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TITLE: Mango Varietal Preference and the Effect of Physiological Changes During Mango Ripening on Host Utilisation by *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae)

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THESIS

MANGO VARIETAL PREFERENCE AND THE EFFECT OF PHYSIOLOGICAL CHANGES DURING MANGO RIPENING ON HOST UTILISATION BY BACTROCERA DORSALIS (HENDEL) (DIPTERA: TEPHRITIDAE)

WIGUNDA RATTANAPUN

A Thesis Submitted in Partial Fulfillment of
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Wigunda Rattanapun 2009: Mango Varietal Preference and the Effect of Physiological Changes During Mango Ripening on Host Utilisation by *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae). Doctor of Philosophy (Entomology), Major Field: Entomology, Department of Entomology. Thesis Advisor: Assistant Professor Weerawan Amornsak, Ph.D. 138 pages.

Most tropical fruit flies lay their eggs only into mature fruit, but a small number can also oviposit into unripe fruit. Little is known about the link between adult oviposition preference and offspring performance in such situations. I examined the influence of different ripening stages of two mango *Mangifera indica* L. (Anacardiaceae) varieties on the preference and performance of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), a fly known to utilise unripe fruit. Work was carried out as a series of laboratory-based oviposition experiments and larval growth trials. The results demonstrated a general preference by *B. dorsalis* for mango variety Oakrong over variety Namdorkmai, but in most cases the single largest dependent variable influencing results was fruit ripening stage. Ripe and fully-ripe mangoes were most preferred for oviposition by *B. dorsalis*. In contrast, unripe mango was infrequently used by ovipositing females, particularly in choice trials. Consistent with the results of oviposition preference, ripe and fully-ripe mangoes were also best for offspring survival, with a higher percentage of larval survival to pupation and shorter development times in these fruits. Changes in total soluble solids (TSS) and firmness correlated with changing host use across the ripening stages. Regardless of the mango variety or ripening stage, *B. dorsalis* had difficulty penetrating the pericarp of all fruits offered in experiments. Under the influence of egg load pressure, high egg-load female flies made more attempts to oviposit into unripe fruit than low egg-load females. Larval survival was also often poor in all experiments. I discuss the possibility that there may be differences in the ability of laboratory and wild flies to penetrate fruit for oviposition, or that in the field flies more regularly utilise natural fruit wounds as oviposition sites. To formalize the adult oviposition preference and larval performance at the "within-fruit" level, experiments were performed to record the number of oviposition attempts made into three fruit parts (top, middle and bottom) and larval behavior within different parts of a fruit, again at three mango ripening stages. Results indicate that female *B. dorsalis* do not oviposit uniformly across a mango fruit, but lay most often in the top of fruit and least in the bottom part, regardless of ripening stage. In contrast, for nearly all data except percent adult emergence from pupae, there was no evidence of larval feeding site preference or performance (development time, pupal weight, percent pupation) being influenced by fruit part, within or across fruit ripening stages. More larval movement in ripe fruit (compared to fully ripe fruit) is probably indicative of larger variation in host nutritional quality during fruit ripening. Differences in mechanical (firmness) and chemical [TSS, titratable acidity (TA), total non-structural carbohydrates (TNC)] traits between different fruit parts were correlated with adult fruit utilisation. The results are ambiguous with respect to supporting, or rejecting, a positive adult preference/offspring performance relationship at within-fruit level for *B. dorsalis*. To further understand the role played by different host cues in female orientation, a third set of experiments were run. These isolated host visual and olfactory cues for three mango ripening stages. Results of these studies indicated that host fruit color played only a minor role in host quality assessment by female flies, whereas host fruit volatiles played an important role in the determination of host quality. Overall results show that while *B. dorsalis* is physiologically capable of utilising green fruit, it much prefers to oviposit into ripe and fully-ripe fruits, and larvae do better in such fruit.

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Wigunda Rattanapun

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TABLE OF CONTENTS

Page

TABLE OF CONTENTS (Continued)

Page

TABLE OF CONTENTS (Continued)

Page

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

MANGO VARIETAL PREFERENCE AND THE EFFECT OF PHYSIOLOGICAL CHANGES DURING MANGO RIPENING ON HOST UTILISATION BY BACTROCERA DORSALIS (HENDEL) (DIPTERA: TEPHRITIDAE)

INTRODUCTION

Tropical fruit flies (Diptera: Tephritidae: Dacinae) are serious pests of economic fruits in Southeast Asia and the Pacific. Adult flies lay their eggs directly into fruit and the resultant maggots feed on the fruit flesh. Dacine fruit flies attack a wide range of different fruit species and cause significant economic loss (White and Elson-Harris, 1992). Fruit flies have been extensively investigated in Thailand as agricultural pests and field surveys of fruit fly hosts have been undertaken (Meksongsee *et al*., 1988; Baimai *et al*., 1998; Chinajariyawong *et al*., 2000; Clarke *et al*., 2001). Economic fruit fly hosts include jackfruit [*Artocarpus heterophyllus* (Moraceae)], guava [*Psidium guajava* (Myrtaceae)], santol [*Sandoricum koetjape* (Meliaceae)] and mango [*Mangifera indica* (Anacardiaceae)]. Non-economic fruits have also been recorded as fruit fly hosts and these may act as alternative sources of fruit flies in agricultural systems. The non-economic host fruits include Tropical almond [*Terminalia catappa* (Combretaceae)], Spanish cherry [*Mimusops elengi* (Sapotaceae)] and fig [*Ficus* spp. (Moraceae)] (Baimai *et al*., 1998; Allwood *et al*., 1999; Clarke *et al*., 2005). The mix of commercial and non-commercial fruit in the environment makes fruit fly population control difficult.

The *Bactrocera dorsalis* complex of tropical fruit flies is one of the most important pest species complexes in world agriculture (Clarke *et al*., 2005). In this use, "complex" refers to a group of morphologically similar, but biologically distinct species. Drew and Romig (1997) accorded pest status of flies within this complex from "significant" [*Bactrocera occipitalis* (Bezzi)], to "serious" (*Bactrocera pyrifoliae* Drew & Hancock) and "major" (*Bactrocera dorsalis* (Hendel) and

Bactrocera carambolae Drew & Hancock), to "the most destructive of all dorsalis complex species" (*Bactrocera papayae* Drew & Hancock). The present study will focus on the Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), a fly found in many areas of central and northern Thailand and which exhibits extreme polyphagy, infesting 124 host species across 42 plant families, (Clarke *et al*., 2001; Clarke *et al*., 2005). *Bactrocera dorsalis* has been observed attacking green fruit at low levels in Southeast Asia (R.A.I. Drew, pers comm.). The detection of incursive Asian papaya fruit fly, *Bactrocera papayae* Drew & Hancock, a sibling species of *B. dorsalis*, in far-north Queensland in the mid-1990's was because of the unusual observation of maggots in green papaya, *Carica papa*ya (Caricaceae) (Drew, 1997). Such observations of *B. dorsalis* complex flies attacking green fruit warrants further investigation as this behavior is uncommon in dacine fruit flies but has important implications for in-field management and market access.

There has been no formal investigation of the influence of host fruit varieties and physiological changes of host fruit during ripening on adult *B. dorsalis* oviposition behavior and larval fruit utilisation. Indeed, this is a very poorly worked area in fruit fly ecology, although it is widely recognised (e.g., as a quarantine tool) that stage of fruit ripeness influences host fruit suitability. Under controlled conditions, this thesis investigates how mango varieties, mango ripeness stages, mango physiological features associated with ripening, and interactions between these factors, influence host preference and performance for female flies and larvae of *B. dorsalis*. To partially address this issue, this study was divided into three parts. Part I presents a detail, laboratory-based analysis of *B. dorsalis* adult oviposition preference and offspring performance across three fruit ripening stages for two locally common mango varieties, Namdorkmai and Oakrong. Both these varieties are subject to commercially significant fly infestation in the field unless protected. Part II further quantified how the host ripening processes impacts on host use by *B. dorsalis* at the adult oviposition preference and larval performance at the "within-fruit" level.

In part III, I seek to tease apart the differential effects of visual and odor cues on female *B. dorsalis* foraging for mangoes of different ripening stage. I asked whether female flies that are exposed to only one host fruit stimuli (visual or volatiles cues), make similar choices depending on the cue received. The result of this study can enhance our understanding of responses of gravid female fly *B. dorsalis* to visual and olfactory cues.

Results of this thesis develop knowledge of the specific mechanisms by which host fruit varieties and ripening influences fruit fly host use. This is of potential value in field management, quarantine and plant breeding using traditional or transgenic approaches, as well as offering significantly theoretical insights into the evolution of host range development of fruit flies and other phytophagous species.

OBJECTIVES

1. To investigate comparative host fruit preference of *B. dorsalis* between two mango varieties.

2. To investigate the effect of physiological changes during mango ripening on adult oviposition behavior and larval feeding of *B. dorsalis*.

3. To identify the fruit physiological traits associated with ripening which influence female flies behavior and host use pattern.

LITERATURE REVIEW

The interaction between tephritid fruit flies and their host plants is complex. Host plants play an important role in all stages of the life cycle of fruit flies and the evolution of fruit flies is considered to be linked with their host plants. Host fruit and foliage attract female flies as they serve as oviposition sites and food substrates. Under natural conditions, female flies rely on many factors to find suitable host fruit for oviposition. These factors may vary depending on the local environment and the physiological status of the female fly. The relationship between fruit flies and their host plants is the topic dealt within this chapter. This review firstly introduces fruit flies of the genus *Bactrocera*, my study organisms, and then the topic of fruit fly host plant interactions. The main bulk of the chapter deals explicitly with host location and host utilisation; very broad area of study in insect herbivore studies for which there is much literature. The purpose of the review is to set the intellectual "scene" for the research chapters which follow.

1. Taxonomy, General Morphology and Biogeography of the Genus *Bactrocera* of the Dipteran Subfamily Dacinae

One of the largest families of true flies (Order Diptera) is the family Tephritidae, the true fruit flies. There are approximately 5,000 tephritid species distributed globally, nearly all of which have phytophagous (i.e., plant feeding) larvae (White and Elson-Harris, 1992). Within the Tephritidae are a number of sub-families, of which the most common within the African, Asian and Pacific regions is the sub-family Dacinae. There are 750 described species of dacine fruit flies worldwide, with approximately 68% of these belonging to the genus *Bactrocera* Macquart and 32% belonging to the genus *Dacus* Fabricius (Drew and Hancock, 2000). *Dacus* species are found predominantly in arid and semi-arid areas of Africa, while the greater number of *Bactrocera* species are found in the humid Indo-Malayan rainforests, extending down into Papua New Guinea and tropical Australia (Drew and Hancock,

2000). Fifty-nine species of dacine fruit fly are described in Thailand (A.R. Clarke pers comm.).

Hardy (1955) described dacine fruit flies as having the following specific characters: reduced chaetotaxy, lacking dorsocentral-, presutural-, sternopleural-, ocellar post vertical-, and humeral-bristles. *Bactrocera* species are separated from *Dacus* through the possession of non-fused tergal plates, with *Dacus* species having fused terga (Drew, 1989). The fused terga may confer an advantage for oviposition into thick-skinned fruit, such as the pods of Asclepiadaceae, and may also help water conservation (White, 2000). The genus *Bactrocera* was subdivided by Drew (1989) into four subgenera according to the length of the posterior lobe of the male, lateral surstylus and the presence or absence of a notch on the hind margin of the fifth male sternite. These subgeneric features within *Bactrocera* suggest some difference in the mechanics of either terminalia retraction and storage or copulation between these subgenera, which in turn may have some behavioral significance (White, 2000). Drew (1989) grouped the subgenera of *Bactrocera* into two key groups, *Zeugodacus* and *Bactrocera*. *Zeugodacus* is associated with host plants in the family Cucurbitaceae, whereas *Bactrocera* has a wider range of host plant families including Anacardiaceae, Combretaceae and Musaceae.

Within the subgenus *Bactrocera* (*Bactrocera*) is a large grouping of closely related, and morphologically similar species known as the Oriental fruit fly (= *Bactrocera dorsalis*) complex. This group of flies, distributed predominantly in Southeast Asia but also east spreading into the Pacific and west to the Indian sub-continent, was first described by Hardy (1969). Drew and Hancock (1994) redefined the *B. dorsalis* complex as one of 20 species complexes within the subgenus *Bactrocera* (*Bactrocera)*. The *Bactrocera dorsalis* complex currently contains 75 described species (Clarke *et al*., 2005). Forty species of the *B. dorsalis* complex are recorded in Thailand and as such they are the dominant group of Thai fruit flies (Drew and Hancock, 1994; Baimai *et al*., 1998; Clarke *et al*., 2005). Species level identification of many flies within the *B. dorsalis* complex remains uncertain. The morphological similarity of most *B. dorsalis* complex species causes significant

difficulty in identification. Significant information on the morphological diagnosis of *Bactrocera dorsalis* complex species has been published (Drew and Hardy, 1981; Elson-Harris, 1988; Drew, 1989; Goh *et al*., 1993; Drew and Hancock, 1994; Iwaizumi *et al*., 1997; Iwahashi, 1999a and 1999b), but even so determining species boundaries for flies within the complex is problematic (Clarke *et al*. 2005).

2 Relationship of Host Plants and Fruit Flies

Sexual behavior (including meeting, courtship and mating) of phytophagous insects may occur principally or exclusively on host plants. Males may purposefully search host plants for females simply because females are likely to visit host plant for feeding and oviposition, resulting in mixed-sex encounters and mating opportunities (Landolt and Phillips, 1997). Adult feeding, mating, and oviposition of tephritid fruit flies are considered to have close evolutionary and ecological associations with their larval host plants (Drew and Lloyd, 1987; Metcalf, 1990; Drew and Hancock, 2000).

Chemicals from host plants play an important role in the production of a wide range of behavioral responses in insects. Semiochemicals from host plants may enhance the response of an insect to sex pheromones (Reddy and Guerrero, 2004). Acquisition or collection of chemicals from plants and their subsequent uses in a sexual role (e.g., as a pheromone) are known for some species of tephritid fly (Shelly and Villalobos, 2004). For example, males of Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), formed tight aggregations and fed on the bark of guava tree which contained high levels of the male attractant α-copaene, resulting in a mating advantage for the flies (Shelly and Villalobos, 2004). The wild tobacco fly, *Bactrocera cacuminata* (Hering) is thought to have their primary mating sites on their larval host plants, wild tobacco, *Solanum mauritianum* (Solanaceae) (Drew *et al*., 2008, but see Raghu *et al*. 2002). Many *Bactrocera* species respond to methyl eugenol, a naturally occurring phenylpropanoid found in many plants (Metcalf, 1990; Clarke *et al*., 2002). Several *Bactrocera* species, such as *B. dorsalis* and *B. papayae*, play a role as pollinators of *Bulbophyllum* species (Orchidaceae) which produce phenylpropanoid volatiles that attract the flies (Clarke *et al*., 2002; Nishida *et al*.,

2004). Shelly (2000) found that male flies of *B. dorsalis* which had eaten methyl eugenol were more successful in courting and mating females than males that have not eaten. In contrast, *B. cacuminata* feeding on methyl eugenol did not gain mating or other physiological advantages over unfed flies (Raghu *et al*., 2002; Raghu and Clarke, 2003). Locating a host plant is crucial for a phytophagous insect to fulfill its nutritional requirements and to find suitable oviposition sites (Bruce *et al*., 2005). Female fruit flies find and assess larval host plants through olfaction, vision and contact (Bell, 1990; Diaz-Fleischer *et al*., 2000). Semiochemicals from larval host plants can stimulate oviposition behavior from female fruit flies and enhance their attractions to male sex pheromones (Metcalf, 1990; Landolts *et al*., 1992).

The large number of volatiles that emanates from fruit can induce insect responses. Polyphagous pest species such as the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) and *B. dorsalis* may respond to a wide range of fruit volatile combinations, whereas monophagous species are likely to respond to a much more specific chemical group (Fletcher, 1987). Some fruit fly species show a distinct preference for certain hosts when they are available, but they will infest other hosts when the preferred hosts are unavailable (Fletcher and Prokopy, 1991). For example, *Bactrocera jarvisi* (Tryon) preferred cocky apple, *Planchonia careya* (Lecythidaceae) both in field and laboratory experiments and it infests this host almost exclusively when this host is available, despite it being recorded from many other fruits (Fitt, 1986). The absence of the most-preferred host may result in prolonged search (Singer *et al*., 1992). For polyphagous flies of the *B. dorsalis* complex, Clarke *et al*. (2001) and Clarke *et al*. (2005) also suggested that different host plants may not be utilised equally. *Psidium guajava* is the host most utilised by fruit flies of the *B. dorsalis* complex, however, disproportionately large numbers of *B. dorsalis* and *B. papayae* were found to infest *T. catappa* in field collections in Southeast Asia (Allwood *et al*., 1999; Clarke *et al*., 2001). Seventy-three and 43 larval host plant species have been recorded in Thailand for *B. dorsalis* and *B. papayae*, respectively (Table 1).

Table 1 Host plants of *Bactrocera dorsalis* and *Bactrocera papayae* recorded in Thailand.

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Anacardiaceae	Cashew	*Anacardium occidentale*	*Bactrocera dorsalis* *Bactrocera papayae*	Chinajariyawong *et al*., 2000 Clarke *et al*., 2001
	Marian plum	*Bouea macrophylla*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
	Mango	*Mangifera indica*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2005 Meksongsee *et al*., 1988
	Horse mango	*Mangifera foetida*	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
	Common hog plum	*Spondias pinnata*	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
	Great hog plum	*Spondias cytherea*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
Annonaceae	Sugar apple	*Annona squamosa*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000
		Annona spp.	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Annonaceae		*Artabotrys siamensis*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Meksongsee *et al*., 1988
Arecaceae	Betel nut	*Areca catechu*	*Bactrocera dorsalis*	Clarke *et al*., 2001 Meksongsee *et al*., 1988 Baimai *et al*., 1998
Burseraceae	Garuga	*Garuga floribunda*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
Caricaceae	Papaya	*Carica papaya*	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005 Clarke *et al*., 2001
Celastraceae		*Salacia verrucosa*	*Bactrocera dorsalis*	Baimai *et al*., 1998
		Siphonodon celastrineus	*Bactrocera dorsalis*	Baimai *et al*., 1998
Clusiaceae	Mundur	*Garcinia dulcis*	*Bactrocera dorsalis* *Bactrocera papayae*	Chinajariyawong *et al*., 2000 Meksongsee *et al*., 1988
		Garcinia costata	*Bactrocera dorsalis*	Baimai *et al*., 1998
		Garcinia atroviridis	*Bactrocera dorsalis*	Meksongsee *et al*., 1988

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Clusiaceae	Mangosteen	*Garcinia mangostana*	*Bactrocera papayae*	Clarke *et al*., 2005
		Mammea siamensis	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
Combretaceae	Tropical almond	*Terminalia catappa*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988
Cucurbitaceae	Cantaloupe	*Cucumis melo*	*Bactrocera dorsalis*	Clarke *et al*., 2005
	Cucumber	*Cucumis sativus*	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005 Meksongsee *et al*., 1988
	Angled luffa	*Luffa acutangula*	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
	Bitter gourd	*Momordica charantia*	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
	Japanese snake gourd	*Trichosanthes oxigera*	*Bactrocera dorsalis*	Clarke *et al*., 2001
Ebenaceae		*Diospyros castanea*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
		Diospyros dasyphylla	*Bactrocera dorsalis*	Baimai *et al*., 1998

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Elaeocarpaceae		*Elaeocarpus madopetalus*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
	Jamica cherry	*Muntingia calabura*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
Euphorbiaceae		*Aporusa villosa*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
		Sapium baccatum	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
Fabaceae		*Afzelia xylocarpa*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
	Twisted cluster bean	*Parkia speciosa*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000 Clarke *et al*., 2001
Ixonanthaceae	Barking deer's mango	*Irvingia malayana*	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
Lauraceae	Avocado	*Persea americana*	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005
Meliaceae	Langsat	*Aglaia domestica*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Meliaceae	Santol	*Sandoricum koetjape*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988
Moraceae	Chempedak	*Artocarpus integer*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
	Jack fruit	*Artocarpus heterophyllus*	*Bactrocera dorsalis* *Bactrocera papayae*	Chinajariyawong *et al*., 2000 Meksongsee *et al*., 1988
	Lakoocha	*Artocarpus lakoocha*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
		Artocarpus lanceolatus	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
	Marang	*Artocarpus odoratissima*	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
		Ficus lepicarpa	*Bactrocera dorsalis*	Baimai *et al*., 1998
Musaceae	Hom thong	*Musa* sp.	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Clarke *et al*., 2001
	Namwa	*Musa x paradisiaca*, ABB Group	*Bactrocera papayae*	Chinajariyawong *et al*., 2000 Clarke *et al*., 2001

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Musaceae		*Musa* spp.	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005 Meksongsee *et al*., 1998
Myristicaceae		*Knema globularia*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
Myrtaceae		*Eugenia paniala*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
		Eugenia spp.	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
	Strawberry guava	*Psidium cattleianum*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
	Common guava	*Psidium guajava*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988
	Rose apple	*Syzygium jambos*	*Bactrocera dorsalis* *Bactrocera papayae*	Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988
	Malay apple	*Syzygium malaccense*	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
	Java apple	*Syzygium samarangense*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Oleaceae		*Myxopyrum smilacifolium*	*Bactrocera dorsalis*	Clarke *et al*., 2001
Oxalidaceae	Carambola, Starfruit	*Averrhoa carambola*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988
Polygalaceae		*Xanthophyllum flavescens*	*Bactrocera dorsalis*	Clarke *et al*., 2001
Rhamnaceae	Common jujube	*Ziziphus jujuba*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988
	Indian jujube	*Ziziphus mauritiana*	*Bactrocera dorsalis* *Bactrocera papayae*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2001 Meksongsee *et al*., 1988
		Ziziphus oenoplia	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000 Clarke *et al*., 2001
		Ziziphus rotundifolia	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
		Ziziphus sp.	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
Rhizophoraceae		*Citrofortunella mitis*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
	Mangrove	*Rhizophora* sp.	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
Rosaceae	Apple	*Malus domestica*	*Bactrocera dorsalis*	Clarke *et al*., 2005
	Plum	*Prunus domestica*	*Bactrocera dorsalis*	Clarke *et al*., 2005
	Peach	*Prunus persica*	*Bactrocera dorsalis*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000 Clarke *et al*., 2001
		Prunus persica var. *nucipersica*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
Rubiaceae	Adam	*Anthocephalus chinensis*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
	Arabica coffee	*Coffea arabica*	*Bactrocera dorsalis*	Chinajariyawong *et al*., 2000
		Ochreinauclea maingayi	*Bactrocera papayae*	Chinajariyawong *et al*., 2000

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Rutaceae	Orange, Lemon, Lime	*Citrus* spp.	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005
		Hesperethusa crenulata	*Bactrocera dorsalis*	Meksongsee *et al*., 1988
		Murraya exotica	*Bactrocera papayae*	Chinajariyawong *et al*., 2000
Sapindaceae	Longan	*Dimocarpus longan*	*Bactrocera dorsalis*	Clarke *et al*., 2005
		Lepisanthes tetraphylla	*Bactrocera dorsalis*	Clarke *et al*., 2001
	Lychee	*Litchi chinensis*	*Bactrocera dorsalis*	Baimai *et al*., 1998 Clarke *et al*., 2005
	Rambutan	*Nephelium lappaceum*	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005 Meksongsee *et al*., 1988
Sapotaceae	Sapodilla	*Manilkara zapota*	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2001 Clarke *et al*., 2005 Chinajariyawong *et al*., 2000
Simaroubaceae		*Irvingia malayana*	*Bactrocera dorsalis*	Baimai *et al*., 1998 Chinajariyawong *et al*., 2000

Table 1 (Continued).

Host plants			Fruit flies species	References
Family	**Common name**	**Scientific name**		
Solanaceae	Bell peper, Capsicum	*Capsicum annuum*	*Bactrocera dorsalis* *Bactrocera papayae*	Chinajariyawong *et al*., 2000 Meksongsee *et al*., 1988
	Tomato	*Solanum lycopersicum*	*Bactrocera dorsalis* *Bactrocera papayae*	Clarke *et al*., 2005 Meksongsee *et al*.,1988
	Eggplant	*Solanum melongena*	*Bactrocera papayae*	Chinajariyawong *et al*., 2000 Clarke *et al*., 2005

3 Host Orientation and Utilisation

3.1 Orientation to host plant or fruit

Host plant searching behavior is an active process by which phytophagous insects recognise and select suitable substrates for food, mates, oviposition, and refuge by using physical cues (color, size, sense of touch) and chemical cues (volatile, nutrition) of host plant (Jolivet, 1992; Panda and Khush, 1995). As for other phytophagous insects, fruit flies use both visual and olfactory cues when searching for their host plants (Dalby-Ball and Meats, 2000; Pinero *et al*., 2006). Vargas *et al*. (1991) indicated that color appears to be the least specific cue in eliciting positive responses in alighting by fruit flies. Rather, after arrival on a host tree where host fruits are apparent and abundant, fruit flies discover these fruits on the basis of vision. If fruits are less apparent or scarce, however, odor appears to interact with vision during the fruit-finding process (Aluja and Prokopy, 1993; Aluja *et al*., 1993). Green *et al*. (1994) believed that color and size, the presence or absence of olfactory cues, distance and environment all influence host-finding by female apple maggot fly, *Rhagoletis pomonella* (Walsh). This section deals with each of these cues independently and in detail.

3.1.1 Visual response cues

a) Shape and size

Visual cues (color, shape and size) play an important role in host plant location and recognition by herbivorous insects (Prokopy and Owens, 1983). Shape and size of host fruit are also an important factor for host finding by fruit flies (Levinson *et al*., 2003). Many species of tephritid fruit fly, such as *B. dorsalis, Bactrocera cucurbitae* (Coquillett), *Bactrocera minax* (Enderlein), *C. capitata* and *Rhagoletis* species, tend to prefer spherical shapes (Reissig, 1976; Nakagawa *et al*., 1978; Vargas *et al*., 1991; Cornelius *et al*., 1999a; Mayer *et al*., 2000; Drew *et al*., 2006; Pinero *et al*., 2006). However, female flies of cherry fruit fly,

Rhagoletis cerasi Loew and black cherry fruit fly, *Rhagoletis fausta* (Osten Sacken) were more commonly captured in a trap of specific shape [the "Rebell" trap, which consists of two yellow plastics, sticky-coated rectangle (15 by 20 cm) that cross each other to form a two dimensional trap] than other commercial traps of different shapes studied (Katsoyannos *et al*., 2000; Liburd *et al*., 1998).

Visual response of fruit flies has also been found to be related with the size of colored spheres (i.e., fruit mimics) (Cornelius *et al*., 1999a; Brevault and Quilici, 2007a). For example, females of apple maggot fly, *R. pomonella*, preferred smaller red models (Moericke *et al*., 1975), while a red sphere of about 10 cm diameter appears optimal for attracting Western cherry fruit fly, *Rhagoletis indifferens* Curran (Mayer *et al*., 2000). Nakagawa *et al*. (1978) reported that the attraction of *C. capitata* increased as the size of fruit models increased from 1.5 to 18 cm.

Preference for larger fruit models reflects fly behavior to real fruit. Within a fruit species, there tends to be a general pattern within the tephritids that female flies tend to prefer larger fruit for oviposition. For example, there was a significant positive correlation between fruit size and the number of larvae of *Rhagoletis turpiniae* Hernandez-Ortiz in a fruit of *Turpinia insignis* (Staphyleaceae) (Aluja *et al*., 2001), while the number of punctures of walnut fly, *Rhagoletis juglandis* Cresson, on a host was positively correlated with fruit volume (Nufio *et al*., 2000). Fruit size, fruit weight and pulp/stone ratio of indian jujube, *Ziziphus mauritiana* (Rhamnaceae) was positively correlated with fruit fly infestation (Singh and Vashishtha, 2002). Diaz-Fleisher and Aluja (2003a) postulated that females of some tephritid fruit fly species tend to deposit larger clutches in larger hosts. However, females of the Mexican fruit fly, *Anastrepha ludens* (Loew), oviposited larger clutches in peach, *Prunus persica* (Rosaceae) than in grapefruit, *Citrus paradise* (Rutaceae), despite the fact that grapefruit is a larger host (Leyva *et al*., 1991). This result indicates that female flies are not always attracted to larger fruit when compare between the different fruit species. Thus, the preference of female flies to host fruit for oviposition may depend on factors other than fruit size.

b) Color

Prokopy and Owens (1983) indicated that the color yellow is a supernormal visual equivalent of plant foliage and is attractive to many phytophagous insects. Color preferences of fruit flies may be related to the color of their host fruits. *Bactrocera dorsalis* is attracted to a yellow color which occurs in almost all their host fruit species (Vargas *et al*., 1991; Cornelius *et al*., 1999a and 1999b; Alyokhin *et al*., 2000). *Bactrocera tryoni*, in contrast, prefers bluish fruit-mimicking spheres which have a slightly enhanced level of ultraviolet reflectance, similar to the reflectance of their native host fruits *Gmelina* spp. (Verbenaceae) and *Elaeocarpus grandis* (Elaeocarpaceae), while yellow or orange spheres, which resemble the color of near-ripe or ripe wild tobacco host fruit, are most attractive to tobacco fruit fly, *B. cacuminata* (Drew *et al*., 2003). *Rhagoletis pomonella*, which attacks red fruits (apple and hawthorn berries), were attracted to red color spheres more than other colors (Reissig, 1975; Prokopy and Hauschild, 1979; Reynolds *et al*., 1996).

c) Background and habitat

Color preference of female flies can be modified by spectral contrast occurring between colored spheres and background influences. Female tomato fruit fly, *Neoceratitis cyanescens* (Bezzi), orientated preferentially to bright orange spheres, irrespective of their natal host fruits (tomato , bug weed, or black nightshade) when placed against a fluorescent yellow background (Brevault and Quilici, 2007a). The visual contrast between an object and its background is the basis for easy fruit detection by fruit flies. For example, female *B. dorsalis* and most *Rhagoletis* species respond positively to dark-pigmented objects against a light background (i.e., foliage and skylight), while *B. cucurbitae* females are attracted to light-pigmented objects against the dark background because they forage for host fruits in the afternoon (Owens and Prokopy, 1986; Cornelius *et al*., 1999a and 1999b; Mayer *et al*., 2000; Pinero *et al*., 2006).

The habitat pattern also plays an important role in the behavior of tephritid fruit flies. Fruit maturity, abundance of host fruit within the canopy and species of host fruit all affect host fruit orientation by female flies (Murphy *et al*., 1991; Katsoyannos *et al*., 1998; Dalby-Ball and Meats, 2000). For example, the efficiency of visual traps tend to decrease when competing with host fruit, but trap efficiency rises when placed within the canopy of host plants without host fruit (Rull and Prokopy, 2003; Brevault and Quilici, 2007b).

d) Fly physiological status

Not only do external factors influence visual response of female flies, but so do the innate factors of female flies, i.e., their physiological states. Immature female flies *R. pomonella* are attracted to yellow panel traps (super-normal visual mimics of foliage) during protein foraging, while mature female flies are attracted to red sphere traps during host fruit foraging for oviposition (Prokopy, 1968; Prokopy, 1972). Thus, shape, size and the environment around host fruits, plus their physiological states, all influence the visual response of female flies during host fruit searching. Other factors, however, particularly host plant volatiles, also play an important role in host fruit orientation by female fruit flies.

3.1.2 Olfactory response cues

Host fruit odors are known to play an important role in the ecology of tephritid fruit flies, for example by stimulating ovarian development (Aluja *et al*., 2001) and increasing mating success (Landolt *et al*., 1992; Landolt, 1994; Shelly and Edu, 2007). Male fruit flies respond to volatile compounds from host and non-host plants largely because of the indirect role such chemicals play in sexual activity (Clarke *et al*., 2002; Nishida *et al*., 2004; Shelly and Villalobos, 2004; Keng-Hong and Nishida, 2005; Shelly and Edu, 2007; Shelly *et al*., 2008). In contrast, mature female flies are attracted to host plant for oviposition and tend to more sensitive to the volatile compounds of host fruit (Cosse *et al*., 1995; Hernandez *et al*., 1996; Jang *et al*., 1997; Malo *et al*., 2005).

The odor arising from a host plant is one of the most important host location cues used by tephritid fruit flies. Orientation to oviposition sites is commonly achieved by following host odors using upwind anemotaxis (Jones *et al*., 1981; Light *et al*., 1988; Light *et al*., 1992; Jang *et al*., 1998; Meats and Hartland, 1999; Jang, 2003). That odor baited traps are more efficient in capturing fruit flies than unbaited traps has been reported by many researchers (Bierbaum and Bush, 1990; Duan and Prokopy, 1992; Liburd *et al*., 1998; Katsoyannos *et al*., 2000; Cornelius *et al*., 2000a and 2000b; Pelz-Stelinski *et al*., 2005). *Rhagoletis pomonella* will respond to apple odor released from a visually neutral polyethylene vial on the tree, demonstrating the importance of this cue alone (Aluja and Prokopy, 1992). Polyphagous fruit flies respond to a wide range of host odors, while monophagous or oligophagous fruit flies may be more sensitive to one or a few host-specific chemicals (Diaz-Fleischer *et al*., 2000; Bernays, 2001). For example, the monophagous species *R. pomonella* and *Rhagoletis mendax* Curran showed responses to only a limited set of host volatile compounds (Lugemwa *et al*., 1989; Zhang *et al*., 1999; Nojima *et al*., 2003a and 2003b; Siderhurst and Jang, 2006), whereas the antennae of *B. dorsalis*, a high polyphagous species, can detect 22 compounds from the volatiles of one host, *T. catappa*, alone (Siderhurst and Jang, 2006).

Even for polyphagous flies, however, not all host odors are equally attractive. A study on host fruit volatiles as attractants concluded that odors of common guava were more attractive to female *B. dorsalis* than papaya and starfruit, whereas they were equally as attractive as strawberry guava, orange and mango (Cornelius *et al*., 2000b). *Cucumis sativus* odor was more attractive to female flies of *B. cucurbitae* than odors of three other host plants: *Cucurbita pepo* (Cucurbitaceae), *C. papaya* and *Solanum lycopersicum* (Solanaceae) (Pinero *et al*., 2006).

The odors of different ripening stages of host fruit can elicit different responses from female flies. Prokopy *et al*. (1973) and Reissig (1974) both suggested that the mechanism which attracts flies to fruit may be an olfaction response to volatile compounds emanating from maturing fruit. The study on preference of *A. ludens* to volatiles of green or yellow mangoes and orange fruits

showed that male and female *A. ludens* were more attracted to green mango variety Haden and orange variety Valencia than yellow fruits (Garcia-Ramirez *et al*., 2004). Flath *et al*. (1990) found that organic compounds released from ripe papaya significantly enhanced attractiveness of the fruit to *B. dorsalis.* This suggests that female flies may use host fruit odors not only to locate suitable hosts for oviposition, but also for assessing fruit ripening.

The olfactory responses of female fruit flies tend to more specific than their responses to visual cues. While yellow color and spherical shape tend to be common across many host fruit species of tephritid fruit flies, attractive host volatile compounds differ among ripening stages, varieties and host fruit species, producing much more specific cues which are differentially used by different fly species (Cosse *et al*., 1995; Hernandez *et al*., 1996; Prokopy *et al*., 1998; Hernandez-Sanchez *et al*., 2001).

3.2 Host acceptance

3.2.1 Host quality

The oviposition choice of female flies is most often related with maximising the performance of their offspring (Fitt, 1981; Peck and McQuate, 2004; Thomas, 2004; Balagawi *et al*., 2005; Navrozidis and Tzanakakis, 2005). Female flies use information from host fruits to determination the quality of that host fruit for offspring growth and survival. Post-alighting examination of fruit by tephritid female flies involves touching of the fruit surface with the antennae and mouthparts and probing the fruit skin with the ovipositor (Eisemann and Rice, 1989; Lugemwa *et al*., 1989; Cosse *et al*., 1995; Hernandez *et al*., 1996; Prokopy *et al*., 1996; Katsoyannos *et al*., 1997; Robacker and Fraser, 2002).

Fruit firmness, associated with the degree of fruit ripeness, is considered to be a likely indicator of host quality for female flies (Messina and Jones, 1990). Many (but not all) fruit flies also use host-marking pheromones at the time of

oviposition. Such pheromones deter other female flies from ovipositing, so as to minimise larval competition (Fitt, 1984; Prokopy *et al*., 1989; Nufio and Papaj, 2004a). Prior infestation, however, need not always deter flies from ovipositing. Larger host fruits tend to be more acceptable than smaller host fruits even if they are infested by conspecific larvae because of the additional food available for larval development (Papaj and Messing, 1996; Diaz-Fleischer and Aluja, 2003b; Nufio and Papaj, 2004b).

The different nutritive value of different host fruit species also has a major impact on larval development (Krainacker *et al*., 1987; Fernandez-Da-Silva and Zucoloto, 1993; Fernandez-Da-Silva and Zucoloto, 1997; Woods *et al*., 2005; Saha *et al*., 2007). For example, *C. capitata* larvae develop faster in bitter gourd, *Momordica indica* (Cucurbitaceae) than quince *Cydonia oblonga* (Rosaceae) (Carey, 1984). Differences in larval development can flow onto adult performance. Males of the West Indian fruit fly, *Anastrepha obliqua* (Macquart) originating as larvae from the native host *Spondias mombin* (Anacardiaceae) exhibited shorter copulations than males developed in the exotic host, *M. indica* (Perez-Staples *et al*., 2008).

3.2.2 Host ripening

The stage of host fruit ripening influences both host plant physical and chemical traits. During fruit ripening, fruits change in attributes such as color, tissue firmness, volatile aroma production, starch accumulation and quantities of other organic compounds (Worrell *et al*., 1998; Bashir and Abu-Goukh, 2003; Ali *et al*., 2004; Balasubramaniam *et al*., 2005; Sane *et al*., 2005; Yashoda *et al*., 2005; Imsabai *et al*., 2006; Yashoda *et al*., 2007). Bidwell (1979) divided ripening of climacteric fruits to four stages: unripe stage, ripening stage, fully ripe stage and overripe stage. The ripening process involves the conversion of acids and starch to free sugars, the development of pectinases and various pigments and the loss of chlorophyll.

Most fruit flies species prefer to oviposit into ripe fruit over ripening or unripe fruit (Messina *et al*., 1991; Vargas *et al*., 1995; Joachim-Bravo *et al*., 2001). As an example, female flies *B. dorsalis* were not only attracted to the organic compounds released from ripe papaya, but also preferred to oviposit into ripe papaya more than mature green papaya (Seo *et al*., 1982; Flath *et al*., 1990; Jang and Light, 1991). This pattern is not, however, universal. Female papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker, *B. papayae* and olive fruit fly *Bactrocera oleae* (Rossi), are reported to prefer to oviposit into the green stage of their host fruits than the mature stage (Pena *et al*., 1986; Leblanc *et al*., 2001; Yokoyama and Miller, 2004).

The preference for ripe fruit for oviposition by females may be explained by ripe fruit being more suitable for larval development (Joachim-Bravo *et al*., 2001; Fontellas-Brandalha and Zucoloto, 2004) and a decline in fruit firmness allowing easier oviposition (Bidwell, 1979; Yashoda *et al*., 2005; Yashoda *et al*., 2007). Additionally, unripe fruit may have resistance mechanisms which are absent or reduced in ripe fruit. Examples include latex containing a high BITC concentration in mature green papaya (Seo *et al*., 1983), the resin from the duct system of unripe Anacardiaceae fruit (Joel, 1978; Joel, 1981) and the resistance to larval growth in immature mango (Hennessey and Schnell, 2001).

3.2.3 Female fly physiological status and experience

Their physiological states (age, mating status, hunger level) significantly impact on the propensity of female flies to be attracted to host fruit (Prokopy *et al*. 1996; Cornelius *et al*., 2000a). Carbohydrate and protein consumed by immature and mature female flies influence ovarian development, with protein required for sexual maturation (Landolt and Davis-Hernandez, 1993). Thus, immature female flies are attracted to protein odors as much or more than host fruit odors, while mature female flies are only more attracted to protein odor than host fruit odors when hungry (Prokopy *et al*., 1991; Prokopy and Vargas, 1996; Robacker *et al*., 1996; Dalby-Ball and Meats, 2000; Rousse *et al*., 2005; Brevault and Quilici, 2007a;

Manrakhan and Lux, 2008). Wild immature female *B. dorsalis* were, however, captured in both protein and orange-baited traps, indicating that immature female flies will respond to both protein and host fruit odors (Cornelius *et al*., 2000a).

Other than hunger, mating status influences the response of mature female flies to host fruit, with mated females more attracted to host fruit than unmated females (Greany *et al*., 1978; Landolt *et al*., 1992; Prokopy and Vargas, 1996; Levinson *et al*., 2003; Garcia-Ramirez *et al*., 2004). This pattern may be caused by the influence of egg load on females. Female flies carrying a large number of mature eggs in the ovaries tend to be more attracted to and accept unsuitable host fruit than female flies carrying few mature eggs in ovaries (Fitt, 1986; Mangel and Roitberg, 1989; Brevault and Quilici, 1999; Prokopy *et al*., 1999).

The prior experience of female flies with host fruit is also an important factor influencing host fruit acceptance. Female flies with prior experience of a host fruit were attracted to, and accepted, the host faster than flies with no prior experience (Averill *et al*., 1996; Robacker and Fraser, 2002; Diaz-Fleischer and Aluja, 2003b). That female flies can learn to select suitable host fruit after exposure to that fruit is illustrated in the study of *R. juglandis* where females with prior experience used different fruit colors to identify infested or uninfested fruits (Henneman and Papaj, 1999). Prior experience with a host may also be crossing generational and be linked to genetic differences between different fruit fly populations (Feder *et al*., 1988). McPheron *et al*. (1988) demonstrated the different populations of the apple maggot, *R. pomonella*, differing in allele frequencies and bred from two different hosts, apple or hawthorn, exhibited different preferences in host acceptance preferentially aligned to the natal host.

The above section identifies a number of factors which interact to influence host acceptance by female flies. These include genetics of the fly, fly physiological state (maturity status, hunger and egg load), prior ovipositional experience, host fruit species, ripening stage of the host fruit, size and nutritional quality of host, and availability of different hosts. This dynamic situation means that,

under natural conditions, the host choice decisions made by any given female at any given time, may be highly variable and difficult to predict. Having chosen a host, the female fly comes to the actual process of oviposition, or host utilisation. Factors influencing adult and larval host utilisation behavior are detailed in the next section.

3.3 Host utilisation

3.3.1 Adult behavior

In nature, gravid female flies may not always be able find suitable host fruit for ovipostion. Female flies in the field may thus be host fruit and factors which may cause this include: only unripe fruits are presented; suitable hosts are scarce; there may high populations of mature female flies in the field; asynchrony between fruit maturation and time of female adult emergence; and resistance of host plants (Fitt, 1981; Greany *et al*., 1983; Messina and Jones, 1990; Messina *et al*., 1991; Aluja *et al*., 2004). Under limiting conditions, female flies may use different strategies of host utilisation. When only unripe fruit or fruit with high firmness are presented, females of many species of fly use soft sites on the fruit, cracks or wounds and existing egg-laying cavities for oviposition (Pritchard, 1969; Papaj *et al*., 1989; Papaj and Messing, 1996; Papaj and Alonso-Pimentel, 1997; Shelly, 1999). This strategy is thought to decrease aculeus wear and save oviposition time (Jones and Kim, 1994; Papaj and Alonso-Pimentel, 1997). Using existing egg-laying cavities or fruit wounds by female flies is considered an evolutionary response to phylogenetic constraints (on host use) (Price, 1991; Aluja and Mangan, 2008).

Stage of fruit ripening and conspefic infestation have both been identified in earlier sections as influencing host location: both these factors also influence host utilisation. The Eastern cherry fruit fly, *Rhagoletis cingulata* (Loew), uses the stage of fruit maturity as the cue for timing first oviposition (Messina *et al*., 1991). Female fruit flies tend to prefer uninfested ripe fruit over infested ripe fruit, but will lay large egg clutches into infested unripe fruit or uninfested unripe fruit as required to ensure some larval survival (Fitt, 1984, Mangel and Roitberg, 1989;

Prokopy *et al*., 1989; Papaj and Messing, 1996; Diaz-Fleischer and Aluja, 2003a and 2003b). Even though utilisation of infested fruit may cause high larval competition, superparasitism of some fruit by fly species such as *R. juglandis* has commonly been found in the field (Nufio and Papaj, 2004b). Large populations of conspecific female flies in the field may lead to competition for hosts among female flies, but in some circumstances this may be positive. For example, female *C. capitata* and *B. tryoni* have a greater propensity to oviposit into host fruit occupied by conspecific female flies than into unoccupied fruit as a means of saving time during host searching and acceptance (Prokopy and Duan, 1998; Prokopy *et al*., 1999; Rull *et al*., 2003). Dukas *et al*. (2001) takes this further by demonstrating that female *C. capitata* have a lower ovipostion preference for host fruit bearing only a single conspecific female fly in comparison to host fruits bearing multiple females. In this case the number of conspecific female flies on the host fruit is used as an assessment of host fruit quality.

Some plant species produce fruit that have mechanisms which can limit fruit fly infestation. These include: the production of callus tissue around fruit fly eggs in "Hass" avocado and lemon (Spitler *et al*., 1984; Aluja *et al*., 2004); the presence of toxic essential oil in the flavedo region of the peel of citrus plant (Greany *et al*., 1983) and the high firmness of "Cherry" tomato (Balagawi *et al*., 2005). In such cases female flies tend to prefer host fruit with low firmness or wounds on the surface for easy ovipositor penetration. Females of some fruit fly species, such as *A. ludens*, have a very long aculeus which allows eggs to be deeply deposited into the nontoxic albedo region of citrus fruits, sites which are suitable for egg hatch and larval growth (Diaz-Fleischer and Aluja, 2003a; Birke *et al*., 2006).

3.3.2 Larval behavior

Nutrition in the insect larval stage is generally directly related to the size of the subsequent adult. Adequate or excess nutrition in the larval stage leads to larger or healthier adult insects, which in turn tend to be the winners in of habitat defense, mating competition and reproductive success (Delisle and Hardy, 1997; Pelletier and Mcneil, 2003; Marazzi and Stadler, 2005; Sciurano *et al*., 2007; Berger

et al., 2008; Gereszek *et al*., 2008; Lee and Heimpel, 2008). For fruit flies, nutrientally adequate host fruits sustain complete larval development. The quality of nutrients available to larvae influences the larval and adult size, immature development time, pupal weight, probability of adult eclosion, and rate of adult reproductive maturation (Bruzzone *et al*., 1990; Economopoulos *et al*., 1990; Khan *et al*., 1999; Chang *et al*., 2000; Kaspi *et al*., 2002).

Although many host plants can sustain full development of tephritid fruit flies, variation in host quality plays a major role in larval survival rate, larval development and adult fecundity (Carey, 1984; Woods *et al*., 2005; Perez-Staples *et al*., 2008). Low fruit fly larval survival in host fruits may indicate the resistance of host plant to larval development, as well as inadequate nuturitional composition (Pree, 1977; Greany *et al*., 1983; Hennessey and Schnell, 2001). Moreover, "unusual" host utilisation of female flies as identified previous section (i.e., superparasitism and oviposition into less suitable hosts) causes pressure on larvae. High larval competition and poor nutritional quality of host fruit may often be experienced by fruit fly larvae in the nature. In such cases the plasticity of host utilisation behaviors found in female fruit flies may also be found in larvae. In case where female *C. capitata* did not oviposit into nutritionally superior parts of fruits, larvae moved within the fruit to parts of the fruit which afforded them better nutrition (Zucoloto, 1987; Zucoloto, 1991; Fernandez-Da-Silva and Zucoloto, 1993; Joachim-Bravo and Zucoloto, 1998). Little is known, however, about the larval biology of most fruit fly species, especially larval behavior and how common the behavior exhibited by *C. capitata* larvae is in other flies is unknown.

The response of female tephritid flies to host fruits relies on external and internal factors. Many studies, as presented in this review, indicate the complex relationship between female flies and their host fruits. Oviposition strategies by female flies under limiting conditions may result in eggs being placed in suboptimal conditions and hence increased pressure on their offspring. Thus, the interaction of external and internal factors which influence oviposition behavior of female flies indirectly affect their larvae. Many points are, however, unclear on the

relationship between oviposition preference and larval performance in fruit flies. One aspect of these, ovipostion choice, larval performance and fruit ripening is the topic of this thesis.

MATERIALS AND METHODS

1. Part I: *Bactrocera dorsalis* Preference for and Performance on Two Mango Varieties at Three Stages of Ripening

1.1 Fruit flies and location of experiment

Bactrocera dorsalis were originally received from a culture maintained by the Entomology and Zoology Group, Plant Protection Research and Development Office, Department of Agriculture, Bang Khen, Bangkok, Thailand. Water and a 3:1 mixture of sugar and yeast hydrolysate were provided in the cage for adult flies. Fruit fly larvae were reared on banana *Musa x paradisiaca*, ABB Group (Musaceae), Namwa variety. Average humidity, temperature, and light intensity within the laboratory were 61%, 25 ºC, and 331 Lux, respectively. Culture lines were nine generations old when used in trials and had undergone a bottle-neck when first established. To convince ourselves that culturing had not dramatically altered the behavior of flies, a subset of the preference/performance trials were repeated using F1 flies from the field after the laboratory studies were completed. These trials showed no obvious difference to the patterns of host use shown by cultured flies. Results of the validation trial are available on request from the contact author. Voucher specimens of flies used in the trials are deposited at the National Biological Control Research Center Headquarters and Department of Entomology, Kasetsart University, Bangkok, Thailand. All research was carried out under laboratory conditions at the National Biological Control Research Center Headquarters, Kasetsart University.

1.2 Fruit hosts

Two local mango varieties (Namdorkmai and Oakrong) were chosen to determine the preference of *B. dorsalis* for fruits of various ripening stages. All fruits were bought from local markets at unripe (hard-green) or ripe (green-yellow; marketable after shipment) stages. Some ripe mangoes were allowed to further ripen

to fully-ripe (yellow; marketable for local use at the production site) stage on the shelf for experiments. Based on discussion with the growers selling their fruits, all mangoes used in experiments had been protected from wild flies by fruit bagging and had not been subjected to pesticide treatments. To check for possible field infestation of the fruit, in every experiment five mangoes were randomly selected and incubated in separate plastic containers to see if pupae were recovered. No pupae were recovered from these control fruits.

1.3 Fruit characteristics

Additional to fruit used in trials, 15 and 20 fruits from each ripening stage of mango varieties Namdorkmai and Oakrong, respectively, were randomly selected for measurements of total soluble solids, TSS (= Brix), measured using a handheld Brix refractometer (OPTIK B-32; ATAGO, Saitama, Japan). Brix degree is used to measure sugar, organic acid, and other components in the juice of fruit (Linskens & Jackson, 1995). Firmness was measured using a penetrometer (FT-327, Effegi, Alfonsine, Italy) with 1 mm diameter probe, mounted on a Black & Decker® test stand (Black & Decker, Berkshire, United Kingdom). The diameter of a punctured hole of a *B. dorsalis* female fly is 0.2 ± 0.01 mm (n = 30) (W Rattanapun, unpubl.). This diameter probe was also used by Balagawi *et al*. (2005) and Diaz-Fleischer and Aluja (2003a) to measure fruit firmness in their studies. Eleven unripe, 13 ripe and 13 fully-ripe fruits of variety Namdorkmai, and 10 unripe, 15 ripe and 15 fully-ripe fruits of variety Oakrong were used to determine firmness. Penetometer readings were taken at three locations on each fruit and averaged for the fruit.

1.4 Experiments

1.4.1 Experiment 1: Effect of mango ripening stages on oviposition preference of *B. dorsalis*

a) No-choice experiment

To evaluate the propensity of *B. dorsalis* females to oviposit into mangoes of differing ripening, fruit of each ripening stage and mango variety were placed individually in a 30 × 30 × 30 cm Perspex observation cage. The place of attachment between the fruit and the mango stem was covered with tape as preliminary observations showed that female flies tended to oviposit at this site, despite this site not being exposed to the fly under natural conditions. An individual, 21–22-day-old, mated female fly was released in an observation cage with one mango per replicate. Twenty single-fly replicates were conducted for each ripening stage of each mango variety. Fruit fly behaviors observed and recorded were: (i) number and duration of fly visits to a fruit, (ii) number of attempted ovipositions (unsuccessful penetration), and (iii) number and duration of successful oviposition events. Observations were done from 07:00–17:00 hours. At the end of the day, females were dissected to check if eggs were presented in their ovaries.

All fruits that female flies had laid eggs into were placed individually into separate gauze covered plastic containers with sand and incubated for 15-16 days until larvae had pupated. The pupae were counted, weighed, and left in plastic containers for adult eclosion. The number of emergent adults was recorded.

b) Choice experiment

A choice experiment was conducted to determine the behavior of individual female *B. dorsalis* when three mango ripening stages (unripe, ripe, and fully ripe) of the one variety were offered simultaneously in a 50 × 50 × 50 cm

laboratory cage. With the exception of simultaneous offering of fruit, all other experimental conditions were as for the no-choice trial.

1.4.2 Experiment 2: Influence of egg load to the responses of female flies to different ripening stages of mango

The mature eggs in ovaries of unsuccessfully oviposited female flies from the no choice experiment of both mango varieties were counted for determination the influence of egg load to host responses. Female flies successfully oviposited into mango were discarded from counted mature eggs in ovaries because of uncertain number of mature eggs in their ovaries.

1.4.3 Experiment 3: Effect of mango ripening stages on larval performance of *B. dorsalis*

Bactrocera dorsalis eggs were collected using an inverted perforated plastic cup swabbed with the flesh of *M. x paradisiaca*, ABB Group. Eggs were placed in water and those that sunk were collected for use: floating eggs are inviable (Balagawi *et al*., 2005). Egg hatchability from the culture used was about 80% (authors' pers. obs.) but was not explicitly tested for this experiment. A narrow slit was made in the mango skin near the stem end of the fruit using a sterile blade. Twenty eggs were inserted into the slit using a brush. The mangoes were subsequently individually incubated over sand for collection of pupae. The pupae were counted, weighed, and left in plastic containers for adult eclosion, with the number of emergent adults assessed. Twenty replicates for each variety and ripening stage were done.

1.5 Statistical analyses

Repeated measures ANOVA was used to analyse the effect of ripening stage to hourly diurnal pattern of female flies. Two-way ANOVA was used to test for effect of variety, ripening stage, and their interactions. If there was no significant interaction effect then the dependent data were pooled across varieties and effect of

ripening stage was tested using one-way ANOVA. If a significant interaction effect was detected, then the effect of fruit ripening stage on the dependent data was analysed by one-way ANOVA for each variety separately. Data were transformed, if required, to meet the assumptions of ANOVA, and then back-transformed for graphical presentation of the number of visits, duration of visits, number of attempted ovipositions, development time, and number of pupae, and also for the fruit properties table. Response variables analysed were number of attempted ovipositions, total number and duration of fly visits to fruit, number of pupae, weight of pupae, percentage adult emergence, duration of egg-to-adult period, and physical characteristics of different mango varieties (i.e., firmness and TSS). Post-hoc, pairwise comparisons of means were made using Tukey tests. Means of fruit length, width, and thickness were compared using t-tests. Regression analysis was used to describe the relationship between the number and weight of pupae in a cohort for all replicates, across all treatments. The data were analysed using SPSS statistics 15.0.

2. Part II: Within-Fruit Oviposition Site Choice and Larval Performance by *Bactrocera dorsalis* on Mango

2.1 Fruit flies and location of experiment

The colony of *B. dorsalis* used in experiments and location of trials was as reported in section 1.1.

2.2 Fruit hosts

Mango varieties Namdorkmai and Oakrong were chosen to determine the oviposition preference of *B. dorsalis* female flies, while only mango variety Namdorkmai was chosen to determine the preference and performance of larvae for different fruit parts. All fruits were bought from local markets at unripe (hard-green), ripe (green-yellow; marketable after shipment) and fully-ripe (yellow; marketable for local use at the production site) stages. Based on discussion with the growers selling their fruits, all mangoes used in experiments had been protected from wild flies by

fruit bagging and had not been subjected to pesticide treatments. To check for possible field infestation of the fruit, in every experiment five mangoes were randomly selected and incubated in separate plastic containers to see if pupae were recovered. No pupae were recovered from these control fruits.

2.3 Fruit properties

Additional to fruit used in trials, 15 and 20 fruits of each ripening stage of mango varieties Namdorkmai and Oakrong, respectively, were randomly selected for measurements of total soluble solids, TSS, (= Brix). Eleven unripe fruits, 13 ripe and fully-ripe fruits of mango variety Namdorkmai, and ten unripe fruits, 15 ripe and fully-ripe fruits of mango variety Oakrong were used for measurements of fruit firmness. Penetometer and Brix degree readings were taken at three different locations on each fruit part and averaged for the position. Methodologies for TSS and firmness are as described in section 1.3.

Six ripe and fully-ripe mangoes variety Namdorkmai were used to determine the percentage of titratable acidity (TA) [following the technique of Hulme (1971)] and total non-structural carbohydrates (TNC) [following the acid extraction technique of Smith *et al*. (1964) and Nelson's reducing sugar procedure (Hodge and Hofreiter, 1962)].

2.4 Experiments

2.4.1 Experiment 1: Oviposition preference of female *B. dorsalis* for different fruit parts

a) No-choice experiment

To evaluate where *B. dorsalis* females oviposited into mangoes of differing ripening, fruit of each ripening stage and mango cultivar were placed individually into a 30 × 30 × 30 cm Perspex observation cage. The place of

attachment between the fruit and the fruit stalk was covered with tape as preliminary observations showed that female flies tended to oviposit at this site, despite this site not being exposed to the fly under natural conditions. A 21-22-day-old, mated female fly was released in an observation cage with one mango per replicate. Twenty single-fly replicates were conducted for each ripening stage for each mango variety. Fruit fly behavior recorded was the number of attempted ovipositions made in each of three fruit parts (i.e., top, middle, bottom). Observations were done continuously from 07:00–17:00 hours. At the end of the day, females were dissected to check if eggs were present in their ovaries.

b) Choice experiment

A choice experiment was conducted to determine the behavior of individual female *B. dorsalis* when mangoes of the one variety at three ripening stages (unripe, ripe and fully-ripe) were offered simultaneously in a 50 × 50 × 50 cm laboratory cage. With the exception of simultaneous offering of fruit, all other experimental conditions were as for the no-choice trial.

2.4.2 Experiment 2: Preference and performance of *B. dorsalis* larvae for different fruit parts

a) The preference of larvae for different fruit parts

Bactrocera dorsalis eggs were collected using an inverted perforated plastic cup swabbed with the flesh of *M. x paradisiaca,* ABB Group. Eggs were placed in water and those which sunk were collected for use: floating eggs are unviable (Balagawi *et al*., 2005). From experience, egg hatchability from the culture used was about 80%, but was not explicitly tested for this experiment. A narrow slit was made in the mango skin near either the top or the bottom of the fruit using a sterile blade. Twenty eggs were inserted into the slit using a brush. The mangoes were subsequently individually incubated over sand. The number of larvae in different parts of the fruit was counted on the fifth day after insertion of eggs. When counting larvae,

upper and lower sides of fruit were divided into four parts. Fruit was first halved into a top (stalk end) and bottom half. The half of the fruit into which the eggs had been inserted was then further equally divided into three parts by length. For fruit where eggs were inserted in the top end, the four parts were numbered sequentially from the top, i.e., parts 1, 2 and 3, and then the bottom half was part 4. For fruit where eggs were placed near the bottom, numbering was reversed, i.e., part one was at the bottom and part 4 was the top half (Figure 1). The number of larvae in each fruit part was counted and recorded. Ten replicates for eggs placed in the top and bottom part of ripe and fully-ripe mango were done.

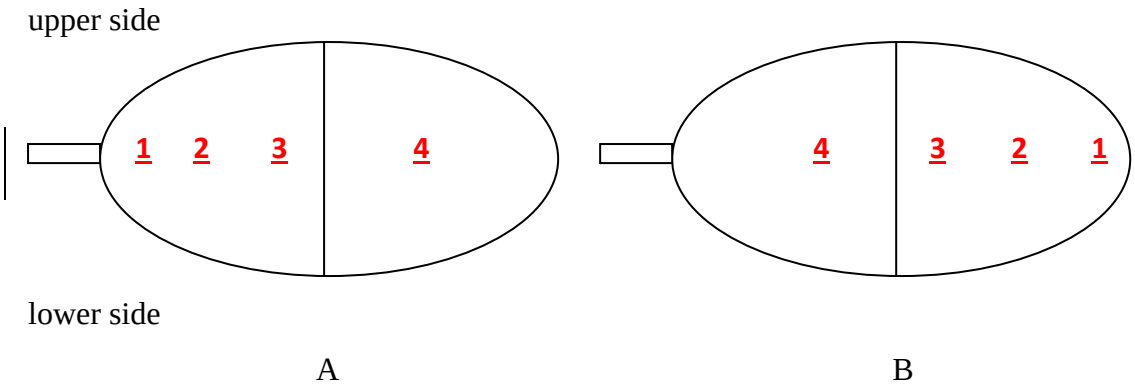

Figure 1 Diagrammatic presentation of mango fruit dividing used to record larval number in different fruit parts (A) fruit fly eggs were inserted in the top end (B) fruit fly eggs were inserted in the bottom end.

b) The performance of larvae in different fruit parts

Bactrocera dorsalis eggs were collected and inserted into fruit (both top and bottom) as for the previous experiment. The mangoes were subsequently individually incubated over sand and pupae collected. The pupae were counted, weighed and left in plastic containers for adult eclosion, when the number of emergent adults were counted and wing length measured (from wing base to wing tip). Wing size is a commonly usually measure of fly size (Yuval *et al*., 1998; Kaspi *et al*., 2000; Kaspi and Parrella, 2003). Ten replicates for top and bottom part of ripe and fully-ripe mango were done.

2.4.3 Experiment 3: Behavior of larvae in fruit of different ripening stages

Unripe, ripe and fully-ripe fruits of mango variety Namdorkmai were used as host in a study of larval behavior. Fruit fly eggs were collected and inserted into the fruit as for the experiments above, with the exception that eggs were inserted under the skin in the middle of one side of the fruit. The number of larvae was counted on the fifth day after inserting eggs. At counting, a mango was peeled and the side of the fruit into which the eggs were inserted was sliced off the seed and laid flat on a tray. A 2 × 2 cm square grid was then laid over the mango, with the centre of the grid being placed over the egg insertion point (i.e., the middle of the mango slice) (Figure 2). Thus gridded out, the number of larvae in each grid square was counted and recorded, along with the grid number. Ten replicates for each ripening stage of mango were done.

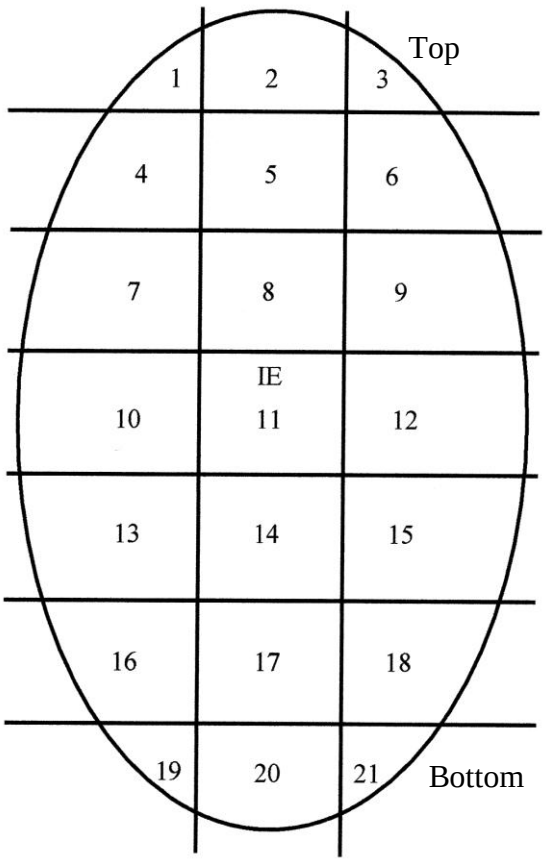

Figure 2 Diagrammatic presentation of mango fruit slice showing the grid pattern used to record larval movement. IE = inserted fruit fly eggs position.

2.5 Statistical analyses

For the oviposition preference of female flies, results were initially analysed using three-way ANOVA to test for effect of variety, ripening stage, fruit part and their interactions. If there was no significant second level interaction effect then the dependent data were pooled across varieties and ripening stage and effect of fruit part was tested using one-way ANOVA. If a significant interaction effect was detected, then the effect of fruit part and ripening stage on the dependent data was analysed by two-way ANOVA for each variety separately. If there was no significant interaction effect detected in the two-way ANOVA then the dependent data were pooled across ripening stage and effect of fruit part was tested using one-way ANOVA. If there was a significant interaction effect then the effect of fruit part on the dependent data was analysed by one-way ANOVA for each ripening stage separately.

For larval feeding site preference, while the data were amenable to analysis using a single three-way ANOVA (i.e., independent variables ripening class, egg placement, fruit part), I did not use this analysis because of the inherent difficulties in interpreting third-order interactions. Rather, I investigated interaction effects using four, two-way ANOVAs. I ran two, two-way ANOVAs to test for differences in larval location depending on where eggs were initially placed within a ripening class [i.e., independent variables, egg placement (top/bottom) and fruit part (1-4); dependent variable, number of larvae; separate two-way ANOVA for each ripening class] and then a further two, two-way ANOVAs to test for differences in larval location when eggs were placed in the same location (either top or bottom) across ripening classes [i.e., independent variables, ripening stage (ripe/fully-ripe) and fruit part (1-4); dependent variable, number of larvae; separate two-way ANOVA for eggs placed at top or bottom of fruit]. Because no significant interactions were found in these analyses, I presented the results graphically as simple mean larval abundance in the four fruit parts for each of the four treatments (i.e., ripe or fully-ripe fruit, eggs inserted in top or bottom of fruit). Differences in abundance between the fruit parts within a treatment were analyzed using one-way ANOVAs with post-hoc, pairwise comparisons of means made using Tukey's-test. Independent-samples t-test was used

to analyse all parameters of larval performance. Paired-samples t-test was used to determine the different of percentage of TA and TNC contents between top and bottom parts. Response variables analysed were the number of attempted ovipositions, the number of pupae, the weight of pupae, percent adult emergence, the duration of the egg to adult period, wing length and the physical characteristics of mango fruit (i.e., firmness, TSS, TA and TNC). Data were transformed using log (n+1), if required, to meet the assumptions of statistical analysis and then back-transformed for presentation in graphs and tables.

3. Part III: Color and Volatiles Responses of Female *Bactrocera dorsalis* to Different Mango Ripening Stages

3.1 Fruit flies and location of experiment

The colony of *B. dorsalis* used in experiments and location of trials was as reported in section 1.1.

3.2 Artificial fruit and color measurement

Three ripening stages of mango variety Namdorkmai were artificially produced in plaster. The color of unripe (hard-green), ripe (green-yellow) and fully-ripe (yellow) stages of mango variety Namdorkmai was measured using the colorimeter (CR-300, Minolta, Osaka, Japan) for creation of the color used for artificial fruits. Color values used in the creation of artificial fruits are given in the Table 2. All artificial fruits were left one month, for the release of chemical compounds, before use.

3.3 Experiments

3.3.1 Experiment 1: Effect of color of artificial mango to host preference of *B. dorsalis*

The artificial mangoes of the three ripening stages were offered to female flies simultaneously in 50 × 50 × 50 cm observation cage (Figure 3). One ovipostionally naive, 21-22-day-old gravid female *B. dorsalis* was released at the center of the cage. Records were made of the first artificial mango visited by the fly. The fly was discarded if not attracted to mangoes within the first ten minutes of observations. Observations were done from 07:00–15:00 hours. Ninety replicates of the trial were done, with the position of the artificial mangoes within the cage changed after every 30 female flies.

Table 2 Color parameters expressed by lightness, redness (+) or greenness, yellowness (+) or blueness and hue values of different fruit part of three ripening stages of mango variety Namdorkmai. [Values represented by mean ± SE. n = number of replicates; *L* = lightness; *a* = redness (+) or greenness (-), *b* = yellowness (+) or blueness (-); h = hue].

Mango ripening stage	*L* n = 6	*a* n = 6	*b* n = 6	h n = 6
Unripe				
top	61.83 ± 0.00	-16.52 ± 0.01	34.20 ± 0.00	115.79 ± 0.00
middle	59.25 ± 0.01	-14.35 ± 0.01	37.28 ± 0.00	111.05 ± 0.00
bottom	64.17 ± 0.01	-16.77 ± 0.01	31.15 ± 0.01	118.30 ± 0.01
Ripe				
top	75.54 ± 1.01	-4.20 ± 1.33	37.95 ± 1.87	96.61 ± 2.23
middle	75.65 ± 0.47	-5.72 ± 1.11	36.37 ± 1.27	99.02 ± 1.91
bottom	75.06 ± 0.84	-6.90 ± 1.30	34.43 ± 0.96	101.44 ± 2.27
Fully-ripe				
top	75.68 ± 0.99	-4.45 ± 0.52	44.08 ± 0.61	84.26 ± 0.63
middle	74.38 ± 0.79	-5.20 ± 0.53	43.34 ± 0.66	83.19 ± 0.62
bottom	74.94 ± 0.50	-4.70 ± 0.25	43.87 ± 0.10	83.86 ± 0.38

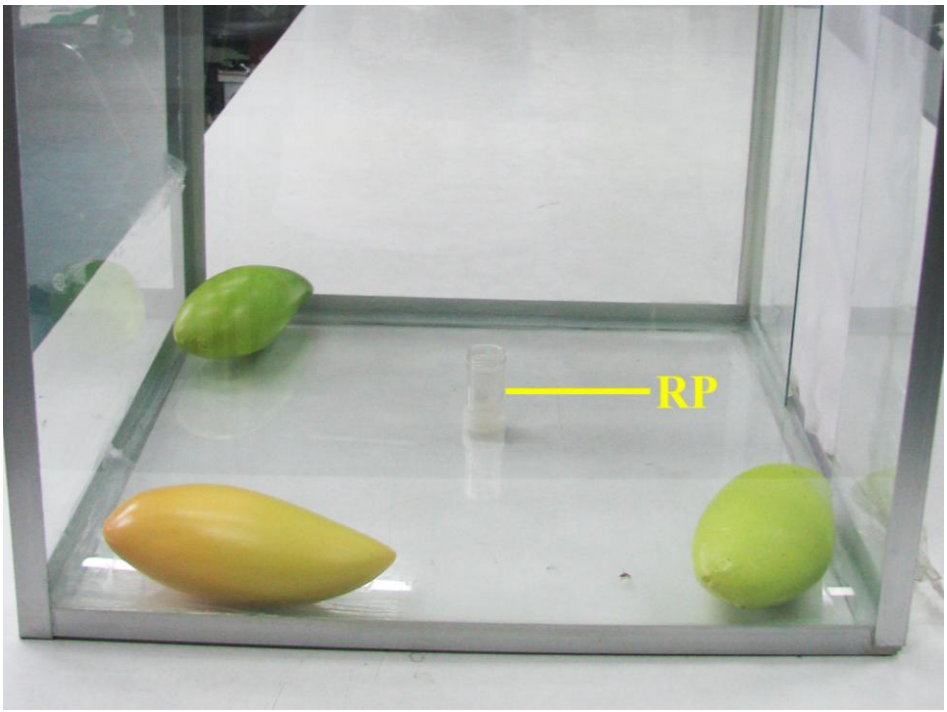

Figure 3 Artificial mango fruits exposed in an observation cage. RP = released fly position.

3.3.2 Experiment 2: Effect of mango volatiles to host preference of *B. dorsalis*

A Y-tube olfactometer, with an 18 cm arm length and 24 cm stem length (Figure 4), was used to determine the preference of *B. dorsalis* female fly for volatiles of each mango ripening stage (unripe, ripe and fully-ripe). Air flow through the olfactometer was created using air pump (Twin majic 8800, China) and flowed at a rate of 250 ml/min. Air was first cleaned by passing it through granular activated charcoal before sending the air to the plastic bottles containing the mangoes and then out through the olfactometer. A 21-22-day-old, gravid female *B. dorsalis*, which had no prior oviposition experience, was placed at the base of the Y-tube. The fly's behavior was recorded when she flew or walked to the one side of the Y-tube. Female flies were discarded if not attracted to either mango within a 10 min period. The sources of sample volatiles were switched between two arms of Y-tube in each trial. Because the Y-tube design does not allow for simultaneous comparison the three fruit, three pair-wise comparative trials had to be done (i.e., green/ripe, green/fully-ripe, ripe/fully-ripe). Thirty replicates were done per trial. Experiments were carried out between 07:00-15:00 hours.

3.4 Statistical analyses

Chi-Square test was used to analyse effect of color and volatiles of three ripening stages of mango. Response variable was number of female fly choice.

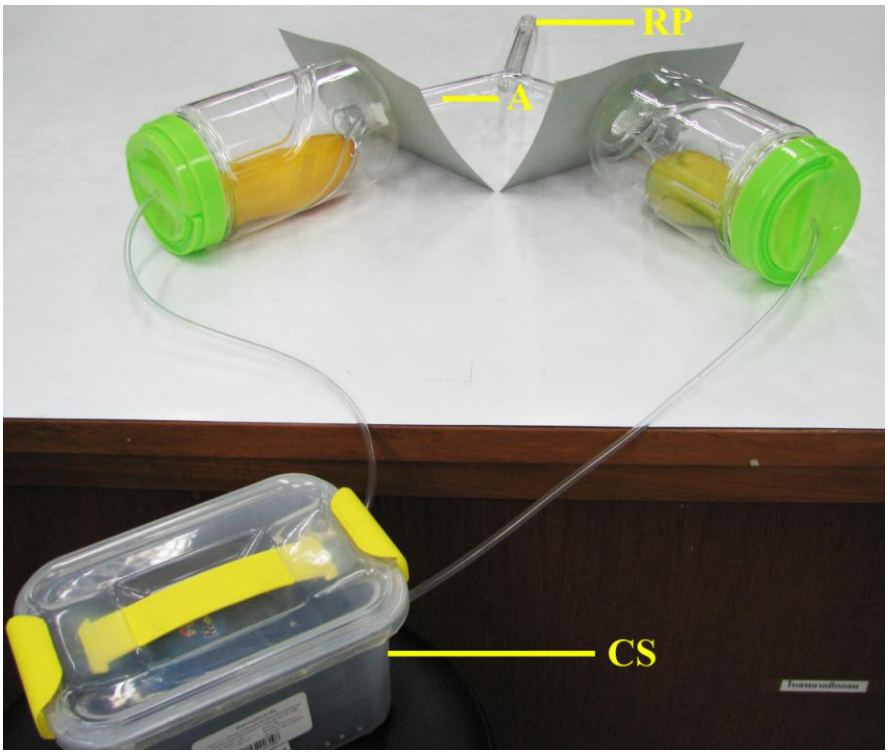

Figure 4 Structure of the Y-tube apparatus used in these experiments.
RP = released fly position, A = arm of Y-tube, CS = clean air source.

RESULTS

1. Part I: *Bactrocera dorsalis* Preference for and Performance on Two Mango Varieties at Three Stages of Ripening

1.1 Fruit characteristics

Variety Namdorkmai is a significantly bigger mango than variety Oakrong (fruit width: t = 6.775, d.f. = 118; fruit length: t = 81.831, d.f. = 106.122; fruit thickness: t = 34.395, d.f. = 100.141; all three P < 0.0001) (Table 1). There were significant differences in TSS between the two mango varieties (ANOVA: $F_{1,99}$ = 9.045, P = 0.003), and the various ripening stages (ANOVA: $F_{2,99}$ = 333.354, P < 0.0001), whereas there was also a significant interaction effect between mango variety and ripening stage (ANOVA: $F_{2,99}$ = 3.609, P = 0.031). Despite the significant interaction effect, general patterns were easily observed and showed variety Oakrong to be the sweeter mango, with fruit sweetening as it ripen (Table 3). As for TSS, mean firmness differed significantly between the two mango varieties (ANOVA: $F_{1,71}$ = 57.944, P < 0.0001), while firmness declined with ripening (ANOVA: $F_{2,71}$ = 1 052.068, P < 0.0001). Again, there was a significant interaction effect between mango variety and ripening stage (ANOVA: $F_{2,71}$ = 62.597, P < 0.0001). Variety Namdorkmai had a tougher exopericarp than Oakrong and firmness decreased as ripening increased (Table 3).

Despite both mango varieties being known hosts of *B. dorsalis*, direct observation of oviposition behavior under laboratory conditions demonstrated that few flies could successfully penetrate the exopericarp of either variety at any stage of ripening: only a few flies achieved successful oviposition. Post-experimental dissection of flies showed that all had eggs in their ovaries and were thus physiologically capable of ovipositing. All flies attempted to oviposit into the fruits and there were distinct behavioral responses to the various mango ripening stages. Thus, in the following section, the number of oviposition attempts, rather than

successful ovipositions, is analysed to determine the preference of female flies to different ripening stages of mangoes. The performance outcomes of successful ovipositions are presented, but performance results where eggs were artificially placed below the fruit skin (section larval performance) give a more reliable performance measure.

Table 3 Fruit attributes (mean ± SE) of two mango varieties (Namdorkmai and Oakrong) at three stages of ripening (n = sample size). Fruit size did not change across the ripening stages measured; TSS = total soluble solids.

Fruit properties	Namdorkmai			Oakrong		
	unripe	ripe	fully-ripe	unripe	ripe	fully-ripe
Width (cm)	8.78 ± 0.14 n = 20			6.90 ± 0.03 n = 20		
Length (cm)	13.90 ± 0.03 n = 20			9.92 ± 0.03 n = 20		
Thickness (cm)	6.84 ± 0.03 n = 20			5.52 ± 0.02 n = 20		
TSS (°Brix)	10.48 ± 0.22 n = 15	15.07 ± 0.30 n = 15	18.64 ± 0.85 n = 15	10.53 ± 0.17 n = 20	17.09 ± 0.27 n = 20	19.14 ± 0.37 n = 20
Firmness (kg/cm^2)	1.09 ± 0.01 n = 11	0.77 ± 0.02 n = 13	0.22 ±0.01 n = 13	1.03 ± 0.02 n = 10	0.55 ± 0.03 n = 15	0.10 ± 0.00 n = 15

1.2 Adult preference

1.2.1 No-choice experiment

Direct observation of *B. dorsalis* oviposition behavior under laboratory conditions demonstrated that only 5.6% of female *B. dorsalis* successfully oviposited into two mango varieties. Thus, the number and duration of visits by flies to fruit within a day (diurnal pattern) is analysed to determine the preference of female flies to different ripening stages of mangoes.

a) Visit number and duration within a day (diurnal pattern)

A repeated measures ANOVA demonstrated that for mango variety Namdorkmai there were significant differences in the number (ANOVA: $F_{14.752,420.436} = 3.189$, $P < 0.0001$) and duration (ANOVA: $F_{13.575,386.90} = 2.650$, $P = 0.001$) of visits by female flies to fruit of different ripening stages across hourly time periods during the day. When observing the hourly response patterns, it can be observed that while flies made similar numbers of visits to fruits of different ripening stages, the visits were nearly always longer to fully-ripe mangoes (Figure 5A). Flies were slower to respond to unripe mangoes and, after a peak in mid-morning, duration of visits to unripe mango declined during the day, a pattern also seen in ripe and fully-ripe fruits (Figure 5B). The diurnal response pattern of flies to mango variety Oakrong differed to those seen in mango variety Namdorkmai. The visit number (ANOVA: $F_{13.600,387.592} = 2.154$, $P = 0.010$), but not the visit duration (ANOVA: $F_{11.320,322.611} = 1.413$, $P = 0.163$), differed between different ripening stages across hourly periods. The number of visits that female flies made to all ripening stages tend to increased during a day, with lowest in unripe fruit (Figure 6A). Unlike mango variety Namdorkmai, initial fly response to mango variety Oakrong of all ripening stages was low, but after the first hour response to ripe and fully-ripe fruit increased and for ripe fruit remained constant throughout the day, but fluctuated for fully-ripe fruit (Figure 6B).

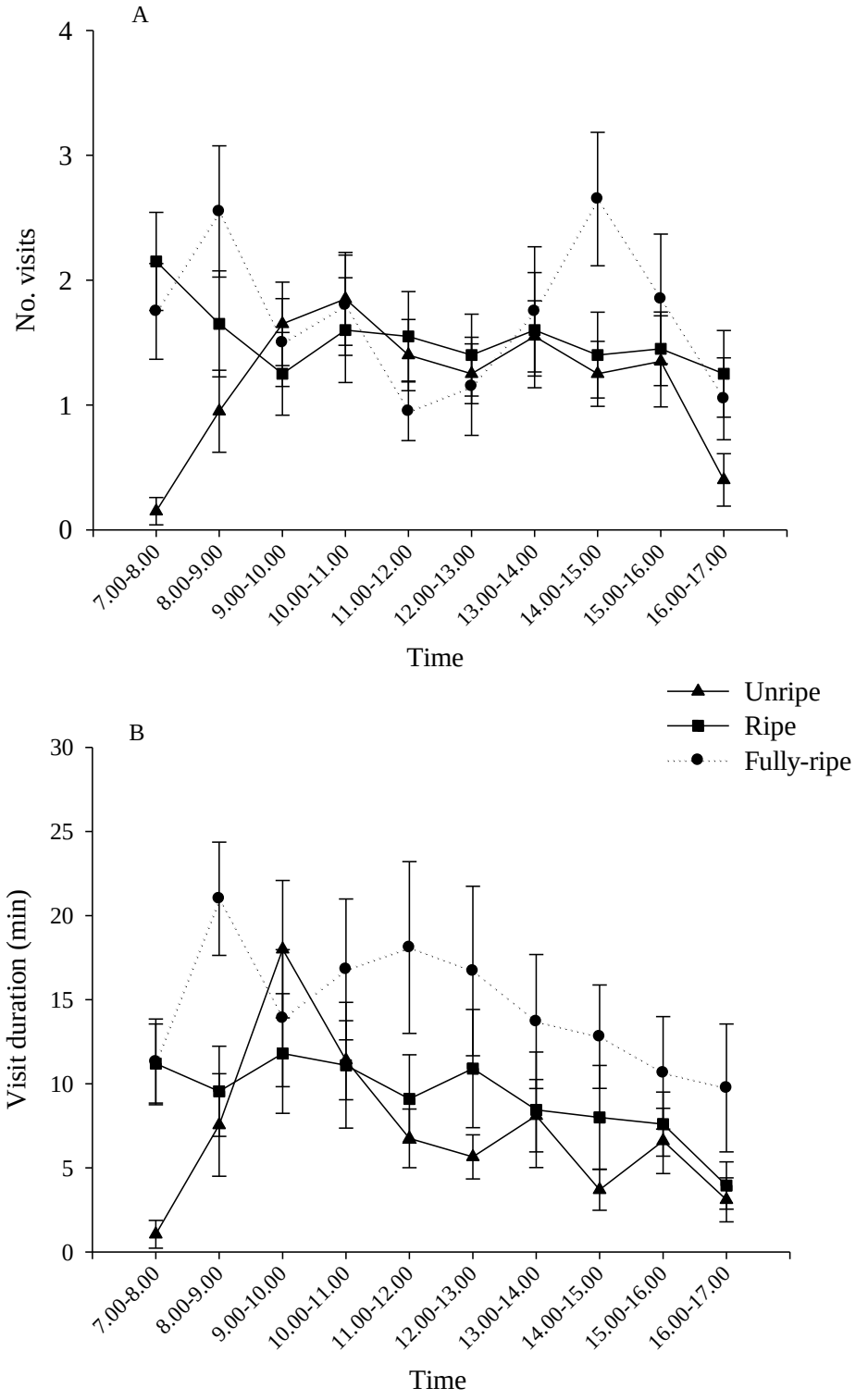

Figure 5 The mean (± SE) hourly visitation (A) number and (B) duration (min) of gravid female *Bactrocera dorsalis* to three ripening categories of mango variety Namdorkmai in a no-choice situation.

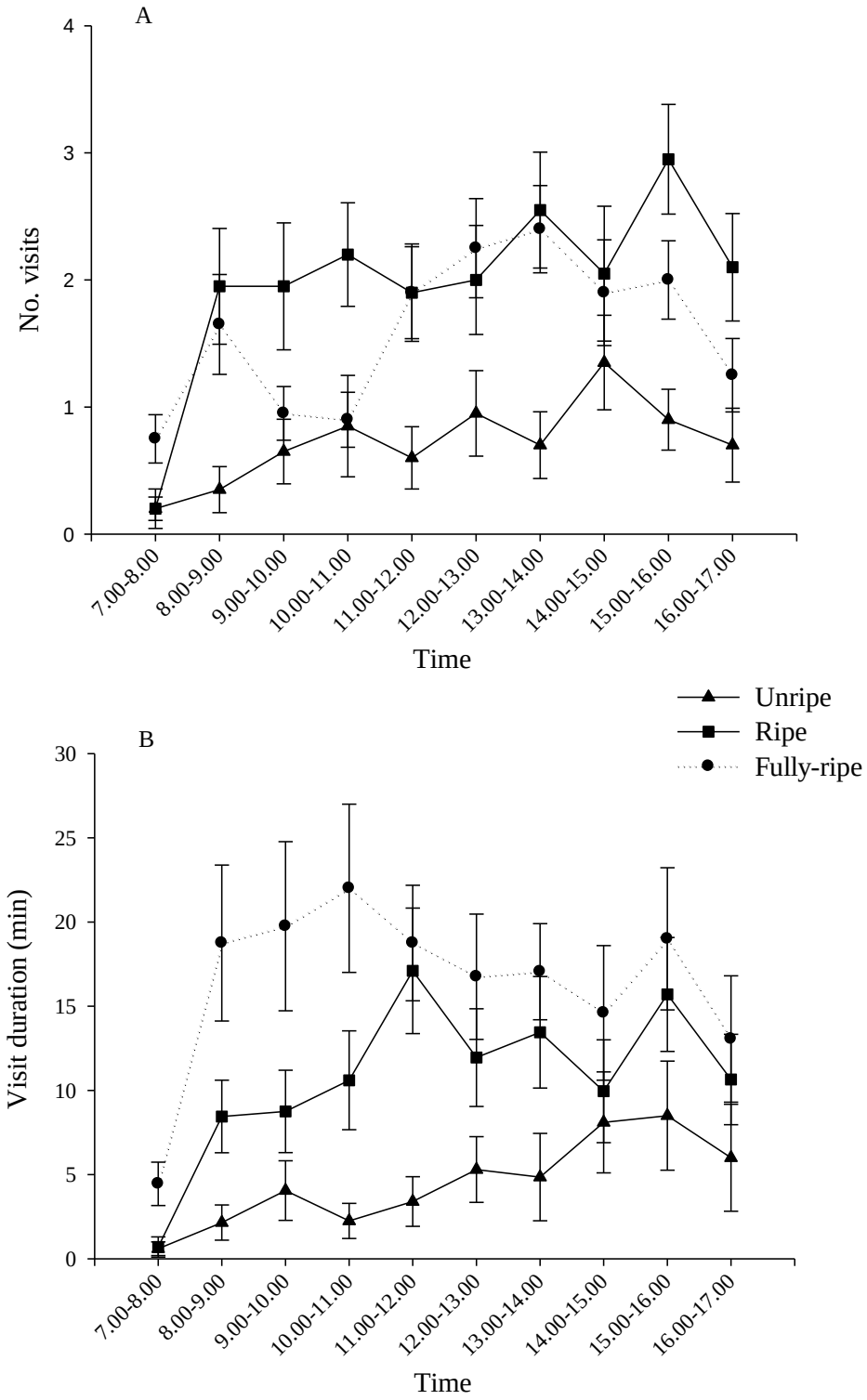

Figure 6 The mean (± SE) hourly visitation (A) number and (B) duration (min) of gravid female *Bactrocera dorsalis* to three ripening categories of mango variety Oakrong in a no-choice situation.

b) Visit number and duration per day

There was no significant interaction effect between stage of ripening and mango variety in the daily number of visits made by female flies (ANOVA: $F_{2,114} = 2.991$, $P = 0.054$), so data were pooled across varieties. The daily number of visits differed significantly between the stages of ripening (ANOVA: $F_{2,117} = 10.224$, $P < 0.0001$), with ripe and fully-ripe fruits being visited in equal numbers and unripe fruit significantly less (Figure 7A).

There was a significant interaction effect between stage of ripening and mango variety in the total duration of visits by female flies (ANOVA: $F_{2,114} = 3.641$, $P = 0.029$), and so results for each variety were analysed separately. For variety Namdorkmai, the total duration of visits differed significantly with ripening stage (ANOVA: $F_{2,57} = 3.823$, $P = 0.028$). On average, flies spent over an hour longer for visits to fully-ripe than to unripe fruit, with visitation duration to ripe fruit intermediate (Figure 7B). For variety Oakrong, there were also significant differences in the duration of visits to fruit of various ripening stages (ANOVA: $F_{2,57} = 15.098$, $P < 0.0001$), but in this case the duration of visits to ripe and fully-ripe fruits did not differ, whereas unripe fruit was visited significantly shorter (Figure 7B).

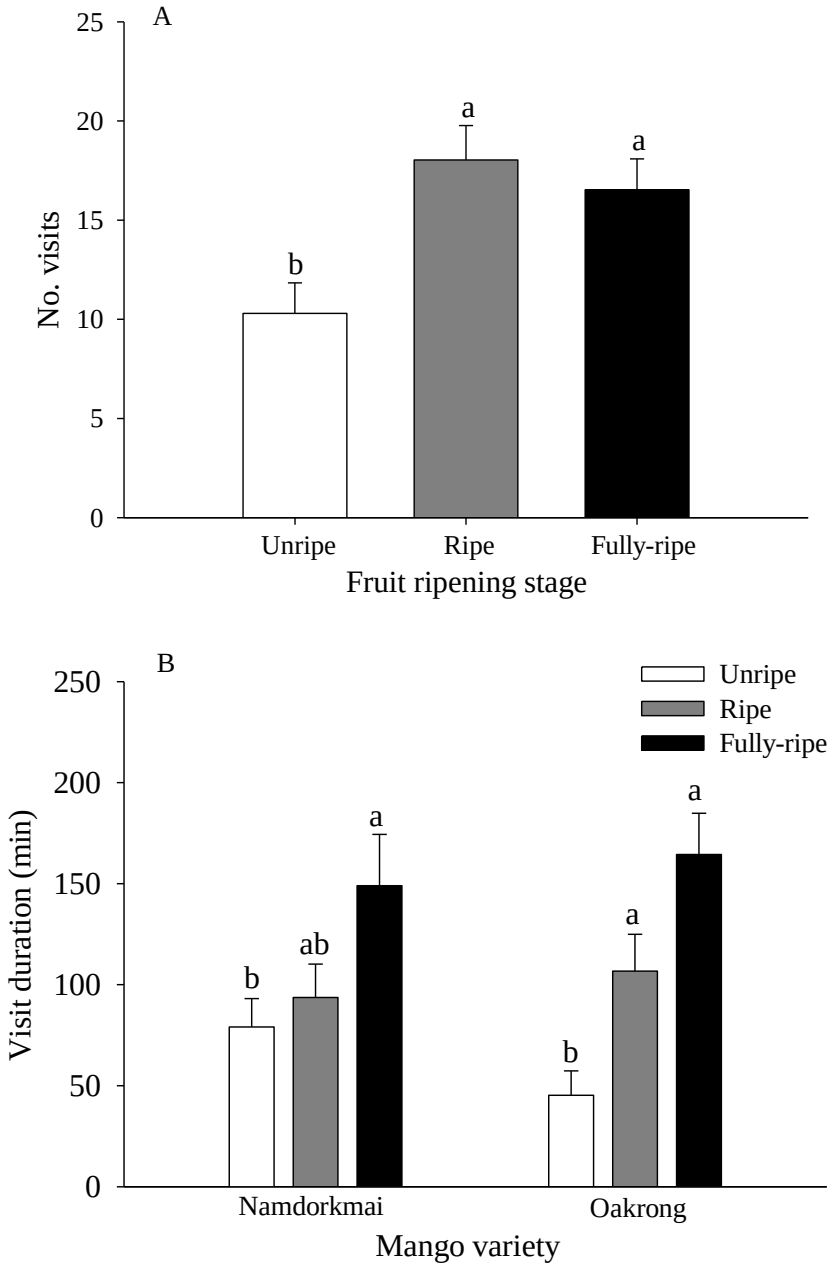

Figure 7 Mean (± SE) (A) number of visits and (B) duration (min) of visits during a day by gravid female *Bactrocera dorsalis* to two mango varieties at three stages of ripening in a no-choice situation. Numbers of visits did not differ between varieties, so data were pooled. Columns capped with different letters are statistically different [Tukey test: $P < 0.05$; n = 40 (A) and n = 20 (B)]. Significance is based on log (x + 1)-transformed data, non-transformed data are plotted.

c) Oviposition attempts and pupal emergence in fruits of different ripening stages

There was no significant interaction effect between stage of ripening and mango variety in the number of attempted ovipositions (fly adopting oviposition stance and attempting to penetrate skin of fruit with ovipositor) (ANOVA: $F_{2,114}$ = 1.378, P = 0.256), hence data were pooled. The number of attempted ovipositions differed significantly between the various fruit ripening stages, with fewer attempted ovipositions into unripe fruit and equal or higher penetration into ripe and fully-ripe fruits (ANOVA: $F_{2,117}$ = 16.595, P < 0.0001) (Figure 8).

Almost no attempted ovipositions led to skin penetration and deposition of eggs. For variety Namdorkmai, only one piece of fully-ripe fruit yielded pupae and this subsequently yielded six adult flies. One female fly successfully oviposited into unripe fruit, but no pupa emerged. For variety Oakrong, there was one successful oviposition per fruit ripening stage, but only two pupae emerged from fully-ripe fruit and neither eclosed as an adult. No pupae emerged from unripe or ripe fruits.

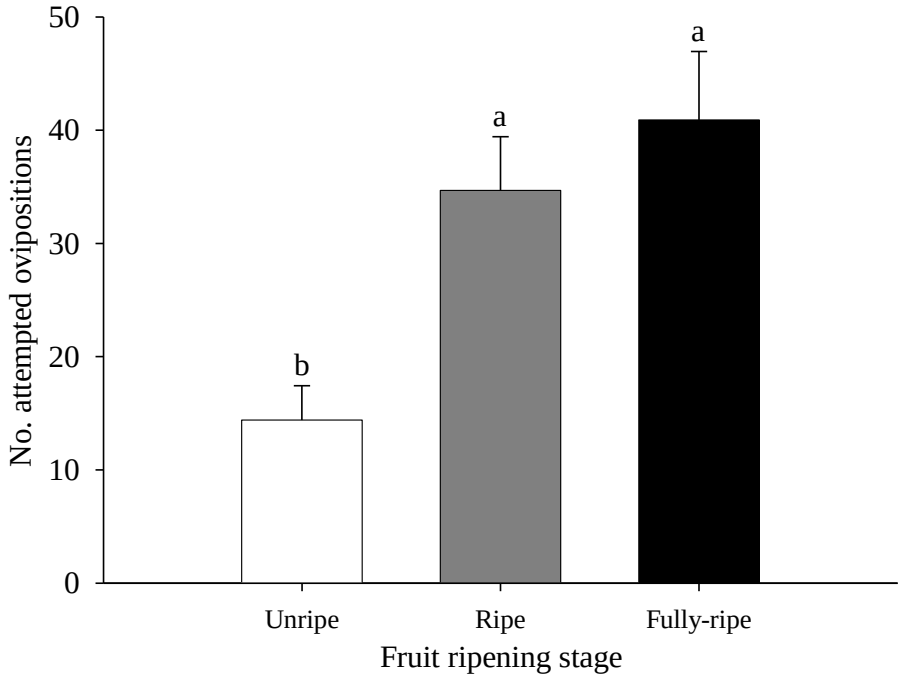

Figure 8 Mean (± SE) number of attempted ovipositions during a day by gravid female *Bactrocera dorsalis* to two mango varieties at three stages of ripening in a no-choice situation. Numbers of attempted ovipositions did not differ between varieties, so data were pooled. Columns capped with different letters are statistically different (Tukey test: $P < 0.05$; $n = 40$). Significance is based on log $(x + 1)$-transformed data, non-transformed data are plotted.

1.2.2 Choice experiment

a) Visit number and duration within a day (diurnal pattern)

A repeated measure ANOVA identified that for mango variety Namdorkmai, under choice conditions, there were no significant differences in the number (ANOVA: $F_{14.243,405.931} = 0.992$, $P = 0.461$) or duration (ANOVA: $F_{13.491,384.497} = 1.403$, $P = 0.151$) of visits to fruit of different ripening stages across hourly time periods during the day. Reflecting the pattern seen for the whole day data, visit number and duration to fully-ripe fruit after 11.00 am was generally greater than visit number and duration to unripe fruit, with ripe fruit intermediate between the two (Figure 9A and 9B). Before late morning, however, there was little obvious difference in the flies' responses to different fruit. The pattern of visits by flies to mango variety Oakrong differed from mango variety Namdorkmai. As for mango variety Oakrong, the number of fly visits to fruit across hourly time periods did not differ significantly among different fruit ripening stages of mango variety Oakrong (ANOVA: $F_{14.529,414.071} = 1.678$, $P = 0.055$; Figure 10A).

However, there were significant differences in the duration (ANOVA: $F_{12.626,359.853} = 1.795$, $P = 0.044$; Figure 10B) of visits. Visitation number to all ripening stages of mango increased during the morning, peaking around midday and then, for unripe and ripe fruit, declining during the afternoon. Visitation number to fully-ripe fruit remained high during the afternoon. With the exception of the first observation period of the day, visitation number and duration were always higher on fully-ripe fruit.

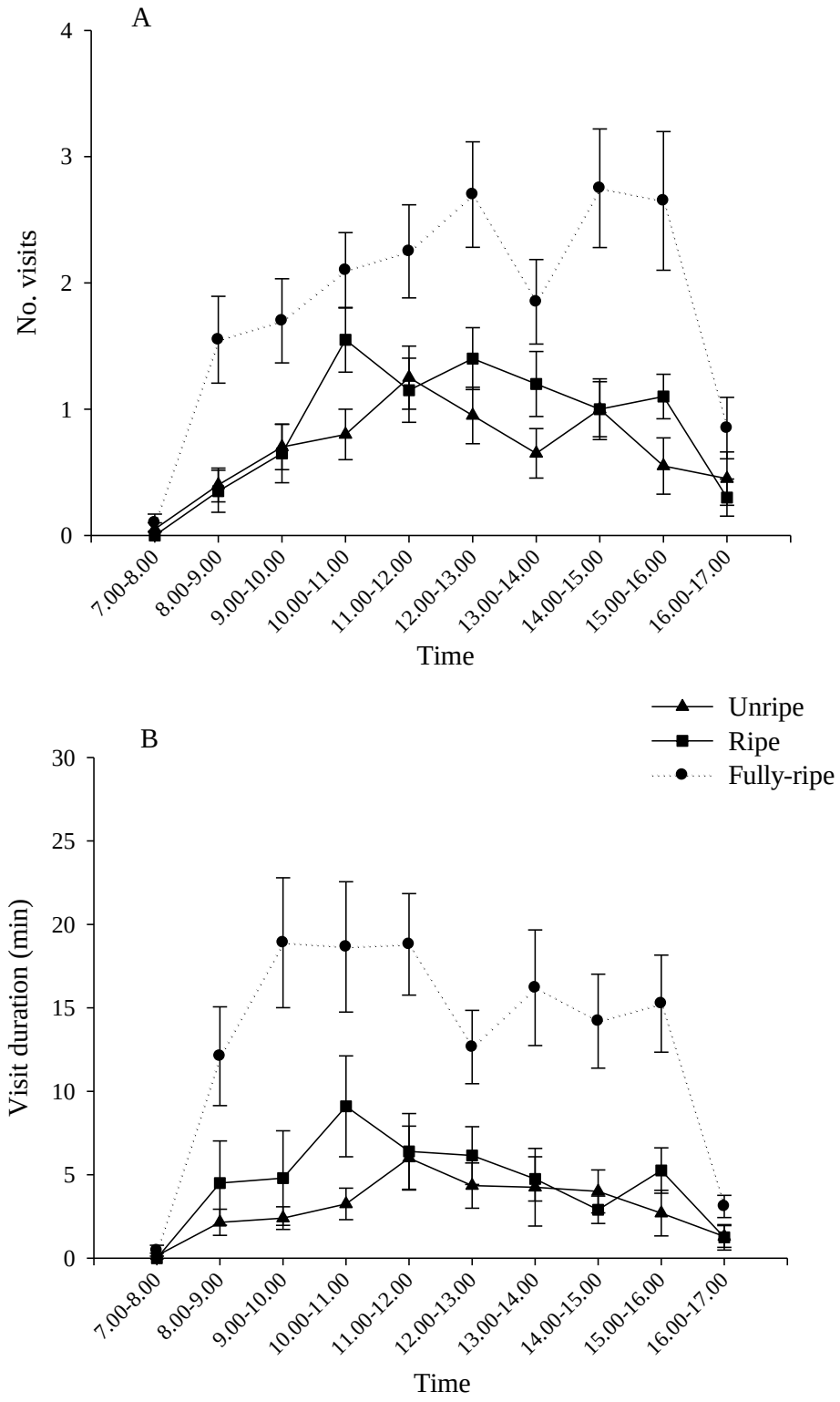

Figure 9 The mean (± SE) hourly visitation (A) number and (B) duration (min) of gravid female *Bactrocera dorsalis* to three ripening categories of mango variety Namdorkmai in a choice situation.

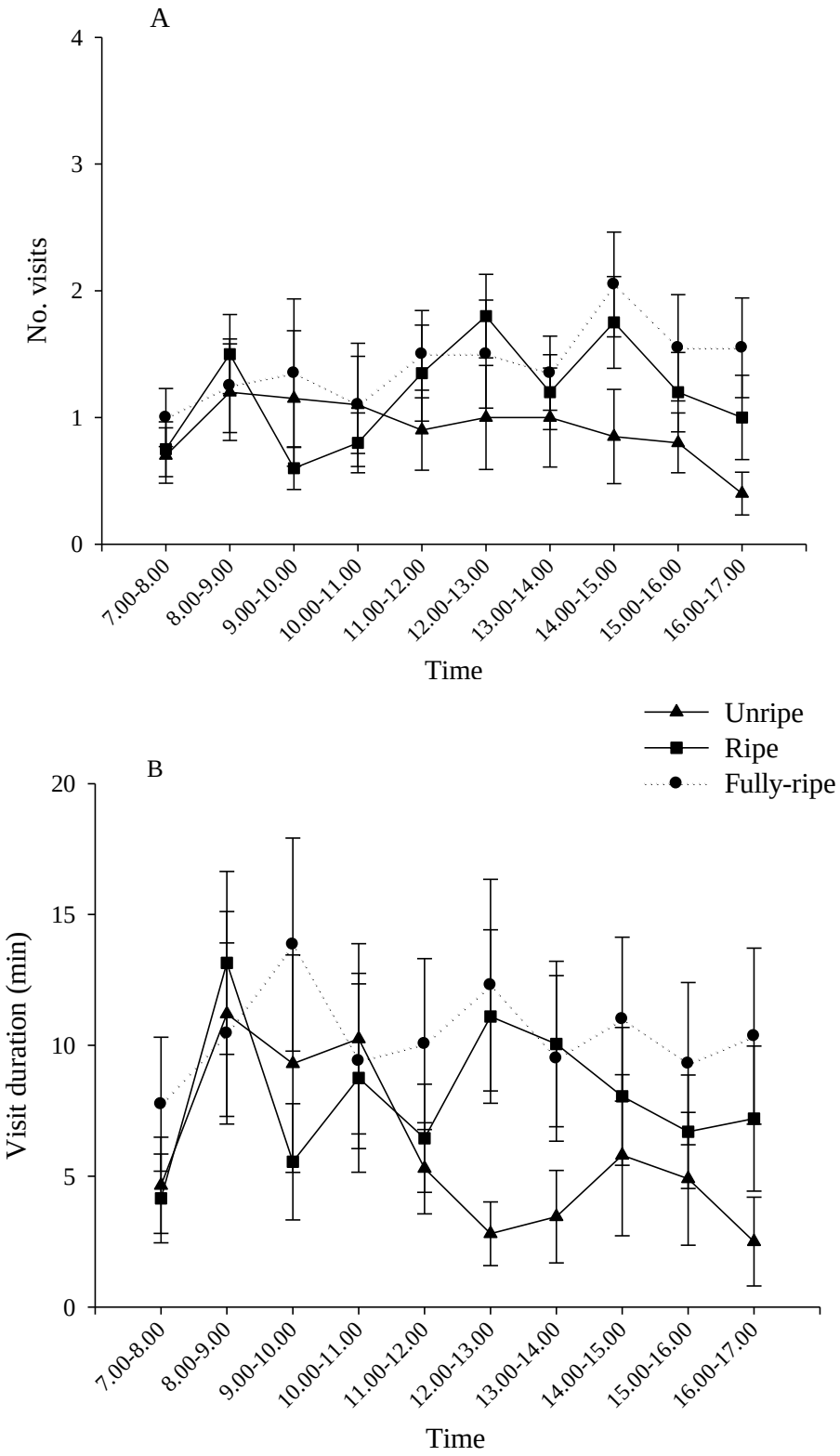

Figure 10 The mean (± SE) hourly visitation (A) number and (B) duration (min) of gravid female *Bactrocera dorsalis* to three ripening categories of mango variety Oakrong in a choice situation.

b) Visit number and duration per day

There was no significant interaction effect between stage of ripening and mango variety in the daily number of visits (ANOVA: $F_{2,114} = 1.580$, $P = 0.210$), so data were pooled for analysis. The daily number of visits made by female flies to fruit of various ripening stages differed significantly (ANOVA: $F_{2,117} = 12.680$, $P < 0.0001$). As for the no-choice trial, flies made least visits to unripe fruit, significantly more to ripe fruit, and again significantly more to fully-ripe fruit (Figure 11A).

There was a significant interaction effect between stage of ripening and mango variety in the duration of visits by female flies (ANOVA: $F_{2,114} = 3.168$, $P = 0.046$). For variety Namdorkmai, under choice conditions, female flies spent equal time periods on ripe and fully-ripe mangoes, and significantly less time on unripe mangoes (ANOVA: $F_{2,57} = 4.958$, $P = 0.010$) (Figure 11B). However, for variety Oakrong, flies spent nearly three times longer on fully-ripe fruit in comparison to unripe or ripe fruits (ANOVA: $F_{2,57} = 19.386$, $P < 0.0001$) (Figure 11B).

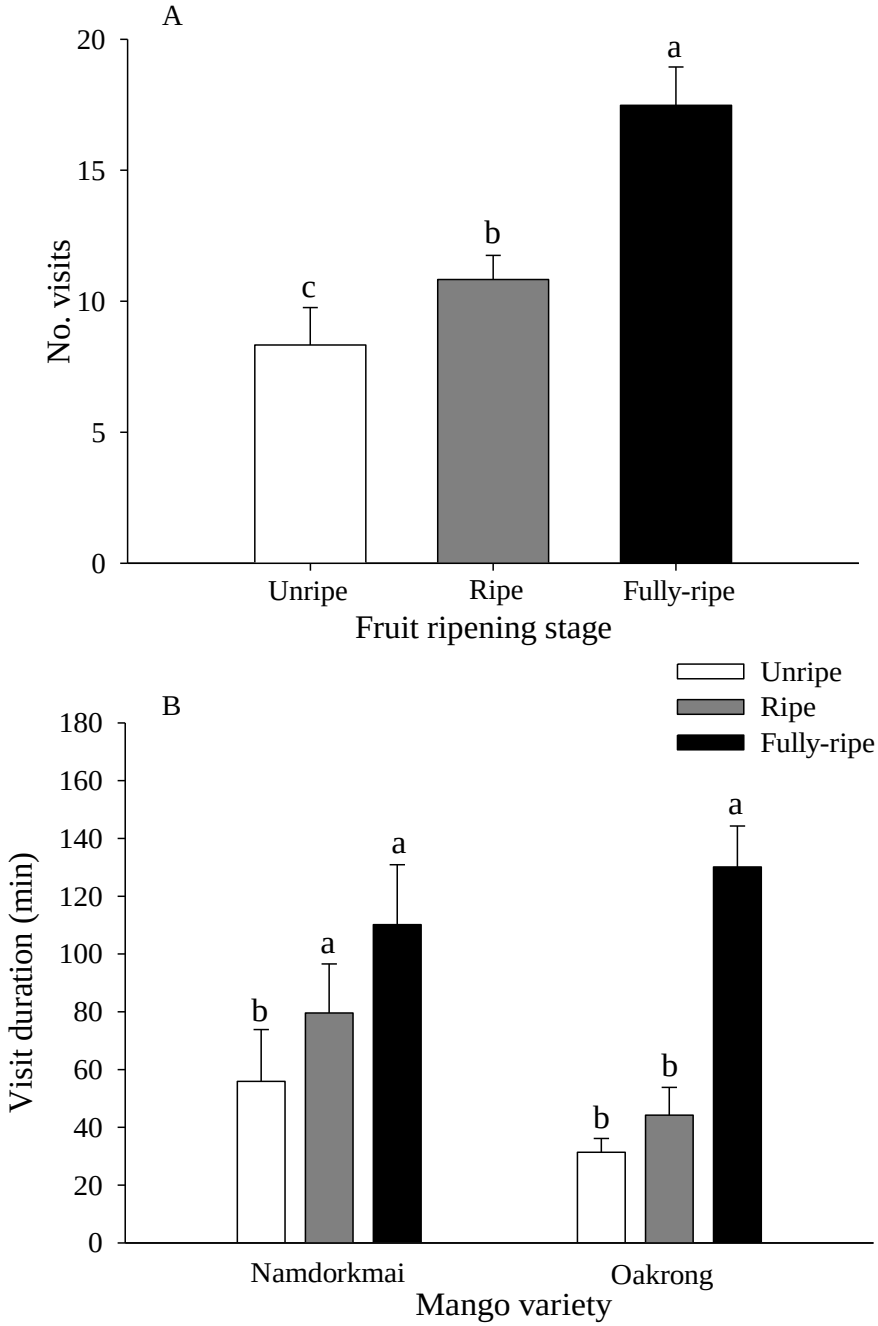

Figure 11 Mean (± SE) (A) number of visits, (B) duration (min) of visits during a day by gravid female *Bactrocera dorsalis* to two mango varieties at three stages of ripening in a choice situation. Number of visits (A) did not differ between varieties, so data were pooled. Columns capped with different letters are statistically different [Tukey test: $P < 0.05$; $n = 40$ (A), and $n = 20$ (B)]. Significance is based on log $(x + 1)$-transformed data, non-transformed data are plotted.

c) Oviposition attempts and pupal emergence in fruits of various ripening stages

There was a significant interaction effect between stage of ripening and mango variety in the number of oviposition attempts under choice conditions (ANOVA: $F_{2,114}$ = 4.429, P = 0.014), hence results were analysed separately for each variety. For Namdorkmai, female flies attempted to oviposit equally into ripe and fully-ripe fruits, but significantly less into unripe fruit (ANOVA: $F_{2,57}$ = 7.353, P = 0.001). For variety Oakrong, flies made significantly more oviposition attempts into fully-ripe fruit than into unripe or ripe fruit (ANOVA: $F_{2,57}$ = 23.102, P < 0.0001) (Figure 12). For variety Namdorkmai, 12 pupae were recovered from one unripe fruit, with eight adults successfully eclosing. For Oakrong, one piece each of fully-ripe and ripe fruits was oviposited into, but neither yielded pupae.

I note here an unusual observation concerning fly oviposition into unripe fruit. For those female flies that successfully penetrated the skin of unripe mango to lay eggs, clear resin immediately flowed from the resultant wound. I directly observed this resin flow pushing deposited fruit fly eggs out off the fruit (Figure 13).

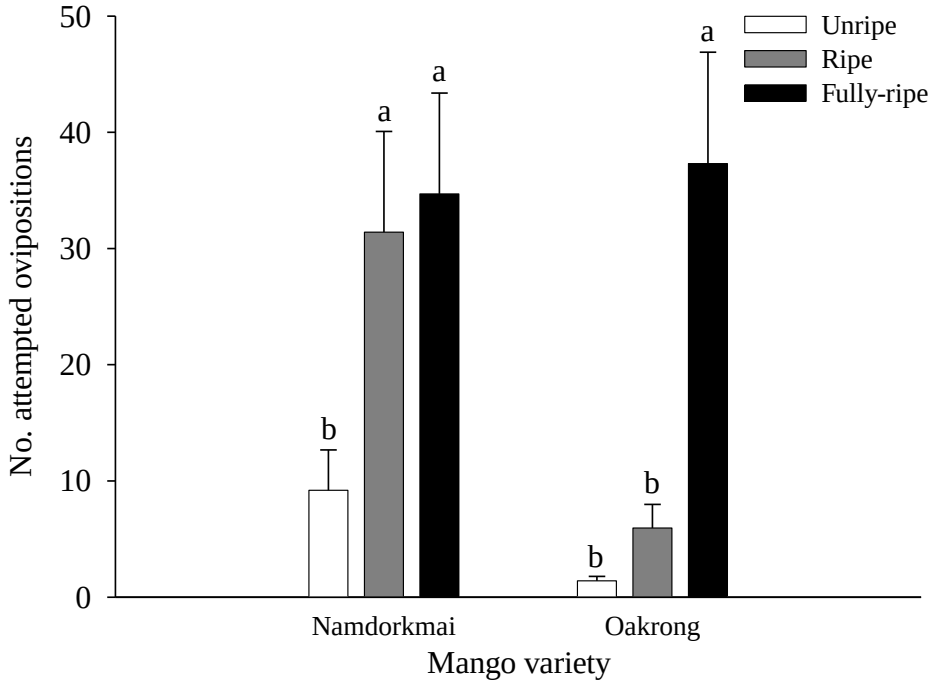

Figure 12 Mean (± SE) number of attempted ovipositions during a day by gravid female *Bactrocera dorsalis* to two mango varieties at three stages of ripening in a choice situation. Columns capped with different letters are statistically different (Tukey test: $P < 0.05$; $n = 20$). Significance is based on log (x + 1)-transformed data, non-transformed data are plotted.

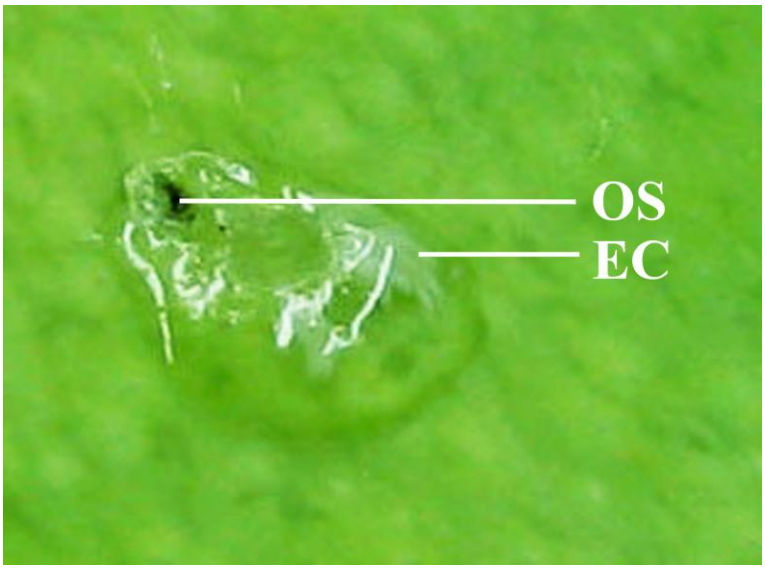

Figure 13 The resin flowed from an oviposition wound on the skin of unripe mango and pushed deposited fruit fly eggs out off the fruit. EC = egg clutch ejected in sap, OS = oviposition scar.

1.3 Influence of egg load

For unripe mangoes, female flies carried high number of mature eggs in ovaries had more significantly responses to unripe mango than female flies carried low number of mature eggs in ovaries (ANOVA, attempted oviposition: $F = 4.271$, d.f. = 2, $P = 0.023$; total duration of visits: $F = 4.461$, d.f. = 2, $P = 0.020$; total time of visits: $F = 3.447$, d.f. = 2, $P = 0.044$). As for the unripe mango, there were the significant differences in the number of oviposition attempts and total time of visits to ripe mango between high eggs load and low eggs load female flies (ANOVA, oviposition attempts: $F = 60.899$, d.f. = 2, $P < 0.0001$; total time of visits: $F = 4.022$, d.f. = 2, $P = 0.027$) even though total duration of visits did not differ (ANOVA, $F = 1.101$, d.f. = 2, $P = 0.345$). In contrast, the responses of female flies carried different number of eggs load did not differ significantly in fully-ripe mango (ANOVA, attempted oviposition: $F = 2.736$, d.f. = 2, $P = 0.083$; total duration of visits: $F = 0.289$, d.f. = 2, $P = 0.751$; total time of visits: $F = 0.098$, d.f. = 2, $P = 0.907$) (Table 4).

Table 4 The responses of female *Bactrocera dorsalis* had the different egg load in their ovaries to different ripening stages of mango. [n = number of replicate. Values (mean ± SE) in the same column followed by the different letter are statistically different (Tukey-test, $P < 0.05$). Significance is based on transformed data using log (x + 1), non-transformed data are presented].

Mature eggs in ovaries	Unripe			Ripe			Fully-ripe		
	Number of attempted oviposition	Duration of visit (min)	Time of visit	Number of attempted oviposition	Duration of visit (min)	Time of visit	Number of attempted oviposition	Duration of visit (min)	Time of visit
1-20	-	-	-	19.23 ± 4.11c	61.77 ± 16.77a	10.92 ± 2.66a	47.57 ± 19.11a	129.93±28.75a	14.93 ± 2.46a
n				13	13	13	14	14	14
21-30	-	-	-	29.45 ± 8.67b	98.91 ± 18.28a	17.00 ± 2.71a	74.14 ± 20.35a	133.71±25.21a	17.29 ± 4.12a
n				11	11	11	7	7	7
≥ 31	-	-	-	37.58 ± 7.00a	89.08 ± 11.65a	25.67 ± 2.82a	23.00 ± 6.83a	156.67±30.39a	14.89 ± 2.45a
n				12	12	12	9	9	9
1-30	2.63 ± 2.09b	20.00 ± 9.52b	3.75 ± 1.54a	-	-	-	-	-	-
n	8	8	8						
31-40	11.50 ± 3.39a	92.25 ± 30.44a	8.38 ± 1.89a	-	-	-	-	-	-
n	8	8	8						
≥ 41	12.63 ± 2.90a	49.74 ± 7.02ab	10.79 ± 1.74a	-	-	-	-	-	-
n	19	19	19						

1.4 Larval performance

1.4.1 Pupal number

Linear regression analysis of the number of pupae in a cohort vs. the weight of pupae in a cohort for all replicates, across all treatments, indicated a strong, positive relationship (ANOVA: $F_{1,119} = 279.988$, $P < 0.0001$, $R^2 = 0.704$; $y = -0.060 + 0.048x$) (Figure 14). There was no significant difference in the number of pupae that developed in fruits between the two mango varieties (ANOVA: $F_{1,114} = 0.335$, $P = 0.564$), but there were significant differences in the number of pupae that recovered from fruits of various ripening stages (ANOVA: $F_{1,114} = 36.200$, $P < 0.0001$), and also the interaction effect between mango variety and ripening stage was significant (ANOVA: $F_{2,114} = 6.735$, $P = 0.002$). Less than 20% of the initial number of eggs placed in unripe fruit of both mango varieties developed into emerging pupae, whereas survival to pupation was > 30% for ripe and fully-ripe fruits of both varieties. In ripe fruit of variety Oakrong 60% of eggs developed to pupae (Figure 15).

1.4.2 Percentage adult emergence from pupae

The interaction effect between stage of ripening and mango variety was not significant (ANOVA: $F_{2,114} = 0.696$, $P = 0.501$), so the data were pooled across mango variety. There was no significant difference in percentage adult emergence from pupae that had emerged from fruits of various ripening stages (ANOVA: $F_{2,117} = 2.243$, $P = 0.111$), with mean (± SE) adult emergence being 70.4 ± 2.90%.

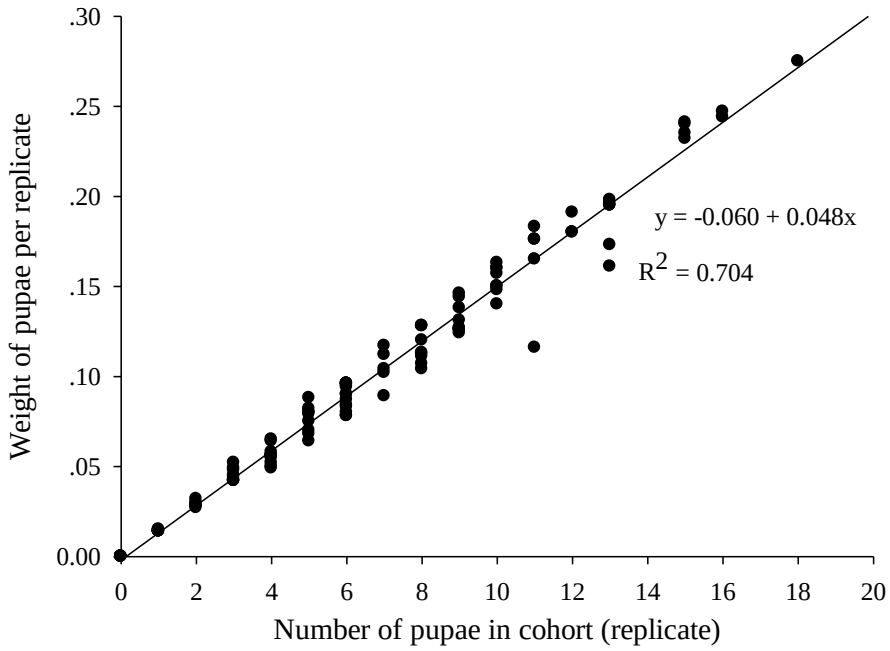

Figure 14 Combined results illustrating the relationship between cohort pupual number and cohort pupal weight for *Bactrocera dorsalis* pupae reared from two mango varieties (Namdorkmai and Oakrong), each at three stages of ripening (unripe, ripe and fully-ripe). Regression analysis was used to describe the relationship between the number of pupae and the weight of pupae in a cohort for all replicates, across all treatments.

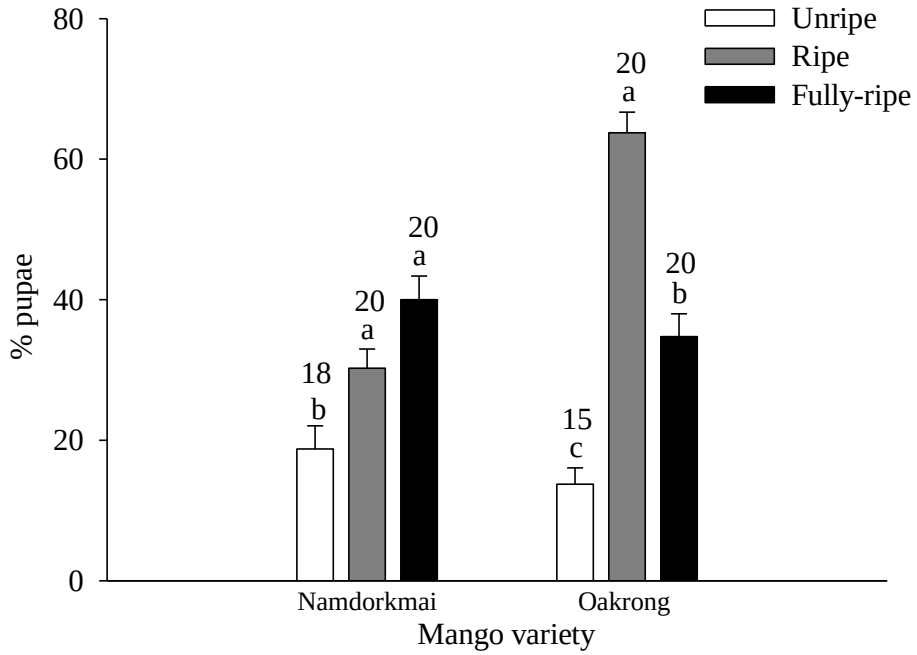

Figure 15 Mean (± SE) percentage of *Bactrocera dorsalis* pupae reared from two mango varieties, each at three stages of ripening. Columns capped with different letters within the same variety are statistically different (Tukey test: $P < 0.05$, $n = 20$). Significance is based on log $(x + 1)$-transformed data, non-transformed data are plotted. Each replicate was initiated as a cohort of 20 eggs per fruit variety and stage. The numbers at the top of each column indicate the fruits yielding at least one pupa.

1.4.3 Egg to adult duration

There was a significant interaction effect between stage of ripening and mango variety in the egg-to-adult duration (ANOVA: $F_{2,114} = 19.115$, $P < 0.0001$), so results for each variety were analysed separately. For Namdorkmai, the immature development was fastest in fully-ripe fruit and slowest in unripe fruit (ANOVA: $F_{2,57} = 6.333$, $P = 0.003$). For variety Oakrong, immature development was slowest in fully-ripe fruit and fastest in ripe fruit (ANOVA: $F_{2,57} = 30.679$, $P < 0.0001$) (Figure 16).

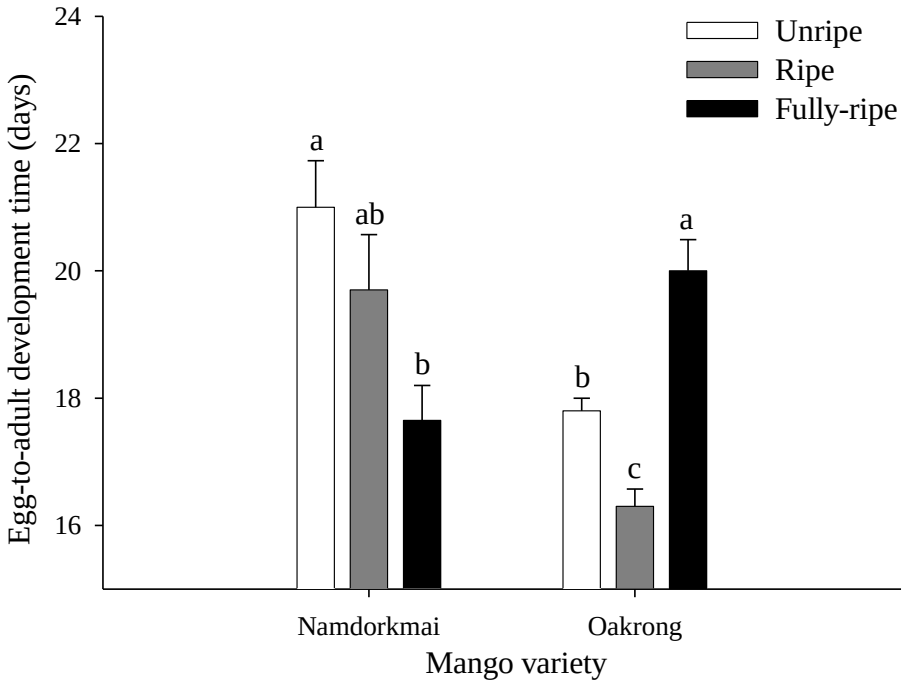

Figure 16 Mean (± SE) development time from egg to adult (days) of *Bactrocera dorsalis* reared from two mango varieties, each at three stages of ripening. Columns capped with different letters within the same variety are statistically different (Tukey test: $P < 0.05$, $n = 20$). Significance is based on log $(x + 1)$-transformed data, non-transformed data are plotted. Each replicate was initiated as a cohort of 20 eggs per fruit variety and stage.

2. Part II: Within-Fruit Oviposition Site Choice and Larval Performance by *Bactrocera dorsalis* on Mango

2.1 Fruit properties

For mango variety Namdorkmai, TSS did not differ significantly among the three fruit parts (i.e., top, middle, bottom) of unripe (ANOVA: $F_{2,42} = 0.389$, $P = 0.680$), ripe (ANOVA: $F_{2,42} = 0.564$, $P = 0.573$) and fully-ripe mangoes (ANOVA: $F_{2,42} = 1.478$, $P = 0.240$). In contrast, there were significant differences in the firmness among the three fruit parts of unripe (ANOVA: $F_{2,30} = 26.656$, $P < 0.0001$) and ripe mangoes (ANOVA: $F_{2,36} = 30.886$, $P < 0.0001$), while the firmness did not differ significantly among three fruit parts of fully-ripe mango (ANOVA: $F_{2,36} = 0.026$, $P = 0.975$) (Table 5).

For mango variety Oakrong, there was no significant difference in TSS among three fruit parts of unripe (ANOVA: $F_{2,57} = 0.987$, $P = 0.379$) and fully-ripe mangoes (ANOVA: $F_{2,57} = 1.387$, $P = 0.258$). TSS differed significantly among the three fruit parts of ripe mango, with the top part having a greater TSS value than the other two sections (ANOVA: $F_{2,57} = 7.799$, $P = 0.001$). The firmness of unripe and ripe mangoes differed significantly across three fruit parts, in both cases with the top part being softer than the other two sections (ANOVA: $F_{2,27} = 22.874$, $P < 0.0001$; $F_{2,42} = 11.440$, $P < 0.0001$), but there was no significant difference in the firmness among three fruit parts of fully-ripe mango (ANOVA: $F_{2,42} = 0.000$, $P = 1.000$) (Table 5).

The percentage TA did not differ significantly among top and bottom parts of ripe stage of mango variety Namdorkmai (t-test: $t = 2.254$, d.f. = 5, $P = 0.074$). However, there was a significant difference in TNC content among top and bottom parts of ripe mango, with TNC being greater in the top (t-test: $t = -5.966$, d.f. = 5, $P = 0.002$). For fully-ripe mango variety Namdorkmai, percentage TA and TNC of both parts did not differ significantly (t-test: $t = 1.222$, d.f. = 5, $P = 0.276$; $t = 0.090$, d.f. = 5, $P = 0.931$) (Table 5).

Table 5 The fruit properties of two mango varieties at three ripening stages. [n = number of replicates. Values (mean ± SE) in the same column of each mango ripening stages followed by a different letter are statistically different based on Tukey-test for TSS and firmness while Paired-samples t-test for TA and TNC at $P < 0.05$. Significance is based on log (x + 1)-transformed data, non-transformed data are presented].

Fruit position	TSS (° Brix)		Firmness (kg/cm^2)		TA (%)	TNC mg D-glucose/ dry weight (g)
	Namdorkmai	Oakrong	Namdorkmai	Oakrong	Namdorkmai	Namdorkmai
Unripe: top	10.63 ± 0.20a	10.73 ± 0.16a	0.96 ± 0.02b	0.86 ± 0.03b	-	-
middle	10.43 ± 0.24a	10.57 ± 0.16a	1.16 ± 0.02a	1.13 ± 0.02a	-	-
bottom	10.37 ± 0.24a	10.41 ± 0.17a	1.16 ± 0.03a	1.09 ± 0.04a	-	-
n	15	20	11	10	-	-
Ripe: top	15.31 ± 0.31a	17.94 ± 0.28a	0.58 ± 0.03c	0.43 ± 0.02b	0.80 ± 0.16a	125.64 ± 11.82a
middle	15.05 ± 0.31a	16.76 ± 0.26b	0.95 ± 0.03a	0.61 ± 0.04a	-	-
bottom	14.85 ± 0.30a	16.55 ± 0.26b	0.79 ± 0.04b	0.62 ± 0.04a	0.99 ± 0.17a	112.54 ± 10.85b
n	15	20	13	15	6	6
Fully-ripe:						
top	19.86 ± 0.96a	19.52 ± 0.33a	0.22 ± 0.01a	0.22 ± 0.00a	0.14 ± 0.03a	127.46 ± 3.16a
middle	18.34 ± 0.92a	19.06 ± 0.36a	0.22 ± 0.01a	0.22 ± 0.00a	-	-
bottom	17.73 ± 0.87a	18.70 ± 0.38a	0.22 ± 0.01a	0.22 ± 0.00a	0.15 ± 0.02a	128.00 ± 3.88a
n	15	20	13	15	6	6

2.2 Experiments

2.2.1 Oviposition preference of female *B. dorsalis* for different fruit parts

a) No-choice experiment

There was no significant difference in the number of oviposition attempts made by female flies to the three fruit parts between different ripening stages of the two mango varieties (ANOVA: $F_{4,342} = 0.395$, $P = 0.812$), so data were pooled across different ripening stages of both mango varieties. Female flies made significantly more oviposition attempts into the top of fruits, followed by the middle of fruit and significantly fewer to the bottom fruit (ANOVA: $F_{2,357} = 35.120$, $P < 0.0001$) (Figure 17).

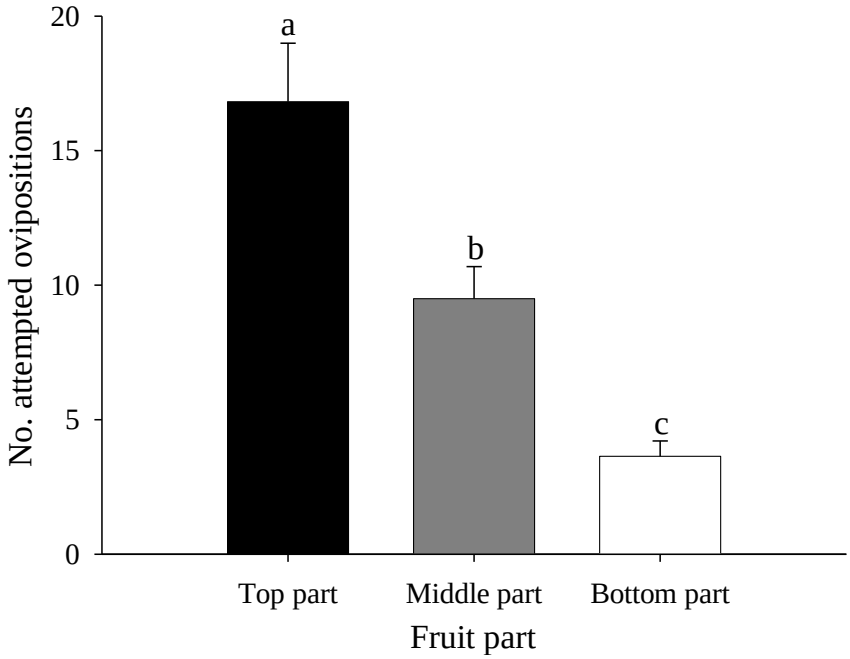

Figure 17 The mean (± SE) number of attempted ovipositions by gravid female *Bactrocera dorsalis* into three fruit parts of two mango varieties in a no-choice situation. The data are pooled from observations made independently on three different ripening stages of both mango varieties.

b) Choice experiment

Under a choice situation, the number of attempted ovipositions into the three fruit parts differed significantly between different ripening stages of both mango varieties (ANOVA: $F_{4,342} = 2.672$, $P = 0.032$), hence results are presented independently for the different ripening stages of each mango variety.

There was a significant difference in the number of oviposition attempts made by female flies to the three fruit parts between different ripening stages of mango variety Namdorkmai (ANOVA: $F_{4,171} = 5.789$, $P < 0.0001$). Female flies made similar, very low numbers of oviposition attempts in all three fruit parts of the unripe mangoes (ANOVA: $F_{2,57} = 0.091$, $P = 0.913$). In ripe mangoes, significantly more oviposition attempts were made into the top part of fruits than either middle or bottom parts of fruits (ANOVA: $F_{2,57} = 28.949$, $P < 0.0001$). For fully-ripe mangoes, female flies made similar numbers of oviposition attempts into the top and middle part of fruits and significantly fewer into the bottom (ANOVA: $F_{2,57} = 10.175$, $P < 0.0001$) (Figure 18).

For mango variety Oakrong, the number of attempted ovipositions into the three fruit parts did not differ significantly across the three different ripening stages (ANOVA: $F_{4, 171} = 2.117$, $P = 0.081$), so data was pooled. Female flies made a similar number of attempted ovipositions into the top and middle part of fruits, but significantly fewer into the bottom part of fruits (ANOVA: $F_{2,177} = 9.201$, $P < 0.0001$) (Figure 19).

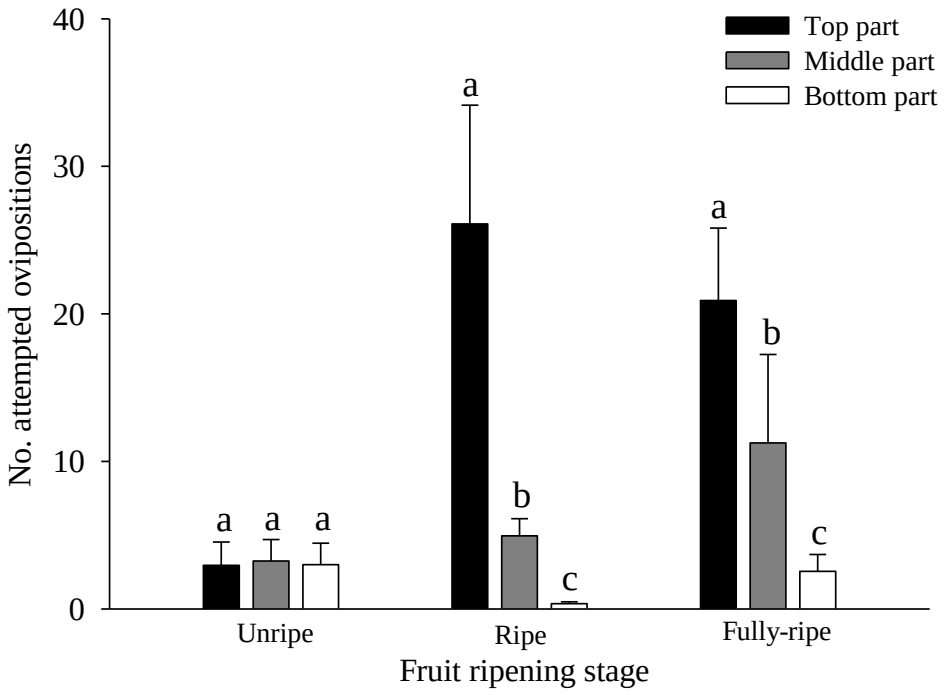

Figure 18 The mean (± SE) number of attempted ovipositions by gravid female *Bactrocera dorsalis* into three fruit parts of three different ripening stages of mango variety Namdorkmai in a choice situation.

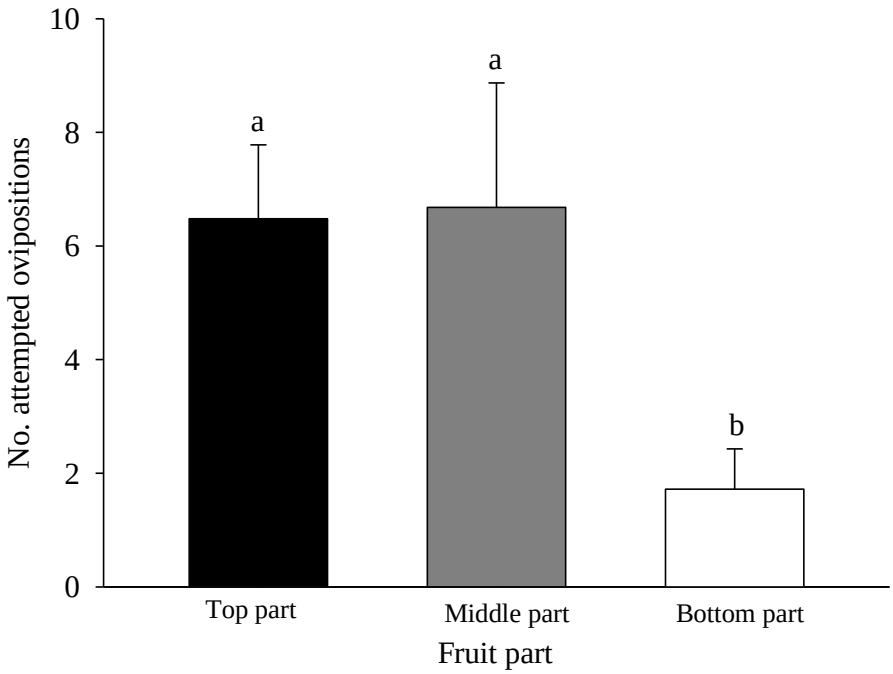

Figure 19 The mean (± SE) number of attempted ovipositions by gravid female *Bactrocera dorsalis* into three parts of mango variety Oakrong in a choice situation. The data are pooled from observations made independently on three different ripening stages of mango variety Oakrong.

2.2.2 Preference and performance of *B. dorsalis* larvae for different fruit parts

a) The preference of larvae for different fruit parts

Two-way ANOVA detected no significant interaction between initial egg insertion point and infestation level of different fruit parts for ripe (ANOVA: $F_{3,72} = 0.772$, $P = 0.513$) or full-ripe mangoes (ANOVA: $F_{2,73} = 1.519$, $P = 0.226$). Nor, when comparing across fruit ripening classes, was there a significant interaction between infestation level of different fruit parts and fruit ripening class when eggs were initially inserted at the top of the fruit (ANOVA: $F_{3,72} = 1.920$, $P = 0.134$), or at the bottom of the fruit (ANOVA: $F_{3,72} = 1.174$, $P = 0.326$).

There was a significant difference in the number of larvae collected from the four fruit parts of ripe mangoes when eggs were inserted in both the top (ANOVA: $F_{3,36} = 15.574$, $P < 0.0001$) and bottom (ANOVA: $F_{3,36} = 6.441$, $P = 0.001$) of fruit. For ripe mangoes with eggs inserted at the top, the number of larvae in fruit part 1 was significantly higher than the number in fruit parts 3 and 4, while the larval number of the fruit part 2 was intermediate between fruit parts 1 and 3. The larval number in the fruit part 4 was significantly fewer than the other parts (Figure 20A). For mangoes with eggs inserted at the bottom, the larval number in fruit parts 1 and 2 were significantly higher than the fruit part 4, while the number of larvae in fruit part 3 was intermediate between these (Figure 20B).

For the fully-ripe mangoes, the larval number differed significantly across the four fruit parts for eggs inserted in the top (ANOVA: $F_{3,36} = 9.036$, $P < 0.0001$) and the bottom (ANOVA: $F_{3,36} = 3.075$, $P = 0.040$) of the fruit. For eggs inserted at the top of fruit, the number of larvae did not differ significantly between fruit parts 1, 2 and 3, but was significantly higher than in fruit part 4 (Figure 21A). For mangoes with eggs inserted at the bottom, the larval number in fruit part 1 was significantly higher than fruit part 4, while the number of larvae in fruit parts 2 and 3 was intermediate between these (Figure 21B).

Observations showed that larvae tended to clump within the pulp of the mango. Clusters of larvae were found in fruit parts 1 and 2 more than fruit parts 3 and 4 for both ripening stages. Most larvae used the wound which was made for egg insertion as the point to exit fruit for pupation. New exit holes made by larvae were found infrequently.

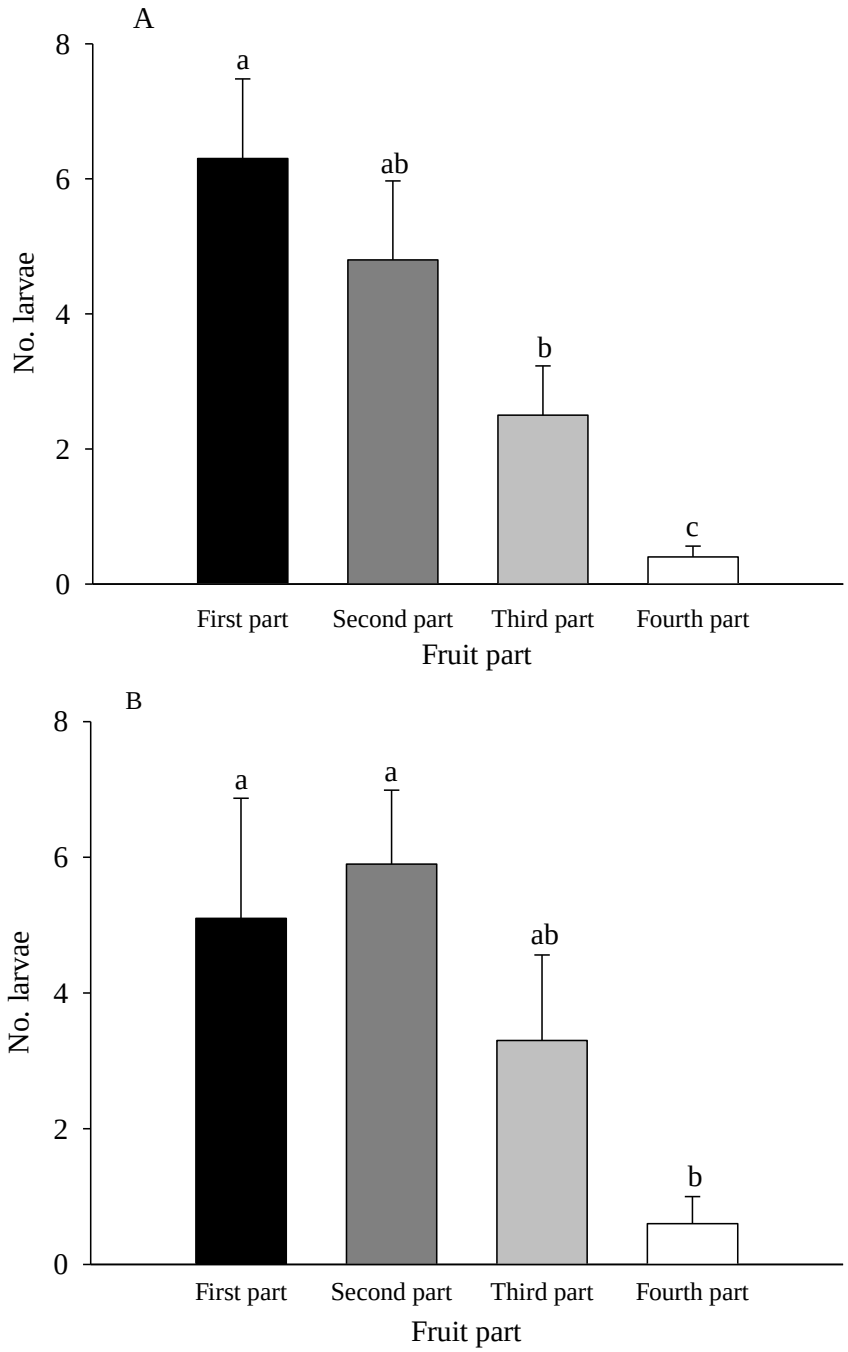

Figure 20 The mean (± SE) number of larvae in four different fruit parts of ripe mango variety Namdorkmai. (A) Eggs were initially placed at the top (stalk) end of the fruit; (B) eggs were initially placed at the bottom end of the fruit. Numbering of parts begins with the position where eggs were placed, so in figure A, "first part" is the top of the fruit and "fourth part" is the bottom on the fruit. In figure B this situation is reversed.

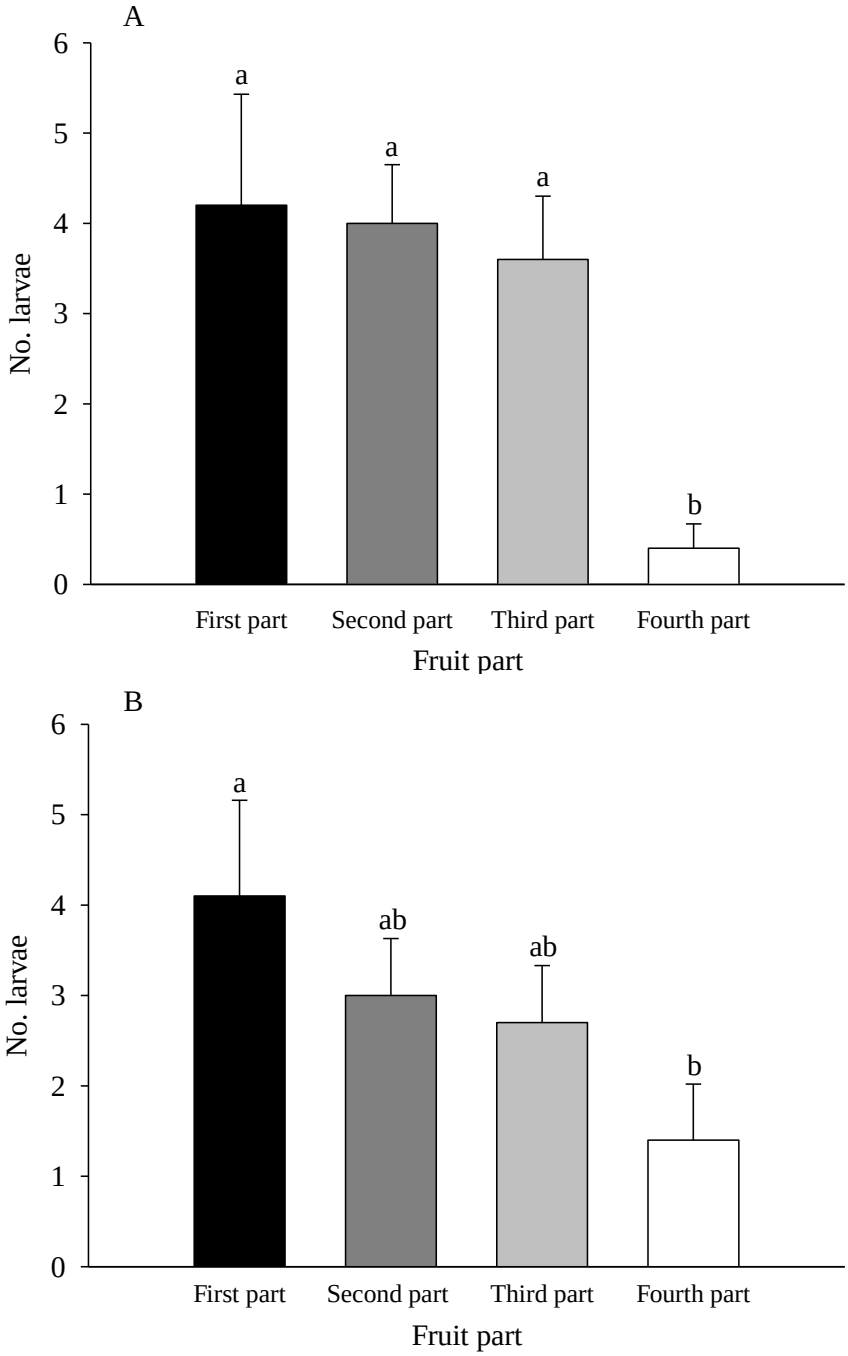

Figure 21 The mean (± SE) number of larvae in different fruit parts of fully-ripe mango variety Namdorkmai. (A) Eggs were initially placed at the top (stalk) end of the fruit; (B) eggs were initially placed at the bottom end of the fruit. Numbering of parts begins with the position where eggs were placed, so in figure A, "first part" is the top of the fruit and "fourth part" is the bottom on the fruit. In figure B this situation is reversed.

b) The performance of *B. dorsalis* larvae in different fruit parts

For ripe mango, between different fruit parts, there were no statistical differences in the average duration of the larval period (t-test: t = 0.550, d.f. = 158.500, P = 0.583), percentage pupal recovery (t-test: t = 1.832, d.f. = 10.241, P = 0.096), pupal weight (t-test: t = 0.816, d.f. = 12.779, P = 0.429), pupal period (t-test: t = 1.082, d.f. = 135, P = 0.281) and wing length of male (t-test: t = -0.259, d.f. = 61, P = 0.796) and female (t-test: t = -0.799, d.f. = 42.343, P = 0.429). There was a significant difference in the percentage of adult emergence between different fruit parts (t-test: t = 2.830, d.f. = 9.189, P = 0.019) (Table 6).

For fully-ripe mango, there were no statistical differences in all parameters of larval performance measurement between different fruit parts. These results were the average duration of the larval period (t-test: t = 1.110, d.f. = 189.409, P = 0.268), percentage of pupal recovery (t-test: t = -0.303, d.f. = 18, P = 0.766), pupal weight (t-test: t = -0.107, d.f. = 18, P = 0.916), pupal period (t-test: t = 0.327, d.f. = 137, P = 0.744), percentage of adult emergence (t-test: t = 0.751, d.f. = 18, P = 0.462) and wing length of male (t-test: t = -1.160, d.f. = 54, P = 0.251) and female (t-test: t = 1.987, d.f. = 81, P = 0.050) (Table 6).

Table 6 The performance of *Bactrocera dorsalis* larvae developed in different fruit parts of each ripening stages of mango variety Namdorkmai. [n = the sample size for numbers >10, or the number of replicated cohorts for where n= 10. Values (mean ± SE) in the same column of each mango ripening stages not followed by the same letter are statistically different based on Independent-samples t-test at $P < 0.05$. Significance is based on log (x + 1)-transformed data, non-transformed data are presented].

Mango ripening stage / fruit part	Larval period (days)	Pupal recovery (%)	Pupal weight (g)	Pupal period (days)	Adult emergence (%)	Wing length (mm)	
						male	female
ripe							
top	11.64 ± 0.33a	56.50 ± 6.67a	0.158 ± 0.017a	10.13 ± 0.16a	73.57 ± 4.48a	6.04 ± 0.06a	6.19 ± 0.03a
n	113	10	113	80	10	34	38
bottom	11.70 ± 0.47a	45.50 ± 12.68a	0.129 ± 0.035a	9.88 ± 0.13a	35.13 ± 11.10b	6.06 ± 0.03a	6.24 ± 0.04a
n	92	10	92	57	10	29	23
Fully-ripe							
top	12.80 ± 0.55a	52.00 ± 5.97a	0.138 ± 0.018a	10.43 ± 0.11a	69.10 ± 7.04a	6.08 ± 0.04a	6.27 ± 0.03a
n	103	10	103	75	10	28	48
bottom	11.83 ± 0.46a	53.00 ± 4.36a	0.140 ± 0.011a	10.41 ± 0.17a	61.26 ± 6.18a	6.13 ± 0.03a	6.19 ± 0.03a
n	103	10	103	64	10	28	35

2.2.3 Behavior of larvae in fruit of different ripening stages

The movement of larvae in the flesh of unripe mango was very restricted. Sixty-five percent of larvae, or evidence of larval feeding, was found at the position where eggs were inserted, with the remaining 35% found in two immediately adjacent sectors. Larval movement was more common in ripe mangoes than unripe mangoes, with larvae distributed across the fruit. Larvae were again found most commonly (71% of individuals) at, or near, the position where eggs were inserted. Larvae moving away from the insertion point tended to move to the top of ripe mangoes. Consistent with the result for ripe mango, larvae tend to move to the top of fully-ripe mango, but with the highest percentage (50%) of larvae found at the egg insertion point. A further 36% of larvae were found in the two grid squares immediately adjacent to the insertion point (Figure 22). General observations showed that larvae moved towards the centre of fruit and were often found near the mango seed. If moving towards the top of fruit, larvae commonly followed the mid line of fruit (i.e., the fruit part with the thickest flesh layer).

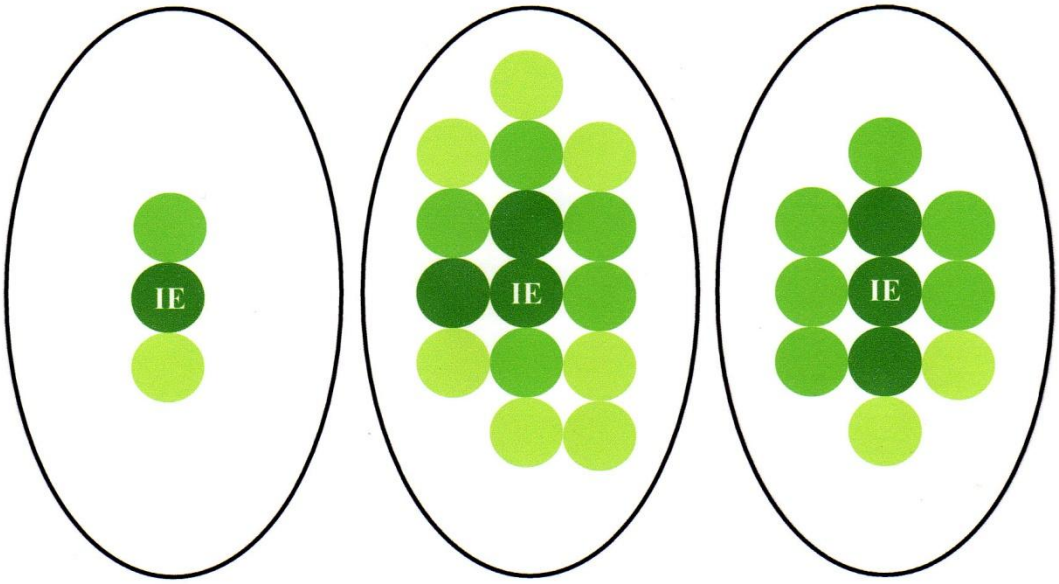

Figure 22 The pattern of *Bactrocera dorsalis* larval movement in different ripening stages of mango. n = 9 replicates per ripening stage. IE = inserted fruit fly eggs position. = larvae or larval feeding hole commonly found (7-9 fruits), = larvae or larval feeding hole often found (4-6 fruits), = larvae or larval hole infrequently found (1-3 fruits).

3. Part III: Color and Volatiles Responses of Female *Bactrocera dorsalis* to Different Mango Ripening Stages

3.1 Effect of color on host location of *B. dorsalis*

Analysis did not detect a significant differential response by female flies to the three different ripening stages of artificial mango (female response to unripe fruit = 23 flies; ripe fruit = 31; fully-ripe = 36; $\chi^2 = 2.867$, d.f. = 2, P = 0.239, n = 90). Many female flies were observed attempting to oviposit in artificial mangoes after arrival at fruit.

3.2 Effect of volatiles on host location of *B. dorsalis*

Female flies showed a significant preference to the volatiles of fully-ripe mango over the volatiles of ripe mango ($\chi^2 = 11.267$, d.f. = 1, P = 0.001, n = 60) and unripe mangoes ($\chi^2 = 48.60$, d.f. = 1, P < 0.0001, n = 60). When female flies were presented with the volatiles of ripe and unripe mangoes, female flies significantly preferred the ripe mango volatiles over the unripe mango volatiles ($\chi^2 = 48.60$, d.f. = 1, P < 0.0001, n = 60). The total number of female flies responding to volatiles of fully-ripe mango was highest, while the total number of female flies responding to volatiles of unripe mango was lowest (Table 7).

Table 7 Response of female *Bactrocera dorsalis* to volatiles of different ripening stages of mango.

Trial	Number of female flies responding to different ripening stages of mango			Total
	Unripe	Ripe	Fully-ripe	
Unripe-Ripe	3	57	-	60
Unripe-Fully-ripe	3	-	57	60
Ripe-Fully-ripe	-	17	43	60
Total	6	74	100	180

DISCUSSION

1. Part I: *Bactrocera dorsalis* Preference for and Performance on Two Mango Varieties at Three Stages of Ripening

1.1 Varietal difference

Independent of ripening stage, total response of flies and rates of larval survival demonstrated a preference for mango variety Oakrong over Namdorkmai. These differences were relatively small and may have been due to a generally lower firmness and higher TSS in Oakrong. In contrast to varietal differences, the most obvious factor influencing adult response and larval performance in these trials was stage of fruit ripening.

1.2 Adult oviposition preference and fruit ripening

The consensus results indicate strongly that female flies show a higher response to ripe and fully-ripe mangoes than to unripe mango. For only two data sets (total duration of visits and number of oviposition attempts in choice trials of variety Oakrong), there was no difference in the response of flies to unripe vs. ripe mangoes. These results may be partially explained by fruit characteristics. The fruit ripening process involves the conversion of acids and starch to free sugars, the development of pectinases which soften and ultimately break down the cell walls, and frequently the development of various pigments, usually anthocyanins, and the loss of chlorophyll (Bidwell, 1979; Yashoda *et al.*, 2007). Thus the ripe and fully-ripe fruits, in comparison to unripe fruit, have a softer exopericarp and higher TSS as well as exhibiting different skin color and odors (authors'pers. obs.).

The firmness of the two mango varieties is likely to play a dominant role in oviposition behavior of female flies. Across all trials, only 5.6% of female *B. dorsalis* successfully oviposited into mangoes of three ripening stages and firmness

was clearly a limiting factor. Female tephritids have been shown on several occasions to have an oviposition preference for ripe fruit or fruit with softer exopericarp, over unripe fruit or fruit with harder exopericarp (Seo *et al*., 1982; Messina and Jones, 1990; Balagawi *et al*., 2005). Resin ducts in the exopericarp of unripe fruit may also be an obstacle for ovipositing female flies. Observations showed that when flies made an oviposition wound in the exopericarp of unripe mango, the resin flowed out immediately and pushed the eggs outside the fruit. In mature mango fruit, resin ducts form a network throughout the fruit both in the exocarp and the inner region of the mesocarp, including the fruit base, whereas the resin itself is released just before ripening (Joel, 1981). Mango resin contains phenol (Keil *et al*., 1946), which in crab apple has been reported as being toxic to larvae of the tephritid *R. pomonella* (Pree, 1977), and this may be a cause of death to eggs or larvae of *B. dorsalis*. Joel (1978) and Herrera (1982) suggested that the Anacardiaceae, by producing secondary compounds such as resins, phenolics, alkaloids, saponins, and volatile oils, have a herbivore defense mechanism which means few insects can attack the fruit of this family. Moreover, Joel (1978) also found that a mango variety with poorly developed duct systems was attacked by *C. capitata*. A similar defensive mechanism has been reported in green papaya, where latex production is thought to deter fruit fly attack (Seo *et al*., 1983).

1.3 Influence of egg load

The high responses to unripe and ripe mangoes by high egg load female flies of *B. dorsalis* (Table 4), is consistent with other tephritid studies. Fitt (1986) presented that the increased in the number of mature eggs carried by female flies of *B. tryoni* influence to acceptability of female flies to unacceptable host. Like for the result of the study in the same fruit fly species, Prokopy *et al*. (1999) indicated that high egg load female flies tend to initiate boring into host fruit rather than low egg load females. Brevault and Quilici (1999) presented that the percentage of females that visited the sphere increased significantly with egg load. Then, under no-choice situation, *B. dorsalis* female flies carried high number of mature eggs in ovaries had more acceptability to less preferred host (unripe mango) than low egg load female

flies distinctly and influence of egg load to female flies responses also found in ripe mango. Interesting, there was no the different responses between high and low egg load female flies for fully-ripe mango. This result may be assumed that under the most preferred host (fully-ripe mango) of no-choice situation, egg load did not influence to the responses of *B. dorsalis* female flies.

In this paper, I report only on the fruit characteristics of firmness and TSS as variables possibly influencing adult preference. The color and odors of fruit, twig, and foliage of host plant are other important cues attracting gravid female fruit flies (Aluja and Prokopy, 1993; Prokopy and Vargas, 1996; Drew *et al*., 2003; Brevault and Quilici, 2007b). Ripe and fully-ripe mangoes may have more attractive characteristics to female *B. dorsalis* than unripe mangoes, for example yellow skin color (Prokopy and Owens, 1983; Vargas *et al*., 1991; Cornelius *et al*., 1999a and 1999b) and stronger volatiles (Jang and light, 1991; Prokopy and Vargas, 1996; Lalel *et al*., 2003). In subsequent work, I will further explore the role of these attributes in our system.

1.4 Larval performance and fruit ripening

Although many host plants can sustain the full development of different tephritid species, host quality plays a major role in differential larval survival (Krainacker *et al*., 1987; Hing, 1991). Larval survival to pupation was less than 20% in unripe mango, indicating that unripe mango is a poor larval host. This result is consistent with those reported by Hennessey and Schnell (2001) for *Anastrepha suspensa* (Loew) and may be related to high acidity and low free sugars in unripe fruit (Bidwell, 1979; Medlicott and Thompson, 1985; Table 3), as well as phenols in the resin ducts. In contrast, ripe and fully-ripe fruits were more suitable for larval development, with higher larval survival and shorter larval development times. The oviposition preference of *B. dorsalis* females for ripe and fully-ripe mangoes, the most suitable hosts for offspring survival, is consistent with other tephritid studies. *Ceratitis capitata* females prefer to oviposit into ripe over unripe papaya fruit and their larvae develop better in ripe papaya (Joachim-Bravo *et al*., 2001), whereas *A.*

obliqua exhibited a preference for an artificial oviposition substrate composed of higher quality nutrients (for offspring performance) (Fontellas-Brandalha and Zucoloto, 2004). In contrast, female flies of *A. ludens* lay larger egg clutches into unripe than ripe fruit, even though larval survival is lower in unripe fruit (Diaz-Fleischer and Aluja, 2003a). The reasons for this counter-intuitive behavior are speculative, but may be based on larger larval clutches modifying an unsuitable host fruit environment (e.g., by increased metabolic heat, increasing bacterial decay), or as an optimizing oviposition strategy by time-limited females (Diaz-Fleischer and Aluja, 2003c).

1.5 Low host suitability of both mango varieties and implications for trade

In contrast to the high infestation rate of fruit flies in the two mango varieties in the fields (as reported by farmers; pers. obs.), the experiments presented here show very low oviposition rates and relatively poor offspring survival in either mango variety. What might be the reason for the discrepancy? Perhaps laboratory flies are less able to oviposit into fruit than wild flies. However, our post-hoc experiments using wild flies did not support this interpretation (results not shown). Rather, many tephritid species prefer to lay their eggs into soft spots or existing wounds in fruit (Pritchard, 1969; Papaj *et al*., 1989; Papaj and Alonso-Pimentel, 1997). In the laboratory, for both mango varieties, I readily observed flies laying eggs into natural or artificial fruit wounds, particularly at the base of the pedicel. Thus, in the field ovipositing female flies may be making use of natural bruises, wounds, or cracks in the fruit, the result of feeding or oviposition by other insects, wind damage, variation in available water, farming practices (harvesting, pruning, bagging), plant diseases, or fruit over-ripening. Similar attributes have been attributed to altering the field susceptibility of fruit in other fruit fly/cropping systems (Greany *et al*., 1983; Greany *et al*., 1985; Liquido *et al*., 1995; Aluja *et al*., 2004) and should be tested for our system in field studies. Not only oviposition rate, but also subsequent larval survival was poor in our two mango varieties and this may be partially due to the secondary compounds known to occur in unripe and ripe fruit of the Anacardiaceae (Joel, 1978; Herrera, 1982). However, for high-quality fruit, particularly if picked

green, I suspect infestation rates will be very low. If these findings are supported by field infestation data, then the results could be incorporated into a system's approach for market access.

2. Part II: Within-Fruit Oviposition Site Choice and Larval Performance by *Bactrocera dorsalis* on Mango

2.1 Oviposition preference of female *B. dorsalis* for different fruit parts

The consensus results indicated strongly that female *B. dorsalis* prefer to oviposit in the top part over the bottom part of ripe and fully-ripe mangoes even though this preference does not exist in unripe fruit of mango variety Namdorkmai in a choice situation (Figure 18). The oviposition preference of female flies for the top part of mango may be partially relate with the physiological changes of mango ripening. The top part of mango fruit ripens earlier than the middle and the bottom parts, and thus have a softer exopericarp and higher TSS, in comparison, to middle and bottom parts (Table 5). Firmness is considered to be a limiting factor for oviposition of female fruit flies (Seo *et al*., 1982; Messina and Jones, 1990; Balagawi *et al*., 2005) and is possibly influencing adult preference.

2.2 The preference and performance of *B. dorsalis* larvae for different fruit parts and their behaviors in fruit of different ripening stages

For nearly all data, there was no evidence of larval preference or performance being influenced by different fruit parts, within or across fruit ripening stages. Two-way ANOVA failed to detect any interaction between larval movement patterns and either egg insertion point or fruit ripening stage, while visual presentation of results (Figures 20 and 21) show a generally common pattern of larvae being in highest density at or near the egg insertion point, becoming less common at greater distances away from that point: normal point dispersal would account for this dispersion pattern. Nearly all measures of larval performance were not significantly

different between larvae developing in the top or bottom of ripe and fully-ripe mangoes, again reinforcing the lack of obvious within-fruit effects.

One very dramatic difference did occur, however, for larvae developing in ripening fruit. Adult emergence from pupae derived from larvae which developed in the bottom half of ripe fruit was only half of that for corresponding pupae from the top of ripe fruit, or for pupae developed from the top or bottom of full-ripe fruit. If host quality influenced this result then it did not show up in other parameters of larval quality, but would be consistent with other research that has demonstrated that the quality of nutrients that larvae have fed on influence emergence of the adult fruit fly (Economopoulos *et al*., 1990; Fernandes-da-Silva and Zucoloto 1993; Chang *et al*., 2000). Significantly lower TNC levels and higher acidity levels in the bottom half of ripe mango (Table 5) may be causal, or at least correlated, with this reduced adult emergence rate. Larval movement was found more in ripe mango than fully-ripe mango, with little movement found in unripe mango (Figure 22). As previously argued, this may be explained by fruit properties of the different ripening stages of mango. Even though the TSS of three fruit parts did not differ significantly, the top and middle parts were slightly sweeter than the bottom. The TSS of the top of ripe mango gradually increases as the fruit continues to ripen, while fewer changes occur in the TSS of fully-ripe mango. Larvae may thus be more likely to track changing TSS in ripe than fully-ripe mango. Most larvae, for all three ripening stage of mango, were found in large clusters at or near where eggs were first inserted. It is possible that this position had a higher bacterial load than other fruit parts because of wound associated with inserting eggs and larvae thus clumped at this position because of the positive link between fruit fly larval feeding and bacteria (Diaz-Fleischer and Aluja, 2003a and 2003b). Most larvae were found away from the fruit exopericarp, often near the mango seed. This result indicates that larvae prefer to be located deeper within the fruit flesh. This behavior may be a parasitoid avoidance mechanism, or may result from difference of fruit properties (i.e., TSS and flesh fruit toughness) at different flesh thickness levels.

While some larval movement occurs, it is not consistent with an expectation that larvae should relocate themselves to the ripest (i.e., top most) part of the fruit. Resolution of the first aim is less clear. Adults prefer to oviposit in the top of fruit, but for one parameter only (from seven parameters of larval performance measured; Table 6) was the top of the fruit better for offspring. That one parameter, adult emergence from pupae, was quite dramatically difference, however, with a 50% reduction in adult emergence from pupae derived from the lower half of fruit. For this performance parameter, I could thus say there is positive relationship between adult oviposition choice and offspring performance at the within-fruit level. Adult oviposition preference may, however, have nothing to do with offspring performance. Fruit flies are well documented as preferring hosts with softer skins and/or flesh (Seo *et al.*, 1982; Messina and Jones 1990; Messina and Jones 1991; Balagawi *et al.*, 2005; Rattanapun *et al.*, in press). Preference for the top of fruit as an oviposition site may thus be a direct mechanical, or longer-term evolved response, to the fact that a host fruit is, or likely to be, softer at the top. I can only conclude therefore, for the system studied in part II, that I have neither supported nor rejected a positive adult preference/offspring performance relationship.

3. Part III: Color and Volatiles Responses of Female *Bactrocera dorsalis* to Different Mango Ripening Stages

When presented with different host fruit information, female flies exhibited different patterns of response. Female flies did not significantly respond to the different colors of the different ripening stages of artificial mango. This result is consistent with those reported by Vargas *et al*. (1991) who found color to be the least specific cue in eliciting positive alighting responses of *B. dorsalis* flies. Color response may also be strongly influenced by the effect of light reflectance (Drew *et al*., 2003) and color of the background (Owens and Prokopy, 1986; Mayer *et al*., 2000; Pinero *et al*., 2006). However, total numbers of female flies responding to fully-ripe artificial mango were greater the number of flies responding to ripe (14% more) and unripe artificial mangoes (36% more). Such differences, especially between unripe and fully-ripe artificial fruit, suggest that there may well have been a real

biological effect (i.e., preferred orientation towards riper fruit) which was not detected by the chi-square analysis used. Thus many female flies tried to oviposit into artificial mango demonstrates that color and shape of host fruit alone can stimulate oviposition behavior of female flies.

In contrast to the results of previous experiments (Part I), where female flies do not differently prefer between ripe and fully-ripe mango when able to use both olfactory and visual cues, the result of this chapter show that when female flies are exposed only to host fruit volatiles almost all females prefer fully-ripe mango. This result is consistent with many experiments that show that female fruit flies are attracted to the volatiles of ripe fruit more than unripe fruit (Bierbaum and Bush, 1990; Flath, 1990; Jang and Light, 1991). Thus, the results suggest that female flies use host fruit volatiles for host quality determination.

Combined results of this and previous chapters demonstrate that female oviposition decisions rely on visual, olfactory and tactile cues if the female can see and touch the fruit surface. Generally, female fruit flies use multiple information cues from host fruit for oviposition decisions, including the presence or absence of wounds or soft sites on the fruit surface (Pritchard, 1969; Papaj *et al*., 1989; Papaj and Alonso-Pimentel, 1997), fruit firmness (Diaz-Fleischer and Aluja 2003a; Balagawi *et al*., 2005), color (Prokopy and Owens, 1983; Vargas *et al*., 1991) and volatiles of host fruit (Jang and light, 1991; Prokopy and Vargas, 1996), including occurrence of larvae (Fitt, 1984) and other female flies (Prokopy and Duan, 1998; Rull *et al*., 2003). With this complex information, female flies vary the oviposition choices they make.

CONCLUSION

Bactrocera dorsalis, a polyphagous fruit fly, has complex host response patterns. This may be related to its large host range and is influenced by the physiological status of individual flies. This thesis investigated in depth two factors which may influence host selection and utilisation in *B. dorsalis*, differences between host fruit (at the varietal level within *M. indica*) and ripening stages of two mango varieties. The specific aims of the thesis were given in Chapter I and I address the outcomes of these aims below. In the second half of this conclusion I present other important ideas and concepts which resulted from the study.

1. Answering the Objectives

1.1 To investigate comparative host fruit preference of *B. dorsalis* between two mango varieties.

Two varieties of one host fruit (i.e., mango) were used in various trials, however, at this varietal level fruit type seemed to have only minor influence on oviposition choice or larval utilisation. This may partially explained by fruit properties (e.g., TSS and firmness) that varied only slightly between the two mango varieties.

1.2 To investigate the physiological changes during mango ripening on adult oviposition behavior and larval feeding of *B. dorsalis*.

Stage of fruit ripening seemed to be the most obvious factors influencing adult response and larval performance in this study. The physical characteristics [yellow color, softness and resin (not measured)] and chemical characteristic (volatiles) of ripe and fully-ripe fruits appear more attractive to female *B. dorsalis* for oviposition than unripe fruit. Female flies used color and host fruit volatiles for host fruit searching and assessment of host quality. Additionally, the results of this study

indicated that host fruit color least influenced the assessment of host quality by female flies, whereas host fruit volatiles played an important role in the dertermination of host quality. If female flies could touch the fruit surface, oviposition decisions also correlated with changes in fruit firmness. Fruit firmness, which gradually declines as the fruit continues to ripen, appears to be the limiting factor of oviposition, with few successful ovipositions recorded in all studies, and very few in unripe (i.e., firmest) fruit. Thus, after arrival on the host fruit, female oviposition decisions depend on combination of visual, olfactory and tactile cues.

Ripe and fully-ripe fruits are not only more suitable for oviposition of female flies, but also for larval development than unripe fruit. This may come from decreases in defense mechanism (resin) and increases in nutritional quality of fruit pulp. Nevertheless, unripe fruit can sustain complete development of larvae, albeit at low levels.

1.3 To identify fruit physiological traits associated with ripening which influence female behavior and host use pattern

Generally, color and volatiles of ripe host fruit play important roles in herbivorous insect responses. For *B. dorsalis* and some other species of tephritid fruit fly, the oviposition preference also relies on fruit firmness. To minimise aculeus wear, female tephritid flies are thought to prefer to oviposit in fruit wounds or softer exopericarp of ripe and fully-ripe fruits over harder exopericarp of unripe fruit (Pritchard, 1969; Fletcher, 1987; Papaj *et al*., 1989; Allwood, 1997; Papaj and Alonso-Pimentel, 1997; Shelly, 1999). In my experiments, female flies preferred to oviposit at the top of fruit rather than the bottom. The top of mango fruit ripens earlier than the middle and the bottom parts, and thus has a softer exopericarp and higher TSS in comparison to other parts of the fruit. However, under the influence of egg load pressure, high egg-load female flies made more attempts to oviposit into unripe fruit than low egg-load females. Moreover, some gravid female *B. dorsalis* did successfully oviposit into unripe fruit. This behavior is uncommon in dacine fruit flies.

For larval preference and performance, there was no evidence of larval feeding site preference or performance being influenced by fruit part, within or across fruit ripening stages. Larvae move deeply into the fruit, away from the exopericarp, possible for parasitoid avoidance or finding more suitable microenvironment. More larval movement in ripe fruit (compared to fully ripe fruit) is probably indicative of larger variation in host nutritional quality during fruit ripening. The results are ambiguous with respect to supporting, or rejecting, a positive adult preference/offspring performance relationship at within-fruit level for *B. dorsalis*.

2 Fruit Ripening and the "Adult Preference/Larval Performance" Model

Host acceptance of female flies relies on many factors in the field. The oviposition preference-larval performance hypothesis states that, due to the action of natural selection, female flies should pick oviposition hosts which are most suitable for offspring performance (Fitt, 1981; Messina *et al*., 1991; Joachim-Bravo *et al*., 2001; Fontellas-Brandalha and Zucoloto, 2004). In my studies, the preference of female *B. dorsalis* to oviposit on ripe and fully-ripe fruits, which best supported larval development and survival, supports this theory. A higher acceptance of unripe fruit by female flies with high egg-load in comparison to low egg-load females, however, combined with an oviposition site preference for fruit surface wounds, means that female have some flexibility in their oviposition strategies. Thus, it is difficult to assume that oviposition preference of female flies relates solely to the performance of their larvae. Other factors acting directly on the parent female, such as the physical ability of her ovipositor to penetrate fruit and internal physiological influences such as egg load, will also impact on her host selection and utilisation decisions. In nature female flies may thus be forced to oviposit into unsuitable hosts if they are subject to different external and internal constraints. Larvae may be negatively affected by this flexibility of female oviposition behavior, but larvae also clearly have the ability to maximise the nutritional value gained from the hosts they are placed within, which may allow for their survival in poorer quality hosts.

There is the conflict between the result of this thesis and high fruit fly infestation rate in the fields as reported by farmers. Under laboratory conditions, even though some female flies successfully penetrated into unripe fruit, almost all female flies were unsuccessful into ovipositing into any of the ripening stages of either mango variety. Moreover, there is poor offspring survival in both mango varieties, even when successful oviposition occurs. Thus, in the nature, fruit fly attack may be supported by other factors such as wounds or cracks in the fruit, created by feeding or oviposition holes made by other insects (including conspecifics), wind damage, variation in available water, farming practices, plant diseases, or fruit over-ripening. Thus the result of this thesis may be the beginning of a model for understanding the relationship between *B. dorsalis* utilisation of mango, however, it is better if similar experiments are also carried out in the field for developing deeper understanding of host utilisation by the fly in cropping systems.

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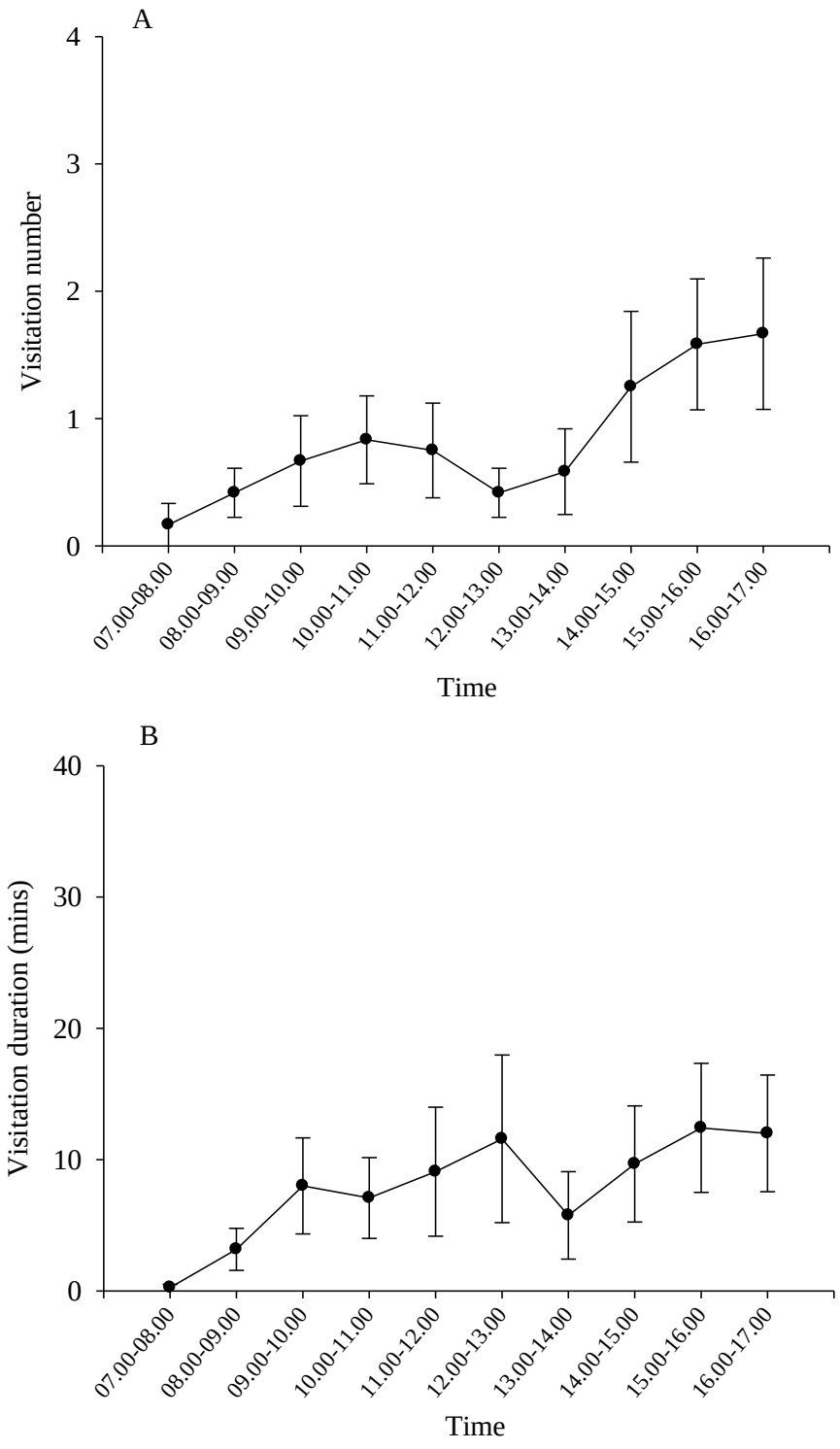
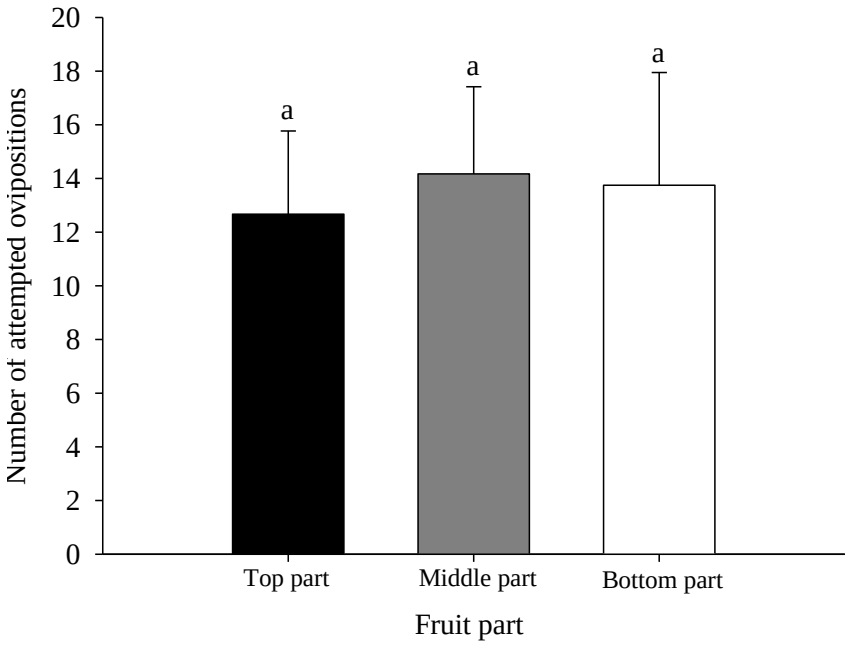
APPENDICES

APPENDIX A

Oviposition Preference of Wild Flies *Bactrocera dorsalis*
for Two Mango Varieties at Three Stages of Ripening



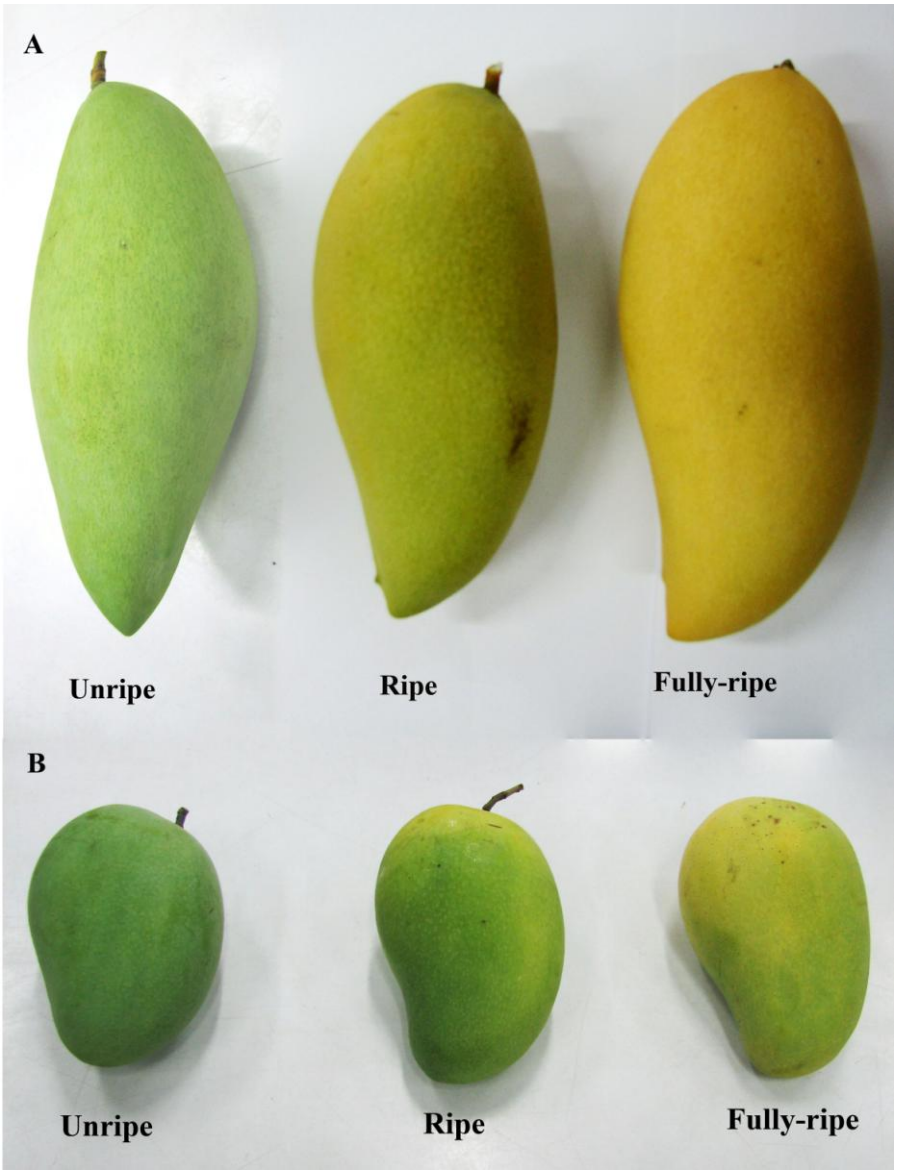
Appendix Figure A1 The mean (± SE) hourly visitation (A) number and (B) duration (minutes) of wild gravid female *Bactrocera dorsalis* to fully-ripe mango variety Namdorkmai in a no-choice situation.



Appendix Figure A2 The mean (± SE) number of attempted ovipositions by wild gravid female *Bactrocera dorsalis* into three fruit parts of fully-ripe mango variety Namdorkmai in a no-choice situation. Columns capped with the same letter are not statistically different ($P \geq 0.05$).

APPENDIX B

Two Mango Varieties and Fruit Property Analysis



Appendix Figure B1 Three ripening stages of two mango varieties. A = Namdorkmai, B = Oakrong.

Percentage of Titratable Acidity (TA)

Titratable acidity (TA) of 2 ml of mango juice was determined by titration against 0.2 N NaOH with 1% phenolphthalein indicator (Hulme, 1971). The percentage of TA was calculated using the formula as follow:

$$\% \text{ TA} = \frac{(\text{ml NaOH})\,(\text{N NaOH})\,(\text{meq.wt. of citric acid})}{\text{ml of sample}} \times 100$$

ml NaOH = ml of NaOH used for titration

N NaOH = normality of NaOH

milliequivalent weight (meq.wt.) of citric acid = 0.0604

ml of sample = ml of mango juice used for titration

Total Non-Structural Carbohydrates (TNC)

Total non-structural carbohydrates (TNC) analysis followed to acid extraction of Smith *et al*. (1964) and Nelson's reducing sugar procedure (Hodge and Hofreiter, 1962).

1. Acid extraction

Fresh ripe and fully-ripe mangoes were dried in a hot air oven at 60˚C for two weeks and then grind for fine-grained. The 0.05 g ground samples were extracted with 40 ml of 0.2 N sulfuric acid in a hot air oven at 100 °C for one hour. All samples were then kept at room temperature for 30 min. The liquid fractions were filtered through Whatman No. 42 filter paper and nutralised (pH = 7.0) with 0.5 N sodium hydroxide. The sample solutions were consequently diluted with distilled water until the desired volume of 50 ml. After that, 1 ml of all samples was obtained for TNC analysis.

2. Nelson’s reducing sugar procedure

One ml of the sample solution was reacted with 1 ml of alkalic copper reagent in a 20 ml test tube. The procedure was also carried out on 1 ml distilled water as a blank and 1 ml glucose solution at various concentrations from 0.05 to 0.3 mg D glucose as a standard. Samples were held in a water bath for 5 min and then kept at room temperature. After that, all samples were reacted with 1 ml Nelson’s reagent and diluted with 9.5 ml of distilled water. Finally, all of these fractions were measured with a spectrophotometer (Genesys 10 series, Minolta, Japan) using a blank fraction for standardization. The readings of optical density value (O.D.) were taken at 540 mm wavelength. The carbohydrate contents were determined using a standard curve of O.D. against mg D glucose for a comparison. Therefore, the TNC concentrations of the tissue samples could be presented at mg D glucose equivalent per dry weight (g).

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