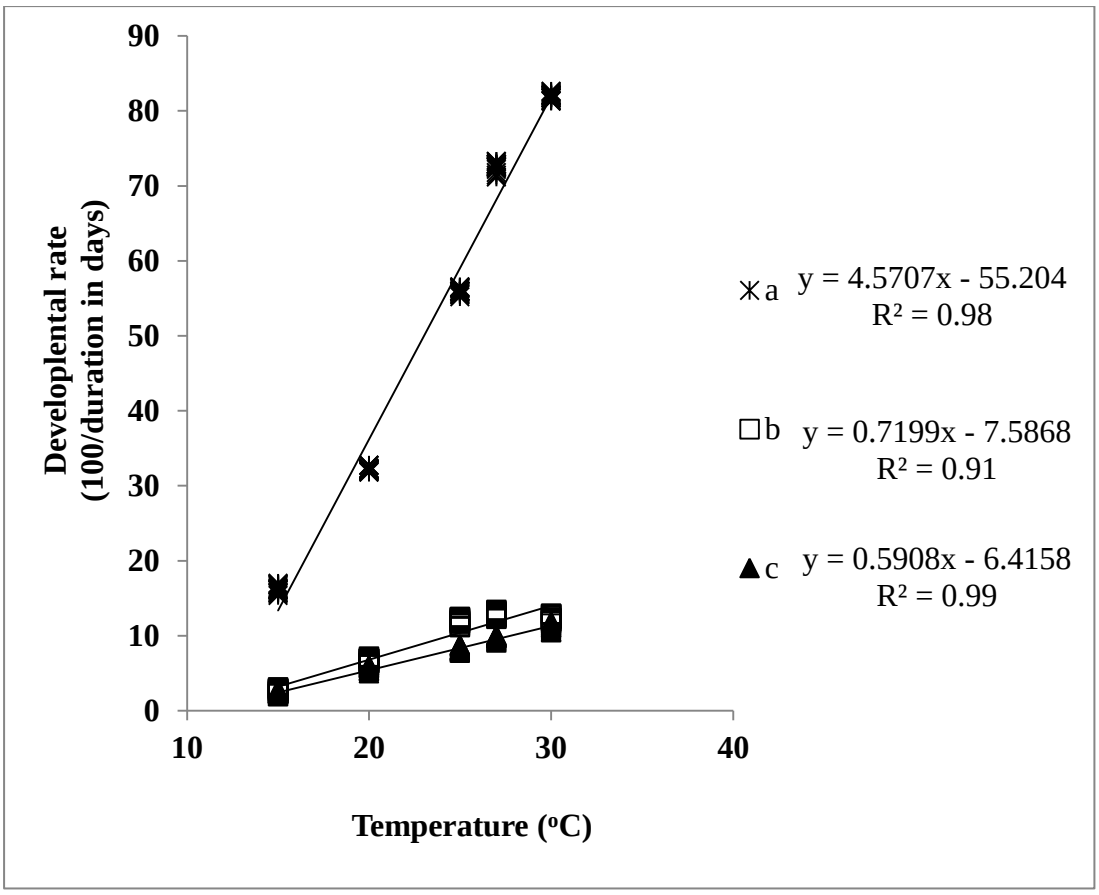


Figure 3. Effect of constant temperature on developmental rate (100/duration in days) of different life stages of *B. papayae*: (a) Egg; (b) Larva; (c) Pupa.

A strong and positive linear relationship was observed between temperature and developmental rate of immature stages of *B. carambolae*, correlation coefficient (R^2) = 0.99, 0.95 and 0.99 ($p<0.0001$, $p<0.0045$ and $p<0.0001$) for egg, larva and pupa, respectively (Fig. 1). The threshold temperatures (*t*) for egg, larva and pupa were 12.44, 11.18 and 11.60^{o}C, respectively. The degree-days (DD) required for completing egg, larva and pupa stages were 25.13, 161.89 and 184.33, respectively. The total DD required to complete all stages was 371.35. Similarly, a strong and positive linear relationship was observed between temperature and developmental rate of *B. papayae*, R^2 = 0.98, 0.91 and 0.99 ($p<0.0010$, $p<0.0101$ and $p<0.0001$) for egg, larva and pupa, respectively (Fig. 2). The *t* for egg, larva and pupa were estimated at 12.08, 10.54 and 10.86^{o}C respectively. The DD were 21.88, 138.91 and 169.26 for egg, larva and pupa respectively. Total DD required to complete all developmental stages was 330.05. *B. carambolae* was found to have exhibited high *t* and consequently, high DD when compared to *B. papayae*.

Effect of temperature on the developmental time of various life stages

The duration of the egg stage varied significantly between the understudied species at each temperature regime (t-test, $p<0.001$) (Table 2). The time required for *B. carambolae* eggs to hatch ranged from 1.12 days at 35^{o}C and increased to 5.49 days at 15^{o}C. For *B. papayae*, the hatchability period ranged from 1.03 days at 35^{o}C and increased to 5.05 days at 15^{o}C. The numbers of days required for egg to hatch decreased with increase in temperature. Except for the hatching time at 35^{o}C for *B. carambolae* and 30^{o}C for *B. papayae* that were not significantly different, all other temperature ranges were significantly different for the two species ($F = 165.08$, d.f. = 11, 15 $p<0.001$) (Table 2). The times required for *B. papayae* eggs to hatch were significantly lower than those observed for *B. carambolae* through all the temperature ranges tested (Table 2). The highest mean range of variation (m.r.v) for *B. carambolae* eggs was 1.54 days and 1.29 days for *B. papayae* eggs at 15^{o}C respectively. The m.r.v for *B. carambolae* were significantly higher than those observed for *B. papayae* eggs, except for 30 and 35^{o}C which were not significant (t-test, $p<0.001$) (Table 2). The highest mean coefficient of variation (m.c.v) was 48.55% recorded at 27^{o}C for *B. carambolae* and 48.54% recorded at 35^{o}C for *B.*

papayae. *B. carambolae* recorded significantly high m.c.v at temperature ranged of 15 – 27^{o}C, while *B. papayae* at 30 and 35^{o}C. All m.c.v values recorded were significantly different for all temperature regime studied (t-test, $p<0.001$) (Table 2).

Larva developmental trend was similar to that observed in the egg stage. The developmental periods for *B. carambolae* increased from 6.05 days at 35^{o}C to 28.94 days at 15^{o}C. Also *B. papayae* larva developed from 5.28 days at 35^{o}C and increased to 27.84 days at 15^{o}C. The developmental time decreased with increase in temperature regime. Except for 30^{o}C which was not significant, all other temperature ranges tested were significantly different (t-test, $p<0.001$). Significant difference were also observed when all developmental times were compared for all temperature regimes ($F = 160.38$, d.f. = 11, 15 $p<0.001$) (Table 2). *B. papayae* significantly revealed a less larva developmental time at all temperature ranges. The m.r.v for *B. carambolae* ranged from 5.81 days at 15^{o}C and decreased to 1.12 days at 30^{o}C, and 1.96 days at 25^{o}C decreased to 1.04 days at 35^{o}C for *B. papayae*. All m.r.v. values were significantly different (t-test, $p<0.001$) (Table 2). The m.c.v for *B. carambolae* ranged from 34.38% at 35^{o}C and decreased to 10.72% at 20^{o}C, and the ranged of 27.49% at 25^{o}C which decreased to 4.42% at 15^{o}C was observed for *B. papayae*. There was no significant different between the m.c.v. of the two flies at 20^{o}C. Other m.c.v values were significantly different (t-test, $p<0.001$) (Table 2).

The pupa period for *B. carambolae* increased from 7.73 days at 30^{o}C to 30.12 days at 15^{o}C. Similarly, *B. papayae* pupa period increased from 7.16 days at 30^{o}C to 29.14 days at 15^{o}C. No emergence was recorded at 35^{o}C for both species. All developmental periods were significantly different for all the temperature ranges tested for the two species of fly understudied ($F = 144.16$, d.f. = 11, 15 $p<0.001$) (Table 2). Lowest pupa developmental periods were recorded for *B. papayae* at each temperature regime when compared to *B. carambolae* (t-test, $p<0.001$) (Table 2). The highest m.r.v of 4.0 days was observed at 15^{o}C and the lowest was 1.0 day observed at 27^{o}C and 30^{o}C for *B. carambolae*. For *B. papayae*, the highest m.r.v of 2.0 days was observed at 15 and 20^{o}C while the lowest value of 1.0 day was recorded for 25 – 30^{o}C. The observed values were significantly different. Except for the temperature bracket of 27 and 30^{o}C which did not differ significantly (t-test, $p<0.001$) (Table 2). The highest m.c.v of 21.01% was observed at 20^{o}C and lowest value of 11.42% at

27^{o}C for *B. carambolae*, and for *B. papayae*, the highest m.c.v of 15.16% was observed at 20^{o}C and the lowest value of 6.86% was observed at 15^{o}C. All values observed were significantly different for both species (t-test, $p<0.001$).

Table 2. Mean developmental time (day ± SE), range of variation and coefficient of variation of immature stages of *B. carambolae* and *B. papayae* at six constant temperatures (n=5, repeated 3 time)

	Stage	Egg		Larva		Pupa	
Temperature	Species	*B. carambolae*	*B. papayae*	*B. carambolae*	*B. papayae*	*B. carambolae*	*B. papayae*
15°C	mean	5.49 ± 0.02aA	5.05 ± 0.02bB	28.94 ± 0.07aA	27.84 ± 0.02bB	30.12 ± 0.07aA	29.14 ± 0.04bB
	m.r.v	1.54a	1.29b	5.81a	1.23b	4.00a	2.00b
	m.c.v	28.05a	25.54b	20.08a	4.42b	13.28a	6.86b
20°C	mean	2.90 ± 0.01aC	2.70 ± 0.01bD	13.25 ± 0.03aC	12.16 ± 0.03bD	14.28 ± 0.06aC	13.19 ± 0.04bD
	m.r.v	0.96a	0.58b	1.42a	1.26b	3.00a	2.00b
	m.c.v	33.10a	21.48b	10.72a	10.36a	21.01a	15.16b
25°C	mean	1.65 ± 0.01aE	1.53 ± 0.01bF	7.80 ± 0.03aE	7.13 ± 0.03bF	10.46 ± 0.04aE	9.73 ± 0.03bF
	m.r.v	0.42a	0.17b	1.64b	1.96a	2.00a	1.00b
	m.c.v	25.45a	11.11b	21.03b	27.49a	19.12a	10.28b
27°C	mean	1.38 ± 0.01aG	1.22 ± 0.01bH	7.14 ± 0.50aF	6.56 ± 0.03bG	8.76 ± 0.04aG	8.40 ± 0.03bH
	m.r.v	0.67a	0.30b	2.25a	1.12b	1.00a	1.00a
	m.c.v	48.55a	24.59b	31.51a	17.07b	11.42b	11.90a
30°C	mean	1.19 ± 0.09aI	1.11 ± 0.01bJ	6.65 ± 0.03aH	6.51 ± 0.05aI	7.73 ± 0.03aI	7.16 ± 0.02bJ
	m.r.v	0.37a	0.37a	1.12b	1.21a	1.00a	1.00a
	m.c.v	34.45b	36.94a	16.84b	18.59a	12.94b	13.97a
35°C	mean	1.12 ± 0.08a J	1.03 ± 0.03bK	6.05 ± 0.03aJ	5.28 ± 0.03bK	0.00a	0.00a
	m.r.v	0.50a	0.50a	2.08a	1.04b		
	m.c.v	44.64b	48.54a	34.38a	19.70b		

Means followed by different small letters in the same row for a specific stage at each temperature are significantly different (t-test, $p<0.05$) and development means followed by different capital letters in the same column and row for each specific stage are significantly different (ANOVA $p<0.05$) *m.r.v., mean range of variation (r.v. = maximum developmental time – minimum developmental time). *m.c.v., mean coefficient of variation [c.v. = (100 x r.v.) / developmental time]. [APPENDIX B. 15-17].

Survivorship at egg, larva and pupa developmental stages for *B. carambolae* and *B. papayae*

Egg survivorship for *B. carambolae* and *B. papayae* ranged from 63.60 - 83.87% and 81.80 - 90.93% for the six temperature regimes respectively. Significantly lower survivorships were observed at 15 and 35^{o}C, whereas, high survivorship were recorded at 20 – 30^{o}C. The survival rates observed at 25^{o}C for the two species were not significantly different. Although survivorship was higher for the two species at 20 – 30^{o}C, *B. papayae* have a significantly higher survival rates when compared to *B. carambolae* at each constant temperature ranges tested (t-test, $p<0.001$). Significant difference were also observed when survivorship were compared for all temperature regimes ($F = 89.76$, d.f. = 11, 15 $p<0.001$) (Table 3). Survival of egg was best at 20 – 30^{o}C for *B. carambolae* and *B. papayae*, respectively.

At larva stage, survival rates exhibited by *B. carambolae* and *B. papayae* ranged from 59.39 – 74.99% and 66.27 - 85.08%, respectively. When survival rates were compared between the tested species, survivorship was low and did not differ significantly for the two species at 15 and 35^{o}C, respectively. On the contrary, survivorships were significantly different for the temperature ranges of 20 – 30^{o}C with *B. papayae* having significantly higher survival rates within each temperature (t-test, $p<0.001$) and among the temperature regimes ($F = 67.08$, d.f. = 11, 15 $p<0.001$) (Table 3), respectively. The survival of larvae was best for the two species between temperatures of 20 – 30^{o}C.

The survivorship range of 0.0 -77.16% and 0.0 – 81.22% were recorded for *B. carambolae* and *B. papayae* pupae, respectively. No survival was observed at 35^{o}C, invariably no adult emergence was observed for both species. At the pupa stage, survivorships were significantly high and best at 25^{o}C for *B. carambolae* and at 25 – 30^{o}C for *B. papayae*. When the survival rates were compared, no significant different were observed for 25 and 30^{o}C, respectively. Other temperatures showed significant different between the two species. It was found that *B. papayae* recorded significantly higher survival rates than *B. carambolae* (t-test, $p<0.001$) and among the temperature regimes ($F = 82.62$, d.f. = 11, 15 $p<0.001$)

(Table 3), respectively. Best survival rates lied in the temperature range of 25–30^{o}C for both species.

Table 3. Mean survivorship (% ± SE) of immature stages of *B. carambolae* and *B. papayae* at six constant temperatures

		Temperature					
Stage	Species	15°C	20°C	25°C	27°C	30°C	35°C
Egg	*B. carambolae*	63.60 ± 2.03bE	81.87 ± 1.77bC	80.67 ± 2.28aC	80.13 ± 1.83bC	83.87 ± 1.74bC	70.93 ± 1.91bD
	B. papayae	81.87 ± 1.35aC	87.20 ± 1.14aB	85.60 ± 1.48aB	88.40 ± 0.90aAB	90.93 ± 0.87aA	81.80 ± 1.88aC
Larva	*B. carambolae*	66.36 ± 4.13aD	64.49 ± 4.13bD	73.68 ± 2.93bC	74.99 ± 2.84bC	70.59 ± 2.85bC	59.39 ± 2.90aE
	B. papayae	73.21 ± 2.79aC	80.79 ± 3.34aB	85.08 ± 2.09aA	83.88 ± 1.76aA	80.09 ±1.32aB	66.27 ± 2.33aD
Pupa	*B. carambolae*	48.65 ± 1.93bE	68.77 ± 1.32bD	77.16 ± 1.80aB	73.59 ± 1.49bC	75.62 ± 2.29aC	0.00aF
	B. papayae	66.80 ± 1.44aD	74.35 ± 2.01aC	80.22 ± 1.58aA	81.52 ± 1.07aA	80.01 ± 1.71aA	0.00aF

Means followed by different small letters in the same column for each specific stage at each temperature are significantly different (t-test $P<0.05$) and mean followed by different capital letters in the same column and row for each specific stage are significantly different (ANOVA $p<0.05$). [APPENDIX B. 18 – 20]

The mean adult emergence for the cohort of 50 eggs ranged were 16.00 – 28.47 and 24.33 – 34.27 adults for *B. carambolae* and *B. papayae*, respectively. The best mean adult emergence was observed at the temperatures of 25 and 27^{o}C for the two flies. The mean adult emergence for *B. papayae* were significantly more than those observed for *B. carambolae* at all temperature regimes tested ($F = 98.85$, d.f. = 9, 15 $p<0.001$) (Table 4).

Table 4. Mean adult emergence / 50 eggs (Mean ± SE) of *B. carambolae* and *B. papayae* at six constant temperatures.

	Temperature					
Species	15°C	20°C	25°C	27°C	30°C	35°C
B.carambolae	16.00 ± 0.88h	22.07 ± 0.71g	28.47 ± 1.35d	27.67 ± 1.09d	26.40 ± 0.83e	0.00i
B.papayae	24.33 ± 0.84f	29.93 ± 1.29c	34.00 ± 0.73a	34.27 ± 0.62a	32.07 ± 0.94b	0.00i

Means followed by different letters in both rows and columns for each species are significantly different (Student-Newman-Keuls, $p<0.05$). [APPENDIX B. 21]

The mean developmental time for all the immature stages increased with decreased temperatures. The developmental times of 15.55 to 64.55 days and 14.73 to 62.03 days at 30 to 15^{o}C were recorded for *B. carambolae* and *B. papayae*, respectively. Though lower mean developmental time were observed for *B. papayae* at all temperature ranges tested, these were not significant for 20 and 25^{o}C, respectively. Other temperature ranges revealed significant different between the two species ($F = 2081.49$, $d.f = 9, 15$ $p<0.001$) (Table 5).

Table 5. Mean developmental time (day ± SE) for all immature stages of *B. carambolae* and *B. papayae* at six constant temperatures

	Temperature					
Species	15°C	20°C	25°C	27°C	30°C	35°C
B.carambolae	64.55±0.59a	30.43±0.74c	19.91±0.19d	17.28±0.34e	15.51±0.13g	0.00i
B.papayae	62.03±0.31b	28.05±0.48c	18.39±0.57d	16.18±0.11f	14.73±0.06h	0.00i

Means followed by different letters in both rows and columns for each species are significantly different (Student-Newman-Keuls, $p<0.05$). [APPENDIX B. 22]

Discussion

Linear approximation is one of the commonly used models in describing the relationship between temperature and developmental rate of insects (Wagner *et al*., 1984). The assumption was that above a certain lower threshold for development, the temperature-development rate is linear (Fletcher, 1989). However, insect development is non-linear at the extremes of low and high temperature (Liu and Ye, 2009). The linear model was used in this research to describe the relationship between temperature and developmental rate because most temperature regimes under examination were within the linear part of development. The linearity of the relationship linking temperature to developmental rate from 15 – 30^{o}C for *B. carambolae* and *B. papayae* was consistent with the previous reports on the development of other species of Tephritidae (Vargas *et al*., 1996; Brévault and Quilici, 2000; Duyck and Quilici, 2002; Duyck *et al*., 2004; Rwomushana *et al*., 2008; Liu and Ye, 2009). The linear regression of the two species revealed that all of the correlation coefficients are close to one, implying a strong linearity between 15 and 30^{o}C. *B. carambolae* and *B. papayae* are species belonging to the *B. dorsalis* complex (Drew and Hancock, 1994). These species are restricted to peninsular Thailand and Malaysia, while the *B. dorsalis* sensu stricto were marginally restricted to central and majorly northern Thailand. *B. dorsalis* and it complex members understudied in this work were prevalently occurring in all seasons throughout the year in their restricted geographical locations in Thailand (Clarke *et al*., 2001). In the on-going guava culturing in our entomology laboratory, both *B. carambolae* and *B. papayae* were found co-infesting guava fruits in peninsular Thailand. Therefore, it could be concluded that ecological niches of the two species are overlapping via host fruit (Duyck *et al*., 2008). Vargas *et al*. (1996) worked on *B. dorsalis* in Hawaii at temperature range of 16 – 32^{o}C and calculated the thermal constant from linear regression to be 358 degree-days for its total development and the lower threshold temperature for eggs, larvae and pupae to be 11.8, 5.6 and 9.3^{o}C, respectively. Similarly, Rwomushana *et al*. (2008) worked on *B. invadens* a member of the *B. dorsalis* complex in Kenya at temperature range of 15 – 35^{o}C and estimated from linear regression the thermal constant of 376 degree-days and the lower threshold

temperature of eggs, larvae and pupae to be 8.8, 9.4, and 8.7^{o}C respectively. Contrastingly, in the present research the lower threshold temperature for *B. carambolae* and *B. papayae* were 12.44, 11.18 and 11.60^{o}C and 12.08, 10.54 and 10.86^{o}C for eggs, larvae and pupae and thermal constant of 371.35 and 330.05 degree-days respectively. Except for the higher threshold temperatures of 12.7, 12.6 and 12.8^{o}C for egg, larvae and pupae, respectively that was reported for *B. zonata* (Duyck *et al*., 2004), these present findings elucidated that the temperature requirement were much higher through all the life stages for both *B. carambolae* and *B. papayae* when compared to other dacine flies of the same complex. This may be because the average temperature of peninsular Thailand is over 24^{o}C. Also biological parameters like developmental zero (Threshold temperature) and the thermal constant (degree-days) are supposed to be the limit factors in the geographical distribution for the fruit flies (Ye, 2001). These differences could also result from the utilization of different rearing diet and rearing conditions (e.g. larval density) (Duyck and Quilici, 2002).

B. carambolae and *B. papayae* have been categorised as highly invasive and polyphagous tephritid flies (Drew and Hancock, 1994). It is pertinent to assess the risk that these notorious pests could pose to fruit production within and outside their range of occurrence. Therefore, the most important factor is to determine the possibilities of eggs hatching as fruits commodity are on transits from field of production to their final destination. Degree days and developmental threshold become important parameters for such risk assessment (Thomas, 1997; Rwomushana *et al*., 2008).

Comparing *B. carambolae* and *B. papayae*, a close range of lower threshold temperature and thermal constant were estimated for both species, although the former showed slightly-higher lower threshold temperature and thermal constant when compared to the latter. In other words, *B. carambolae* required high thermal constant to complete it developmental processes. To buttress this, their seasonal pattern as recorded by Clarke *et al*. (2001) showed that *B. carambolae* are less in population and possessed an irregular distribution pattern. Therefore, apart from host fruits, thermal requirement may be used to explain why *B. carambolae* was much narrower in distribution and less in population when compared to *B. papayae*. This

might have led to their varying distribution statuses in Southeast Asian countries and South America where they have been found. This may also be due to some physiological and ecological factors. Therefore a thorough study into their physiology and ecology may reveal some other factors.

Temperature has effect on the developmental time of immature stages of *B. carambolae* and *B. papayae* with the duration of each stage increasing as temperature decreased. Development were prolonged at 15 and 20^{o}C, and shortened at 30 and 35^{o}C through all developmental stages for both *B. carambolae* and *B. papayae*. Though this phenomenon was common to the two species understudied, *B. papayae* was faster in development at all temperature ranges for all preimaginal stages. At 35^{o}C, egg and larva were able to develop but with high mortality, no emergences from pupae were recorded indicating total mortality rate (100%). This revealed that the upper temperature threshold lies between 30 and 35^{o}C. Therefore, it will be pertinent to investigate their development at temperatures ranging from 30 – 35^{o}C in detail in order to establish their upper threshold temperatures. Generally, there is a favourable and or desirable temperature at which development is at its best which may be referred to as "intermediate optimum temperature" for development (Howe, 1967; Rwomushana *et al*., 2008). In this work, the optimum temperature was found to be between 25 and 27^{o}C, though narrow temperature range, but falls within broader temperature range reported for other tephritid flies. In *B. invadens*, the optimum temperature have been reported to lie between 25 and 30^{o}C (Rwomushana *et al*., 2008), 26 and 30^{o}C for *B. cucurbitae*, *B. dorsalis* and *B. olae* (Messenger and Flitter, 1958; Tsitsipis, 1980). But on the contrary, Liu and Ye (2009) reported optimum temperature range of 30 – 33^{o}C for *B. correcta*.

Rwomushana *et al*. (2008) reported high rate of survival for *B. invadens* at 20 and 30^{o}C for all immature stages. Similarly, Duyck *et al*. (2004) reported the range of 20 – 30^{o}C for high surviving rate for *B. zonata*. Lower survival rates were generally been observed for the extreme temperatures of 15 and 35^{o}C for all developmental stages of Tephritid fruit flies (Brévault and Quilici, 2000; Duyck and Quilici, 2002; Duyck *et al*., 2004; Rwomushana *et al*., 2008). In the present work, the survival rates observed for *B. carambolae* and *B. papayae* followed the same trend of the aforementioned workers. Comparison of survival rates between the species

revealed that they both differ in all developmental stages. *B. carambolae* has significantly lowest surviving rates at all stages. The survival trends were also reflected on the mean adult emergence recorded for both species. The mean adult emergence was low at 15^{o}C and high at 25 and 27^{o}C for both flies, but *B. papayae* has higher number of adult emergence at all temperature regimes. Although this present work is in agreement with the results of other workers on tephritid flies who reported temperature range of 20 – 30^{o}C as the best for adult emergence, but the present optimum temperature range is narrow (Brévault and Quilici, 2000; Duyck and Quilici, 2002; Duyck *et al*., 2004; Rwomushana *et al*., 2008). The lowest surviving rate observed at 15^{o}C might be the reason why *B. carambolae* and *B. papayae* were limited to low altitude peninsular Thailand and Malaysia. This phenomenon was also observed with *B. invadens* (*B. dorsalis* complex member as *B. carambolae* and *B. papayae*) that was restricted to low altitude of Kenya (Ekesi *et al*., 2006). Insects are cold-blooded organisms, the temperature of their bodies is approximately the same as that of the environment. Therefore, temperature is probably the single most important environmental factor influencing insect behaviour, distribution, development, survival, and reproduction. Some researchers believe that the effect of temperature on insects largely overwhelms the effects of other environmental factors (Brévault and Quilici, 2000; Bale *et al*., 2002). Tephritid distribution and abundance are notably dependent on several abiotic factors (e.g., temperature, relative humidity, and rainfall) and several biotic factors (e.g., host plants and natural enemies) (Vayssières *et al*., 2008). For tephritid flies, the ability to complete their life cycle represents a successful adaptation to both their host plant and to the climatic environment in which they are found.

The high survival rates of *B. carambolae* and *B. papayae* over a narrow range of intermediate optimum temperature of 25 – 27^{o}C may explain their strategic occurrences in some tropical countries of the world. Presently, *B. papayae* is prevalence in Indonesia and Paupa New Guinea, while *B. carambolae* was found restricted to Indonesia, India, French Guiana and Brazil. Both species were also found to co-exist in the status of present in Singapore and restricted in Malaysia and Thailand (Drew and Hancock, 1994). Before eradication, *B. papayae* was recorded in northern Australia near Cairns in 1995 (Drew and Romig, 1997). Its occurrence in the

Northern territory of Australia could be linked to tropical climatic conditions that persist in this region. From the records of their distribution, both species seems much more adapted to tropical climate rather than any other type of climate as evidenced from their occurrence. The tropical climate present throughout the year mean temperature above 18^{o}C and the temperature remains relatively constant throughout the year and seasonal variations are dominated by precipitation. Many of the *B dorsalis* complex members have been recorded in many tropical countries. For instance, *B. invadens* have been recently discovered in Kenya (Lux *et al*., 2003) and have been described to be very invasive and polyphagous. This species have now rapidly spread across most of the sub-saharan African region and currently reported from 24 countries with a record of 30 host plants (Drew *et al*., 2005). Therefore, *B. carambolae* and *B. papayae* with wider hosts and tolerant of tropical climate conditions, could be highly invasive and notorious if mistakenly introduced to other tropical regions.

The study revealed that though the two species understudied cohabitate the same niche overlap (Guava fruit), they exhibited different developmental time and survivorship rates. *B. papayae* survived better and completed its development faster than *B. carambolae*. It was also found that the two flies fall within the same optimum developmental temperature range (25 – 27^{o}C). Although *B. papayae* showed slightly-higher lower threshold temperature, *B. carambolae* required high thermal constant to complete it developmental process. The results obtained from this work offers comprehensive and valuable information about the biology and ecology of these pests. Additionally, these findings contribute immensely to the improvement of rearing methods of these two species studied. A suitable compromise between short developmental time and high survival could be achieved if the preimaginal stages of the two species were maintained between temperatures ranged of 25 – 27^{o}C. It would be helpful for optimizing environmental condition for mass rearing of the two fly species for sterile insect technique programme which can be implored for their control and eradication. However, before undertaken mass rearing, it would be worthwhile to compare the quality of the diets developed for *B. carambolae* and *B. papayae* by other Scientists. The range of thermal parameters generated could help in making precise decisions regarding the quarantine risk associated with this flies. Also, the

combination of the data generated with other field trapping and phenological studies should be useful in the construction of computer simulation models of fruit fly population dynamics that will enhance better environmental and ecological friendly monitoring and management practices for these flies.

Morphology of eggs

Introduction

In the *B. dorsalis* complex are certainly the most significant fruit fly pest species in Asia / South-east Asia (Drew and Hancock, 1994). Greater difficulty has been encountered in identifying *B. dorsalis* and its related species than any other group of Dacinae. The history of confusion in the nomenclature of the *B. dorsalis* complex was documented by Hardy (1969). For every complex member, accurate identification is essential for appropriate ecological study and application of quarantine restrictions law placed on fruits and fruit fly from one country to another.

The major focus of this study is on *B. carambolae* and *B. papayae* which are sibling species belonging to *B. dorsalis* complex (Drew and Hancock, 1994; Tan and Nishida, 1996; Wee and Tan, 2005). These two species have been found to be well established and distributed in Southern Thailand affecting different kind of fruits and vegetables. Drew and Hancock (1994), Ranganath and Veenakumari (1995) and Allwood *et al*. (1999) had worked extensively on the host plant records for fruit flies (Diptera: Tephritidae) in Southeast Asia. Their work revealed that *B. carambolae* and *B. papayae* are polyphagous species of tephritid flies found in Southeast Asia. They reported 76 and 193 host species for *B. carambolae and B. papayae* in this region, respectively.

It was observed from the list of the hosts available that the two species shares common hosts. Invariably, they share common ecological niche overlap in peninsula Thailand through host plants (Danjuma *et al*., 2013). Accurate identification of these species is a prerequisite for control and regulatory measures. However, identification has been difficult between these sibling species (Drew and Hancock, 1994; Iwaizumi *et al*., 1997; Iwahashi, 1999). But black band on the abdomen, the colour of the occiput and the wing coastal band were used to distinguish these species (Drew and Hancock, 1994). But some of the distinguishing characters were not reliable because their intermediate states are frequently found in both species (Iwaizumi *et al*., 1997; Iwahashi, 1999). Furthermore, Iwaizumi *et al.* (1997) and Iwahashi (1999) did an extensive morphometric study on the male aedeagus and the female aculeus. The observed differences in the length of the aedeagus and aculeus

were also being use to distinguish the male and female of these species, respectively. Ebina and Ohto (2006) study the morphological characters and PCR-RFLP Markers in the interspecific hybrids. They therefore, concluded that in both species, the inconsistency between the morphological characters and the DNA markers, and the continuous variation of the aculeus length, were mainly caused by interspecific hybridization in the distribution area. The blending of traits observed between the sibling species suggested that heterospecific crosses between them might be occurring under natural conditions and if this is true, it would be interesting to examine the length of the terminalia of hybrid males and females resulting from this crosses (Iwaizumi, 1997). This was confirmed recently by Schutze *et al*. (2013) that these species demonstrated by significant deviation from random mating towards assortative mating.

The need to explore additional morphological characters is pertinent at this juncture in order to generate other characters that may be used to separate this species. In our previous study on the effect of constant temperatures on the survival and developmental stages of *B. carambolae* and *B. papayae*, the whole range of constant temperatures verified revealed that *B. papayae* was faster at each stage (Danjuma *et al*., 2013). The disparity observed for egg developmental time for both fly species triggered a thought that lead to the screening of the morphology of the eggs with the aid of Scanning Electron Microscope (SEM). Because the eggs of insect species present morphological peculiarities which are related to their life strategies (Hinton, 1969). The relationships of these morphological adaptations to evolution patterns were clearly demonstrated for some group of insects (Kafatos *et al*., 1987; Zeh *et al*., 1989; Kambyselis, 1993). Among the tephritid fruit flies of genus *Anastrepha*, the importance of egg morphology for taxonomy and phylogenetic inferences was predicted by Norrbom *et al*. (2000). Hence, the objective of this study was to improve on the ability to identify the egg stage of *B. carambolae* and *B. papayae* that will enhance the better understanding of the disparity of their developmental time and to serve as distinctive taxonomic characters between the two species. This study is paramount as it will lead to improvement on the rearing of the flies in the laboratory and for mass production of the flies for control program.

Material and methods:

The study was carried out at the Entomology Research Unit of the Department of Biology, Faculty of Science, and Central Laboratory of the Prince of Songkla University (PSU), Hat Yai, Thailand.

Insect culture

This study was conducted on the first filial generation, F_1 laboratory reared fruit fly. The population was initially generated from infested guava fruits sampled from PSU (7^o00'13.05"N and 100^o29'57.11"E) and Ban koyai (7^o00'52.98"N and 100^o27'35.18"E) guava orchards, respectively. The fruit fly colonies were reared and maintained at the Entomology Unit of the Department of Biology, PSU, Hat Yai, Thailand. Rearing conditions were maintained at 25 ± 1^oC, 75 ± 5% relative humidity (RH) and Photoperiod of L12:D12.

Egg collection

Eggs were collected from *B. carambolae* and *B. papayae* stock colony with the aid of an artificial egg-laying device offered to the 10 F_1 females of both flies maintained separately in 27 x 27 x 27cm cages.

Morphometric study

From each species egg dome, 60 eggs each were collected with the aid of a camel brush under a Stereo microscope. Eggs were carefully placed in a vial of 2 ml from where 30 eggs per species were randomly picked and morphometric data (length and width) were taken with the aid of Olympus microscope with inbuilt ocular micrometer. Furthermore, the eggs were examined and the images of 5 eggs each were captured with the aid of Olympus DP72 Universal Camera at the Department of Biology microscopy room, PSU, Hat Yai, Thailand. The remaining eggs were further held in vial of 2 ml containing 2.5% glutaraldehyde (CH2(CH2CHO)2) organic compound. These vials were immediately taken to the Central Laboratory, PSU for preparation for electron microscopy.

Electron microscopy process

Egg preparation followed the method of Selivon and Perondini (1998). Thirty eggs of each species were transferred into 0.1M cacodylate buffer (pH 7.4), washed, post-fixed in an aqueous solution of 1% Osmium tetroxide (OsO_4) for an hour. These eggs were dehydrated in an ethanol series then critical point dried in CO_2

for 3 hours and sputter-coated with gold layer (Selivon *et al*., 2003; Dutra *et al*., 2011). The eggs were then examined under scanning electron microscope (Quanta 400, FEI, Czech Republic) at high vacuum, 10.00kv. All scanning were done at the Central Laboratory of the PSU, Hat Yai. Thailand. SEM was used to examine the chorion in at least 10 eggs of each species. The anterior pole (the end of the egg that bears the pedicel or a slight projection with the micropyle and aeropyles) and the posterior pole (the end opposite of the pedicel which is usually smooth and bluntly rounded and bears no external opening or structure) were also examined. The convex side of the egg is referred to as the ventral side and the concave side as the dorsal side (Dutra *et al*., 2011).

Results

The eggs of *B. carambolae* and *B. papayae* have similar characteristics in their gross morphology. Observations under Olympus DP72 Universal Camera microscope revealed that the eggs of these species were white in colour and tapered towards anterior and posterior ends concurrently. The anterior pole possessing a micropyle is more tapered than the posterior pole which end bluntly and rounded (Figure 4, a and b).

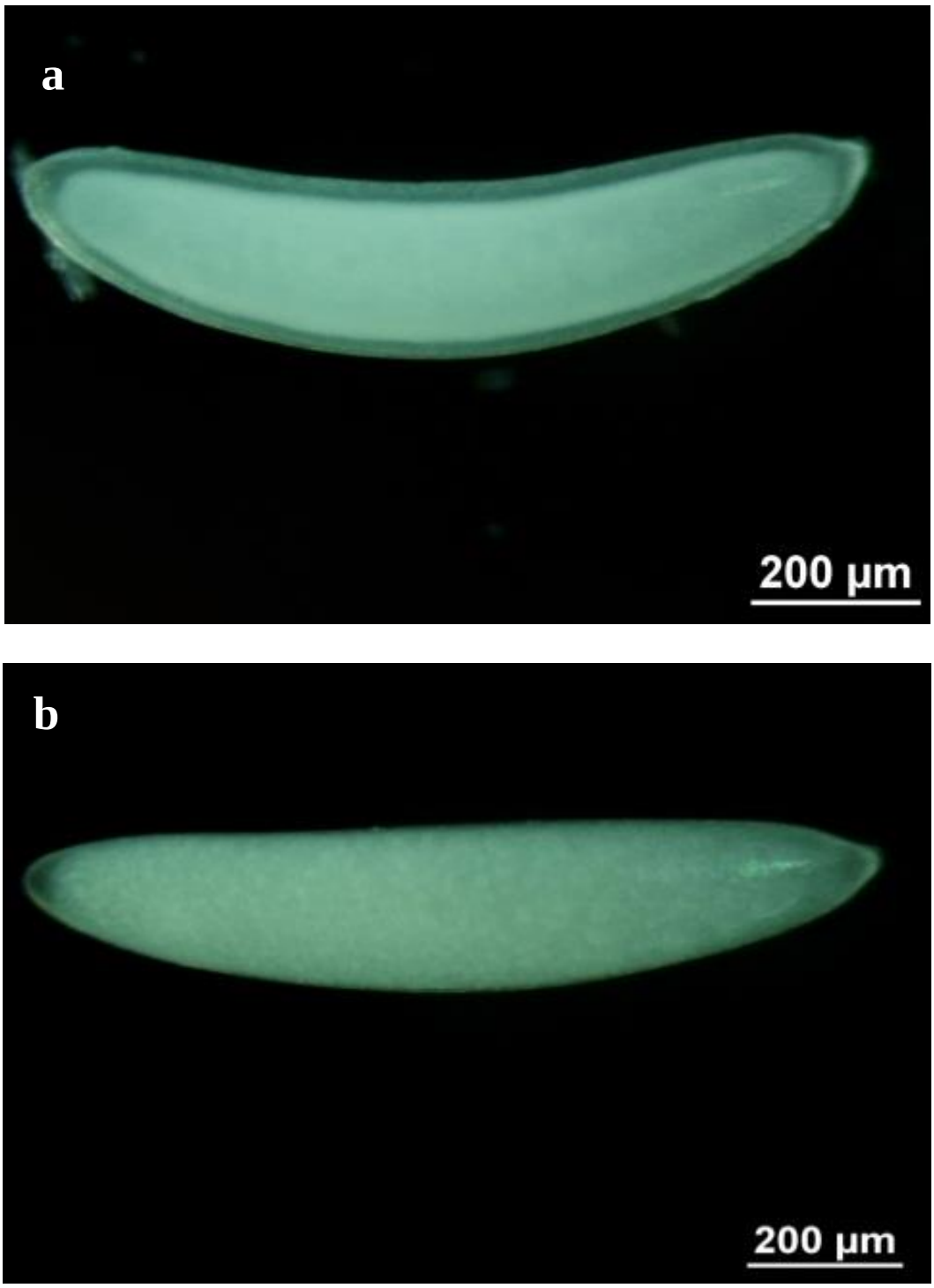


Figure 4. *Bactrocera* eggs (a) *B.carambolae* egg (b) *B.papayae* egg

Diagnostic characters to differentiate between these two species eggs include chorion ornamentation, location of aeropyles and a pronounced rim of the chorion with a woolly appearance surrounding the micropyle (Dutra *et al*., 2011). None of the eggs of the studied species had a conspicuous respiratory appendage.

Bactrocera carambolae

Material Examined

In total 30 eggs were examined from 10 F_1 females emanating from larva culture from guava collected from Ban Koyai and PSU guava orchards, Hat Yai, Songkhla province.

General features

Length, 0.88-1.23mm and width, 0.21-0.23mm. Eggs are white in colour, elongate, elliptical and strongly curved. Broader from the middle towards the anterior pole, tapering gradually towards both ends (Figure 4a and Fig. 5. a1, b1).

Chorionic Sculpturing

The apex of the anterior pole bears a micropyle, surrounded by a conspicuous ring-shaped rim (papilla) of chorion which is strongly ornamented by woolly substance (Figure 5. a1 y). Chorion reticulation was less conspicuous and present well defined threadlike-linesnwhich presents the shell with firmed, solid and rigid polygonal wall (Figure 5. c1). The irregular polygonal patterns covered all the egg surfaces and present a fine grainy textured within the polygon formed by the chorion reticulation (Figure 5. a1, b1 and c1). Aeropyles were rarely seen on the surface of the eggs. Between 1-5 aeropyles minute openings were observed in the egg of this species (Figure 5. c1, arrow head x).

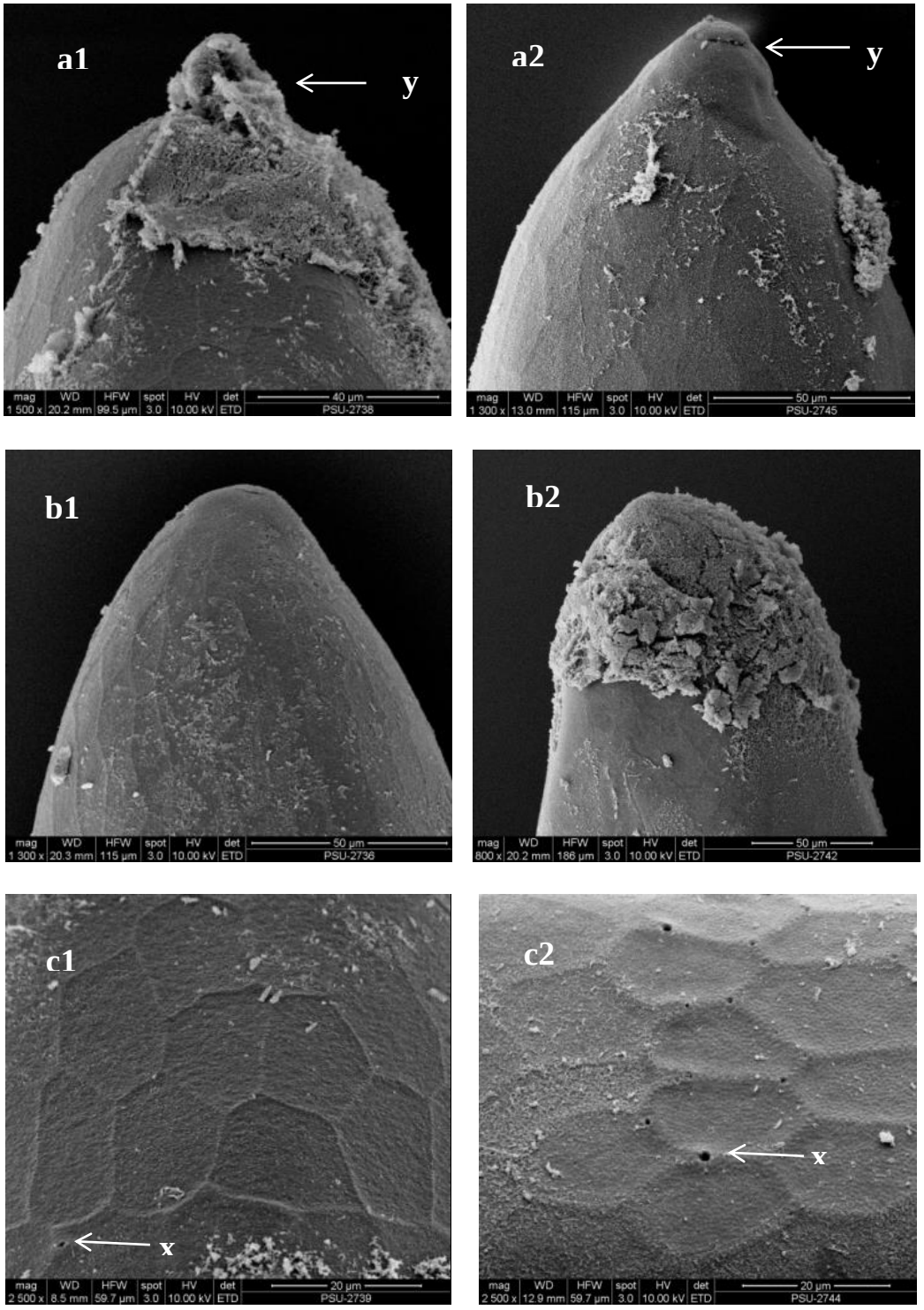


Figure 5. *B. carambolae* and *B papayae* egg scanned with the aid of electron microscope (a1) anterior poles of *B. carambolae* and (a2) *B. papayae* eggs (b1) posterior poles of *B. carambolae* and (b2) *B. papayae* eggs (c1) pre-anterior poles of *B. carambolae* and (c2) *B papayae* eggs (x) aeropyle (y) micropyle.

Bactrocera papayae

Material examined

In total 30 eggs were examined from 10 F_1 females emanating from larva culture from guava collected from Ban Koyai and PSU guava orchards, Hat Yai, Songkhla province.

General features

Length, 0.91-1.16mm and Width, 0.20-0.26mm. Eggs are white, elongate, elliptical and slightly curved (Figure 4b). Broader from the middle towards the anterior pole, tapering gradually towards both ends. But bluntly rounded at the posterior pole (Figure 5. a2 and b2)

Chorionic sculpturing

The apex of the anterior pole bears a papilla and limited chorion ornamentation with less pronounced reticulation in a polygonal arrangement (Figure 5. c2), and the surface is roughly textured within the polygons. Between 15-25 aeropyles are located on the egg at the vertices of the polygons mostly pronounced at both the dorsal and ventral side (Figure 5. c2). The aeropyles openings are of variable diameters (Figure 5. c1 x). The reticulation were poorly developed forming into a rough bulge or protuberance which get fainted towards the posterior pole. The micropyle is located at the apex of the anterior pole and ornamented by a pronounced rim (papilla) of the chorion. This rim is ringed-shaped and has a smooth appearance devoid of woolly materials (Figure 5. a2 y). The main diagnostic characters of these species eggs are shown in Table 1.

Table 6. Diagnoses of the eggs of the two sibling species analysed in this study.

Bactrocera spp.	Chorion		Micropyle		Aeropyle		
	Reticulation	Sculpturing in reticular	Location	Rim	Location	No	Diameter
B. carambolae	threadlike-lines distinguishing each polygon	none fine grained	apex of anterior	clumsy and woolly	anterior lateral side	1-5	minute
B. papayae	wide and poorly developed and distinguish each polygons	poor protuberance	apex of anterior	Clear and smooth	all sides	15-25	variables

Discussion

The eggshell morphology of the two *Bactrocera* species examined in this study correspond to the general pattern of tephritid fly eggs with reference to their gross morphology such as colour, shape and chorion, especially in being similar to other *Bactrocera* species eggs (White and Elson-Harris, 1992). The eggshell chorion revealed some specific characters for the two species examined.

The chorionic sculpturing of the two species fall under the broad category of eggs of Diptera Cyclorrhapha as designated by Ferrar (1987). *B. carambolae* and *B. papayae* have their eggs chorion faintly reticulated. The reticulation observed in *B. carambolae* was threadlike-lines devoid of protuberance and present the chorion as firmed and solid fine-grained surface. Poor protuberance of reticulate was observed on the chorion of *B. papayae* and this present the chorion as roughed surface. Faint reticulation was already observed in the eggs of *B. tryoni* (White and Elson-Harris, 1992) and *Anastrepha luden* (Carroll and Whartson, 1989), *A. coroilli* and *A.distincta* (Dutra *et al*., 2011). Well-developed chorionic reticulation is known to occur in some *Anastrepha* species such as *A.* sp.1 aff. *fraterculus, A.* sp. 2 aff. *Fraterculus* (Selivon and Perondini, 1998), *A.obliqua* (Murillo and Jirón, 1994), and *A. sororcula* (Selivon and Perondini, 1999). *B. carambolae* and *B. papayae* eggs present chorion reticulation on all sides and were found all over the chorion in *B. carambolae*. But become fainter towards the posterior pole in *B. papayae*. Studies have shown that sculpturing may be related to the differential activity of the follicle epithelium and to an adaption to the fly habitat (Cônsoli *et al*., 1999). It is also believed that reticulation together with aeropyles plays some significant role in embryo respiration (Selivon and Perondini, 1998) and also provides protection against desiccation (Cônsoli *et al*., 1999).

The posterior poles for the two species show similarities in tapering and ending bluntly. The anterior poles though shows similarities in ending pattern and possession of rim ring-shaped micropyle, but differs in the presence of clumsy and woolly structure on the mycropyle of *B. carambolae* which was absent in that of *B. papayae*. Aeropyles of minute openings small in number of between 1-5 were observed on the lateral sides of the *B. carambolae* eggs. But aeropyles of 15-25 of

distinct variable diameters were revealed on all sides of the chorion of eggs belonging to *B. papayae*. In both cases, all aeropyles were more to the anterior than to the posterior region and were sighted on the reticular ridges. Dutra *et al*. (2011) reported aeropyles location on *Anastrepha* species eggs, ventral position in *A. antunesi, A. bahiensis* and *A. coronilli* whereas, in *A. turpiniae, A. distincta* and *A.zenildae* they were observed on both sides (dorsal and ventral) in large numbers. Their work also revealed variations in the aeropyle diameters and confirmed that in *A.distincta* aeropyles with larger diameters are located on the ventral side and those with smaller diameters were located on the dorsal side. In the present work, aeropyles of variable diameters were observed concurrently on both side of *B. papayae* egg only. This might be so because the present flies belong to a different genus (*Bactrocera*) and occurring in a distinct region and habitat. No respiratory appendage found on the eggs of both species. Dutra *et al*., (2011) also reported similar phenomena in six *Anastrepha* species (*A. antunesi, A. bahiensis, A. coronilli, A. distincta, A. turpiniae* and *A.zenildae*). It was only in *A. barbiellinii, A. manihoti, A.obliqua, A. nigrifacia* and *A.pittieri* that presence of respiratory appendage has been reported (Murillo and Jirón, 1994; Norrbom *et al*., 1999; Norrbom and Kortytkowski, 2009). It has been suggested that the structure of chorion and the number of aeropyles are related to adaption strategy to the environment where they eggs were deposited (Dutra *et al*., 2011). The number of aeropyles also was reported by Cônsoli *et al*. (1999) to be related to the species metabolic rate, need for gas exchange and control of water loss. Distinct papilla was observed in the two species, located at the anterior pole of the eggs analysed. However, it is more pronounced in *B. carambolae*, similar to what has been reported for *A. coronilli, A. distincta, A. turpiniae* and *A.zenildae* (Dutra *et al*., 2011), *A. grandis* (Steck and Wharton, 1988), *A. luden* (Carroll and Wharton, 1989), *A.* sp.1 aff. *fraterculus* (Selivon and Perondini, 1998, Selivon *et al*., 2003) and *A. sorocula* (Selivon and Perondini, 1999).

The mycropyle of the eggs of the two species studied were located directly on the apex of their anterior poles. This is similar to the work of Dutra *et al*., (2011) that reported mycropyle location on the anterior pole apex for *A. antunesi, A. bahiensis, A. coronilli, A. distincta* and *A.zenildae*, respectively. However slightly displaced mycropyle from the apex has been reporte in *A. turpiniae* (Dutra *et al*.,

2011), and *A.* sp.1 aff. *Fraterculus* (Murillo and Jirón, 1994; Selivon and Perondini, 1998, Selivon *et al*., 2003). A dislocated mycropyle due to respiratory appendage has also been reported in *A. oblique* (Murillo and Jirón, 1994; Norrbom and Kortytkowski, 2009).

The present study of the two sibling species eggs with the aid of SEM revealed some basic similarities between the species studied and among other *Anastrepha* species reported before as there was rarely such studies of eggs of *Bactrocera* species except for scanty documentation in few texts. The combinations of the characteristics displayed by these eggs, such as chorion ornamentation, location of aeropyles and of mycropyle are useful as taxonomic characters (Dutra *et al*., 2011). The results of this work will increase the understanding of eggshell morphology and the reasons behind the variations observed in the hatching time of the species eggs and there life history strategies. This will enhance the rearing of this species for mass production with reference to Sterile Insect Technique and for other control strategies. It is worth mentioning that further work on other *Bactrocera* species especially, the *B. dorsalis* complex members are required to better our understanding of this monophyletic group with reference to their phylogenetic relationship.

CHAPTER 5

LIFE TABLE OF *B. CARAMBOLAE* AND *B. PAPAYAE*

Introduction

The carambola fruit fly *B. carambolae* and the Asian papaya fruit fly *B. papayae* are members of the *B. dorsalis* complex. These and other species of the genus *Bactrocera* are native to southeast Asia (White and Elson-Harris, 1992; Drew and Hancock, 1994). The *B. carambolae* and *B. papayae* are prevalence in their regions of occurrence globally and present different statuses of occurrence where they are found. *B. papayae* is highly invasive and prevalence in Indonesia and Paupa New Guinea, while the *B. carambolae* was found to be restricted to Indonesia, India, Suriname, Guyana, French Guiana and northern Brazil. Both species were also found to co-exist in the status of present in Singapore and restricted in Malaysia and Thailand (White and Elson-Haries, 1992; Drew and Hancock, 1994). Both species have been reported as polyphagous and major pest causing enormous damage to fruits (Allwood & Leblanc, 1997). This was evidence in the report of Drew and Hancock (1994), Allwood *et al*. (1999) and Sauers-Muller (2005) who documented 76 and 193 host species for *B. carambolae* and *B. papayae* in this region, respectively. The adult female fly lays eggs in batches in groups of 4 – 5 under the skin of fruits with a needle like ovipositor (egg-laying tube at the tip of the abdomen). While puncturing the fruit, the fly pushes bacteria from the skin into the flesh. These bacteria cause fruit decay, which results in a substrate in which the larvae feed (Fletcher, 1987; Drew and Lloyd, 1989), consequently leading to economic and nutritional loss (Lux, 1999).

To effectively manage these pests population, it is necessary to understand their ecology which will provide concise knowledge about the population biology of these invasive species, hence, provide more precise focus on specific characteristics involved in invasiveness (Crawley, 1986). Understanding population growth rate, dispersal ability, voracity and fitness of an invasive species are of primary importance in their control program (Hou and Weng, 2010). Among the abiotic factors, temperature is the most important and a critical factor that greatly exert pressures on the biological characteristics of invasive pests (Haghani *et al*.,

2007). Therefore, effect of temperature on the growth, survival and establishment of this species need to be evaluated. Life table is an important tool in the study of population ecology and invasiveness of species (Sakai *et al*., 2001; Chi, 1990). Therefore demographic models are essentials in identifying the life history stages where management would be most effective.

Cohort life table is a longitudinal perspective study of a population which includes the mortality experience of a particular cohort from moment of birth through consecutives ages until no individuals remain in the original cohort (Carey, 1993). Hence *B. carambolae* and *B. papayae* were examined from cohort population. Danjuma *et al*. (2013) had reported an intensive effect of temperature regimes on the preimaginal stages of these species. To develop better pest management strategies for fruit flies, some researchers have applied demographic analysis to species of economic importance (Carey, 1982, Carey, 1989; Vargas *et al*., 1984; Carey and Vargas, 1985; Vargas and Nishida, 1985; Vargas and Carey, 1990; Vargas *et al*., 2000). No reported published work on the life table of the adults of *B. carambolae* and *B. papayae* before now. Life table provide survival, growth/development and fecundity parameters of the target population and the basic data on population growth parameters give the most comprehensive description of population ecology (Hou and Weng, 2010). Life table of a population has diverse applications among which are; predicting life history traits, analyzing population stability and structure, estimating extinction probabilities, predicting outbreaks in pest species, and examining the dynamics of colonizing or invading species (McPeek and Kalisz, 1993). Therefore, the present work evaluated the cohort population of both species under four constant temperatures in order to determine their post-imaginal population behaviours viz; survival, fecundity and life table parameters. Apart from gaining basic understanding of these species post-imaginal behaviours, the work would be useful in the application of various management strategies as detailed in the IPM practices.

Materials and methods

Fly colony establishment

Colonies of *B. carambolae* and *B. papayae* were established at the Entomology Research Unit of the Department of Biology, Prince of Songkla University (PSU), Hat Yai, Thailand from larvae emanating from infested guava fruits collected from PSU (7^{o}00'13.05"N and 100^{o}29'57.11"E) and Ban koyai (7^{o}00'52.98"N and 100^{o}27'35.18"E) guava orchards, respectively. The concurrent recovery of these fruit flies from the guava fruits was an indication of the overlap in their ecological niche via plant host (Duyck *et al*. 2008; Danjuma *et al*. 2013). Ecological information on utilization of guava fruits by both species was summarized in Danjuma *et al*. (2013). The procedures for rearing the larvae and pupae of these species from infested guava follow that documented in Copeland *et al*. (2002).

Insect rearing

The fruit fly colonies were reared and maintained at the automated room of Entomology Research Unit of the Department of Biology, PSU, Hat Yai, Thailand. Rearing conditions were maintained at 25 ± 1^{o}C, 75 ± 5% relative humidity (RH) and Photoperiod of L12:D12. Separate colony of each fly species contained a mixed population of 150 males and 100 females in a cage of 27 × 27 × 27 cm, respectively. Flies were fed ad-libitum with 3:1 volumetric mixtures of sugar and enzymatic yeast hydrolysate (Becton Dickson Company, USA), sugar and water were provided in sponged filled plastic trough. Eggs were collected over 3-4 hours period from *B. carambolae* and *B. papayae* stock colony with the aid of an artificial egg-laying device (pierced half yellow plastic ball) as described in Danjuma *et al*. (2013). Random samples of 150 eggs were counted under a stereo microscope and placed on 3 cm diameter tissue paper placed on 200g of guava diet (Danjuma *et al*., 2013) in screen-covered Plexiglas boxes of 20cm × 15cm × 7cm. Each experiment was conducted with 10 cups of guava diet at each temperature regime (5 cups for each of the 2 species). Experiments were replicated 5 times with different generations of fruit flies.

Matured third instar larvae were allowed to leave the rearing cups and pupate in a 1 cm thickness layer of sawdust in Plexiglas boxes of 20cm × 15cm × 7cm.

Pupae were separated from the pupation medium and held in Plexiglas boxes of 10cm × 7.5cm × 5.5cm lined with moist tissue paper until eclosion.

Experimental set up

The rearing procedures was repeated thrice and the adult emanating from the F_3 to F_6 were used consecutively for the life table analysis over temperature ranges of 20^{o}C, 25^{o}C, 27^{o}C and 30^{o}C (1±^{o}C), 70 ± 5% relative humidity (RH) and Photoperiod of L12:D12 in thermostatically controlled environmental chambers (Contherm phytotron climate simulator, New Zealand). At eclosion 10 pairs of newly emerged adults were placed in separate cage to assess fecundity. Eggs were collected by placing an egg receptacle at the mid of each cage (Danjuma *et al*., 2013). Eggs were removed from the receptacles with the aid of camel brush and counted daily and immediately placed on 50g of guava diet in petri dishes of 9cm diameter for the determination of eclosion. Records of life cycle survivorship, pre-oviposition and oviposition periods, fecundity and fertility were taken. Dead males were immediately replaced with another male of the same age. Daily survival rate of both sexes and fecundity of females were recoded until all cohort individuals died. Data were not collected at 15^{o}C and 35^{o}C because the preliminary studies on the preimaginal stages revealed a protracted emergence and no emergence at 15^{o}C and 35^{o}C, respectively. Also the average temperature of Southern Thailand is above 20^{o}C throughout the year.

Data analysis

Life table parameters and population age structures were calculated from daily records of mortality, fecundity and fertility of cohorts of *B. carambolae* and *B. papayae*. Data on both flies life history were analysed according to cohort life table theory (Carey, 1993). Life table parameters were calculated by using XLSTAT 2013. The age specific survival rate, daily fecundity and sex ratio were used to construct l_x m_x life tables from which the following population growth parameters were calculated using the detailed formulae in Carey (1993, 2001) (Table 1).

Table 1. Notations and formulae for various life table of *B. carambolae* and *B. papayae*

Notation	Parameter	Formula
r	Intrinsic rate of increase	InR_o/T
λ	Finite rate of increase	e^r
GRR	Gross reproductive rate	$\sum m_x$
R_o	Net reproductive rate	$\sum l_x m_x$
DT	Doubling time	In(R_o)/r
e_x	Expectation of life at age *x*	$\sum l_y/l_x$ or ½ +(l_{x+1}+ l_{x+2}+… l_z/ l_x)

The interpretations of the formulae are itemised below:

Where;

In; is natural logarithm ($\log_e$)

x; is the age in days of the individuals in the cohort.

l_x; refers to the cohort survival at age *x* and this is calculated by the formula; N_x / N_0 (N_x: Individual surviving to age *x* and N_0: Initial number of individual starting a cohort).

l_y; is the summation of l_{x+1}+ l_{x+2}+… l_z.

m_x; is number of female offspring produced at a specific age (total number of daughters produced by female cohort from age *x* to *x*+1 / total number of females at midpoint of interval *x* to *x*+1).

Effect of temperature regimes on adults of *B. carambolae* and *B. papayae* on different parameters was analysed by the application of one way analysis of variance (ANOVA). Where significant difference were observed, multiple comparison were then made by using Student-Newman-Keul (SNK) ($P<0.05$). Statistical analysis was carried out by using Sigmaplot 11 (2008).

Results

Preimaginal development and survival

Development and survival of preimaginal stages of *B. carambolae* and *B. papayae* has been detailed in Danjuma *et al*. (2013). The durations varied with temperature regime. Egg, larva and pupa stages of the two species were markedly longer at 20^{o}C and shorter at 30^{o}C for both species, respectively. *B. papayae* had significantly shorter developmental periods at all stages for all temperature ranges. The optimum developmental and survival temperatures are 25^{o}C and 27^{o}C for both fly.

Survival rate and fecundity

Age-specific survival rate (l_x), gross and net fecundity (M_x) of *B. carambolae* and *B. papayae* on guava fruits at different temperature regimes are presented in figure 1- 4. Survivorship of *B. carambolae* and *B. papayae* on guava at different temperature regimes depicts both type III and type I survivorship curves. The type III occurred at lower temperature of 20^{o}C and type I occurred at 25, 27 and 30^{o}C for both flies understudied, respectively. In type III, most of the mortality occurred at early stage of life and type I showed that most of the mortality occurred late in life. Egg production and adult emergence was low at 20^{o}C and 30^{o}C, but high at 25^{o}C and 27^{o}C for the flies, respectively.

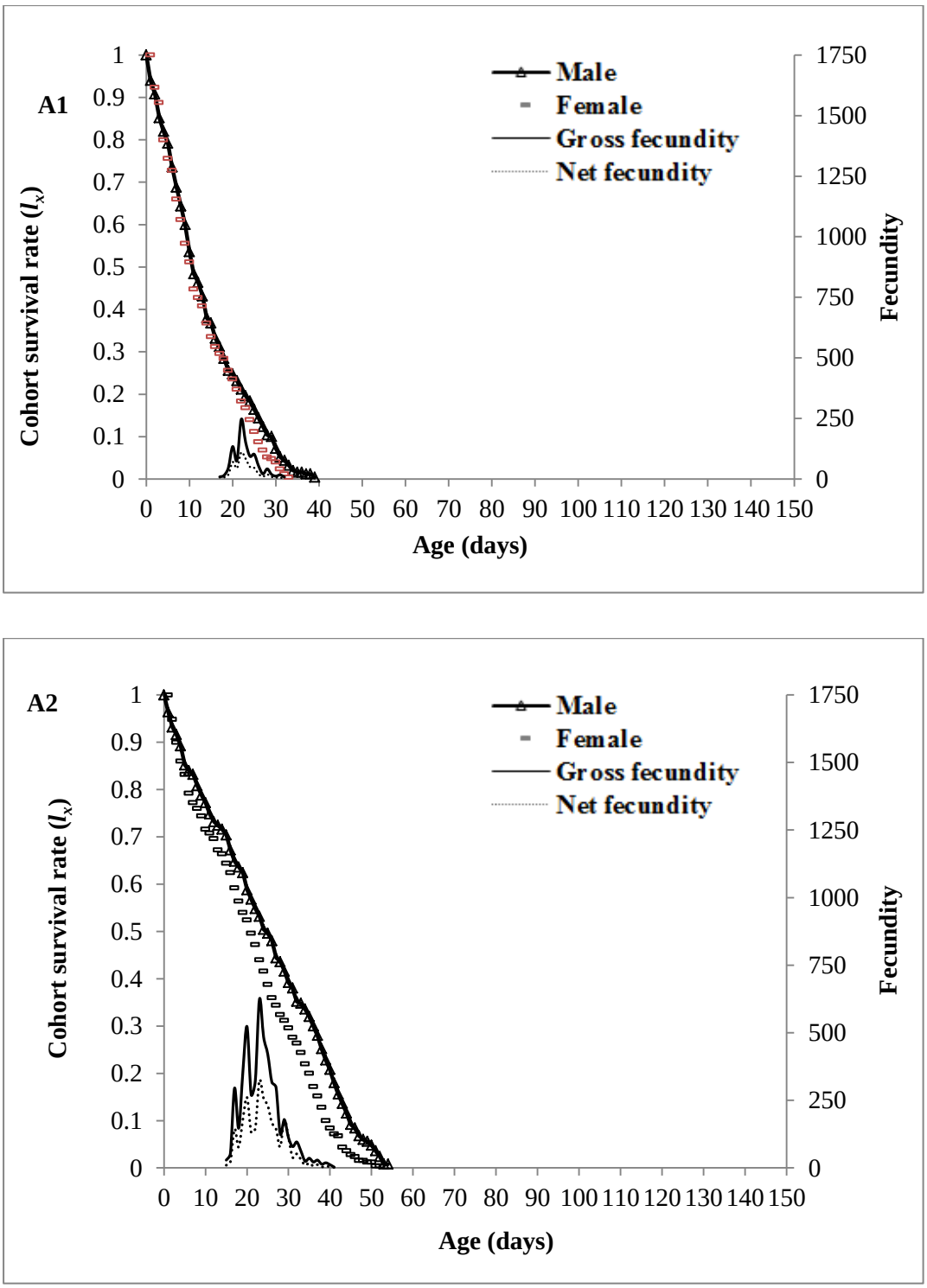


Figure 1. Survivorship (l_x), gross and net fecundity (m_x) curves of (A1) *B. carambolae* and (A2) *B. papayae* reared at 20°C.

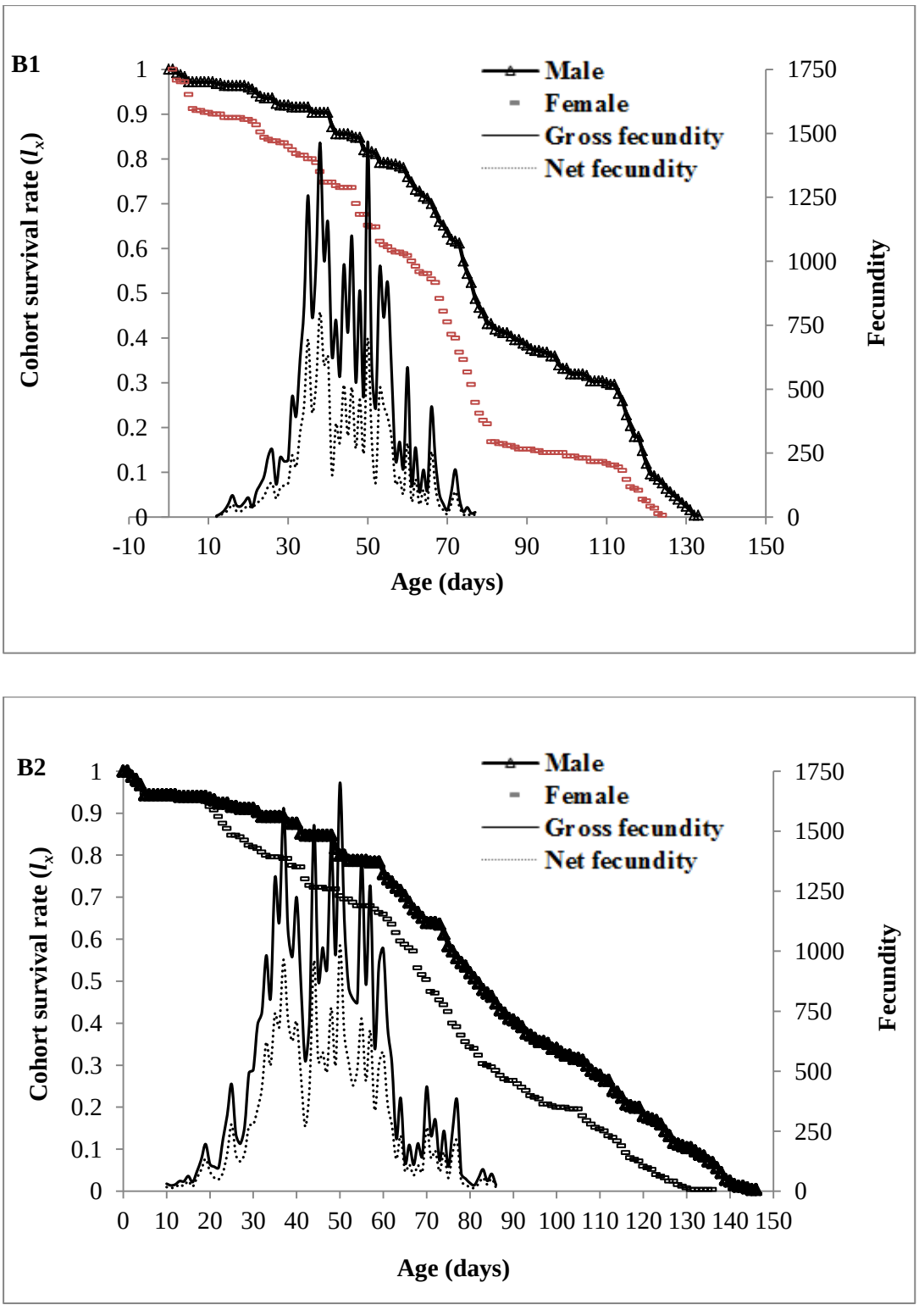


Figure 2. Survivorship (l_x), gross and net fecundity (m_x) curves of (B1) *B. carambolae* and (B2) *B. papayae* reared at 25°C.

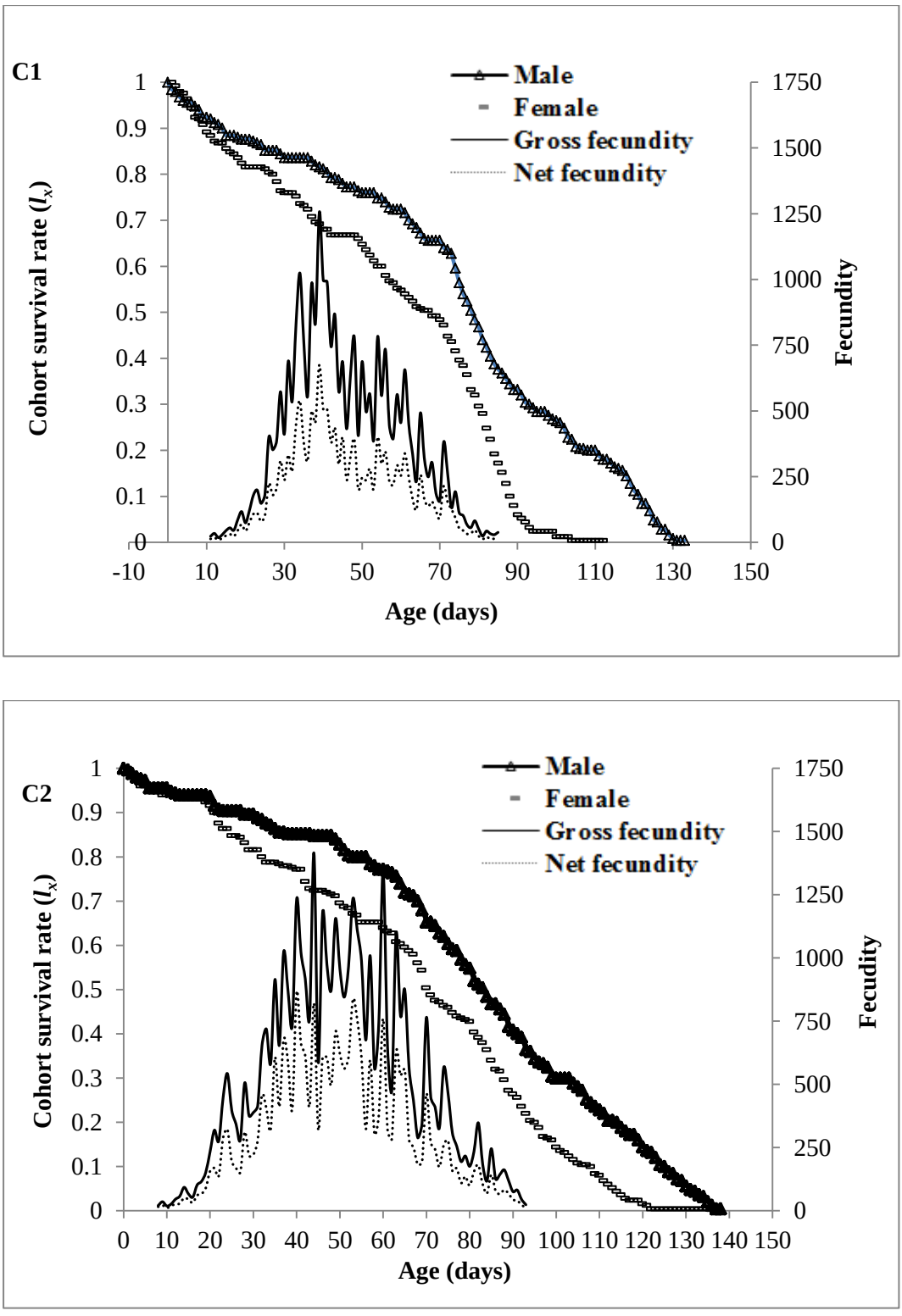


Figure 3. Survivorship (l_x), gross and net fecundity (m_x) curves of (C1) *B. carambolae* and (C2) *B. papayae* reared at 27°C.

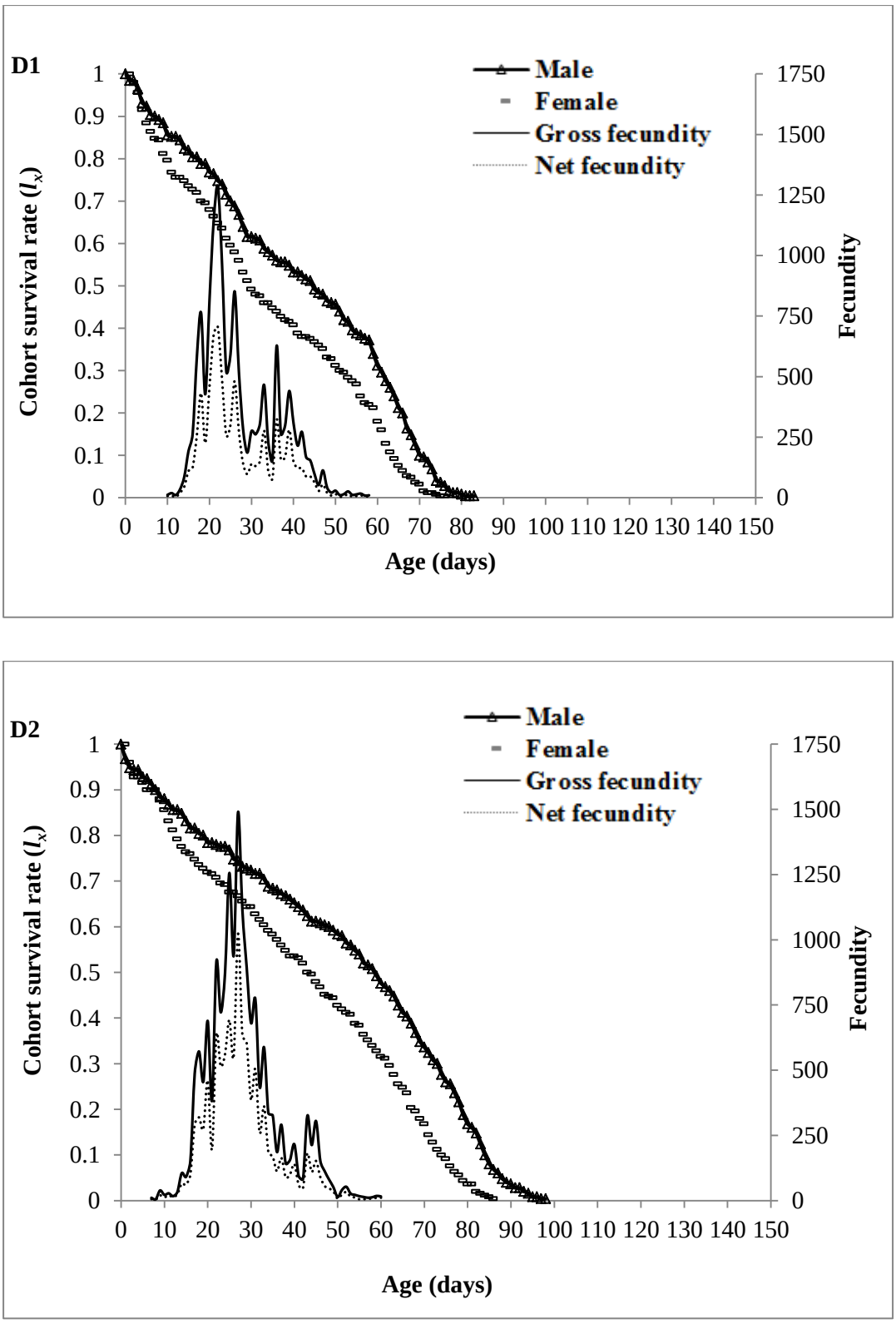


Figure 4. Survivorship (l_x), gross and net fecundity (m_x) curves of (D1) *B. carambolae* and (D2) *B. papayae* reared at 30°C.

Reproductive parameters

Pre-oviposition period

Pre-oviposition period varied significantly with temperature regime within species ($F = 106.78$, d.f. = 3, 9 $p < 0.001$ and $F = 65.23$, d.f. = 3, 9 $p < 0.001$ for *B. carambolae* and *B. papayae*, respectively) and between species ($F = 86.31$, d.f. = 7, 9 $p < 0.001$) (Table 2). Although pre-oviposition periods were observed to be longer at 20^{o}C for both species, but *B. papayae* duration was significantly shorter than for those observed for *B. carambolae*. No significant difference was observed between the temperatures of 25^{o}C and 27^{o}C for *B. carambolae*, but contrary was the case with *B. papayae*.

Oviposition period

The oviposition period revealed significant difference within species ($F = 620.84$, d.f. = 3, 9 $p < 0.001$ and $F = 668.95$, d.f. = 3, 9 $p < 0.001$ for *B. carambolae* and *B. papayae*, respectively) and between species ($F = 571.82$, d.f. = 7, 9 $p < 0.001$) (Table 2). Oviposition periods were shorter at 20^{o}C followed by 30^{o}C for both species. The temperatures of 25^{o}C and 27^{o}C revealed longer oviposition periods. This was not significant for *B. papayae*, but the contrary was the case for *B. carambolae*. At all temperature regimes, oviposition periods were longer for *B. papayae* than for *B. carambolae*.

Gross fecundity

Gross fecundity varied significantly with temperature regime ($F = 279.59$, d.f. =7, 9; $p<0.001$ between species) and ($F = 154.99$, d.f. =3, 9 $p < 0.001$ and $F = 175.71$, df=3, 9 $p < 0.001$ for *B. carambolae* and *B. papayae*, respectively) (Table 2). Gross fecundity was lower at 20^{o}C compared to any other temperature regime. This scenario was also observed at temperature of 30^{o}C. The optimum temperature for gross fecundity for both species was at 25^{o}C. Except at 30^{o}C which was not significantly different for both species, *B. papayae* gross fecundity was significantly more than those observed for *B. carambolae* at 20-27^{o}C.

Net fecundity

Net fecundity varied significantly with temperature regime ($F = 152.92$, d.f. = 7, 9 $p < 0.001$) and within species ($F = 61.11$, d.f. = 3, 9 $p < 0.001$ and $f=94.88$: df=3, 9; $p<0.001$ for *B. carambolae* and *B. papayae*, respectively) (Table 2).

Net fecundity was lower at 20^{o}C and higher for other temperature regimes, with highest value recorded at 25^{o}C for both species intra-specifically. Observed net fecundity for *B. papayae* at 20-27^{o}C was greater than for those observed for *B. carambolae*, But the values for 30^{o}C does not varied inter-specifically.

Daily egg production

The daily egg production varied significantly with temperature regime ($F = 118.28$, d.f. = 7, 9 $p < 0.001$) and within species ($F = 188.24$, d.f. = 3, 9 $p < 0.001$ and $f=83.98$: df=3, 9; $p<0.001$ for *B. carambolae* and *B. papayae*, respectively) (Table 2). Intra-specifically, daily egg production decreased with lowest and the highest temperature in the order of 20^{o}C<30^{o}C<27^{o}C<25^{o}C. This scenario was common to both species. Inter-specifically, the daily egg production for *B. papayae* was always greater than for *B. carambolae* at 20-27^{o}C, and no variation was observed at 30^{o}C.

Observed longevity

Female longevity was significantly different with temperature regime ($F = 536.97$, d.f. = 7, 9 $p < 0.001$) and within species ($F = 501.64$, d.f. = 3, 9 $p < 0.001$ and $f=753.93$: df=3, 9; $p<0.001$ for *B. carambolae* and *B. papayae*, respectively) (Table 2). Life span of female increased according to the pattern 20^{o}C<30^{o}C<27^{o}C<25^{o}C. Female longevity differed significantly between species according to the pattern *B. papayae* > *B. carambolae*.

Male longevity varied significantly with temperature regime ($F = 613.03$, d.f. = 7, 9 $p < 0.001$) and within species ($F = 616.99$, d.f. = 3, 9 $p < 0.001$ and $f=847.53$: df=3, 9; $p<0.001$ for *B. carambolae* and *B. papayae*, respectively) (Table 2). Male life span was highest at 25-27^{o}C, and lowest at other temperature ranges in the increasing pattern of 20^{o}C<30^{o}C. Intra-specifically, male life span of *B. carambolae* was not significantly different at temperatures of 25-27^{o}C, but the contrary was the case for male life span of *B. papayae* which varied significantly at all temperature ranges. Male of *B. papayae* had higher life span than male of *B. carambolae* at all temperature ranges.

The comparisons between male and female life span varied significantly (paired t-test $p < 0.005$) for both species (Table 3). The male life spans were longer than that observed for the females at all temperature regimes for *B.*

carambolae. Except for the comparison at 27^{o}C for *B. papayae* that was not significant, all other comparisons of life spans between male and female were significantly different in all the remaining temperature ranges.

Table 2. Mean (±SE) of reproductive parameters and longevity of life between *B. carambolae* and *B. papayae* reared at 4 temperature regimes (n=5, repeated 5x).

		Temperature °C			
Parameter	Species	20	25	27	30
Preoviposition	*B. carambolae*	21.10 ± 0.62aA	14.61 ± 0.31bB	13.73 ± 0.26bC	11.81 ± 0.25cE
period (days)	*B. papayae*	17.00 ± 0.33aA	13.11 ± 0.30bD	11.72 ± 0.39cE	10.71 ± 0.34dF
Oviposition	*B. carambolae*	17.42 ± 0.63dG	61.70 ± 0.82bC	66.00 ± 1.31aB	45.52 ± 0.65cE
period (days)	*B. papayae*	22.83 ± 0.88cF	72.25 ± 0.94aA	74.01 ± 1.15aA	50.43 ± 0.67bD
Gross fecundity	*B. carambolae*	243.41 ± 9.53dF	1383.40 ± 28.94aB	1302.48 ± 17.39bC	1229.81 ± 16.86cD
(eggs/female)	*B. papayae*	587.83 ± 16.87dE	1702.44 ± 34.8aA	1329.66 ± 20.56bC	1271.34 ± 54.69cD
Net fecundity	*B. carambolae*	119.45 ± 5.76cE	684.62 ± 10.78aB	651.28 ± 8.43abC	627.45 ± 20.12bC
(eggs/female)	*B. papayae*	296.54 ± 9.74dD	873.55 ± 39.23aA	681.61 ± 21.97bB	624.23 ± 17.55bC
Daily eggs	*B. carambolae*	4.17 ± 0.17dF	9.82 ± 0.19aB	9.04 ± 0.25bC	8.21 ± 0.14cD
(eggs/day)	*B. papayae*	6.33 ± o.13dE	11.01 ± 0.28aA	9.65 ± 0.26bB	8.65 ± 0.16cCD
Female longevity	*B. carambolae*	32.80 ± 1.53cG	121.11 ± 1.73aC	118.56 ± 2.21aC	72.83 ± 1.88bE
(days)	*B. papayae*	48.22 ± 1.59dF	130.61 ± 1.44bB	138.21 ± 1.41aA	81.82 ± 1.72cD
Male longevity	*B. carambolae*	40.43 ± 0.93cF	136.32 ± 2.11aB	137.22 ± 2.81aB	85.27 ± 1.07bD
(days)	*B. papayae*	56.79 ± 1.27dE	147.28 ± 1.16aA	139.84 ± 1.71bB	92.86 ± 1.67cC

Means in same row followed by the same lowercase letter are not significantly different (intraspecifically). Means in the same column followed by the same uppercase letter are not significantly different (interspecifically). All significant differences identified by Student-New-Man (SNK) test at $p<0.005$. [APPENDIX B. 23-29]

Table 3. Mean (±SE) life span of male and female flies.

Temperature regime	*B. carambolae*		*B. papayae*	
	male	female	male	female
20°C	40.43 ± 0.93a	32.80 ± 1.53b	56.79 ± 1.27a	48.22 ± 1.59b
25°C	136.32 ± 2.11a	121.11 ± 1.73b	147.28 ± 1.16a	130.61 ± 1.44b
27°C	137.22 ± 2.81a	118.56 ± 2.21b	139.84 ± 1.71a	138.21 ± 1.41a
30°C	85.27 ± 1.07a	72.83 ± 1.88b	92.86 ± 1.67a	81.82 ± 1.72b

Means in the same row for each fly followed by different lowercase letters are significantly different (paired t-test $p < 0.001$).

Population parameters

The results accrued from population parameters studies for both *B. carambolae* and *B.* papayae were presented in table 4.

Both species exhibited highest intrinsic rates of increase (r) at 27-30°C and 25-27°C for *B. carambolae* and *B.* papayae, respectively. These were significantly different for temperature ranges ($F = 47.72$, d.f. = 3 $p < 0.001$ for *B. carambolae* and $F = 85.46$, df=3 $p < 0.001$ for *B. papayae*) and among species ($F = 100.36$, d.f. = 7 $p < 0.001$). *B. papayae* present the highest values and the lowest values were recorded for *B. carambolae*.

Finite rate of increase (λ) were high at 27-30°C and 25-27°C for *B. carambolae* and *B. papayae*, respectively. These were significantly different for temperature ranges ($F = 45.90$, d.f. = 3 $p < 0.001$ for *B. carambolae* and $F = 70.60$, d.f. = 3 $p < 0.001$ for *B. papayae*) and among species ($F = 88.82$, d.f. = 7 $p < 0.001$).

Net Reproductive Rates (R_o) of the two species revealed marked increase with increase in temperature, and the highest values falls in the temperature range of 25-27°C. These were significantly different for temperature ranges ($F = 2286.56$, d.f. = 3 $p < 0.001$ for *B. carambolae* and $F = 2737.43$ d.f. = 3 $p < 0.001$ for *B. papayae*) and among species ($F = 2570.25$, d.f. = 7, $p < 0.001$). A decline in Net Reproductive Rates was observed at 30°C for both species, respectively. The values recorded for *B. papayae* were greater than for those recorded for *B. carambolae*.

The Gross Reproductive Rate (*GRR*) for both species were highest at temperatures of 25-27^{o}C. These were significantly different for temperature ranges ($F = 920.16$, d.f. = 3 $p < 0.001$ for *B. carambolae* and $F = 3437.54$, d.f. = 3 $p < 0.001$ for *B. papayae*) and among species ($F = 2045.55$, d.f. = 7 $p < 0.001$). In the same vain, *B. papayae* values were greater than those observed for *B. carambolae*.

Life expectancy (e_x) for both sexes of the two flies revealed that 25-27^{o}C temperature ranges recorded the highest life spans. It was also revealed that males of both flies had higher life expectancy than the female. *B. papayae* also had higher values of life expectancy than *B. carambolae*. These were significantly different for temperature ranges ($F = 965.36$ d.f. = 3 $p < 0.001$ for *B. carambolae* male, $F = 542.27$, d.f. = 3 $p < 0.001$ for *B. papayae* male, $F = 733.30$, d.f. = 3 $p < 0.001$ for *B. carambolae* female and $F = 497.63$, d.f. = 3 $p < 0.001$ for *B. papayae* female) and among species of the same sex ($F = 624.90$, d.f. = 7 $p < 0.001$ for male fly and $F = 532.61$, d.f. = 7 $p < 0.001$for female fly).

Doubling time (*DT*) revealed lowest values at 25-27^{o}C for both flies. These values were significantly different for temperature ranges ($F = 48.991$, d.f. = 3 $p < 0.001$ for *B. carambolae* and $F = 7.09$, d.f. = 3 $p < 0.001$ for *B. papayae*) and among species ($F = 32.34$, d.f. = 7 $p < 0.001$).

Table 4. Mean (±SE) of population parameters and life expectancy between *B. carambolae* and *B. papayae* reared at 4 temperature regimes (n=5, repeated 5x).

		Temperature °C			
Parameter	Species	20	25	27	30
Intrinsic rate of	*B. carambolae*	0.102 ± 0.014 dD	0.216 ± 0.012cC	0.309 ± 0.014aB	0.258 ± 0.010bB
increas / time (r)	*B. papayae*	0.219 ± 0.011cC	0.553 ± 0.014aA	0.594 ± 0.032aA	0.283 ± 0.018bB
Finite rate of	*B. carambolae*	1.108 ± 0.016dE	1.242 ± 0.015cD	1.362 ± 0.019aB	1.294 ± 0.013bBC
increase / time (λ)	*B. papayae*	1.248 ± 0.012bD	1.740 ± 0.025aA	1.814 ± 0.057aA	1.328 ± 0.024bB
Net reproductive	*B. carambolae*	1.16 ± 0.10dH	28.13 ± 0.30bD	30.64 ± 0.31aC	15.902 ± 0.359cF
rate / generation (Ro)	*B. papayae*	5.79 ± 0.36dG	46.37 ± 0.51bB	51.92 ± 0.44aA	21.118 ± 0.321cE
Gross reproductive	*B. carambolae*	10.02 ± 0.41dH	39.94 ± 0.56bD	50.17 ± 0.82aC	29.092 ± 0.360cF
rate / generation (GRR)	*B. papayae*	15.39 ± 0.51dG	67.15 ± 0.51bB	80.89 ± 0.53aA	34.294 ± 0.459cE
Life expectancy	*B. carambolae*	21.97 ± 0.40cF	60.13 ± 0.71aB	61.90 ± 0.63aB	40.510 ± 0.639bD
/ day (Male)	*B. papayae*	27.70 ± 0.71dE	65.36 ± 0.99aA	61.49 ± 0.28bB	47.788 ± 0.751cC
Life expectancy	*B. carambolae*	18.92 ± 0.58dG	58.73 ± 0.53aB	49.98 ± 0.49bC	40.468 ± 0.863cE
/ day (Female)	*B. papayae*	26.52 ± 0.85dF	61.41 ± 0.84aA	58.41 ± 0.65bB	43.208 ± 0.468cD
Doubling time	*B. carambolae*	8.22 ± 0.53aA	2.82 ± 0.30cC	2.98 ± 0.29cC	3.02 ± 0.24bC
/ generation	*B. papayae*	3.94 ± 0.29aB	1.92 ± 0.32cE	2.35 ± 0.34cD	3.04 ± 0.37bC

Means in same row followed by the same lowercase letter are not significantly different (intraspecifically). Means in the same column followed by the same uppercase letter are not significantly different (interspecifically). All significant differences identified by Student-New-Man (SNK) test at $p<0.005$.

[APPENDIX B. 30 – 36].

Discussion

The life table analysis of *B. carambolae* and *B. papayae* which are congeneric sympatric species was comparatively studied for the first time on guava at four different temperature regimes occurring in Thailand. Previously, tephritid fly Scientists have research into interspecific (Vargas *et al*., 1984; 2000) and intraspecific (Carey, 1982; Muniz and Gil, 1984; Yang *et al*., 1994a, b; Carey *et al*., 2005) of demographic parameters of fruit flies. Among the flies studied were *B.cucurbitae, B. capitata, B. dorsalis* and *Anastrepha ludens.* Summary of demographic parameters of insects have been documented in Carey (1993). The present tephritid fly studied are *B. dorsalis* complex members which were notoriously affecting fruit production in southern Thailand. The life table analysis of these two flies studied at constant temperature regimes in the laboratory revealed that adult survival, longevity, fecundity, net reproductive and gross reproductive rates, doubling time, finite and intrinsic rate of increase varied by species and temperature (Vargas *et al*., 1997, 2000).

Survival and longevity of *B. carambolae* and *B. papayae* revealed the same pattern; both flies are relatively long lived. At the lowest temperature, life span was short and type III survival curve was observed. At high temperature type I survival curve was observed with relatively longer life span which declined at 30^{o}C. Hence mortality of flies was high at extreme temperatures. Male flies were also observed to have lived longer than the females of the same cohort. Between species, *B. papayae* survived and had extended life span more than it sympatric relative. Survival and longevity disparities in favour of male flies have been reported by Vargas *et al*. (2000) for *B. cucurbitae*, *B. dorsalis* and *C. capitata*. Slowing of mortality at older ages has been exhaustively documented in the medfly (Carey *et al*., 1992; Carey, 2003) and was also observed in the Mexfly (Vaupel *et al*., 1998) as well as in the current study. Life expectancy was greater for male at all temperature regimes. Generally, the life expectancy of *B. papayae* was greater than those observed for *B. carambolae*. The life expectancy was low at the lowest temperature regime (20^{o}C) and decline at the highest temperature regime (30^{o}C). It is not unexpected for life expectancy to share the same pattern as survival because the latter is a subset of the former. Other tephritid scientists also reported seemingly high life expectancy

within the temperature range of 25-30^{o}C and lower life expectancy at temperatures outside the aforementioned range (Carey, 1982, 2005; Vargas *et al*., 1984, 1997, 2000; Yang *et al*., 1994a, b). In southern Thailand, the temperature ranges from 24-33^{o}C throughout the seasons, hence, *B. carambolae* and *B. papayae* survival is favoured by temperature within this region. This might also be a strong reason why their survival and prevalence in South-East Asia is enhanced. The distributions of these flies majorly are relatively limited to most tropical countries of the world (Drew *et al*., 2005). Notwithstanding, some of the temperate zones of the world that present alternating temperatures of temperate and tropical zones (Northern part of Australia, Brazil, French Guyana) were also found to be supportive of the survival of these flies (Drew *et al*., 2005).

Pre-oviposition periods of *B. carambolae* and *B. papayae* were observed to be extended at the lowest temperature. Hence, increase in temperature also corresponds to short pre-oviposition periods for both flies. On the other hand, oviposition period of both flies was short at the lowest temperature and become extended as temperature increases to the optimum and thereafter decline at 30^{o}C. Oviposition reduced drastically with age and extends into post-oviposition period. This scenario was also peculiar to other tephritid flies studied previously (Vargas *et al*., 1997). The discrepancies observed with pre- and oviposition periods in relation to temperature regimes were also peculiar to other insects other than fruit flies. For instance, temperature significantly affected the lengths of the lesser cornstalk borer pre-oviposition, oviposition and post-oviposition periods (Sandhu *et al*., 2013).

At favourable temperature range of 25-27^{o}C, both tephritid species are capable of laying 10–30 eggs per day during peak reproductive ages and 5–10 eggs per day at many of the older ages. Thus, the observed lifetime egg production in both of these species was extraordinarily high with fecundity ranging from 680 - 1400 and 870 – 1700 eggs/female for *B. carambolae* and *B. papayae*, respectively. A relatively high fecundity results have been reported for Mexfly and medfly (Carey, 2003) and *B. dorsalis* (Vargas *et al*., 2000). Low daily egg production and fecundity have been recorded with *B. cucurbitate* and *C. capitata* (Vargas *et al*., 2000). Daily egg production and fecundity reduced drastically with extreme temperatures. The fecundity of the female flies may not only be determined by temperature alone;

success of mating, diet richness and the fly physiology are also very significant factors. Furthermore, the relationships between reproduction and longevity that may also be present in the both flies includes: (i) the rate of decrease in egg laying for the individual at young ages were positively correlated with their probability of death at subsequent ages (Müller *et al*., 2001; Carey *et al*., 2005); and (ii) individual-level reproduction can be characterized in a three-stage pattern: Stage I—reproductive stage (maturation); Stage II—a maturity stage characterized by a constant rate of production; and Stage III—a reproductive senescent stage with exponentially-decreasing pattern of egg production with age (Noveoseltsev *et al*., 2004).

Temperature exerted strong effects on reproductive parameters. Both species exhibited fluctuations in both gross and net reproductive rates with reference to temperature regimes. Extreme temperature regimes lead to reduction of these rates in both flies due to less fertile egg production resulting from poor mating. Optimum reproductive rates fall in the temperature range of 25-27^{o}C. The constant temperature of 24^{o}C and alternating temperatures of 29:18^{o}C were reported earlier for *B. cucurbitae*, *B. dorsalis* and *C. capitata* (Vargas *et al*., 1997, 2000). In the previous studies on preimaginal stages of these flies, it was revealed that the newly emerged adults could not survive at 15^{o}C and 35^{o}C (Danjuma *et al*., 2013). These suggested that extreme temperatures were more detrimental to all stages of these flies. Hence cold storage of fruits at lower temperature could limit the development of preimaginal stages.

The present studies have revealed the differences in reproductive and demographic parameters between both sympatric species. This may be used for species differentiation and to predict areas where these pestiferous species may survive and reproduce (Messenger and Flitters, 1958).

The finite and intrinsic rates of increase were high for both species with *B. papayae* presenting higher values. One of the most valuable applications of these concepts is in delineation of the liveable environment of a species (Laughlin, 1965; Vargas *et al*., 2000). Although both species understudied were of tropical origin (Drew and Hancock, 1994), distribution history revealed that both species have extended to some warm temperate countries. The present studies also have implications for examining the dynamics of colonizing or invading species.

Population sizes, growth rates and structure can be projected in relation to environmental conditions. Likewise, survival and adult longevity measured under different temperature regimes are important in understanding fruit fly invasion biology and overwintering behaviour (Papadopoulos *et al*., 1998). These factors are important when fruit flies are introduced accidentally into new areas and eradication is considered (Vargas *et al*., 2000).

In conclusion, both species shared common characteristics of r-k strategies, but demographic parameters studied for both species suggested that *B. papayae* can invade and colonise a new area faster than *B. carambolae*. This may be the reason behind it more prevalence and abundance in field over the *B. carambolae*.

CHAPTER 6

CONCLUSION

The dacine fruit flies, especially the genus *Bactrocera* (Diptera: Tephritidae) has posed major threat to the development of horticulture in southern Thailand. These are the key pest groups of Asia and Pacific (Waterhouse, 1993, 1997; Drew, 1989, 2004), with the larval stages feeding on a wide range of fruits and vegetables (Allwood *et al*., 1999). Consequently, causing direct fruit and vegetable damages and loss of export markets through quarantine restrictions. All these are mechanisms by which fruit fly infestation causes economic loss (Clarke *et al*., 2005). With adult traits that include high mobility and dispersive powers, high fecundity, and in some species, extreme polyphagy, the genus *Bactrocera* are well-documented invaders and rank high on quarantine target list (White and Elson-Harries, 1992; Drew and Hancock, 1994; Duyck *et al*., 2004; Clarke *et al*., 2005). Allwood *et al*. (1999) reported an extensive host list of fruit fly in south-east Asia with the plants in the family Myrtaceae as the most substantive host of fruit fly in this region. In southern Thailand, plants in this family are well cultivated and consumed. But no sufficient documentation of fruit fly biodiversity on this family before now. Knowledge of the fruit fly associated with this family, the ecology and life history strategies of the key factor pests are paramount to enhance adequate prevention and control of fruit fly in order to produce pest-free fruits and vegetables that would be acceptable in local and international markets.

In this thesis, I studied the biodiversity and elucidated those species of the genus *Bactrocera* associated with the plants in the family Myrtaceae considering *P. guajava* as a model host for the members of this family. I also identified and investigated about the ecology of the key factor pests of this host by detailing their seasonality, biology of the pre-imaginal stages, egg morphology, and the life table analysis of the adult at different constant temperatures.

Thailand fauna is rich in biodiversity, but few diversity studies were known to be carried out on the tephritid flies (Hardy, 1973). The present biodiversity

study in southern Thailand revealed 31 species belonging to the genus *Bactrocera*. Of which 17 were recorded before (White and Elson-Harris, 1992; Drew and Hancock, 1994) and 14 were new record in this region. History of trapping revealed that 14 of the species were caught on *P. guajava* and 22 species were around the orchard (Chapter 2). Richness of species was towards the border provinces with Malaysia (Songkhla and Narathiwat). This could be due to cross introduction from adjacent countries (Chua, 2002, 2010). Other provinces further away from the border were less rich in species may be due to environmental conditions and the type of vegetation around the orchards. *B. carambolae* and *B. papayae* were trapped abundantly on and around orchards than any other species, hence, are the key factor pests. These species were caught in large numbers throughout the sampling sites and prevalence all over south of Thailand infesting different types of fruits (Drew and Hancock, 1994; Clarke *et al*., 2001). Their prevalence in this region is due to the average weather conditions, availability of host plants and the ability to invade and colonize a new environment. The duo has been found to be sharing the same ecological niche overlap and outcompeting other species (Duyck *et al*., 2004). These may be threatening to the development of fruit production in southern Thailand, except if effective and efficient control measures of these notorious flies are put in place. This also call for judicious and timely checking of imported fruits by the quarantine stations at the various border lines and or between the adjacent countries and Thailand.

B. carambolae and *B. papayae* as the key factor pests lead to their ecological studies to ascertain about their seasonality (abundance and distribution) on and around *P. guajava* orchards (Chapter 3). The ecology was studied alongside with the weather conditions that prevailed in the pest occurrence areas. Movement, dispersal, and habitat selection are keys to understanding the dynamics and spatial distribution of animal population over time (Senger *et al*., 2009). Sites were selected from macro- and micro-climate type of environments and samples collected with the aid of methyl eugenol and Steiner trap. Both species were found in abundant at both types of environments throughout the sampling period of a year. *B. papayae* revealed a bimodal abundance pattern and irregular patterns was observed for *B. carambolae* (Clarke *et al*., 2001). The months of August-September and May were more supportive of fly

population. This may be due to prevailing favourable weather conditions (Amice and sales, 1997) and host availability (ToraVueti *et al*., 1997; Mwatawala *et al*., 2006b). Both species also share the same ecological niche overlap via host fruits as revealed from the *P. guajava* fruits experiment, and *B. papayae* recovery was greater than *B. carambolae*. *P. guajuva* yielded large number of both flies than was observed for other host fruits and this could be said to be the primary host or most preferred hosts and this was in tandem with the report of Allwood *et al*. (1999). The riped stage of *P. guajava* yielded more of the two fruit flies population than the remaining developmental stages. This suggested that more of sugars and other nutrient required for development are more available and easily accessible by the developing larva. This also gives an insight into when cultural control strategies should be employed. For instance, timely harvest, bagging stage and appropriate disposition of discarded fruits. Among all the weather factors considered during the study, temperature happens to exert higher pressure on fly populations (Bale *et al*., 2002). Intriguingly, the fly trapped in town orchards were greater than those trapped at the agro-forested orchards. This suggested that *B. carambolae* tends to predominate in orchard and urban areas (Vijaysegaran *et al*., 1991). But *B. papayae* were trapped in rainforest areas that were relatively close to urban areas (Meat *et al*., 2008). Hence, they are tolerance of both urban and fairly forest habitat. *B. tryoni* had a similar trend in (Raghu *et al*., 2000). It may therefore, be presumed that suburbia was now the major breeding habitat of tephritid flies (Courtice and Drew, 1984). It may be concluded that, the transformation of rainforest into suburbia and cultivation of tamed hosts enhanced the abundance and distribution of *B. carambolae* and *B. papayae.*

Apart from the ecological studies, effect of temperature regimes and guava diet was test on the preimaginal developmental stages of *B. carambolae* and *B. papayae* (Chapter 4). Temperature is the main abiotic factor affecting survival and development of insects (Fletcher, 1987). Both species responded differently to the temperature regimes, but share the same range of "intermediate optimum temperature" (25-27^{o}C) for development (Howe, 1967; Danjuma *et al*., 2013). All other temperature regimes were extreme cases and do not sufficiently support the preimaginal developmental stages. Total failure of the pre-imaginal stages was the case at highest

temperature of 35^{o}C. The narrow range of favourable temperature for these two species may explain their co-occurrence in some warm temperate and tropical countries of the world. The result thus accrued from this study contributes immensely to the biology of the preimaginal stages of these flies and would be handy in improving on the rearing and for other control measures.

The eggs of *B. papayae* were faster in hatching compared to the eggs of its sympatric relative. Therefore, the differential developmental time between the eggs of these two species at each specific temperature regime led to the study of the egg morphology (Chapter 4). Eggs were scanned with the aid of electron microscope and the major differences were observed in chorion reticulation, micropyle structure and a distinct aeropyles of different variations in diameters and numbers. All these factors were considered to have led to the variations in the eggs developmental time of both species. With further cross examination by other tephritid scientists, these characters could be used to further differentiate this sibling species.

Cohort life table of the adult of *B. carambolae* and *B. papayae* was also studied for complete and appropriate comparisons of both species at different temperature regimes as obtainable in southern Thailand (Chapter 5). Both flies responded to temperature in similar way and share the same intermediate optimum temperature as their pre-imaginal developmental stages. It worth mentioning that *B. papayae* survived and brings forth to more fecundity than *B. carambolae*. Similarly, *B. papayae* live longer than its sympatric relative. Generally, the females of both flies are short-lived when compared to the males of the same cohort. This may be because egg laying for the individual female correlate with the probability of death at a subsequent age (Müller *et al*., 2001; Carey *et al*., 2005). Mortality of adult fly was rapid at extreme temperature regimes of coldness and hotness, and subsequently led to variations in survivorships of both fly.

REFERENCES

Allwood, A. J., Chinajariyawong, A., Drew, R. A. I., Hamacek, E. L., Hancock, D. L., Hengsawad, C., Jinapin, J. C., Jirasurat, M., Kong Krong, C., Kritsaneepaiboon, S., Leong, C. T. S. and Vijaysegaran S. 1999. Host plant records for fruit flies (Diptera: Tephritidae) in South-East Asia. *Raffles Bulletin of Zoology*. Supplement No 7. 92 pp.

Allwood, A. J. and LeBlanc, L. 1997. Losses caused by fruit flies in seven Pacific island countries. In: Allwood, A. J. and Drew, R. A. I. (eds). Management of fruit flies in the Pacific. Canberra, *Proceedings of Australian Centre for International Agricultural Research (ACIAR)*. 76: 208–211.

Allwood, A. J, Leblanc, L., Vueti, E. T. and Richard, B. 2001. Fruit fly control methods for Pacific Island countries and territories. Plant Protection Service. /Secretariat of the Pacific Community. Pest Advisory Leaflet No. 40.

Aluja, M. and Birke, A. 1993. Habitat use by adults of *Anastrepha obliqua* (Diptera: Tephritidae) in a mixed mango and tropical plum orchard. *Annals of Entomological Society of America*. 86: 799–812.

Aluja, M., Guillén, J., De La Rosa, G., Cabrera, M., Celendonio, H., Liedo, P. and Hendrichs, J. 1987. Natural host plant surve of the economically important fruit flies (Diptera: Tephritidae) of Chiapas, Mexico. *Florida Entomologists*. 70: 329–328.

Aluja, M. and Mangan, R. L. 2008. Fruit fly (Diptera:Tephritidae) host status determination: critical conceptual, methodological and regulatory considerations". *Annual Review of Entomology*. 53: 473–502.

Aluja, M., and Norrbom, A. 2000. Fruit flies (Diptera: Tephritidae): Phylogeny and evolution of behaviour. Boca Raton, Fl, USA. CRC Press.

Aluja, M., Ordano, M., Guillen, L. and Rull, J. 2012. Understanding long-term fruit fly (Diptera: Tephritidae) population dynamics: implications for area wide management. *Journal of Economic Entomology*. 105: 823–836.

Aluja, M. and Prokopy, R. J. 1992. Host search behaviour by *Rhagoletis pomonella* flies: inter-tree movement patterns in response to wind-borne fruit volatiles under field conditions . *Physiological Entomology*. 93: 403–412.

Aluja, M. and Prokopy, R. J. 1993. Host odour and visual stimulus interaction during intra-tree host finding behavior of *Rhagoletis pomonella* flies. *Journal of Chemical Ecology*. 19: 2671–2696.

Amice, R. and Sales, F. 1997. Seasonal abundance of fruit flies in New Caledonia, pp 134-139. In: Allwood, A. J. and Drew R. A. I. (eds). Management of fruit flies in the Pacific. *Proceedings of Australian Centre for International Agricultural Research (ACIAR)*. 76: 134–139.

Andrew, D. H. and Anthony, R. C. 2006. The influence of soil type and moisture on pupal survival of *Bactrocera tryoni* Froggatt (Diptera: Tephritidae). *Australian Journal of Entomology*. 45: 16–19.

Armstrong, J. W. and Jang, E. B. 1997. An overview of present and future fruit fly research in Hawaii and the US mainland. In: Allwood, A. J. and Drew, R. A. I. (eds). Management of fruit flies in the Pacific. *Proceedings of Australian Centre for International Agricultural Research (ACIAR)*. 76: 30–42.

Arnold, C. Y. 1959. The determination and significance of the base temperature in a linear heat unit system. *Proceeding of American Society for Horticultural Science.* 74: 430–445.

Baimai, V. and Brockelman, W. Y. 1998. Biodiversity research and training program in Thailand. *Pure and Applied Chemistry*. 70: 2073–2078.

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, J., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D. and Whittaker, J. B. 2002. Herbivory in global climate change research: direct effects of rising temperatures on insect herbivores. *Global Change Biology*. 8:1–16.

Bateman, M. A. 1972. The ecology of fruit flies. *Annual Review of Entomology*. 17: 493–518.

Batra, H. N. 1964. The population, behaviour, host specificity and development potential of fruit flies bred at constant temperature in winter". *Indian Journal of Entomology*. 26: 195–206.

Bernays, E. A. and Chapman, R. F. 1994. Host selection by phytophagous insects. Chapman and Hall, New York.

Bhatnagar, K. N. and Yadava, S. R. S. 1992. An insecticidal trial for reducing the damage of some cucurbitaceous fruits due to *Dacus cucubitae* Coq. *Indian Journal of Entomology*. 54:66–69.

Birch, L. C. 1957. The role of weather in determining the distribution and abundance of animals. Cold Spring Harbour. *Symposia on Quantitative Biology*. 22: 203–18.

Bokonon-Ganta, A. H., McQuate, G. T. and Messing, R. .H. 2007. Natural establishment of a parasitoid complex on *Bactrocera latifrons* (Diptera: Tephritidae) in Hawaii. *Biological Control*. 42: 365–373.

Boykin, L. M., Schutze, M. K., Krosch, M. N., Chomic, A., Chapman, T. A., Englezou, A., Armstrong, K. F., Clarke, A. R., Hailstones, D. and Cameron, S. L. 2013. Multi-gene phylogenetic analysis of south-east Asia pest members of

the *Bactrocera dorsalis* species complex (Diptera: Tephritidae) does not support current taxonomy". *Journal of Applied Entomology*. (in press) doi: 10.1111/jen.12047.

Brévault, T., Duyck, P. F. and Quilici, S. 2008. Life-history strategy in an oligophagous tephritid: the tomato fruit fly, *Neoceratitis cyanescens*. *Ecological Entomology*. 33: 529–536.

Brévault, T. and Quilici, S. 2000. Relationship between temperature, development and survival of different life stages of tomato fruit fly, *Neoceratitis cyanescens*. *Entomologia Experimentalis et Applicata*. 94: 25–30.

Brown, J. H. 1995. Macroecology. University of Chicago Press.

Brown, J. H., Marquet, P. A. and Taper, M. L. 1993. Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist*. 142: 573–584.

Brown, V. K. 1991. The effects of changes in habitat structure during succession in terrestrial communities. In: Siemann, E., Haarstad, J., and Tilman, D. 1999. Dynamics of plant and arthropod diversity during old field succession. *Ecography* 22: 406–414.

Carey, J. R. 1982. Demography and population dynamics of the Mediterranean fruit fly. *Ecology Model*. 16: 125–150.

Carey, J. R. 1993. Applied demography for biologists with special emphasis on insects. Oxford University Press. New York.

Carey, J. R. 2001. Insect biodemography. *Annual Review of Entomology*. 46: 79–110.

Carey, J. R. 2003. Longevity: The Biology and Demography of Life Span. Princeton: Princeton University Press.

Carey, J. R. and Dowell, R. V. 1989. Exortic fruit pests and Carlifonia agriculture. *Carlifonia Agrciulture*. 43: 38–40.

Carey, J. R., Liedo, P., Müller, H. G., Wang, J. L., Senturke, D. and Harshman, L. 2005. Biodemography of a long-lived tephritid: Reproduction and longevity in a large cohort of female Mexican fruit flies, *Anastrepha ludens*. *Experimental Gerontology*. 40: 793–800.

Carey, J. R., Liedo P., Orozo, D. and Vaupel, J. W. 1992. Slowing of mortality rates at older ages in large medfly cohorts. *Science.* 258: 457–461.

Carey, J. R. and Vargas, R. I. 1985. Demographic analysis of insect mass rearing: a case study of three tephritids. *Journal of Economic Entomology* 78: 523–527.

Caroline, G. S., Frances, D. L. and Jonathan, D. M. 2008. Determination of host status of citrus fruits against the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann (Diptera: Tephritidae). *Australian Journal of Entomology*. 47: 184–187.

Carroll, L. E. and Wharton, R. A. 1989. Morphology of the immature stages of *Anastrepha ludens* (Diptera: Tephritidae). *Annals of Entomological Society of America*. 82: 201–214.

Carroll, L. E., White, I. M., Freidberg, A., Norrbom, A. L., Dallwitz, M. J. and Thompson F. C. 2004. Pest fruit flies of the world: identification, descriptions, illustrations, and information retrieval. Diptera Data Dissemination Disk (CD-ROM) 2.

Casida, J. E. and Quistad, G. B. 1998. Golden age of insecticide research: past, present, or future? *Annual Review of Entomology*. 43: 1–16.

Chi, H. 1990. Timing of control based on the stage structure of pest population: a simulation approach. *Journal of Economic Entomology*. 83: 1143–1150.

Chinajariyawong, A., Clarke, A. R., Jirasurat, M., Kristsaneepaiboon, S., Lahey, H. A., Vijaysegaran, S. and Walter, G. H. 2000. Survey of Opiine parasitoids of fruit flies (Diptera: Tephritidae) in Thailand and Malaysia. *Raffle Bulletin of Zoology*. 48: 1–38.

Chinajariyawong, A., Kristsaneepaiboon, S. And Drew, R. A. I. 2003. Efficacy of protein bait sprays in controlling fruit flies infesting angle luffa and bitter gourd in Thailand. *Raffles Bulletin of Zoology*. 51: 7–15.

Christenson, L. D. and Foote, R. H. 1960. Biology of Fruit Flies. *Annual Review of Entomology*. 5: 171–192.

Chua, T. H. 2002. New records of Trypetinae from Brunei Darussalam (Diptera: Tephritidae). *Malayan Nature Journal*. 56: 43–48.

Chua, T. H. 2010. Fruit flies (Diptera: Tephritidae) from Malaysia and Brunei Darussalam: New species and records. *Florida Entomologist*. 93: 483–488.

Clarke, A. R., Allwood, A. J., Chinajariyawong, A., Drew, R. A. I., Hengsawad, C., Jirasurat, M., Kong Krong, C., Kristsaneepaiboon, S. and Vijaysegaran, S. 2001. Seasonal abundance and host use patterns of seven *Bactrocera* macquart species (Diptera: Tephritidae) in Thailand and Peninsular Malaysia. *Raffles Bulletin of Zoology*. 49: 207–220.

Clarke, A. R., Armstrong, K. F., Carmichael, A. E., Milne, J. R., Raghu, S., Roderick, G. K. and Yeates, D. K. 2005. Invasive phytophagous pests arising through a recent tropical evolutionary radiation: The *Bactrocera dorsalis* Complex of Fruit Flies. *Annual Review of Entomology*. 50: 293–319.

Claudianos, C., Russell, R. J. and Oakeshott, J. G. 1999. The same amino acid substitution in orthologous esterases confers organophosphate resistance on the house fly and a blowfly. *Insect Biochemistry and Molecular Biology*. 29: 675–686.

Cobert, G. B. and Hill, J. E. 1992. The mammals of the Indomalayan Region: A Systematic Review. Oxford University Press: Oxford. UK.

Collins, N. M., Sayer, J. A. and Whitemore, T. G. 1991. The conservation atlas of tropical forests: Asia and the Pacific IUCN. Gland Switzerland.

Cônsoli, F. L., Kitajima, E. W. and Parra, J. R. P. 1999. Ultrastructure of the natural and factitious host eggs of *Trichogramma galloi* Zucchi and *Trichogramma pretiosum* Riley (Hymenoptera:Trichogrammatidae). *International Journal of Insect Morphology and Embryology*. 28: 211–229.

Convey. P. and Block, W. 1996. Antarctic diptera: Ecology, physiology and distribution. *European Journal of Entomology*. 93: 1–13.

Copeland, R. S., Wharton, R. A., Luke, Q. and De Mayer, M. 2002. Indigenous hosts of *Ceratitis capitata* (Diptera: Tephritidae) in Kenya. *Annals of Entomological Society of America*. 95: 672–694.

Copeland, R. S., Wharton, R. A., Luke, Q., De Mayer, M., Lux, S., Zenz, N., Machera, P. and Okuinu, M. 2006. Geographical distribution, host fruits and parasitoids of the African fruit fly pests *Ceratitis capitata*, *Ceratitis cosyra*, *Ceratitis fasciventris* and *Ceratitis rosa* (Diptera: Tephritidae) in Kenya. *Annals of Entomological Society of America*. 99: 261–278.

Corbet, S. A. 1995. Insects, plants and succession: advantages of long-term set aside. *Agriculture, Ecosystems and Environment*. 53: 201–217.

Courtice, A. C. and Drew, R. A. I. 1984. Bacterial regulation of abundance in tropical fruit flies (Diptera: Tephritidae). *Australian Journal of Zoology*. 21: 251–268.

Coviella, C. and Trumble, J. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology*. 13: 700–712.

Cowley, J. M., Baker, R. T. and Harte, D. S. 1992. Definition and determination of host status for multivoltine fruit fly (Dipteral: Tephritidae) species. *Journal of Economic Entomology*. 85: 312–317.

Cranston, P. S. 2009. Biodiversity of Australasian insects. In: R. G. Foottit and P. A. Adler (eds). Insect biodiversity. Science and Society, Willey-Blackwell. A John Wiley and Sons, Ltd, Publication. United Kingdom.

Crawley, M. J. 1986. The population biology of invaders. Philosophical transsactions of the Royal Society of London. Series B, *Biological Science*. 314: 711–729.

Daniel, F. L., Vicente, H. O, and Liliana, L. M. 2009. Description of the third-instar of *Anastrepha leptozona* Hendel (Diptera: Tephritidae). *Neotropical Entomology*. 38: 491–496.

Danjuma, S., Thaochan, N., Permkam, S. and Satasook, C. 2013. Effect of temperature on the development and survival of immature stages of the carambola fruit fly, *Bactrocera carambolae* and the Asian papaya fruit fly, *Bactrocera papayae* reared on guava diet. *Journal of Insect Science*. (In Press).

Dhillon, M. K., Singh, R., Naresh, J. S. and Sharma, H. C. 2005. The melon Fruit Fly, *Bactrocera cucurbitae*: A review of its biology and management. *Journal of Insect Science*. 5: 1–16.

Diamantidis, A. D., Carey, J. R. and Papadopoulus, N. T. 2008. Life-history of an invasive tephritid. Journal of Applied Entomology. 132: 695–705.

Diaz-Fleischer, F. D., Propoky, P. R. J., Norrbom, A. I. and Aluja, M. 1999. Evolution of fruit fly behaviour," in *Phylogeny and evolution of behaviour*. In: Aluja, M. and Norrbom, A. L. (eds). Fruit flies (Tephritidae). CRC. Boca Raton, FL.

Diaz, F. A. and Vasquez, R. B. 1993. Época de oviposición de la mosca de las frutas (*Anastrepha* spp.), relacionada con la fenologia de la guayaba nativa. *Rev. ICA*. 4: 323–333.

Drew, R. A. I. 1989. The tropical fruit flies (Diptera: Tephritidae: Dacinae) of the Australasian and Oceanian regions. *Memoirs of the Queensland Museum*. No 26. 521 pp.

Drew, R. A. I. 2004. Biogeography and speciation in the Dacini (Diptera: Tephritidae: Dacinae). *Bishop Museum Bulletin of Entomology*. 12: 165–178.

Drew, R. A. I. and Hancock, D. L. 1994.The *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. *Bulletin of Entomological Research*. Supplement Series. Supplement 2. 68 pp.

Drew, R. A. I. and Hooper, G. H. S. 1983. Population studies of fruit flies (Diptera: Tephritidae) in South East Queensland. *Oecologia*. 26: 153–159.

Drew, R. A. I. and Lloyd, A. C. 1989. Biology and Physiology; nutrition; bacteria associated with fruit flies and their host plants, In: Robinson, A. S. and Hooper, G. H. S. (eds). Fruit flies; Their Biology, Natural Enemies and Control. Elsevier. Amsterdam, Netherlands.*World Crop Pests*. 3(A). pp. 131–140.

Drew, R. A. I. and Romig, M. C 1997. Overview - Tephritidae in the Pacific and Southeast Asia. In: Allwood, A.J. and Drew, R.A.I. (eds). Management of fruit flies in the Pacific. *Proceedings of Australian Centre for International Agricultural Research (ACIAR)*. 76: 46–53.

Drew, R. A. I. and Romig, M. C 2007. Record of Dacine fruit flies and new species of *Dacus* (Diptera: Tephritidae) in Bhutan. *Raffles Bulletin of Zoology*. 55: 1–21.

Drew, R. A. I., Tsuruta, K., White, I. M. 2005. A new species of pest fruit fly (Diptera: Tephritidae: Dacinae) from Sri Lanka and Africa. *African Entomology*. 13: 149–154.

Dutra, V. S., Ronchi-Teles, B., Steck, G. J. and Silva, G. J. 2011. Egg morphology of *Anastrepha* spp. (Diptera: Tephritidae) in the fraterculus group using scanning electron microscopy. *Annals of Entomological Society of America*. 104: 16–24.

Duyck, P. F., David, P. and Quilici, S. 2004. A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae)". *Ecological Entomology*. 29: 511–520.

Duyck, P. F., David, P., Pavoine, S. and Quilici, S. 2008. Can host-range allow niche differentiation of invasive polyphagous fruit flies (Diptera: Tephritidae) in La Réunion? *Ecological Entomology*. 33: 439–452.

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.

Duyck, P. F., Sterlin, J. F. and Quilici, S. 2004. Survival and development of different stages of *Bactrocera zonata* (Diptera: Tephritidae) reared at five constant temperatures compared to other fruit fly species. *Bulletin of Entomological Research*. 94: 89–93.

Dyer, L. A. Singer, M. S. Lill, J. T. Stireman, J. O. Gentry, G. L. Marquis, R. J. Ricklefs, R. E. Greeney, H. F. Wagner, D. L. Morais, H. C. Diniz, I. R. Kursar T. A. and Coley, P. D. 2007. Host specificity of Lepidoptera in tropical and temperate forests. *Nature*. 448**:** 696–699.

Ebina, T. and Ohto, K. 2006. Morphological characters and PCR-RFLP Markers in the interspecific hybrids between *Bactrocera carambolae* and *B. papayae* of the *B. dorsalis* Species Complex (Diptera: Tephritidae). *Research Bulletin of Plant Protection, Japan*. 42: 23–34.

Ekesi, S., Nderitu, P. W. and Rwomushana, I. 2006. Field investation, life history and demographic parameters of *Bactrocera invadens* Drews, Tsuruta and White, a new invasive fruit fly species in Africa. *Bulletin of Entomological Research*. 96: 379–386.

Esculdero-Colomar, L. A., Vilajeliu, M. and Batllori, L. 2008. Seasonality in occurrence of the Mediterranean fruit fly [*Ceratitis capitata* (Wied.) F] in north-east of Spain. *Journal of Applied Entomology*. 132: 714–721.

FAO, 2006. Requirements for the establishment of pest free places of production and pest free production sites. SPM No.10, 2005 Edition. Food and Agriculture Organization, Rome. pp.105–111.

Faith, D. P. 2007. Biodiversity. In: E. N. Zalta, U., Nodelman and C. Allen (eds). Stanford Encyclopedia of Philosophy. Metaphysics Research Lab, Stanford University, Stanford, California. http//plato.stanford.edu/entries/biodiversity/ [Accessed 13th February, 2013].

Fay, H. A., Drew, R. A. I., Lloyd, A. C. 1997. The eradication program for papaya fruit fly (*Bactrocera papayae* Drew and Hancock) in North Queensland. in: Allwood, A.J., and Drew, R.A.I. 1997. Management of fruit flies in the Pacific. *Proceedings of Australian Centre for International Agricultural Research (ACIAR).* No 76. pp. 259–261.

Fein, B. L., Reissig, W. H. and Roclofs, W. L. 1982. Identification of apple volatiles attractive to apple maggot fly. *Journal of Chemical Ecology*. 8: 1473–1487.

Ferrar, P. 1987. A guide to the breeding habits and immature stages of Diptera Cyclorrhapha. *Entomonograph.* 8: 1–907.

Fletcher, B. S. 1987. The biology of dacinae fruit flies. *Annual Review of Entomology.* 32: 115–144.

Fletcher, B. S. 1989. Movements of tephritid fruit flies. In: A. S. Robinson and Hooper, G. H. S. (eds). Fruit flies: their biology, natural enemies and control. *World Crop Pests*. pp. 209–219.

Fletcher, B. S., Pappas, S. and Kapatos, E. T. 1978. Changes in the ovaries of olive flies (*Dacus oleae* (Gmelin)) during the summer, and their relationship to temperature, humidity and fruit availability. In: Kendra, P. E., Montgomery, W. S., Epsky, N. D. and Heath, R. R. (eds). Assessment of female reproductive status in *Anastrepha suspensa* (Diptera: Tephritidae). *Florida Entomologist*. 89: 144–151.

Fletcher, B. S. and Prokopy, R. J. 1991. Host location and oviposition in tephritid fruit flies. Reproductive behaviour of insects. In: Bailey, W. J. and Ridsdill-Smith, J. (eds). Chapman and Hall, New York. pp 139–171.

Foote, R. H. 1981. The genus *Rhagoletis* Leow south of the United State (Diptera: Tephritidae). United State Department of Agriculture. *Technical Bulletin*. 1607. 1–75.

Frías, L. D., Hernández-Ortiz, V., Vaccaro, N., Bartolucci, A. and Salles, L. A. 2006. Comparative morphology of immature stages of some frugivorous species of fruit fies (Diptera: Tephritidae). *Israel Journal of Entomology*. 37: 536–545.

Gallo, J. 2007. Integrated plant control: System and management. *Encyclopedia of Pest Management*. 2: 279–287.

Genc, H. and Nation, J. L. 2008. Survival and development of *Bactrocera oleae* Gmelin (Diptera: Tephritidae) immature stages at four temperatures in the laboratory. *African Journal of Biotechnology*. 7: 2495–2500.

Girolami, V. 1983. Fruit fly symbiosis and adult survival: general aspects. In: Cavalloro, R. (ed), Fruit Flies of Economic Importance. Balkima, Rotterdam. Athens. *Proceedings of the CEC/IOBC International Symposium.* pp. 74–76.

Gupta, J. N. and Verma, A. N. 1982. Effectiveness of fenitrothion bait sprays against melon fruit fly, *Dacus cucurbitae* Coquillett in bitter gourd. *Indian Journal of Agricultural Research.* 16: 41–46.

Haghani, M., Fathipour, Y., Talebi, A. A. and Baniameri, V. 2007. Thermal requirement and development of Liriomyza sativae (Diptera: Agromyzidae) on cucumber. *Journal of Economic Entomology*. 100: 350–356.

Hamilton, J. G., Dermody, O., Aldea, M., Zangerl, A. R., Rogers, A. Berenbaum, M. R. and Delucia, E. 2005. Anthropogenic changes in tropospheric composition increase susceptibility of soybean to insect herbivory. *Environmental Entomology*. 34: 479–485.

Hancock, D. L., Hamacek, E., Lloyd, A. C., Elson-Harris, M. M. 2000. The distribution and host plants of fruit flies (Diptera: Tephritidae) in Australia. Queensland Department of Primary Industries. Information Series QI990. pp. 67–75.

Hardy, D. E. 1969. Taxonomy and distribution of the Oriental fruit fly and related species (Diptera: Tephritidae). *Proceedings of the Hawaiian Entomologcal Society*. 20: 395–428.

Hardy, D. E. 1973. The fruit flies (Tephritidae – Diptera) of Thailand and borederin countries. *Pacific Insects Monograph*. 31: 1–353.

Hardy, D. E. 1974. The fruit flies of Philippines (Diptera: Tephritidae). *Pacific Insects Monograph*. 32: 1–266.

Hardy, D. E. 1977. Tephritidae (Tephritidae, Trupaneidae). In: Delfinado, M. D. and Hardy, D. E. (eds). *A catalogue of the Oriental Region*, University of Hawaii, Honolulu. 3: 44–134.

Hardy, D. E. 1988. Fruit fly of the subtribe Gastrozonina of Indonesia, New Guinea and the Bismarck and Solomon Islands (Diptera, Tephritidae, Trypetinae, Acanthonevrini). *Zoologica Scripta*. 17: 77–121.

Harris, E. J., Nakagawa, S.and Urago, T. 1971. Sticky traps for detection and survey of three tephritids. *Journal of Economic Entomology*. 64: 62–65.

Harris, E. J., Takara, J. M. and Nishida, T. 1986. Distribution of the melon fly, *Dacus cucurbitae* (Diptera: Tephritidae), and Host plants on Kauai, Hawaiian Islands. *Environmental Entomology*. 15: 488–493.

Harris, E. J., Vargas, R. I. and Gilmore, J. E. 1993. Seasonality in occurrence and distribution of Mediterranean fruit fly (Diptera: Tephritidae) in Upland and Lowland areas on Kauai, Hawaii. *Environmental Entomology*. 22: 404–410.

Hendrichs, J. and Hendrichs, M. A., 1990. Mediterranean fruit fly (Diptera: Tephritidae) in nature: location and diel pattern of feeding and other activities on fruiting and nonfruiting hosts and nonhosts. *Annals of the Entomological Society of America*. 83: 632–641.

Hendrichs, J., Katsoyannos, B. I., Papaj, D. R. and Prokopy, R. J. 1991. Sex differences in movement between natural feeding and mating sites and tradeoffs between food consumption, mating success and predator evasion in Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia*. 86: 223–231.

Higley, L. G., Pedigo, L. P. and Osile, K. R. 1986. DEGDAY: a program for calculating degree days, and assumptions behind the degree-day approach. *Environmental Entomology*. 15: 999–1016.

Hinton, H. E. 1969. Respiratory systems of insect eggshells. *Annual Review of Entomology*. 14: 343–368.

Hodkinson, I. D. 1997. Progressive restriction of host plant exploitation along a climatic gradient: the willow psyllid Cacopsylla groenlandica in Greenland. *Ecological Entomology*. 21: 47–54.

Hodkinson, I. D., Webb, N. R., Bale, J. S., Block, W., Coulson, J. S. and Strathdee, A. T. 1998. Global change and Arctic ecosystems: Conclusions and predictions from experiments with terrestrial invertebrates on Spitsbergen. *Arctic and Alpine Research*. 30: 306–313.

Hollingsworth, R. and Allwood, A. 2000. Melon Fly. Pest advisory leaflet. Secretariat of the Pacific Community. Plant Protection Service, 31. In: Victor M. G. S. (2009), Monitoring and pest control of Fruit flies in Thailand: New knowledge for integrated pest management. *SLU* Institutionen för ekologi, Box 7044, 750 07 Uppsala. pp.1–42.

Hou, Y. and Weng, Z. 2010. Temperature-dependent and life table parameters of *Octodonta nipae* (Coleoptera: Chrysomelidae). *Physiological Ecology*. 39: 1676–1684.

Howard, D. J. 1989. Biology and physiology; nutrition; the symbionts of *Rhagoletis*, In: Robinson, A. S. and Hooper, G. H. S. (eds), Fruit flies; their biology, natural enemy and control. *World Crop Pests*. 3: 121–129.

Howe, R. W. 1967. Temperature effects on embryonic development in insects. *Annual Review of Entomology*. 12: 15–42.

Hsu, J. C. and Feng H. T. 2006. Development of resistance to spinosad in Oriental Fruit Fly (Diptera: Tephritidae) in laboratory selection and cross-resistance. *Journal of Economic Entomology*. 99: 931–936.

Hughes, J., Round, P. and Woodruff, D. S. 2003. The Indochinese-Sundaic faunal transition at the Isthmus of Kra: an analysis of resident forest birds species distribution. *Journal of Biogeography*. 30: 569–580.

Hunter, M. D. 2001. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Agricultural and Forest Entomology*. 3: 153–159.

IAEA. 1996. Standardization of medfly trapping for use in sterile insect technique programmes. Final report of coordinated research programme 1986–1992. IAEA-TECDOC-883

IAEA. 1998. Development of female medfly attractant systems for trapping and sterility assessment. Final report of a Coordinated research programme 1995-1998. International Atomic Energy Agency (IAEA) TECDOC-1099. 228 pp.

IAEA. 2003, Trapping guidelines for area-wide fruit fly programmes. International Atomic Energy Agency (IAEA) 47pp.

Ibrahim, A. G. and Ibrahim, R. 1990. Handbook on identification of Fruit Flies in the Tropics. Universiti Pertanian Malaysia, Serdang.

Itô, S. 1983-5. Die Japanischen Borhfliegen. Osaka. [Privately published in 7 parts.]

Itô, Y., Kakinohana, H. Yamagishi, M. and Kohama. T. 2003. Eradication of the melon fly, *Bactrocera cucurbitae*, from Okinawa, Japan, by means of the sterile insect technique, with special emphasis on the role of basic studies. *Journal of Asia-Pacific Entomology*. 6: 119–129.

Iwahashi, O. 1999. Distinguishing between the two sympatric species *Bactrocera carambolae* and *Bactrocera papayae* (Diptera: Tephritidae) based on aedeagal length. *Annals of the Entomological Society of America*. 92: 639–643.

Iwaizumi, R. 2004. Species and host record of the *Bactrocera dorsalis* complex (Diptera: Tephritidae) detected by the plant quarantine of Japan. *Applied Entomology and Zoology*. 39: 327–333.

Iwaizumi, R., Kaneda, M. and Iwahashi, O. 1997. Correlation of length of terminalia of males and females among nine species of *Bactrocera* (Diptera: Tephritidae) and differences among sympatric species of *B. dorsalis* complex. *Annals of the Entomological Society of America*. 90: 664–666.

Jalali, M. A., Tirry, L., Arbab, A. and De Clercq, P. 2010. Temperature-dependent development of the two-spotted ladybeetle, *Adalia bipunctata*, on the green peach aphid, *Myzus persicae*, and a factitious food under constant temperatures. *Journal of Insect Science*.10 124. www.insectscience.org/10.124

Jang, E. B. 1997. Attraction of female oriental fruit fly, *Bactrocera dorsalis* to volatile semiochemicals from leaves and extracts of a non-host plant, panax (*Polyscias guilfoylei*) in laboratory and olfactometer assays. *Journal of Chemical Ecology*. 23: 1389–1401.

Kafatos, F. C., Mitsialis, S. A., Nguyen, H. T., Spoerel, N., Tsitilou, S. G. and Mazur, G. D. 1987. Evolution of structural genes and regulatory elements for the insect chorion. In Raff, R. A. and Raff, E. C. (eds.). Development as an evolutionary process. New York, Alan R Liss Inc., pp.161–178.

Kambyselis, M. P. 1993. Ultrastructural diversity in the egg chorion of hawaiian Drosophila and Scaptomiza: ecological and phylogenetic considerations. *International Journal of Insect Morphology and Embryology*. 22: 417–446.

Kapoor, V. C., Hardy, D. E., Agarwal, M. L. And Grewal, J. S. 1980. Fruit fly (Diptera, Tephritidae) Sytematics of the Indian Subcontinent. Export India Publications, Jullunder.

Katsoyannos, B. I. 1989. Response to shape, size and colour. In: Robinson, A. S. and Hopper, G. H. S. (eds). Fruit flies: their biology, natural enemies. Vol.3A, 307–324.

Katsoyannos, B. I., Koloussis, N. A. and Carey, J. R. 1998. Seasonal and annual occurrence of Mediterranean fruit flies (Diptera: Tephritidae) on Chios Island, Greece: difference s between two neighboring citrus orchards. *Annals of Entomological Society of America*. 91: 43–51.

Kendra, P. E., Montgomery, W.S., Epsky, N. D. and Heath, R. R. 2006. Assessment of female reproductive status in *Anastrepha suspensa* (Diptera: Tephritidae). *Florida Entomologist*. 89: 144–151.

Korneyev, V. A. 1999. Phylogenetic relationships among higher group of Tephritidae. In: Aluja, M. and Norrhom, A. L. (eds). Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior. CRC Press.

Krosch, M. N., K. Schutze, M., Armstrong, K. F., C. Graham, G., Yates, D. K. and Clarke, A. R. 2012. A molecular phylogeny for the tribe Dacini (Diptera: Tephritidae): Systematic and biogeographic implications". *Molicular Phylogenetic and Evolution.* 64: 513–523.

Kuba, H., and Koyama, J. 1982. Mating behavior of the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae): Comparative studies of one wild and two laboratory strains. *Applied Entomology and Zoology*. 17:559–568.

Kuba, H., Koyama, J., and Prokopy, R. J. 1984. Mating behaviour of wild melon flies, *Dacus cucurbitae* Coquillet (Diptera: Tephritidae), in a field cages: Distribution and behavior of flies. *Applied Entomology and Zoology*. 19: 367–373.

Laughlin, R. 1965. Capacity for increase: a useful population statistic. *Journal of Animal Ecology*. 54: 77–91.

Leblanc, L. and Allwood, A. J. 1997. Mango fruit fly (*Bactrocera frauenfeldi*): Why so many in federal state of Micronesia? In: Allwood, A. J. and Drew, R. A. I. (eds). Management of fruit flies in the Pacific. *Proceedings of Australian Centre for International Agricultural Research (ACIAR)*, Canberra, 125–130.

Lekagul, B. and Round, P. D. 1991. A guide to the Birds of Thailand, Bangkok.

Lewinsohn, T. M. Novotny, V. and Basset, Y. 2005. Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecology, Evolution and Systematics*. 36: 597–620.

Lewis, T. 1997. Thrips as crop pests. CAB International, Cambridge: University Press.

Liquido, N. J., Chan, H. T. and McQuate, G. T. 1995. Hawaiian tephritid fruit fly (Diptera): Integrity of the infestation-free quarantine procedure for sharwil avocado. *Journal of Economic Entomology*. 88: 85–96.

Liu, S. S. and Meng, X. D. 1999. Modelling development time of *Myzus persicae* (Hemiptera: Aphididae) at constant and natural temperatures. *Bulletin of Entomological Research.* 89: 53 –63.

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

Liu, S. S., Zhang, G. M. and Zhu, J. 1995. Influence of temperature variations on rate of development in insects: analysis of case studies from entomological literature. *Annals of Entomological Society of America*. 88: 107–119.

Lloyd, A. C. 1991. The distribution of alimentary tract bacteria in the host tree by *Dacus tryoni*. In: Vijaysegaran, S. and Ibrahim, A. G. (eds). First International Symposium on Fruit Flies in the Tropics, Kuala Lumpur. Malaysian Agricultural Research and Development Institute, Kuala Lumpur. pp. 289–295.

Lux, S. A. 1999. African fruit fly Initiative: Pan African initiative to promote productivity and trade of fruit and vegetables through management of African fruit flies. Nairobi, ICIPE. Kenya.

Lux, S. A., Copeland, R. S., White, I.M., Manrakhan, A. and Billah, M. K. 2003. A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. *Insect Science and its Application*. 23: 355–360.

Magurran, A. E. 2004. Measuring biological diversity". Blackwell Publishing Company, Cowley road, Oxford. UK.

Malavasi, A.D., Midgarden, Sauers-Muller van A. 1998. Operations manual. Regional project for the control of the Carambola fruit fly in South America.

Malavasi, A., Morgante, J. S. and Zucchi, R. A. 1980. Biologia de "moscas-das-frutas" (Diptera: Tephritidae). I. Lista de hospedeiros e ocorrência. *Brazilian Journal of Biology*. 40: 9–16.

May, R. M. 1986. Biological diversity: How many species are there? *Nature.* 324, 514–515.

McLnnis, D.O., Tam, S.Y.T., Grace, C. and D. Miyashita. 1994. Population suppression and sterility rates induced by variable sex-ratio insect releases of

Ceratitis capitata (Diptera: Tephritidae) in Hawaii. *Annals of the Entomological Society of America*. 87: 231–240.

McPeek, M. A. and Kalisz, S. 1993. Population sampling and bootstrapping in complex designs: demography analysis. In: Scheiner S. M. and Gurevitch, J. (eds). Design and analysis of ecological experiments, Chapman and Hull, New York.

McPhail, M. 1939. Protein lures for fruit flies. *Journal of Economic Entomology*. 32: 758–761.

McQuate, G. T. and Vargas, R. I. 2007. Assessment of attractiveness of plants as roosting sites for the melon fly, *Bactrocera cucurbitae*, and oriental fruit fly, *Bactrocera dorsalis*. *Journal of Insect Science*. 7:57, availableonline: insectscience.org/7.57

Mcvean, R. and A. F. G. Dixon. 2001. The effect of plant drought-stress on populations of the pea aphid *Acyrthosiphon pisum*. *Ecological Entomology*. 26: 440–443.

Meat, A., Fay, H. A. C. and Drew, R. A. I. 2008. Distribution and eradication of an exortic tephritid fruit fly in Australalia: relevance of invasion theory. *Journal of Applied Entomology*. 132: 406–411.

Messina, F. J. and Jones, V. P. 1990. Relationship between fruit phenology and infestation by the apple maggot (Diptera: Tephritidae) in Utah. *Annals of Entomoligical Society of America*. 83: 742–752.

Messenger, P. S. and Flitters, N. E. 1954. Bioclimatic studies of three species of fruit flies in Hawaii. *Journal of Economic Entomology*. 47: 756–765.

Messenger, P. S. and Fltters, N. E. 1958. Effect of constant temperature environments on the egg stage of three species of Haiwaiian fruit flies. *Annal of Entomological Society of America.* 51, 109–119.

Metcalfe, J. 1996. Pre-cretaceous evolution of SE Asia terranes. In: Hall R. and Blundell, D. J. (eds). Tectonic Evolution of Southeast Asia, Special Publication 106, Geological Society, London.

Miyatake T. 1997. Correlated responses to selection for developmental period in *Bactrocera cucurbitae* (Diptera: Tephritidae): time of mating and daily activity rhythms. *Behaviour Genetics*. 27: 489–498.

Müller, H. G., Carey J. R., Wu D. and Vaupel, J. W. 2001. Reproductive potential determines longevity of female Mediterranean fruit flies. *Proceedings of Royal Society,* London B. 268: 445–450.

Müller, H. G., Wang, J. L., Carey, J. R., Caswell-Chen, E. P., Chen, C., Papadopoulos, N. and Yao, F., 2004. Demographic window to aging in the wild: Constructing life tables and estimating survival functions from marked individuals of unknown age. *Aging Cell*. 3: 125–131.

Muniz, M. and Gil, A. 1984. Desarrollo y reproduccion de *Ceratitis capitata* Wied. en condiciones artificiales. *Biological Service Plaga, Fuera de series*. 2:1–139.

Murillo, T. and Jirón, L. F. 1994. Egg morphology of *Anastrepha oblique* and some comparative aspectswith eggs of *Anastrepha fraterculus* (Diptera: Tephritidae). *Florida Entomologist*. 77: 342–348.

Muthuthantri, S., Maelzer, D., Zalucki, M. P. and Clarke, A. R. 2010. The seasonality of *Bactrocera tryoni* (Froggatt) (Diptera; Tephritidae) in Queensland. *Australian Journal of Entomology*. 49: 221–233.

Mwatawala, M. W., De Meyer, M., Makundi, R. H., Maerere, A. P. 2006a. Seasonality and host utilization of the invasive fruit fly, *Bactrocera invadens* (Diptera: Tephritidae) in central Tanzania. *Journal of Applied Entomology*. 130: 530–537.

Mwatawala, M. W., De Meyer, M., Makundi, R. H. and Maerere, A. P. 2006b. 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., Makundi, R. H. and Maerere, A. P. 2009. Host range and distribution of fruit infesting pestiferous fruit flies (Diptera, Tephritidae) in selected areas of Central Tanzania. *Bulletin of Entomological Research*. 99: 629–641.

Nakashizuka, T. 2004. The role of biodiversity in Asian forests. *The Japanese Forestry Research.* 9: 293–298.

New, T. R. 2008. Insect conservation in early succession on island: lessons from Surtsey, Iceland, and the Krakatau Archipelago, Indonesia. *Journal of Insect Conservation*. 12: 307–312.

Newell, I. M. and Haramoto, F. H. 1968. Biotic factors influencing population of *Dacus dorsalis* in Hawaii. *Proceedings of Hawaii Entomological Society*. 20: 81–139.

Norrbom, A. L. 2004. Updates to Biosystematic Database of World Diptera for Tephritidae through 1999. Diptera Data Dissemination Disk (CD-ROM) 2.

Norrbom, A. L. and Korytkowski, C. A. 2009. A revision of the *Anastrepha robusta* species group (Diptera: Tephritidae). *Zootaxa*. 2182: 1–91.

Norrbom, A. L., Zucchi, R. A. and Hern•ndez-Ortiz, V. 1999. Phylogeny of the genera *Anastrepha* and *Toxotrypana* (Trypetinae: Toxotrypanini) based on morphology. In: Aluja, M. and Norrbom, A. L. (eds). Fruit flies (Tephritidae): phylogeny and evolution of behaviour. Boca RatÛn, CRC Press. New York.

Norrbom, A. L., Zucchi, R. A. and Hern•ndez-Ortiz, V. 2000. Phylogeny of the genera *Anastrepha* and *Toxotrypana* (Trypetinae: Toxotrypaninae) based on morphology. In Aluja, M. and Norrbom, A.L. (eds.). Fruit flies (Tephritidae): Phylogeny and Evolution of Behavior. Boca RatÛn, CRC Press. New York

Novoseltsev, V. N., Carey, J. R., Novoseltseva, J. A., Papadopoulos, N. T., Blay, S., Yashin, A. I. 2004. Systemic mechanisms of individual reproductive life history in female medflies. *Mechanisms of Ageing and Development*. 125: 77–87.

Novotny, V. and Basset, Y. 2005. Host specificity of insect herbivores in tropical forests. *Proceeding of Royal Society of Biological Sciences*. 272: 1083–1090.

Novotny, V., Miller, S. E., Hulcr, J., Drew, R. A. I., Basset, Y., Janda, M., Setliff, G. P., Darrow, K., Stewart, A. J. A., Auga, J., Isua, B., Molem, K., Manumbor, M., Tamtiai, E., Mogia, M. and Weiblen, G. D. 2007. Low beta diversity of herbivorous insects in tropical forests. *Nature.* 448: 692–695.

Novotny, V. and Weiblen, G. D. 2005. From communities to continents: beta-diversity of herbivorous insects. *Annales Zoologici Fennici.* 42: 463–475.

Papachristos, D. P. and Papadopoulos, N. T. 2009. Are citrus species favourable hosts for the Mediterranean fruit fly? A demographic perspective. *Entomologia Experimentalis et Applicata*. 132: 1–12.

Papadopoulos, N. T., Katsoyannos, B. I. and Carey, J. R. 1998. Temporal changes in composition of the overwintering larval population of the Mediterranean fruit

fly (Diptera: Tephritidae) in Northern Greece. *Annals of Entomological Society of America*. 91: 430–434.

Papadopoulos, N. T., Katsoyannos, B. I. and David, N. 2003. Spatial autocorrelation analysis of a *Ceratitis capitata* (Diptera: Tephritidae) adult population in mixed deciduous fruit orchard in northern Greece. *Environmental Entomology*. 32: 319–326.

Pedigo, L. P. and Zeiss, M. R. 1996. Analyses in Insect Ecology and Management. Iowa State University Press, Ames, IA.

Permkam, S. 1995. Bamboo shoot fruit flies in Southern Thailand. *Songklanakarin Journal of Science and Technology*. 17: 229–238.

Permkam, S. 2005. Bamboo-shoot fruit flies (Diptera: Tephritidae) of southern Thailand. *Songklanakarin Journal of Science and Technology*. 27: 223–237.

Permkam, S., Saibon, S. and Hancock, D. L. 1997. Survey and biology of bamboo-shoot fruit flies in southern Thailand. Final Report to the National Research Council of Thailand. Prince of Songkla University. Songkhla.

Peter, R. H. 1983. The ecological implication of body size. Cambridge University Press.

Pike, E. L. and Corcoran, R. J. 1998. *Bactrocera papayae* (Diptera: Tephritidae) incursion – cairns, Australia. *Acta Horticulture*. 464: 321–324.

Prokopy, R. J., Cooley, S. S., Prokopy, J. J., Quan, Q. and Buonaccorsi, J. P., 1994. Interactive effects of resource abundance and state of adults on residence of apple maggot (Diptera: Tephritidae) flies in host tree patches. *Environmental Entomology*. 23: 304–315.

Prokopy, R. J. and Owens E. D. 1983. Visual detection of plants by herbivorous insects. *Annual Review of Entomology*. 28: 337–364.

Pruess, K. P. 1983. Day-degree methods for pest management. *Environmental Entomology*. 12: 613–619.

QDPI. 1998. Queensland Department of Primary Industries, Australia.

Raghu, S., Clarke, A. R., Drew, R A. I. and Hulsman, K. 2000. Impact of habitat modification on the distribution and abundance of fruit flies (Diptera: Tephritidae) in southeast Queensland. *Population Ecology*. 42: 153–160.

Ramadan, M. M. and Messing R. H.. 2003. A survey for potential biocontrol agents of *Bactrocera cucurbitae* (Diptera: Tephritidae) in Thailand. *Proceedings of Hawaii Entomological Society*. 36: 115–122.

Ranganath, H. and Veenakumari, K. 1995. Notes on the Dacine fruit flies (Diptera: Tephritidae) of Andaman and Nicobar Islands. *Raffle Bulletin of Zoology*. 43: 235–238.

Reiners, S. and Petzoldt, C. 2005. Integrated crop and pest management guidelines for commercial vegetable production. Cornell cooperative extension publication 124VG http://www.nysaes.cornell.edu/recommends/

Rohdendorf, B. B. 1961. Palaearctic fruit flies (Diptera, Trypetidae) of the genus *Rhagoletis* Leow and closely related genera. *Entomological Review*. 40: 89–102.

Rosenzweig, M. L. and Abramsky, Z. 1993. How are diversity and productivity related? In: Siemann, E., Haarstad, J. and Tilman, D. Dynamics of plant and arthropod diversity during old field succession. *Ecography*. 22: 406–414.

Rwomushana, I., Ekesi, S., Ogol, C. K. P.O., and Gordon, I. 2008. Effect of temperature on development and survival of immature stages of *Bactrocera invadens* (Diptera: Tephritidae)**.** *Journal of Applied Entomology*. 132: 832–839.

Sakai, A. K., Allendorf, E. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J E., Ellstrand, N. C., McCauley, D. E., Neil, P. O., Parker, I. M., Thompson, J. N. and Weller, S. G. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics*. 32: 305–332.

Sandhu, H. S., Nuessly, G. S., Webb, S. E., Cherry, R. H. and Gilbert, R. A. 2013. Temperature-dependent reproductive and life table parameters of *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on sugarcane. *Florida Entomologists*. 96: 380–390.

Sauers-Muller, van A. 1991. An overview of the Carambola fruit fly *Bactrocera* species (Diptera: Tephritidae), found recently in Suriname. *Florida Entomologists*. 74: 432–440.

Sauers-Muller, van A. 1993. Pilot eradication project for the Carambola fruit fly in Coronie, Suriname. In: Aluja, M. and Liedo, P. (eds). Fruit flies Biology and Management. pp. 439–442.

Sauers-Muller, van A. 2005. Host plants of carambola fruit fly, *Bactrocera carambolae* Drew and Hancock (Diptera: Tephritidae), in Suriname, south America. *Neotropical Entomology*. 34: 203–214.

Schutze, M. K., Jessup, A., Ul-Haq, I., Vreysen, M. J. B,, Wornoayporn, V., Vera, M. T. and Clarke, A. R. 2013. Mating compatibility among four pest members of the *Bactrocera dorsalis* fruit fly species complex (Diptera: Tephritidae). *Journal of Economic Entomology*. 106: 695–707.

Segura, D. F., Vera, M. T. and Cladera, J. L. 2004. Host utilization by Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). In: Barnes, B. N. (ed). Proceedings of the 6th International Symposium on fruit flies of economic importance. Stellenbosch, South Africa. Isteg Scientific Publications, Irene, South Africa.

Sei-Woong, C. 2008. Effects of weather factors on the abundance and diversity of moths in a temperate deciduous mixed forest of Korea. *Zoological Science*. 25: 53–58.

Selivon, D. and Perondini, A.L.P. 1998. Eggshell morphology in two cryptic species of the *Anastrepha fraterculus* complex (Diptera, Tephritidae). *Annals of Entomological Society of America*. 91: 473–478.

Selivon, D. and Perondini, A.L.P. 1999. Description of *Anastrepha sororcula* and *A. serpentine* (Diptera: Tephritidae) eggs. *Florida Entomologist.* 82: 347–353.

Selivon, D, Vretos, C. and Perondini, A. L. P. 2003. Evaluation of egg morphology from ethanol preserved females of *Anastrepha* sp.2 aff. *fraterculus* (Diptera: Tephritidae). *Neotropical Entomology*. 32: 527–529.

Senger,S. E., Tyson, B., Roitberg, B. D., Thistlewood, H. M. A., Harestad, A. S. and Chandler, M. T. 2009. Influence of habitat structure and resource availability on the movements of *Rhagoletis indifferens* (Diptera: Tephritidae). *Environmental Entomology*. 38: 823–835.

Sieman, E. 1998. Experinmental test of the effects of plant productivity and plant diversity on grassland arthropod diversity. *Ecology*. 79: 2057–2070.

Siemann, E., Haarstad, J., and Tilman, D. 1997. Short-term and long-term effects of burning on oak savannah arthropods. *American Midland Naturalist*. 137: 349–361.

Siemann, E., Haarstad, J., and Tilman, D. 1999. Dynamics of plant and arthropod diversity during old field succession. *Ecography*. 22: 406–414.

SigmaPlot. 2008. Version 11.0 Systat Software, San Jose, CA.

Smith, P. H. 1989. Behavioural partitioning of the day and circadian rhythmicity. In: Robinson, A. S., and Hooper, G. H. S. (eds.), Fruit Flies: Their Biology, Natural Enemies and Control, Elsevier, Oxford. Vol. 3B. pp. 325–341.

Souza-Filho, M. F., Raga, A., Azevedo-Filho, J. A., Strikis, P. C., Guimarães, J. A. and Zucchi, R. A. 2009. Diversity and seasonality of fruit flies (Diptera: Tephritidae and Lonchaeidae) and their parasitoids (Hymenoptera: Braconidae and Figitidae) in orchards of guava, loquat and peach. *Brazilian Journal of Bioliogy*. 69: 31–40.

Srinivasan, K. 1991. Pest management in cucurbits – An overview of work done under AICVIP. In: Group Discussion of Entomologists Working in the Coordinated Projects of Horticultural Crops. Central Institute of Horticulture for Northern Plains, Lucknow, Uttar Pradesh, India. pp. 44–52.

Steck, J. and Wharton, R. A. 1988. Description of immature stages of *Anastrepha interrupta*, *A. limae* and *A. grandis* (Diptera: Tephritidae). *Annals of Entomological Society of America*. 81: 994–1003.

Steffan-Dewenter, I. and Tscharntke, T. 1997. Early succession of butterfly and plant communities on set-aside fields. *Oecologia*. 109: 294–302.

Steiner, L. F. 1952. Low-cost plastic fruit fly traps. *Journal of Economic Entomology*. 50: 508–509.

Stork, N. E. 1999. The magnitude of biodiversity and its decline. The living Planet in crisis: Biodiversity science and policy. In: Cracraft, J.and Grifo, F. T. (eds). Columbia University Press, New York.

Subhadrabandhu, S. and Wongwanich, O. 1996. Status of the fruit and vegetable industry in Thailand. *Kasetsart Journal of Social Sciences*. 17: 170–180.

Syed, R. A. 1971. Studies on trypetids and their natural enemies in west Pakistan. *Dacus* (Strumeta) *cucurbitae* Coquillett. *Technical Bulletin of the Commonwealth Institute of Biological Control*. 14: 63–75.

Tan, K. H. and Nishida, R. 1996. Sex pheromone and mating competition after methyl eugenol consumption in the *Bactrocera dorsalis* complex. In: McPheron, B. A. and Steck, G. J.(eds.). Fruit Fly Pests. St. Lucie, Florida.

Thomas, D. B. 1997. Degree-day accumulations and seasonal duration of the pre-imaginal stages of the Mexican fruit fly (Diptera: Tephritidae). *Florida Entomologist*. 80: 71–79.

Thapinta A. and Hudak, P.F. 2000. Pesticide use and residual occurrence in Thailand. *Environment Monitoring and Assessment*. 60: 103–114.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos*. 58: 3–15.

Tobin, J. 1990. Fruit fly control. ACIAR Economic Assessment Series 2, Canberra. In: Fruit fly in Malaysia and Thailand. Collins Business Development and Analysis.

ToraVueti, E., Ralulu, L., Walker, G. P., Allwood, A. J., Lewiniqila, L. and Balawakula, A. 1997. Host availability – its impact on seasonal abundance of fruit flies, In: Allwood A J, Drew R E I (eds). Management of fruit flies in the

Pacific. *Proceedings of Australian Centre for International Agricultural Research (ACIAR)*, Canberra, Australia. No 76. pp 105–110.

Tscharnike, T. and Greiler, H. 1995. Insect communities, grasses, and grasslands. *Annual Review of Entomology*. 40: 535–558.

Tsitsipis, J. A. 1980. Effect of constant temperatures on larval and pupal development of olive fruit flies reared on artificial diet. *Environmental Entomology* 9: 764–768.

Turner, H. Hovenkamp, P. and van Welzen, P. C. 2001. Biogeography of Southeast Asia and the West Pacific. *Journal of Biogeography*. 28: 217–230.

Udevitz, M. S. and Ballachey, B. E. 1998. Estimating survival rates with age-structure data. *Journal of Wildlife Management*. 62: 779–792.

Vargas, R. I. and Carey, J. R. 1990. Comparative survival and demographic statictics for wild oriental fruit fly, Mediterranean fruit fly, and melon fruit fly (Diptera: Tephritidae) on papaya. *Journal of Economic Entomology* 83: 1344–1349.

Vargas, R. I. and Nishida, T. 1985. Life history and demographic parameters of *Dacus latifrons* (Diptera: Tephritidae). *Journal of Economic Entomology* 78: 1242–1244.

Vargas, R. I., Nishida, T. and Beardsley, J. W. 1983. Distribution and abundance of *Dacus dorsalis* (Diptera: Tephritidae) in native and exotic forest areas on Kauai. *Environmental Entomology*. 12: 1185–1189.

Vargas, R. I., Miyashi, D. and Nishida, T. 1984. Life history and demographic parameters of three laboratory reared tephritids (Diptera: Tephritidae). *Annals of Entomological Society of America* 77: 651–656.

Vargas, R. I., Stark, J. D and Nishida, T. 1989.Abundance, distribution, and dispersion indices of the oriental fruit fly and melon fly (Diptera:Tephritidae) on Kauai, Hawaiian Islands. *Journal of Economic Entomology* 82: 1609–1615.

Vargas, R. I., Strak, J. D. and Nishida, T. 1990. Population dynamics, habitat preference and seasonal distribution patterns of Oriental fruit fly and Melon fruit fly (Diptera: Tephritidae) in an agricultural area. *Environmental Entomology*. 19: 1820–1828.

Vargas, R. I., Walsh, W. A., Jan, E. B., Armstrong, J. W. and Kanehisa, D. T. 1996. Survival and development of immature stages of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Annals of Entomological Society of America* 89: 64–69.

Vargas, R. I., Walsh, W. A., Kanehisa, D. T., Jang, E. B. and Armstrong, J. W. 1997. Demography of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Annals of Entomological Society of America* 90: 162–168.

Vargas, R. I., Walsh, W. A., Kanehisa, D. T., Stark, J. D. and Nishida, T. 2000. Comparative demography of three Hawaiian fruit flies (Diptera: Tephritidae) at alternating temperatures. *Annals of Entomological Society of America*. 93: 75–81.

Vaupel, J. W., Carey, J. R., Christensen, K., Johnson, T. E., Yashin, A. I., Holm, N. V., Iachine, I. A., Kannisto, V., Khazaeli, A. A., Liedo, P., Longo, V. D., Zeng, Y., Manton, K. G. and Curtsinger, J. W. 1998. Biodemographic trajectories of longevity. *Science*. 280:855–860.

Vayssières, J. F., Carel, Y. Coubes, M. and Duyck, P. F. 2008. 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: 307–314.

Vayssières, J., Goergen, G., Lokossou, O., Dossa, P. and Akponson, C. 2005. A new *Bactrocera* species in Benin among mango fruit fly (Diptera: Tephritidae) species. *Fruits*. 60: 371–377.

Vernon, P., Vannier, G. and Trehen, P. 1998. A comparative approach to the entomological diversity of polar regions. *Acta Oecologica*. 19: 303–308.

Victor, M. G. S. 2009. Monitoring and pest control of Fruit flies in Thailand: new knowledge for integrated pest management. Examensarbete, *SLU* Institutionen för ekologi, Uppsala. 32 pp.

Vijaysegaran, S. and Shamsudin, O. M. 1991. Fruit flies in Malaysian peninsular: their economic importance and control strategies. In: Kawasaki, K., Iwahashi, O. and Kaneshiro, K. Y. (eds). *Proceedings of the International Symposium on the biology and control of fruit flies*. Okinawa.

Wagner, T. L., Wu, H. I., Sharpe, P. J. H., Schoolfield, R. M. and Coulson, R. N. 1984. Modeling insect development rate: a literature review and application of a biophysical model. *Annals of Entomological Society of America* 77: 208–225.

Warburg, M. S. and Yuval, B. 1997. Effects of energetic reserves on behavioral patterns of Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia*. 112: 314–319.

Waterhouse, D. F. 1993. The major arthropod pests and weeds of Agriculture in Southeast Asia. Canberra, Australia. *Australian Centre for International Agricultural Research* (*ACIAR*) *Monograph.* No. 21 141pp.

Waterhouse, D. F. 1997. The major invertebrate pests and weeds of agriculture and plantation forestry in southern and western Pacific. Canberra, Australia. *Australian Centre for International Agricultural Research* (*ACIAR*) *Monograph*. No 44, 99pp.

Wee, S. L. and Tan, K. H. 2005. Evidence of natural hybridization between two sympatric sibling species of *Bactrocera dorsalis* complex on pheromone analysis. *Journal of Chemical Ecology*. 31: 845–853.

Weems, H. V. Jr. and Heppner, J. B. 1999. Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Insecta: Diptera: Tephritidae). Florida Department of Agriculture and Consumer Services, Division of Plant Industry, and T.R. Fasulo, University of Florida. University of Florida Publication EENY- 083.

Wharton, R. A. 1989. Classical biological control of fruit infesting Tephritidae. In: Robinson, A. S. and Hooper, G. H. S. (eds). Fruit flies: their biology, natural enemies and control. Elsevier Science, Amsterdam. *World crop pests.* Vol. 3B. 303-313.

White, I. M. and Clement, S. L. 1987. Systematic notes on Urophora (Diptera, Tephritidae) species associated with *Centaurea solstitialis* (Asteraceae, Cardueae) and other Palaearctic weeds adventive in North America. *Proceedings of the Entomological Society of Washington*. 89: 571–580.

White, I. M. and Elson-Harris, M. M. 1992. Fruit flies of economic significance: Their identification and bionomics. CAB International, Wallingford, 601pp.

Whitmore, T. C. 1975. Tropical rainforest of the far East. Clarendon Press. Oxford.

Wikramanayake, E., Dinerstein, E., Loucks, C., Olson, D., Morrison, J., Lammoreux, J., McKnight, M. and Hedao, P. 2002. Terrestrial ecoregions of the Indo-Pacific: a conservation assessment. Island Press, U.S.A.

Yamamura, K. and K. Kiritani. 1998. A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. *Applied Entomology and Zoology*. 33: 289–298.

Yang, P., Carey, J. R. and Dowell, R. V. 1994a. Temperature influences on the development and demography of *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Environmental Entomology*. 23: 971–974.

Yang, P., Zhou, C., Liang, G., Dowell, R. V. and Carey, J. R. 1994b. Temperature studies on a chinese strain of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae). *Pan-Pacific Entomology*. 70: 269–275.

Ye, H. 2001. Distribution of the oriental fruit fly (Diptera: Tephritidae) in Yunnan Province. *Insect Science*. 8: 175–182.

Yong, H. S. 1994. Host fruit preference in two sympatric taxa of the *Bactrocera dorsalis* complex (Insecta: Diptera: Tephritidae). In: Allwood, A. J., Chinajariyawong, A., Drew, R. A. I., Hamacek, E. L., Hancock, D. L., Hengsawad, C., Jinapin, J. C., Jirasurat, M., Kong Krong, C., Kritsaneepaiboon, S., Leong, C. T. S., and S. Vijaysegaran. 1999. Host plant records for fruit flies (Diptera: Tephritidae) in South-East Asia. *Raffles Bulletin of Zoology*. Supplement 7. 92 pp.

Yong, H. S., Rosli, H., Moh'd, S. A., Siti. and Z. M. D. 2010. Diversity and abundance of dacinae fruit flies (Insecta: Diptera: Tephritidae) in Pantai Melawi and Delising, Kelantan, Peninsular Malaysia. *Malaysian Journal of Science*. 29: 63–66.

Zeh, D. W., Zeh, J. A. and Smith, R. L. 1989. Ovipositors, amnions and eggshell architecture in the diversification of terrestrial arthopods. *Quarterly Review of Biology*. 64: 147–168.

Zwölfer, H. 1983. Life sytems and strategies of resource exploitation in tephritids, In: Cavalloro, R. (ed). Fruit Flies of Economic Importance. Proceedings of the CEC/IOBC Innternational Symposium, Athens, Balkima, Rotterdam. pp. 16–30.

APPENDIX A. List of genus *Bactrocera* and *Dacus* species reported in this study.

(1) *B. albistigata* (F)

(4) *B. carambolae* (M)

(2) *B. atrifemur* (M)

(5) *B. caryae* (M)

(3) *B. bimaculata* (M)

(6) *B. caudata* (M)

(7) ***B. correcta*** **(M)**

(10) ***B. floresiae*** **(M)**

(8) ***B. cucurbitae*** **(M)**

(11) ***B. holtmanni*** **(M)**

(9) ***B. diversa*** **(M)**

(12) ***B. irvingiae*** **(M)**

(13) ***B. kandiensis*** **(M)**

(16) ***B. lombokensis*** **(M)**

(14) ***B. kinabalu*** **(M)**

(17) ***B. malasiensis*** **(M)**

(15) ***B. latifrons*** **(F)**

(18) ***B. melastomosis*** **(M)**

(19) ***B. musae*** **(M)**

(22) ***B. osbeckiae*** **(M)**

(20) ***B. neocognata*** **(M)**

(23) ***B. papayae*** **(M)**

(21) ***B. neopropinqua*** **(M)**

(24) ***B. philippinensis*** **(M)**

(25) ***B. propinqua*** **(M)**

(28) ***B. tau*** **(F)**

(26) ***B. quasipropinqua*** **(M)**

(29) ***B. umbrosa*** **(M)**

(27) ***B. raiensis*** **(M)**

(30) ***B. zonata*** **(M)**

(31) ***B. sp1*** **(M)**

(32) ***D. lounsburyii*** **(F)**

(33) ***D. smeiroides (M)***

APPENDIX B. Statistical tables

1. **Summary of one way ANOVA for *B. carambolae* comparison for town orchards (PSU X HN)**

Source of Variation	DF	SS	MS	F	P
Between Groups	23	276789.258	12034.316	14.265	<0.001
Residual	82	69176.600	843.617		
Total	105	345965.858			

2. **Summary of one way ANOVA for *B. papayae* comparison for town orchards (PSU X HN)**

Source of Variation	DF	SS	MS	F	P
Between Groups	23	5644490.226	245412.619	19.144	<0.001
Residual	82	1051158.500	12819.006		
Total	105	6695648.726			

3. **Summary of one way ANOVA for *B. carambolae* and *B. papayae* comparison at (PSU)**

Source of Variation	DF	SS	MS	F	P
Between Groups	23	5665087.636	246308.158	30.663	<0.001
Residual	82	658676.600	8032.641		
Total	105	6323764.236			

4. **Summary of one way ANOVA for *B. carambolae* and *B. papayae* comparison at (HN)**

Source of Variation	DF	SS	MS	F	P
Between Groups	23	3319229.434	144314.323	25.633	<0.001
Residual	82	461658.500	5629.982		
Total	105	3780887.934			

5. **Summary of one way ANOVA for *B. carambolae* comparison for agro forest BK (AGO X GO)**

Source of Variation	DF	SS	MS	F	P
Between Groups	23	2839092.149	123438.789	9.641	<0.001
Residual	82	1049841.700	12802.948		
Total	105	3888933.849			

6. **Summary of one way ANOVA for *B. carambolae* comparison for agro forest BP (AGO X GO)**

Source of Variation	DF	SS	MS	F	P
Between Groups	23	492029.406	21392.583	6.238	<0.001
Residual	82	281229.500	3429.628		
Total	105	773258.906			

7. **Summary of one way ANOVA for *B. papayae* comparison for agro forest BK (AGO X GO)**

Source of Variation	DF	SS	MS	F	P
Between Groups	23	54233809.162	2357991.703	22.334	<0.001
Residual	81	8551820.400	105578.030		
Total	104	62785629.562			

8. Summary of one way ANOVA for *B. papayae* comparison for agro forest BP (AGO X GO)

Source of Variation	DF	SS	MS	F	P
Between Groups	23	6985006.943	303695.954	8.787	<0.001
Residual	82	2833950.500	34560.372		
Total	105	9818957.443			

9. Summary of one way ANOVA for *B. carambolae* and *B. papayae* comparison at BK (AGO)

Source of Variation	DF	SS	MS	F	P
Between Groups	23	3133128.590	136222.982	21.893	<0.001
Residual	81	503999.600	6222.217		
Total	104	3637128.190			

10. Summary of one way ANOVA for *B. carambolae* and *B. papayae* comparison at BK (GO)

Source of Variation	DF	SS	MS	F	P
Between Groups	23	54936673.434	2388551.019	21.529	<0.001
Residual	82	9097662.500	110947.104		
Total	105	64034335.934			

11. Summary of one way ANOVA for *B. carambolae* and *B. papayae* comparison at BP (AGO)

Source of Variation	DF	SS	MS	F	P
Between Groups	23	6835838.784	297210.382	11.127	<0.001
Residual	82	2190262.650	26710.520		
Total	105	9026101.434			

12. Summary of one way ANOVA for *B. carambolae* and *B. papayae* comparison at BP (GO)

Source of Variation	DF	SS	MS	F	P
Between Groups	23	4001121.150	173961.789	15.423	<0.001
Residual	82	924917.350	11279.480		
Total 105	4926038.500				

13. Summary of one way ANOVA for *B. carambolae* at Urban, GO and AGO

Source of Variation	DF	SS	MS	F	P
Between Groups	2	12653.659	6326.830	12.405	<0.001
Residual	309	157602.926	510.042		
Total	311	170256.585			

14. Summary of one way ANOVA for *B. papayae* at Urban, GO and AGO

Source of Variation	DF	SS	MS	F	P
Between Groups	2	310904.015	155452.008	18.908	<0.001
Residual	309	2540433.235	8221.467		
Total	311	2851337.250			

15. Summary of Kruskal-Wallis One Way ANOVA on ranks for egg developmental time of *B. carambolae* and *B. papayae*

H = 165.084 with 11 degrees of freedom. (P = <0.001)

16. Summary of Kruskal-Wallis One Way ANOVA on ranks for larva developmental time of *B. carambolae* and *B. papayae*

H = 160.377 with 11 degrees of freedom. (P = <0.001)

17. Summary of Kruskal-Wallis One Way ANOVA on ranks for pupa developmental time of *B. carambolae* and *B. papayae*

H = 144.155 with 9 degrees of freedom. (P = <0.001)

18. Summary of Kruskal-Wallis One Way ANOVA on ranks for egg survival of *B. carambolae* and *B. papayae*

H = 89.764 with 11 degrees of freedom. (P = <0.001)

19. Summary of Kruskal-Wallis One Way ANOVA on ranks for larva survival of *B. carambolae* and *B. papayae*

H = 67.083 with 11 degrees of freedom. (P = <0.001)

20. Summary of Kruskal-Wallis One Way ANOVA on ranks for pupa survival of *B. carambolae* and *B. papayae*

H = 82.622 with 9 degrees of freedom. (P = <0.001)

21. Summary of Kruskal-Wallis One Way ANOVA on ranks for adult emergence of *B. carambolae* and *B. papayae*

H = 98.850 with 9 degrees of freedom. (P = <0.001)

22. Summary of one way ANOVA for mean developmental time of *B. carambolae* and *B. papayae*

Standard Analysis of Variance

Source of Variation	DF	SS	MS	F	P
Between Groups	9	9711.231	1079.026	2081.489	<0.001
Residual	20	10.368	0.518		
Total	29	9721.599			

23. Summary of one way ANOVA for pre-oviposition

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	489.400	163.133	106.778	<0.001
Residual	36	55.000	1.528		
Total	39	544.400			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	229.400	76.467	65.232	<0.001
Residual	36	42.200	1.172		
Total	39	271.600			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	815.600	116.514	86.307	<0.001
Residual	72	97.200	1.350		
Total	79	912.800			

24. Summary of one way ANOVA for oviposition

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	14538.100	4846.033	620.844	<0.001
Residual	36	281.000	7.806		
Total	39	14819.100			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	17147.500	5715.833	668.953	<0.001
Residual	36	307.600	8.544		
Total	39	17455.100			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	32722.400	4674.629	571.820	<0.001
Residual	72	588.600	8.175		
Total	79	33311.000			

25. Summary of one way ANOVA for gross fecundity

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	4288456.200	1429485.400	754.993	<0.001
Residual	16	30294.000	1893.375		
Total	19	4318750.200			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	3235046.800	1078348.933	175.705	<0.001
Residual	16	98196.400	6137.275		
Total	19	3333243.200			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	7858759.100	1122679.871	279.599	<0.001
Residual	32	128490.400	4015.325		
Total	39	7987249.500			

26. Summary of one way ANOVA for net fecundity

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	1081173.750	360391.250	461.109	<0.001
Residual	16	12505.200	781.575		
Total	19	1093678.950			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	862662.000	287554.000	94.880	<0.001
Residual	16	48491.200	3030.700		
Total	19	911153.200			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	2040366.375	291480.911	152.917	<0.001
Residual	32	60996.400	1906.138		
Total	39	2101362.775			

27. Summary of one way ANOVA for daily egg produced

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	94.853	31.618	188.237	<0.001
Residual	16	2.687	0.168		
Total	19	97.541			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	58.154	19.385	83.979	<0.001
Residual	16	3.693	0.231		
Total	19	61.847			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	165.096	23.585	118.282	<0.001
Residual	32	6.381	0.199		
Total	39	171.477			

28. Summary of one way ANOVA for female longevity

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	25922.200	8640.733	501.639	<0.001
Residual	16	275.600	17.225		
Total	19	26197.800			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	26971.750	8990.583	753.927	<0.001
Residual	16	190.800	11.925		
Total	19	27162.550			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	54784.575	7826.368	536.972	<0.001
Residual	32	466.400	14.575		
Total	39	55250.975			

29. Summary of one way ANOVA for male longevity

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	32253.400	10751.133	616.995	<0.001
Residual	16	278.800	17.425		
Total	19	32532.200			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	27396.550	9132.183	847.534	<0.001
Residual	16	172.400	10.775		
Total	19	27568.950			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	60505.575	8643.654	613.025	<0.001
Residual	32	451.200	14.100		
Total	39	60956.775			

30. Summary of one way ANOVA for Intrinsic Rate of increase (*r*)

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	0.116	0.0386	47.721	<0.001
Residual	16	0.0129	0.000808		
Total	19	0.129			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	0.534	0.178	85.460	<0.001
Residual	16	0.0333	0.00208		
Total	19	0.567			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	1.015	0.145	100.356	<0.001
Residual	32	0.0462	0.00144		
Total	39	1.061			

31. Summary of one way ANOVA for Finite Rate of increase (λ)

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	0.173	0.0578	45.898	<0.001
Residual	16	0.0202	0.00126		
Total	19	0.194			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	1.225	0.408	70.663	<0.001
Residual	16	0.0925	0.00578		
Total	19	1.318			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	2.188	0.313	88.815	<0.001
Residual	32	0.113	0.00352		
Total	39	2.301			

32. Summary of one way ANOVA for Net Reproductive Rate (R_o)

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	2734.256	911.419	2286.560	<0.001
Residual	16	6.378	0.399		
Total	19	2740.634			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	7033.010	2344.337	2737.432	<0.001
Residual	16	13.702	0.856		
Total	19	7046.712			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	11289.825	1612.832	2570.254	<0.001
Residual	32	20.080	0.627		
Total	39	11309.905			

33. Summary of one way ANOVA for Gross Reproductive Rate (*GRR*)

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	4421.803	1473.934	920.162	<0.001
Residual	16	25.629	1.602		
Total	19	4447.433			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	13455.405	4485.135	3437.544	<0.001
Residual	16	20.876	1.305		
Total	19	13476.281			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	20809.351	2972.764	2045.548	<0.001
Residual	32	46.505	1.453		
Total	39	20855.856			

34. Summary of one way ANOVA for Life Expectancy (e_x) of male

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	5300.614	1766.871	965.360	<0.001
Residual	16	29.284	1.830		
Total	19	5329.898			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	4344.203	1448.068	542.265	<0.001
Residual	16	42.726	2.670		
Total	19	4386.930			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	9843.648	1406.235	624.900	<0.001
Residual	32	72.011	2.250		
Total	39	9915.659			

35. Summary of one way ANOVA for Life Expectancy (e_x) of female

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	4393.119	1464.373	733.300	<0.001
Residual	16	31.951	1.997		
Total	19	4425.070			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	3855.181	1285.060	497.630	<0.001
Residual	16	41.318	2.582		
Total	19	3896.498			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	8536.400	1219.486	532.605	<0.001
Residual	32	73.269	2.290		
Total	39	8609.669			

36. Summary of one way ANOVA for Doubling time (*DT*)

B. carambolae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	94.065	31.355	48.991	<0.001
Residual	16	10.240	0.640		
Total	19	104.305			

B. papayae

Source of Variation	DF	SS	MS	F	P
Between Groups	3	11.688	3.896	7.093	0.003
Residual	16	8.789	0.549		
Total	19	20.477			

B. carambolae X *B. papayae*

Source of Variation	DF	SS	MS	F	P
Between Groups	7	134.607	19.230	32.337	<0.001
Residual	32	19.029	0.595		
Total	39	153.637			

VITAE

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MPhil. Entomology	University of Ghana, Legon	2002
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List of Publication and Proceeding

1. Solomon Danjuma, Narit Thaochan, Surakrai Permkam and Chutamas Satasook, 2013. Effect of temperature on the development and survival of immature stages of the carambola fruit fly, *Bactrocera carambolae* and the Asian papaya fruit fly, *Bactrocera papayae* reared on guava diet. Journal of Insect Science (In press).

2. Solomon Danjuma, Singtoe Boonrotpong, Narit Thaochan, Surakrai Permkam and Chutamas Satasook, 2013. Biodiversity of the genus *Bactrocera* (Diptera: Tephritidae) in guava *Psidium guajava* L. orchards in different agro-forested locations of southern Thailand. International Journal of Chemical, Environmental and Biological Sciences (IJCEBS). Vol 1, Issue 3, 538-544.

3. Solomon Danjuma, Singtoe Boonrotpong, Narit Thaochan, Surakrai Permkam and Chutamas Satasook, 2013. Seasonality of the Carambola fruit fly *Bactrocera carambolae* and Asian papaya fruit fly *Bactrocera papayae* (Diptera: Tephritidae) on guava *Psidium guajava* in peninsular Thailand. International Journal of Pest Management (In process).