COMPARATIVE ECOLOGY OF BACTROCERA CUCUMIS (FRENCH) AND BACTROCERA TRYONI (FROGGATT) (DIPTERA: TEPHRITIDAE) - UNDERSTANDING THE LIFE HISTORY CONSEQUENCES OF HOST SELECTION AND OVIPOSITION BEHAVIOUR

B. cucumis

B. tryoni

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B. Sc. (BIOLOGY)

M. Phil. Qualifying (ENVIRONMENTAL STUDIES)

Submitted in fulfillment of the requirements of the degree of Doctor of Philosophy

Faculty of Environmental Sciences

Griffith University

2006
ABSTRACT

The host use patterns of tephritids (fruit flies) range from those that are highly specific (monophagous, oligophagous) to those that use a wide range of hosts from different plant families (polyphagous). Knowledge of the mechanisms responsible for such host use patterns is critical in understanding the insect-plant relationship and developing successful population management strategies. Several studies have revealed that the behavioural and environmental factors play a significant role in host use. A key theory thought to explain host use patterns of phytophagous insects has been optimality theory (preference-performance hypothesis), however, this has seldom been investigated in fruit flies.

In this thesis I compared the host use pattern of the specialist (oligophagous) cucumber fruit fly, *Bactrocera cucumis* (French), and the generalist (polyphagous) Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae: Dacinae), both serious agricultural pests in Queensland, Australia. I primarily focussed on investigating the role of the preference-performance hypothesis in explaining the host use pattern of these two species at different plant taxonomic levels. I also examined the life history consequences of host use patterns by investigating the demographics of these two dacines on different host plants.

The preference-performance hypothesis postulates that the host preference executed by an insect should be positively correlated to its offspring performance. While there were some correlations between preference and performance parameters for both *B. cucumis* and *B. tryoni*, these were dependent on the parameter used and were more relevant in explaining host use patterns in *B. cucumis* than *B. tryoni*. Both species exhibited significant host discrimination among the different hosts presented to them. More significantly, they preferentially used certain host plants even when hosts of purportedly equivalent status were presented to them simultaneously. The efficiency with which they used their hosts differed even when offered different varieties of a host species from their primary host family. These patterns, observed in both these dacine species, indicated that host use is more plausibly explained by behavioural and physiological factors associated with host use.
Abstract

Key factors affecting host acceptance behaviour and subsequent host use of dacine fruit flies include pre-alighting factors (e.g., host plant structure, fruit colour, shape and size) and post-alighting factors (e.g., pericarp toughness, fruit volatiles and chemical composition of fruit). I investigated the role of fruit size and pericarp toughness in explaining host use patterns. Pericarp toughness appeared to strongly affect host acceptance and subsequent host use in both dacine species. Although some fruit species were readily accepted for oviposition by receiving a high proportion of oviposition attempts from both fly species, very few of these oviposition attempts resulted in pericarp penetration (oviposition event). This behaviour was primarily attributed to the differences in pericarp toughness; fruits with a tougher pericarp provided greater resistance to ovipositor penetration, thus resulting in less use than those with a softer pericarp.

In addition to the behavioural aspects of fruit fly-host plant relationships, life history parameters of tephritid species play a significant role in host use. Investigations of the demography of these species on different hosts revealed that the polyphagous B. tryoni has higher fecundity and net reproductive rate, and shorter generation time while the oligophagous B. cucumis has a lower fecundity and net reproductive rate with a longer generation time. While the demographic patterns of the B. cucumis appeared to conform to preference-performance hypothesis, B. tryoni showed some interesting departures from the predictions of the preference-performance hypothesis. For B. tryoni, it was evident that some hosts that may yield lower survival in terms of larval survival (e.g., plum) may still be demographically suitable because of the enhanced reproductive performance of adults emerging from these fruits. This highlights the significance of the quality of adult feeding resource in the demography of this species.

Organizing demographic data and analysing them using population projection models also enabled me to identify critical life stages that influence the demography of these two species across different host fruits. This study found that for both the specialist B. cucumis and the generalist B. tryoni, population growth rate is highly sensitive at the adult reproductive stage, indicating that manipulating probability of survival at this life stage would be critical to manage the population of these pest species. This may
explain the success of protein bait sprays as a technique to manage these pest species. Predators or pathogens that target the adult reproductive stage may also provide successful biological control of these pest fruit fly populations. In addition to survival of reproductive individuals, pupal survival was also important to the demography of these species, suggesting that biological control targeting pupal stage may also yield population suppression across different fruit production systems.

In summary, my studies showed that, while the preference-performance hypothesis may be a useful heuristic tool in explaining comparative host use patterns in the Dacinae, it may be more valuable in understanding primary adaptations of different species that enable them to use different host plants. This understanding combined with the life-history consequences of host use would not only shed light on their ecology, but also prove valuable in designing suitable management strategies for pest dacines.
ACKNOWLEDGEMENTS

My sincere thanks go to the many people who assisted me throughout the course of this study. In particular, my supervisors, Professor Richard Drew, Dr. Vijay Shanmugam and Dr. S. Raghu deserve special mention for being an integral part of my Ph.D. project by providing the direction, encouragement and support. I thank my principal supervisor, Professor Richard Drew for being supportive for my research and always making time available whenever I needed to see him. I am also grateful for his time in reading through the thesis. I thank my associate supervisor, Dr. Vijay Shanmugam for always being available for any discussion regarding this study.

Special thanks go to my external associate supervisor Dr. S. Raghu. Although an associate supervisor on paper, he has practically been the engineer and the mentor behind my research project. I thank him for the intellectual discussions on subjects involving insect-plant interaction as well as for introducing me to the general ecology literature. His attentive and constructive criticism on each thesis chapter has been invaluable. I thank Dr. Raghu for being a mentor, colleague as well as a close friend during my Ph.D. journey and cannot adequately express my gratitude in words.

I thank Dr. Anthony Clarke (Queensland University of Technology) for his support and help in securing my Ph.D. scholarship and also for providing direction in the initial phase of this research project. I thank Assoc. Prof. Gimme Walter (University of Queensland) for inviting me to be part of his stimulating student discussion group. These meetings have broadened my knowledge on ecological research and science in general.

Staffs of the International Centre for Management of Pest Fruit Flies are also acknowledged for helping and facilitating my research. I thank Meredith Romig for her help in facilitating the smooth flow of my research. Lynita Howe, Peter Halcoop, Cameron Drew, Travis Romig, Sarah Romig are also acknowledged here for providing some help and a relaxed working environment. Other university staffs that have been helpful during my candidacy include Bruce Mudway, David Henstock and Donald Dennis. I thank each of them for all their help.
I also acknowledge the help of Dr Rod Jordan and Dr Paul Exley from the Queensland Department of Primary Industries for helping and allowing me to use their fruit penetrometer for quantifying the pericarp toughness of fruits used in this study.

The Australian Centre for International Agricultural Research (ACIAR) funded both the research reported herein and my fellowship. I sincerely thank ACIAR for its generosity. I also thank Griffith University for providing research funds towards this Ph.D. project.

Without the approval of my employer, it would have been impossible for me to take up the ACIAR scholarship. I therefore thank my employer, Papua New Guinea National Agricultural Research Institute (NARI), for its wisdom in releasing me to undertake this Ph.D. project.

Most importantly, I dedicate this thesis to my mother (who passed away during the course of my candidacy) and my first daughter (who was born during the Ph.D. candidacy period). A special lady who has always been present to cheer me up when I encountered difficulties or got frustrated with my research has been my wife, Monica Balagawi. I dearly thank her for her patience and support throughout the course of this study.
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STATEMENT OF ORIGINALITY

This work has not been previously submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where acknowledged in the thesis.

..........................

Solomon Balagawi
1.1 GENERAL INTRODUCTION

The family Tephritidae (true fruit flies) is one of the largest families of Diptera and is highly diverse with more than 4200 known species in 471 genera (Norrbom et al. 1998). Tephritids (hereafter referred to as fruit flies) are distributed throughout the tropical, subtropical and temperate regions of the world (Christenson and Foote 1960), but the greatest diversity of species occurs in the tropical regions (Wang 1996, Norrbom et al. 1998). Habitats they occupy range from rainforest through to open grassland and suburbia (Michaux and White 1999). The vast majority of species within this family are phytophagous, although species in the subfamily Tachiniscinae are parasitoids, while most species of the subfamily Phytalmiinae are saprophagous (Diaz-Fleischer and Aluja 2000).

Larvae of some tephritid species, especially those of the subfamilies Dacinae and Trypetinae, are frugivorous and feed on fruit pulp of both wild and cultivated plants, hence, bearing the name ‘fruit flies’. Larvae of the remaining species feed on stems, shoots and flowers (Christenson and Foote 1960, Diaz-Fleischer et al. 2000). The feeding habit of the frugivorous larvae of some species causes extensive damage to cultivated fruits. Hence, fruit flies are regarded as one of the most serious pests of horticultural crops (Christenson and Foote 1960, White and Elson-Harris 1992, Landolt and Quilici 1996).

Fruit flies exhibit a diverse array of host use patterns that range from strict monophagy to extreme polyphagy. Females of some fruit fly species such as Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae: Dacinae), oviposit in fruits of many plant families (Drew 1989, Fitt 1990) and are “polyphagous”, but other species such as olive fruit fly, *Bactrocera oleae* (Gmelin), oviposit in only olive fruit and are “monophagous” in their host use pattern (White and Elson-Harris 1992). However, many species are “oligophagous”, breeding predominantly in plant species within the same family (Norrbom et al. 1998). A typical example of an oligophagous species is the cucumber fruit fly, *Bactrocera cucumis* (French), which primarily breeds in plant species within the family Cucurbitaceae (Smith et al. 1988).
In the following section, I review the mechanisms involved in host use and host plant choice of phytophagous insects in general and specifically of fruit flies, and the effect of host plant choice and use on their life history.

1.2 Host use and host plant choice in phytophagous insects

“Host use” in phytophagous insects is generally defined as the plant species being fed or oviposited upon by an insect species, whereas the likelihood of using different plant species under the same environmental conditions is referred to as “host preference/choice” (Singer 1983). Phytophagous insects use host plants or plant parts as refuges or for feeding, mating, oviposition and larval development (Thorsteinson 1953), but different insect species differ considerably in the range of plant species that they use as hosts (Thompson 1988a).

Depending on the number of plant species used for feeding or oviposition, phytophagous insects are commonly categorized as either being polyphagous, use of plants from several plant families; oligophagous, use of plants from a single family; or monophagous, use of plants from a single or few closely related plant species of the same genus, (Cates 1980, 1981). However, labelling phytophagous insects as polyphagous implies that the frequency of the use of plants is proportionate to the plant abundance in the local habitat and that the “fitness”, rate of survival and reproduction, of the insect on the various plant species used is similar irrespective of the plant species (Walter and Benfield 1994, Thompson 1998, Walter 2003). Host use categorizations of individual insect species have often been inconsistent in the literature, probably due to the use of different plant taxonomic levels at different habitat scales by different researchers (Cates 1981, Hayes 1982, Dyer and Floyd 1993, Menken 1996). Nevertheless, the mechanisms which cause the observed host use patterns to occur are more important, than problems of definition, in understanding the evolution of host plant choice and host use in phytophagous insects.

Several non-mutually exclusive hypotheses and models have been postulated to explain the evolution of the mechanisms shaping host plant choice and the subsequent host use patterns by phytophagous insects. These include the chemical coevolution hypothesis (Ehrlich and Raven 1964), plant apparency and chemical defense

1.2.1 Chemical coevolution hypothesis

The chemical coevolution hypothesis suggests that the present day insect-plant associations are a result of a reciprocal stepwise interaction between insects and plants over evolutionary time (Ehrlich and Raven 1964). That is, plants (angiosperms) through occasional mutation and recombination produce defensive chemical compounds against herbivory. Such plants enter a new adaptive zone, which is free of herbivores and gives rise to an entire family or group of families, which are chemically diverse. In response to these physiological obstacles, phytophagous insects may acquire means to overcome such defensive plant traits. Those insect species that evolve the capacity to use these plants may also use these defensive chemical compounds as cues for locating their host plants. The chemical coevolution hypothesis contends that such reciprocal interactions continued over evolutionary time have led to the present day host specialization (monophagy or oligophagy) behaviour of phytophagous insects in which taxonomically related insects use chemically related plant species (Ehrlich and Raven 1964).

A typical example of the chemical coevolution hypothesis was exhibited by the leaf beetle genus, *Phratora*. Closely related species of beetles in this genus generally fed on related species of plants. Two species, *P. atrovirens* (Cornelius) and *P. laticollis* (Suffrian) specialize on poplar tree species, while two other species *P. vulgatissima* (Linnaeus) and *P. aklaviki* (Carr) feed on willow trees and pilose leaves with low concentration of phenolic glucosides (Kopf et al. 1998). Yet another species, *P. vitellinae* (Linnaeus), fed on poplars and willows that contain high concentration of salicin and salicortin, and also on other available plants containing salicylates, hence, exhibited host specialization in relation to plant chemistry (Kopf et al. 1998).
Similarly, in a recent phylogenetic study of host plant association in the leaf beetle genus, *Trirhabda* LeConte, Swigonova and Kjer (2004) showed that host shifts were phylogenetically conservative and that host shifts were mostly between taxonomically related plants. The phylogeny also revealed that *Trirhabda* spp. were adapted to tolerate complex secondary compounds of its host plants. Such empirical studies provide evidence for the chemical coevolution hypothesis shaping current patterns of host specificity in some insect-plant associations. However, other theories are required to explain host choice and host use for other insect plant associations (Thompson 1988a).

### 1.2.2 Plant apparency and chemical defense hypothesis

The host plant apparency and chemical defense hypothesis emphasizes plant chemical compounds, as well as the predictability of plants in a given time period in a particular, to be the major contributing factors that influence host choice and host use by herbivorous insects (Feeny 1976, Rhoades and Cates 1976). This hypothesis postulates that, in the initial phase, the apparent or predictable plants are conspicuous and long-lived and provide enough time for insects to adapt and specialize on these plants. Conversely, the unapparent plants are less conspicuous and short-lived and therefore escape from specialist herbivores but are used by herbivores with a generalized feeding habit. However, in response to herbivory by insects, plants evolve the capacity to produce chemical defense mechanisms that result in new host use patterns that differ from the initial host use patterns. The predictable (apparent) plants invest most of their resources in producing less toxic but costly digestibility-reducing compounds that select for generalist herbivores that are able to circumvent the less toxic compounds, but not the digestibility-reducing substances. On the other hand, the unpredictable, ephemeral/unapparent plants produce highly toxic compounds that inhibit its generalist feeders, but are selected by specialist species that have developed mechanisms to overcome these toxic compounds (Rhoades and Cates 1976). The plant apparency and chemical defense hypothesis has been validated by several empirical studies.

When testing whether pyrrolizidine alkaloids (PA) in *Cynoglossum officinale* L. serve as antifeedants against herbivores, Vanda et al (1995) showed that PA extracts of
the leaf significantly deterred a polyphagous but not a monophagous herbivore. They specifically demonstrated that the PA extract deterred the polyphagous larvae of *Spodoptera exigua* (Hubner) whereas the monophagous weevil, *Mogulones cruciger* (Herbst), on rosette plants, consumed more of the younger leaves that had the highest PA content. In the field, the polyphagous herbivore avoided the young leaves with highest PA levels and preferentially fed on the more abundant (apparent) oldest leaves. Similar results were demonstrated in other studies where larvae of six polyphagous lepidopteran species preferred the less nutritious, tough and mature leaf tissue of their host plants, and avoided younger leaves that contain protein complexing phenolics (Cates 1980). In contrast, the monophagous and oligophagous species preferred the more nutritious and highly toxic young leaf tissue of their host plants (Cates 1980). In some insect-plant systems, host plant predictability (apparency) in a given time period in a particular habitat determines the host use patterns exhibited by insects (Kuussaari et al. 2000).

1.2.3 Time-limitation hypothesis

Similar to the plant apparency hypothesis, the time-limitation hypothesis uses host plant predictability and availability in time and space as well as herbivore life span as the main parameters influencing host choice and host use patterns in phytophagous insects. Levins and MacArthur (1969), making the assuming that insects do not distinguish between good and poor hosts, postulated that when acceptable plants are rare or the insect’s life-span is short, the insect will accept less suitable plants as hosts. This behaviour results in polyphagy because the loss in average fitness from accepting low quality hosts no longer outweighs the loss in time spent searching for the most suitable host (e.g., Wiklund 1981).

Similarly, when the most suitable plant is rare, insects which produce eggs continuously oviposit on less suitable plants thereby resulting in polyphagy (e.g., Singer 1971, Courtney and Forsberg 1988). Polyphagous feeding behaviour is executed in this circumstances because as time progresses, it becomes risky for the insect to leave the low quality host without laying any eggs because a suitable host may not be found before the next batch of eggs are to be laid (Jaenike 1978a, b). Furthermore, if an insect’s search time is small, it is assumed to be time-limited and,
therefore, less discrimination between plants would be expected resulting in the use of a broad host range (Courtney 1982). However, if the search time is large, the insect is egg-limited and, therefore, promotes host discrimination behaviour, which consequently results in a narrow host use pattern (Larsson and Ekbom 1995, West and Cunningham 2002).

1.2.4 Hierarchy threshold model

Chemical and physical stimuli of the plant play a major role in directing the insect to either accept or reject a plant as a host. However, the behavioural decision and the response on the part of the insect, is largely determined by the sensory information processed in the central nervous system, which in most instances is determined by the insect’s physiological status (Schoonhoven et al. 1998b, Walter 2003). The hierarchy threshold model predicts that insects rank hosts in a hierarchical fashion, and that the acceptability of the plant is determined by the interaction between the plant stimuli received by the insect and the insect’s physiological status. The hierarchy threshold model (Courtney et al. 1989) uses physiological parameters, such as the female egg load, to predict host choice and host use patterns (Mayhew 1997).

If factors influencing the acceptance threshold level are not host specific, an individual insect that accepts a lower ranking host will also accept all hosts above that host in the rank-order (Courtney et al. 1989). Higher egg loads decrease the threshold for acceptance and, therefore, lower ranking hosts are accepted which results in polyphagy. In contrast, high discrimination in host selection will occur with less fecund females because the lower egg load increases the acceptance threshold level which consequently leads to only the highly ranked hosts being accepted, hence, resulting in host specialization (Courtney et al. 1989). Such discrimination in oviposition behaviour can occur within a species based on egg-load. In a field study, Nomakuchi et al. (2001) reported that the host acceptance of both the old and young adult pierid butterflies, *Anthocharis scolymus* (Butler), was determined by their egg load. Younger butterflies with greater egg loads laid eggs on plants that already had eggs laid on them (poor host) and those with no eggs laid on them (suitable host). In contrast, older females with fewer mature eggs in their ovaries selectively laid eggs on plants which never had eggs deposited on them. Similarly, the unpredictable
occurrence of the primary host of *Helicoverpa punctigera* (Wallengren) encourages some adult females to migrate and oviposit on newly emerged cotton plants. The threshold for host acceptance in these individuals was decreased because they were physiologically stressed by possessing higher egg load (Walter 2003). In contrast to the plant apparency hypothesis that suggests plant traits/stimuli as the influencing factors in host choice and host use, the hierarchy threshold model postulates that host choice and host use patterns in phytophagous insects are the net result of both the plant traits and the insect’s biological or physiological constraints or requirements.

### 1.2.5 Density-dependent models

Density-dependent models predict host use patterns to be determined by density dependent factors such as natural enemies (predators and parasites), interspecific competition and the abundance of suitable host plants (Futuyma 1983a, Jaenike 1990, Mayhew 1997). These factors can cause insects to either restrict or broaden their host range.

Natural enemies of phytophagous insects cause mortality to insects and, therefore, provide a selection pressure for herbivores to either restrict or widen their host range depending on other ecological factors, such as plant diversity (Bernays and Graham 1988, Bernays 1988). In habitats with low plant diversity, specialization of host use may occur by avoiding the plant with enemies and shifting onto restricted host plants that are not used by the natural enemy. In contrast, in habitats with high plant diversity, natural enemies would drive herbivores to use a wide range of ‘enemy-free’ plant species. In this case, specific host finding would result in longer search times which results in increased vulnerability of the insect to discovery by the natural enemies (Beaver 1979, Bernays 1988). Furthermore, in habitats where natural enemies concentrate their efforts on plants where herbivorous prey are plentiful, polyphagy may be favoured because the prey, in response to predation, would be distributed across various plant species resulting in a lower prey densities and, hence, lower predation rate (Brower 1958).

Attack by natural enemies may further promote host specialization as the herbivore may develop cryptic mechanisms or means to sequester toxic compounds from its
host plants to protect itself from the natural enemy (Bernays and Graham 1988, Bernays 1998, Karban and Agrawal 2002). Moving away from the host plant may increase its vulnerability to natural enemies. For example, when both the specialist and generalist lepidopteran larvae were fed on their host plants and offered to the tropical ant predator, *Paraponera clavate* (Fabricius), the ant frequently rejected the cryptic specialist despite the absence of the correct host plant background. This response suggests that the chemical defense derived from the host plant deterred the ant from preying on the larvae (Dyer and Floyd 1993).

In some instances, populations of phytophagous insects experience density-dependent competition for resources (Futuyma 1983a). If fitness of herbivorous insects using a particular host plant increases with increasing number of conspecifics using the same plant, then host specialization may result. Conversely, an insect may widen its host range if fitness decreases with conspecific insect density, provided that the resources are available locally (Rausher 1984, Jaenike 1990, Walter 2003). Similarly, host plant density within a given habitat may also affect the host use pattern of herbivorous insects. In habitats where insects are faced with high abundance of inferior hosts and rarity of high quality hosts, selection may favour the use of the abundant inferior hosts, resulting in increased host range. However, if high quality hosts are abundant, then the insects may only use this plant species, thereby promoting a specialized host-use pattern (Jaenike 1978b, Courtney 1983, Courtney et al. 1989).

### 1.2.6 Optimality theory

Optimality theory predicts that herbivorous insects will restrict their feeding or oviposition behaviour depending on the host plant quality. Plants species that enhance herbivore fitness will always be used, resulting in a restricted host-use pattern (Kennedy 1965, Jaenike 1978a). However, in habitats where several potential host plants with similar quality are present ‘host confusion’ may occur if the insects have difficulty in finding the most suitable host (Fox and Lalonde 1993, Larsson and Ekbom 1995). Therefore, it would be advantageous for the insect to use all the available hosts because avoiding one host could result in avoiding the most suitable host. Hence, the result may be the use of a wider host range by the local insect population (Jaenike 1978a, Michaud 1990).
A key prediction of optimality theory in the context of host use is that “oviposition preference” and “offspring performance” are positively correlated (Thompson 1988a). Oviposition preference is defined as the non-random choice shown by an ovipositing female to plant resources offered simultaneously, whereas offspring performance describes the survival of all life stages, i.e., larval growth and efficiency, pupal mass, and adult fecundity and longevity (Thompson 1988a). Apart from the host plant traits and the ecological factors, oviposition preference of the adult female may be determined by the performance of its offspring in relation to the nutritional quality of the plant (Abrahamson and Weis 1997). The “preference-performance hypothesis” predicts that the plant with optimal nutritional and chemical quality that increases the fitness of the offspring will be preferred over those that do not (optimal host choice strategy) (Cates and Orians 1975).

Several studies have illustrated that ovipositing females choose plants which are suitable for the survival of their offspring (Kouki 1993, Carr et al. 1998, Bruyn et al. 2002). However, other studies have shown contradictory results, suggesting other ecological, behavioural, and/or physiological factors influencing host choice and host use (Fitt 1986a). These contradictory results suggest a need for a closer look at the relationship between adult preference and offspring performance and how this relationship may determine host plant choice and host use patterns in phytophagous insects.

1.3 Host plants and host use in fruit flies

Host plants of phytophagous insects are usually the plants in which the adult insect and larvae feed, or in which the adult oviposits. In some insect groups, (e.g., some lepidopteran species), the adult oviposits on one plant species and the larvae may migrate to another plant species or conspecific plant for feeding (Berdegue et al. 1998). In contrast, other insect groups, especially those with less mobile larvae (e.g., fruit flies), have a larval feeding behaviour that is restricted to the same plant used by the adult female for oviposition.
Fruit flies can use host plants for feeding, mating, oviposition, larval development, and as refuge from natural enemies. However, unlike oviposition and larval development, the other activities of adult fruit flies are not always restricted to the host plants (Prokopy 1983, Raghu et al. 2002). Because of the close interaction of the ovipositing females and the subsequent development of the larvae on this plant, the host plants for fruit flies are those plants that the female chooses for oviposition and in which subsequent larval development may occur (Prokopy and Owens 1983). These host plants are sometimes referred to as ‘larval hosts’.

Larvae of different fruit flies species can feed on different plant parts other than fruits (White and Elson-Harris 1992; Christenson and Foote 1960). Although fruit flies of the subfamily Dacinae are mostly frugivorous, a few, especially those attacking species of Cucurbitaceae (e.g., B. diversa (Coquillett) and B. scutellaris (Bezzi)) can infest the flowers. Larvae of some species within the tribe Ceratitini develop in bamboo shoots (White and Elson-Harris 1992, Wang 1996, Allwood et al. 1999). Similarly, larvae of the subfamily Trypetinae (e.g., Coelotrypes, Acidoxantha and Macrotryptera spp.) infest fruits, flowers and growing shoot tips, while others are also leaf miners. In contrast, almost all species of the subfamily Tephritinae are associated with flowers, while a few are stem miners (White and Elson-Harris 1992).

The host use patterns of the frugivorous tephritid species of Dacinae and Trypetinae range from those that are highly polyphagous to those that are more specialized (oligophagous and monophagous) on certain host fruits (Aluja et al. 1987, Allwood et al. 1999). Fruit fly studies that quantify both the level of host fruit infestation and rank the preference for host plant species are rare (e.g., Aluja et al. 2000, Clarke et al. 2001). Most studies only document fruit fly host plants based on host records without reference to infestation rate with respect to relative abundance of the host plants in the field. Ultimately, too many documented host records are based on a single record (e.g., Smith et al. 1988, Allwood et al. 1999, Hancock et al. 2000). Classifications of tephritids based on host use (i.e., polyphagous, oligophagous or monophagous) are subsequently made based only on host records. This may be ecologically uninformative because a truly polyphagous insect species must use host plants in proportion to their occurrence in its habitat (Walter and Benfield 1994, Clarke et al.
Similarly, the use of the terms, monophagy and oligophagy, must also be placed within an ecological context.

Allwood et al. (1999) reported fruit fly species that infested fruits from several families as polyphagous irrespective of the level of fruit infestation with respect to the local host abundance or size of the fruit sample collected. Reanalysis of the Allwood et al. (1999) data clearly showed a preference ranking of host species by the different fruit fly species (Clarke et al. 2001). For example, *Terminalia catappa* L. yielded up to five times the number of *B. papayae* (Drew & Hancock) and *B. dorsalis* (Hendel) than all other fruits, and *Averrhoa carambola* L. yielded three times the number of *B. carambolae* (Drew & Hancock) as all other fruit species (Clarke et al. 2001). Allwood et al. (1999) reported that *B. latifrons* (Hendel) was reared from fourteen species across ten families of host fruits. Hence, this species would be described as polyphagous. However, 90-95% of *B. latifrons* were reared from *Solanum* spp, indicating a more restricted oligophagous host use pattern (Clarke et al. 2001). These data reanalyses demonstrate that supposedly polyphagous fruit flies have a clear preference hierarchy among the host species they use. Similar detailed preference ranking studies on other species previously labelled as polyphagous (e.g., *B. tryoni* and *Anastrepa ludens* (Loew)) (Smith et al. 1988, Hancock et al. 2000), also may show variations in their host preference ranking and host use patterns.

Host use patterns of frugivorous tephritids are based primarily on surveys of cultivated or edible fruits in altered habitats by human activities with little or no information on the primary hosts in the natural habitats, such as rainforest. This further complicates our understanding of the evolution of host choice mechanisms and host use patterns of the fruit fly species. Therefore, studies on host choice and host use patterns should incorporate the natural/primary hosts in the endemic habitat in order to clearly understand the evolution of host choice mechanisms of the fly species (Walter and Benfield 1994). Furthermore, studies reporting host use patterns of an insect-plant association should clearly state the host preference ranking of polyphagous species; information vital to the understanding of how insects and plants become distributed within the community over time (Thompson 1988b). For pest species, such preference ranking information is crucial for understanding the
population dynamics of the pest species in relation to the host plant(s) and is useful for developing appropriate control methods for pest species that are polyphagous.

1.4 Host choice mechanisms for oviposition in fruit flies

Host choice in tephritid fruit flies is made by the ovipositing adult female and the developing larvae have no choice and must feed on the plant substrate in which eggs were deposited to complete development. Whether the oviposition preference of the female is made based on its behavioural, ecological and/or physiological associations with the plant (acceptability of the fruit for oviposition) or the suitability of the fruit for offspring development is often difficult to verify. Nevertheless, thorough studies on the biotic and abiotic ecological factors that affect host choice, behavioural responses caused by plant cues, and physiological constraints of the insect may improve our understanding of host choice mechanisms of frugivorous tephritids. (Futuyma 1983b, Walter 2003).

In the following section, I review the mechanisms of host plant choice in fruit flies, concentrating mainly on of the genus Bactrocera that is distributed throughout the tropical and subtropical regions of Australasia and Oceania (Drew 1989). Also included are information from other frugivorous tephritid genera, such as Anastrepha, Ceratitis and Rhagoletis, which have been well studied in other parts of the world. I also explore the influence of host use patterns on the life history and demography of fruit flies.

1.4.1 Ecological influences on host plant choice of fruit flies

Ecological factors, such as host plant availability and phenology, habitat type (Nishida 1963), climatic conditions (Bateman 1968), and parasites and predators (Drew and Hooper 1983), all influence host plant choice exhibited by dacine fruit flies in their natural habitat. Although these factors contribute to host plant choice in the natural habitat, the influence of habitat type and the availability (predictability) and phenology of host plants play an important role in host recognition by the foraging fruit flies.
Host choice and host use are conditional on a hierarchical sequence of behavioural steps made by the gravid female (Table 1.1). Once a female makes a host seeking flight, she forages to locate a group of hosts, and then a host plant within the group with suitable fruits is chosen for oviposition (Fletcher and Prokopy 1991). If no potential fruiting hosts are present, she leaves the group of host plant in search for another group that can sometimes result in long distance dispersal. Fletcher (1974) reported that mature *B. tryoni* travelled considerable distances from their point of release when fruiting host plants were rare. Although the availability of host plants may cause the female to remain in the habitat, it may not necessary stimulate oviposition if suitable fruits are not available. Various fruit traits such as fruit volatiles, ripening stage or colour may influence both fruit selection and oviposition activities.

For most polyphagous fruit fly species, host plant fruiting phenology influences host use patterns in which the female alternates between the primary hosts and secondary hosts. The polyphagous species, *B. jarvisi* (Tryon), generally oviposits into its primary native fruit, *Planchonia careya* (F. Muell). However, when *P. careya* is absent, *B. jarvisi* readily oviposits into other fruits (Fitt 1986a); behaviour indicative of a time-limited oviposition strategy. In contrast, host shift behaviour does not occur in highly monophagous species, such as *B. opiliae* (Drew and Hardy), which only oviposits in its natural host, *Opilia amentacea* Roxb, (Fitt 1981). These species exhibit an egg-limited oviposition strategy.

Other studies have shown that monophagous or oligophagous fruit fly species rely more heavily on visual cues to locate the host plants and fruits than polyphagous species. This suggests that host predictability within a habitat may play an important role in host location for specialist species. Field cage studies demonstrated that when fruits were abundant and visually conspicuous, the specialist *Rhagoletis pomonella* (Walsh) alighted more frequently on the fruit, than when fruit were scarce and inconspicuous (Aluja and Prokopy 1993). Similar behaviour also was observed in the specialist olive fly, *B. oleae*, (Prokopy and Haniotakis 1976).

Plant density also has been shown to affect host choice and host use patterns of two polyphagous *Anastrepha* spp. The single egg laying species, *A. obliqua* (Macquart),
visited fewer hosts and reduced the rate of eggs laid per female when exposed to a low host density, an indicative of egg-limitation constraints. Conversely, *A. ludens* which lays clutches of eggs per oviposition, accepted a low quality host when exposed to low host density, an indicative of time-limited oviposition behaviour (Diaz-Fleischer and Aluja 2003b). In studies where *Ceratitis capitata* (Wiedemann) females were released into field cages of fruiting kumquats, the flies visited more fruits and oviposited more into fruits on plants with higher fruit densities (Prokopy et al. 1987). These empirical studies with fruit flies demonstrated that host plant apparence and predictability (Feeny 1976, Rhoades and Cates 1976) can impact on both their host choice mechanisms and host use patterns.

Host plant predictability over time in a particular habitat could cause insects to evolve behavioural mechanisms to avoid competition that would otherwise result in low offspring performance (Dukas et al. 2001). This adaptation may only occur if resources are ephemeral and scarce within the habitat. The fruit or other plant parts used by fruit flies for oviposition are generally limited resources and, as a consequence, some fruit fly species (especially those infesting smaller fruits) have evolved mechanisms to produce host-marking pheromones that reduce larval competition among the same or different fly species (Prokopy and Koyama 1982). After oviposition, the female deposits a host-marking pheromone on the oviposition site to deter other females from ovipositing at that site. Some tephritid species that deposit host-marking pheromones include *Rhagoletis* spp (Prokopy et al. 1976), *C. capitata* (Prokopy et al. 1978) and *A. suspensa* (Lowe) (Prokopy et al. 1977).

With the exception of *B. oleae* (Girolami et al. 1981), no other *Bactrocera* spp. have been found to deposit host-marking pheromones. However, the presence of larvae in fruits may deter females of the same or different species from ovipositing in the infested fruit (Fitt 1984) and change their oviposition preference to alternative, non-infested host fruits. Avoidance of infested fruit as oviposition sites may not only be due to larval presence (competition *per se*), but may also be caused by chemical changes associated with fruit tissue decomposition resulting from larval feeding (Fitt 1984). Larval competition in host fruits generally results in smaller body size, especially at higher larval densities (Fletcher 1989a).
The capacity of host-marking pheromones to influence host use or host shift in nature is not well understood. To date, studies done to explain the effect of host-marking pheromones on host choice used infested and non-infested fruit of the same host plant species (Prokopy et al. 1987) and that it was not clear whether the deterrent effect of host-marking pheromones would cause the females to use alternate hosts. Furthermore, host-marking pheromones lose effectiveness within minutes (Mangel and Roitberg 1989) thereby allowing other females to oviposit in the previously oviposited host (Roitberg and Prokopy 1983), hence, further complicating the role of host marking pheromone in host use.

1.4.2 Behavioral influences on host plant choice of fruit flies

Most of the studies done to understand host choice mechanisms in fruit flies have been those related to the insects’ responses to plant cues. Physical properties of the plant, such as size, shape and colour, are the initial plant stimuli for host location activities of fruit flies (Prokopy and Owens 1983). These visual plant properties facilitate fruit location, but do not necessarily stimulate oviposition (Table 1.1). Prokopy and Haniotakis (1976) reported that the females of *B. oleae* located fruits by using only visual cues of size, shape and colour, rather than fruit odour. However, other species respond differently to specific sizes, shapes and colours. For example, the monophagous *R. pomonella*, was more attracted to the hues of the yellow colour than to that of orange, red, green, grey or black (Prokopy 1972). In contrast, the polyphagous *C. capitata*, was more attracted to both the hue and the reflectance of blue and red colours than those of yellow and white (Katsoyannos et al. 1986). Similar studies reported that *B. tryoni* responded positively to blue colour (colour of its primary rainforest host) and the monophagous *B. cacuminata* (Hering) responded strongly to orange or yellow colours that resemble the colour of its near-ripe to ripe host fruit, wild tobacco fruit, *Solanum mauritianum* Scop., (Drew et al. 2003).

Size and shape are important cues for attracting fruit flies whose host plants are trees, with shape generally more important than size (Katsoyannos 1989). Moericke et al. (1975) demonstrated that *R. pomonella* was attracted more strongly to larger models of its host tree than to smaller ones. Similar to the colour responses, different fruit fly species vary in their responses to dissimilar fruit sizes. For example, *R. pomonella*
was strongly attracted to larger fruit models while \textit{R. fausta} (Osten Sacken) and \textit{R. cingulata} (Loew) were strongly attracted to smaller fruit models (Prokopy 1977). Studies done on the attractiveness of different shapes (Prokopy and Haniotakis 1976), showed that spheres were more attractive than other shapes with the probable association that the circular outline resembled the outline of many of its natural host fruits (Prokopy and Boller 1969, Katsoyannos 1989).

When the female fly arrives at the fruit, it explores the fruit surface before attempting to oviposit. Therefore, physical fruit traits (other than colour, shape and size) may also determine fruit suitability for oviposition. For example, \textit{B. tryoni} oviposited into ‘Grosse Lisse’ and ‘Roma’ tomato varieties that had soft pericarp more readily than into ‘cherry’ tomatoes that had a tougher pericarp (Balagawi et al. 2005). In some species, such as \textit{B. tryoni}, this exploration behaviour is done to locate favourable oviposition sites (e.g., holes made by previously oviposited females or damage done by other agents) (Pritchard 1969). Other species, such as \textit{B. cucurbitae} and \textit{B. dorsalis} also exhibited exploration behaviour to find breaks in the skin in which to oviposit (Prokopy and Koyama 1982). If the preferred fruit is found to be too smooth, oily or tough, the female will seek other fruits, because she cannot grip the fruit with her tarsi in order for the ovipositor to penetrate the fruit skin (Pritchard 1969). This may be one reason why most fruit fly oviposition occurs at the later stages of ripening, when the fruit becomes softer and more prone to damage (Matanmi 1975).

Unlike the visual stimuli of colour, size and shape that attract fruit flies within the vicinity of the a fruiting plant, many compounds released by the plant can both attract flies and enable them to discriminate between host and non-host plants, and can further stimulate ovipositor probing on host fruits (Fitt 1981) (Table 1.1). In some species (e.g., \textit{B. tryoni}), volatile compounds are responsible for the exploratory behaviour and ovipositional activity on the fruit (Fletcher 1987). Volatile compounds that have been shown to attract and stimulate oviposition in \textit{B. tryoni} include, respiratory CO$_2$ (Stange 1999), \textit{n}-butyric acid, methyl butyrate, ethyl butyrate, 2-butanone, ethyl acetate, ethanol, 2-propanone, \textit{alpha}-farnesene (Eisemann and Rice 1992) and 2-chloro-ethanol (Fletcher and Watson 1974). Other compounds that stimulate oviposition are \textit{beta}-D(-) fructose (Eisemann and Rice 1985). Moisture
content also has been found to stimulate ovipositional activities (Eisemann and Rice 1989).

The response of ovipositing females to different physical and chemical plant traits and their importance in the size of host range are largely unknown and provide a vast area for scientific investigation.

1.4.3 Host choice as a function of physiological constraints

The behavioural responses exhibited by the female flies are the net result of plant stimuli and the physiological state of the fly. The physiological state of phytophagous insects is one of the major factors that drive insects to forage for feeding or oviposition resources (Courtney and Kibota 1990) (Table 1.1). Several factors, such as age, feeding status, mating status, and egg load contribute to the physiological state of female tephritids. Although not all tephritid females mate and feed on their host plants (Fletcher and Prokopy 1991, Raghu et al. 2002), foraging for larval hosts is obviously critical. Therefore, egg load may have a significant influence in host seeking behaviour of mated female fruit flies.

Some highly polyphagous species of the genera, *Bactrocera*, *Ceratitis* and *Anasptrepha* develop mature eggs throughout their life and have larger lifetime fecundity than specialist species (Fitt 1990). These physiological traits, combined with the unpredictable nature of host fruit abundance, can increase egg load and influence host use patterns of fruit flies (Fitt 1990). Their host use patterns would then be consistent with the hierarchy threshold model (Courtney et al. 1989), where low ranking hosts in the preference hierarchy should be accepted with increasing egg load to result in a polyphagous host use pattern.

Several empirical studies have shown that fruit flies exhibit a wider host range as a function of high egg load. Fitt (1986b) found that the polyphagous *B. tryoni* oviposited on low ranking hosts in both choice and no choice tests whereas the monophagous *B. cacuminata* and oligophagous *B. cucumis* did not oviposit on low ranking hosts even when their preferred host was absent. Fitt (1990) attributed the broad host range of *B. tryoni* to the fact that it has many ovarioles per ovary that result
in higher fecundity, whereas the specialized host use patterns of *B. cucumis* and *B. cacuminata* resulted from possessing fewer ovarioles and lower fecundity.

These studies demonstrate that, in some species, host choice patterns are consistent with the hierarchy threshold model. Higher net fitness to the polyphagous species may result because mortality caused by the use of lower-ranking (unsuitable) hosts would be compensated by exploiting a wider host range.

1.4.4 Optimality theory (preference - performance hypothesis) in host choice of fruit flies

Tephritid larval development is completed inside the fruit oviposited by the adult female. According to the preference-performance hypothesis, natural selection should favour ovipositing females to use those plants that maximize fitness (Thompson 1988a). Non-frugivorous tephritids have shown a high correlation between adult oviposition preference and offspring performance. For example, the gall forming *Eurosta solidaginis* Fitch, while unable to discriminate between plant genotypes in some instances (Craig et al. 1999), did discriminate between plants and laid more eggs in plant genotypes which sustained high larval survival (Carr et al. 1998). Studies on other Diptera species with less mobile larvae, such as Hessian fly, *Mayetiola destructor* (Say) (Kanno and Harris 2002), and the willow-galling sawfly, *Euura lasiolepis* Smith (Craig et al. 1989), showed a strong correlation between oviposition preference and offspring performance. These results suggested that host choice was a function of the availability of a rich larval resource for growth and survival.

While several studies have identified ecological and behavioural factors influencing host use in frugivorous tephritids, few studies have investigated the value of optimality theory (preference-performance hypothesis) to explain host use patterns (Fitt 1986a, Balagawi et al. 2005). When comparing the oviposition preference of the adult and larval survival for five *Bactrocera* spp on seven cultivated fruits, Fitt (1986a) concluded that the host choice of most of the species was based on the behavioural association of the ovipositing female with the host plant rather than any relationship between oviposition preference and larval performance. Fitt (1986b) reported that the oligophagous *B. cucumis* exhibited a greater preference for
ovipositing in its primary host (cucumber) and had higher larval survival on this host than on other novel hosts. He also reported a similar result for the monophagous *B. opiliae* (Fitt 1981). Consequently, it appears that the preference-performance hypothesis would be more likely to explain host use patterns in specialist dacines.
Table 1.1. Host plant and insect factors of importance to different components in the sequential steps leading to host use.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Host searching ➔</th>
<th>Host selection ➔</th>
<th>Host acceptance ➔</th>
<th>Host use</th>
</tr>
</thead>
</table>
| Insect factors | Physiological status of insect  
- hunger/nutritional status  
- reproductive status (e.g., egg-load)  
- Quality and sensitivity of olfactory receptors (chemoreception)  
- Development and sensitivity of sensory organs (e.g., antennae, ovipositor sensilla and the central nervous system) | Spectral dimension and sensitivity of insect vision  
- Spectral dimension and sensitivity of insect vision  
- Quality and sensitivity of olfactory receptors (chemoreception)  
- Development and sensitivity of sensory organs (e.g., antennae, ovipositor sensilla and the central nervous system) | Development and sensitivity of sensory organs (e.g., antennae, ovipositor sensilla and the central nervous system)  
- Development and sensitivity of sensory organs (e.g., antennae, ovipositor sensilla and the central nervous system) | Physiological status of insect  
- egg load  
- insect age  
- host deprivation period  
- preference-performance relationships |
| Host plant factors | Visual cues  
- Plant structure (shape, size)  
- Plant colour (reflectance wavelength) | Olfactory cues  
- Plant volatiles  
- Plant volatiles | Mechano-sensory cues  
- Plant’s surface texture (e.g., trichomes, wax crystals)  
- Palatability and toughness of surface plant tissue  
- Surface plant chemistry affecting taste or oviposition | Physical cues  
- Palatability of plant tissue for feeding  
- Toughness of plant tissue for oviposition penetration  
- Chemical cues  
- Chemical composition of plant tissue |

- Olfactory cues  
- Plant volatiles  
- Palatability of plant tissue for feeding  
- Toughness of plant tissue for oviposition penetration

- Mechano-sensory cues  
- Plant’s surface texture (e.g., trichomes, wax crystals)  
- Palatability and toughness of surface plant tissue  
- Surface plant chemistry affecting taste or oviposition
1.5 Biology, life history and demography of dacine fruit flies

1.5.1 Biology

Knowledge of the biology and life history of phytophagous insects is a prerequisite to understanding their relationships to their host plant(s). The general biology of fruit flies has been reviewed by Christenson and Foote (1960), while Fletcher (1987) reviewed the biology specific to the subfamily Dacinae. With exception of some univoltine species, such as B. opiliae (Fitt 1981) and B. minax (Enderlein), the majority of known dacines are multivoltine species (Fletcher 1989a) and have a similar life cycle. The gravid females lay either a single egg or egg clutch inside fruits and fleshy vegetables, which within few days hatch into first instar larvae. The immature larvae feed on bacteria, the decaying fruit pulp and macerated tissue until they develop into mature third instar larvae. These larvae leave the fruit and burrow into the soil for pupation or may pupate in the decayed fruit if it as dried adequately. After emergence, teneral adults feed for several days on sugars for survival, and need protein from the habitat to attain sexual maturity (Fletcher 1987). Mating then occurs which subsequently triggers a behavioural switch in the female from mating behaviour to oviposition behaviour and the search for suitable host plants (Jang 1995, Meats and Leighton 2004) (Figure 1.1).
1.5.2 Factors affecting life history parameters

Despite having the same general life cycle, the time required to advance through each developmental stage can vary considerably between and within tephritid species found in different, and even similar, habitats. Although various factors may contribute to these differences, major factors include climatic or environmental conditions (Christenson and Foote 1960, Bateman 1972), adult food intake (Christenson and Foote 1960, Vijaysegaran 1995), and the predictability and quality of larval diet (host plant) (Fletcher and Prokopy 1991).

Distribution of the different tephritid groups is restricted to various macro-climatic or geographical zones that contribute to the differences in the life history and annual
generation times of the species across these different zones. For example, tephritids such as those from the genus *Rhagoletis*, of holarctic origin, have a pupal diapause for most of the year and are univoltine (Prokopy 1968, Boller and Prokopy 1976), whereas the Dacinae are mostly tropical and subtropical in origin, lack pupal diapause and are mostly multivoltine (Bateman 1972, Fletcher 1987, Fletcher 1989a). However, even within a similar habitat, the microclimatic or environmental conditions such as temperature, humidity, moisture and rainfall directly affect the development rate of both immature and adult fruit flies (Fletcher and Zervas 1977, Fletcher and Kapatos 1983). Studies in both laboratory and natural conditions have shown the effect of abiotic environmental factors on the life history parameters of various fruit fly species (Fletcher and Kapatos 1983, Dimou et al. 2003).

Adult feeding behaviour and food sources in the fruit flies are very different to that of the larvae. In addition to environmental conditions, adult life history parameters (fecundity, pre-mating period, pre-oviposition period, and longevity) are dependent on the adult food intake (Yuval et al. 2002). Although in some species egg hatch and the larval developmental rates may be high, the adults may not feed on proteinaceous resources and, therefore, attain low fecundity. Carey et al. (2002), reported that when the frequency of exposure to food resources (protein) was alternated in *C. capitata*, both the life time reproduction and mortality of this species increased with greater availability of protein. Additionally, life expectancy was increased in females exposed to a prolonged sugar-only diet and decreased in females exposed to shorter periods of a sugar-only diet (Carey et al. 2002). Similarly, mated *B. tryoni* that were fed protein *ad libitum* from two days after emergence produced more eggs than those fed with a lower quantity of protein (Meats and Leighton 2004).

Host plant predictability and larval diet also have a considerable influence on the life history parameters of tephritids. In a recent study, Kaspi et al. (2002) reported that the progeny of *C. capitata* that fed on high protein larval diet had higher growth and reproductive rates than those fed on a protein-deprived larval diet. Fitt (1990) reported that *B. cucumis* had a shorter egg development time in cucumber (24h) in contrast to 53h for the egg development of *B. cacuminata* in its host plant, *S. mauritianum*. When the fitness of five different species was compared across different fruit species, *B. cucumis* had a higher larval developmental rate in cucumber than in banana, and did
not develop at all in *S. mauritianum* (Fitt 1986a). The strict monophagous, univoltine life history strategy of *B. opiliae* was hypothesized to be a result of the unpredictable availability of its host plant, *O. amentacea*, in its natural habitat (Fitt 1981). These studies provide evidence for the evolutionary impact of food resource availability on tephritid life cycle parameters.

Demographic variation related to host use have been demonstrated in several tephritid species (Carey 1982). A comparative demographic study of *C. capitata* revealed that life history parameters compensated one another resulting in high intrinsic rate of increase on different hosts (Krainacker et al. 1987). For example, the low adult survivorship of flies reared from mammee apple was offset by high fecundity, and long developmental times of flies reared on blackberry was offset by higher rate of larval survival (Krainacker et al. 1987). Similarly, Filchak et al. (1999) tested the fitness of *R. pomonella* reared on field apple and hawthorn to those reared in the laboratory on artificial diet, and concluded that the observed fitness trade-off was a net result of selection pressure acting on multiple life stages rather than any one particular stage.

In nearly all the hypotheses and models discussed above, host plant suitability and variability of plant abundance over time in the particular habitat are some of the major factors determining host choice and host use in phytophagous insects. Plant suitability, however, is a function of many variables, such as the chemical and physical plant properties and level of infestation (Jaenike 1978a), while availability of host plants is largely driven by the ecological factors operating within the habitat. The hypotheses and models developed to explain the mechanisms responsible for host plant choice and host use patterns in one insect-plant interaction system may not apply in another system. Therefore, it is important that individual studies be done for each insect-plant system in order to understand the mechanisms involved in host plant choice and host use patterns in the different systems.
1.6 Thesis objectives and rationale

Behavioural steps involved in host location establish the host use patterns of tephritids. Once a fly makes a host-seeking flight, it must first find a potential host, accept the host and then utilizes it. Most studies done on host choice of fruit flies have focused on host location (e.g., Drew et al. 2003) and rarely on host acceptance or host use (e.g., Fitt 1986a, Balagawi et al. 2005, Dhillon et al. 2005). This study is focused on the latter aspects of host acceptance and use (Figure 1.2).

Because fruit flies have great economic impact on agriculture, their host use has largely been defined on the basis of trade and quarantine regulations. Therefore, even when a single larvae or pupa is recovered from a fruit, that fruit is thereafter labelled a ‘host’, especially by regulatory agencies. This practice has resulted in several dacine species being classified, albeit potentially, as polyphagous (May 1953, Hancock et al. 2000). Therefore, classifying of fruit flies as monophagous, oligophagous or polyphagous is vague and largely devoid of any ecological context. My study investigated the relevance of these classifications through detailed testing of host use patterns in two non-monophagous species, \textit{B. cucumis} and \textit{B. tryoni}.

I previously discussed how host use patterns directly impact tephritid population dynamics. However, with few exceptions (e.g., Carey 1982), most life history studies conducted on dacine fruit flies investigated only the rate of development and mortality of restricted life history parameters (e.g., larvae and pupal mortality) and ignored other important parameters, such as adult age-specific mortality and life time fecundity. Gathering comprehensive life-table data is significant to the development of control measures for pest species in agricultural systems. For example, knowing which life stages that have the most influence on population dynamics would provide information useful in the development of efficient management tool that targeted these stages. Therefore, I also explored the link between host use patterns and demography.

These objectives were achieved through comparative studies of host use patterns by a polyphagous (\textit{B. tryoni}) and an oligophagous (\textit{B. cucumis}) species, and by comparing their demography as a function of host use.
1.7 The study species – *Bactrocera cucumis* (French) and *Bactrocera tryoni* (Froggatt)

I investigated the ecology of, *B. cucumis* and *B. tryoni*. These species were selected because they represent model systems that facilitated my objective of elucidating host use patterns. The oligophagous host use pattern of *B. cucumis* and the polyphagous host use pattern of *B. tryoni* serve as an ideal system for comparative ecological studies with respect to host choice mechanisms and life history strategies. Additionally, *B. cucumis* and *B. tryoni* are easily reared under laboratory conditions that facilitate both life history and demography studies under finite conditions.

Both species are endemic to Australia. *B. cucumis* occurs throughout the eastern coastal region from Cape York to northern New South Wales, while the distribution of *B. tryoni* further extends southwards along the eastern coast to East Gippsland in Victoria (Drew et al. 1982, Drew 1989). Prior to European settlement, these species were believed to have been endemic to rainforest habitats (May 1963, Zalucki et al. 1984), but the cultivation of fruits and vegetables post colonization allowed them to spread by utilizing these crops. The economic loss in fresh fruits and vegetable production caused by these species resulted in their shift from innocuous rainforest insects to attaining major pest status (May 1958, 1963).

The two species differ considerably in the range of plant species that they use as hosts for larval development (May 1953, Hancock et al. 2000). The oligophagous *B. cucumis* primarily uses plants in the family Cucurbitaceae, but occasionally has been reported to use plants in the families Passifloraceae and Solanaceae (May 1953). It does not respond to any known chemical male lures used worldwide to attract fruit flies. In contrast, the polyphagous *B. tryoni* uses a wide range of plant species (> 30 families), including the families Myrtaceae, Rosaceae and Rutaceae as the principal hosts (May 1953, Hancock et al. 2000) and, unlike *B. cucumis*, *B. tryoni* is attracted to cue-lure (4-(p-acetoxyphenyl)-2-butanone).

Because this study investigated the host choice mechanisms and host use patterns of the two species, plants regarded as primary and alternate hosts were used. Primary
host fruits selected from the Cucurbitaceae and alternate hosts from Passifloraceae, Solanaceae and Myrtaceae were used for studies with *B. cucumis*. Fruit hosts from the Myrtaceae, Rosaceae, Solanaceae, and Cucurbitaceae were selected for studies with *B. tryoni* with Myrtaceae and Rosaceae regarded as primary host families.

1.8 Thesis structure

After reviewing the theory and empirical studies that elucidate each of the steps involved in host choice and host use in this introductory chapter (Chapter 1), I present the results of a series of experiments focusing on the host acceptance and host use pattern of the two species involved (Figure 1.2). In Chapter 2, I present the general materials and methods that are common to all research chapters. Procedures that are specific to each research chapter are discussed under the Materials and Methods sections of the respective chapters.

The preference-performance hypothesis predicts that in insects with especially less mobile larvae, such as in tephritid fruit flies, females should preferentially use plants that result in high offspring performance (Thompson 1988a). This has seldom been tested in the case of tephritid fruit flies (Diaz-Fleischer et al. 2000). I specifically tested this hypothesis by using the oligophagous *B. cucumis* and polyphagous *B. tryoni* in Chapter 3. To explain host use patterns in fruit flies, previous studies have shown or proposed physical or chemical factors influencing the oviposition behaviour of tephritid fruit flies (Fitt 1986a, Eisemann and Rice 1989). I also identify some of these factors in Chapter 3.

Knowledge of the life history, population dynamics and demography of tephritid fruit flies would help facilitate a clearer understanding of the consequences of using different host plants (Fitt 1990). This thesis therefore further delves into understanding the life history and demography of *B. cucumis* and *B. tryoni* as a consequence of using the primary and alternate hosts. These findings are presented and discussed in Chapter 4. The concluding chapter (Chapter 5) summarizes the salient findings of the thesis and highlights avenues for further investigation.
Sequential steps towards Host use

1. **Host searching**
2. **Host finding**
3. **Host selection**
4. **Host acceptance**
5. **Host use**

### Preference/Performance

- **Within plant species variety**
  - *Bactrocera cucumis* (Cucumber)
  - *Bactrocera tryoni* (Apple)

- **Within plant family**
  - *Bactrocera cucumis* (Cucurbitaceae)
  - *Bactrocera tryoni* (Rosaceae)

- **Between plant family**
  - *Bactrocera cucumis* (Cucurbitaceae)
  - *Bactrocera tryoni* (Myrtaceae)

### Life History studies

- **Bactrocera cucumis**
  - Alternate hosts (secondary hosts):
    - Solanaceae
    - Passifloraceae
    - Myrtaceae

- **Bactrocera tryoni**
  - Alternate hosts (secondary hosts):
    - Solanaceae
    - Passifloraceae
    - Myrtaceae

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**Figure 1.2.** Thesis structure
CHAPTER 2: GENERAL MATERIALS AND METHODS
2.1 GENERAL MATERIALS AND METHODS

Standardised procedures and experimental methods used in every study are reported here to avoid repetition. Procedures and experimental methods specific to individual studies are reported in the Materials and Methods sections of their respective chapters.

2.1.1 Experimental conditions

All studies were done in the fruit fly laboratory at Griffith University from September 2003 through to March 2006. Because the developmental rate of both the wild and laboratory reared fruit flies is strongly influenced by temperature and humidity (Messenger and Flitters 1958, Pritchard 1970, Bateman 1972, Tsitsipis 1980, Tsitsipis and Abatzis 1980, Fletcher 1989b), the flies were reared and all experiments done in a controlled environment room at 26 ± 1 °C and 65 ± 10 % RH. The experimental room was artificially illuminated with fluorescent tube lights from 0700 – 1700 hours, and this allowed natural dawn and dusk periods each day. Average light intensity was 331 lux with a photoperiod of 12:12 (light:dark).

2.1.2 Laboratory rearing of adult flies

Rearing wild adult *B. cucumis* from field-collected fruit was not possible because field infestation levels were too low at the time of this study. Instead, adults were reared initially from laboratory-reared pupae obtained from Queensland Department of Primary Industry (QDPI), Cairns. The pupae were placed in moist sterilized sawdust in plastic containers and placed in a 60 x 60 x 60cm laboratory cage constructed from 25 x 25mm aluminium square frame covered with very fine, 0.6mm x 0.25mm, mesh. The same procedure was used to maintain adult *B. tryoni* except that they were initially reared from mango fruits and maintained in the fruit fly laboratory at Griffith University.

The procedures used for rearing adults where those of Heather and Corcoran 1985, Fay 1989 and Walker et al. 1996, with adults fed on sugar, water and enzymatic autolysate yeast protein (ICN Biomedicals Inc Aurora, Ohio) from the time of
eclosion. When adults were 17-28 days old, eggs were collected using fruit domes for experimental and maintaining laboratory colony.

2.1.3 Laboratory rearing of immature fly stages

Numerous artificial larval diets have been developed for rearing immature flies in both laboratory and mass-rearing situations (Tzanakakis and Economopoulos 1967, Manoukas 1975, Tsitsipis 1977, Nakamori and Kakinohana 1980, Heather and Corcoran 1985, Vargas and Mitchell 1987). These diets often include a bulking agent, Torula yeast as the protein source, Nipagin as an anti-fungal agent, and hydrochloric acid to maintain the diet at optimal pH. Plants from the Cucurbitaceae family are readily used by *B. cucumis* as hosts and as a consequence, a suitable larval diet for this species has been developed using pumpkin (Swaine et al. 1978, Pike et al. 2001). Throughout this study, the recipe used for the larval diet for *B. cucumis* was adopted from that of Pike et al. (2001).

Organically grown pumpkins, *Cucurbita moschata* (Duchesne), and zucchinis, *Cucurbita pepo* L., were purchased from the Brisbane Markets at Rocklea. A zucchini was washed, sliced in half and its flesh extracted to make egging domes (Monro and Osborn 1967, Fay 1989, Walker et al. 1996). Domes were then pierced with entomological pins and placed inside the laboratory cage holding adults for egg collection. The pumpkins were washed, sliced, and the seeds and the endocarp layer were removed. The pumpkin slices were chopped into smaller pieces and 1kg of the chopped pieces was blended using a 2 litre capacity blender (model 38BL44, Conair Corporation, Torrington USA). Forty grams of Torula yeast (Sanitarium Health Food Company, Sydney), 2g of Nipagin (Nipa Industrial Estate, Mid Glamorgan, Britain) and 6ml Hydrochloric acid (32% concentration) were added to the blended pumpkin and thoroughly mixed using the blender. The prepared diet mixture was poured onto 500g capacity diet trays, covered with dark lids and allowed to cool.

Eggs deposited into the zucchini domes were collected after 30-60 minutes by washing the eggs into a clean beaker with tap water using a clean hand sprayer. All fruit particles were removed from the eggs before the eggs were placed on the diet trays at a ratio of 2 eggs/gram of diet (1000 eggs in 500g of diet) using a 1ml plastic
pipette. These diet trays were placed on cool, heat sterilized (60 °C for 12h) sawdust in a ventilated container and covered with a cardboard box to provide a dark environment to inhibit yeast growth. After all surviving larvae had pupated, the sawdust was sieved and the pupae were counted, weighed and placed on fresh, sterilized sawdust in an open plastic container. The container of pupae was placed inside a clean laboratory cage (60cm³) to begin the next cycle of eclosion and egg collection for the next fly generation.

The same procedures were used for rearing immature *B. tryoni* except that apple fruit domes were used to collect eggs instead of zucchini domes and a carrot base diet was used instead of a pumpkin based diet. The carrot based diet consisted of 300g dehydrated sliced carrot, 100g torula yeast, 10g nipagin, 21ml hydrochloric acid and 2000ml of water. The carrot, yeast and nipagin were mixed together and soaked in 1000ml of water overnight. The remaining 1000ml of water and the hydrochloric acid were added while blending until a consistency of a thick paste was obtained. The diet was placed in three diet trays and eggs of *B. tryoni* were placed on the diets at a ratio of 3 eggs/gram of diet (Pike et al. 2001).

### 2.1.4 Test plant species selection procedure

Host choice and host use patterns of both *B. cucumis* and *B. tryoni* were compared at three plant taxonomic levels that included (1) plants across different plant families, (2) plants within a single plant family, and (3) plant varieties within a single plant species. These plants were selected on the basis of their phylogenetic relationship (Figure 2.1) to the known primary hosts; Cucurbitaceae for *B. cucumis*, and Myrtaceae and Rosaceae for *B. tryoni* (Judd et al. 2002, Angiosperm Phylogeny Group 2003), and on records of primary and alternate hosts reported for these species (May 1957, Allwood and Angeles 1979, Smith et al. 1988, Hancock et al. 2000). Plant species from within the Cucurbitaceae, Solanaceae, Passifloraceae and Myrtaceae were used for *B. cucumis* while species from within Myrtaceae, Rosaceae, Solanaceae and Cucurbitaceae were used for *B. tryoni*. Individual plant species used for the three plant taxonomic levels are described in the respective chapters.
Figure 2.1. Classification of Orders and Families of flowering plants. (Source: Angiosperm Phylogeny Group (2003)).
CHAPTER 3: HOST PREFERENCE AND HOST USE OF BACTROCERA CUCUMIS (FRENCH) AND BACTROCERA TRYONI (FROGGATT) ACROSS PLANT FAMILIES, WITHIN PLANT FAMILIES AND WITHIN PLANT VARITIES
Chapter 3. Host preference and host use of B. cucumis & B. tryoni at three plant taxonomic levels

3.1 INTRODUCTION

Generalist phytophagous insects accept and respond to a wide array of host plant cues and as a result exhibit minimal host ranking behaviour, resulting in the use of a wider host range than that for specialist insects (Michaud 1990, Aluja et al. 2000). However, distinct host ranking behaviour by generalist species has been reported in some cases (Berdegue et al. 1998, Rodriguez-Saona and Trumble 1999, Clarke et al. 2001). Most phytophagous insects are highly specific and exhibit high host discrimination behaviour which in turn result in specialization on plant species within groups of related plant families, one plant family, or even be restricted to a lower plant taxonomic level (genus, species, variety) (Ehrlich and Raven 1964, Singer 1971, Wiklund 1975, Thompson 1998). Whether the oviposition preference executed by phytophagous insects correlates with their fitness consequences (preference-performance hypothesis) or a function of other behavioural/physiological insect-plant associations has been debated in several empirical studies (Rausher 1980, Fitt 1986a, Barton-Browne 1993, Berdegue et al. 1998, Carr et al. 1998, Thompson 1998, Marques et al. 2000, Sipura and Tahvanainen 2000, Gonzalez-Megias and Gomez 2001, Singer 2001, Bruyn et al. 2002, Jallow and Zalucki 2003). Such contradictory observations indicate a need for a closer examination of the generality of the preference-performance hypothesis in shaping host choice and host use of the various insect-plant interacting systems.

In fruit flies, the ovipositing female determines the larval host plant and hence provides an ideal system to test the validity of the preference-performance hypothesis. Since the quality, abundance and frequency of occurrence of potential host plants vary greatly in the natural habitat, ovipositing tephritid females have to make decisions to either accept or reject a potential host or vary the proportion of eggs laid (Leather 1994, Roitberg et al. 1999, Awmack and Leather 2002, Diaz-Fleischer and Aluja 2003a). The preference-performance hypothesis predicts that in such circumstances natural selection will select against female tephritids ovipositing in plant species that decrease offspring performance. However, this hypothesis has seldom been tested in frugivorous tephritids.
In this study, I investigated the patterns of host choice and host use of the specialist cucumber fruit fly, *B. cucumis*, and the generalist Queensland fruit fly, *B. tryoni*, with respect to their hypothesized primary and alternate hosts (May 1957, Smith et al. 1988, Hancock et al. 2000). The study investigated both the prediction of the preference-performance hypothesis and evaluated the host preference ranking of these two species at three distinct plant taxonomic levels. The study began by investigating the preference-performance relationship at the broader taxonomic level (across plant families), followed by species within single plant family, and finally, plant varieties within a species. Other post-alighting physical fruit traits that could explain their host use patterns of these two species were also investigated.

3.2 MATERIALS AND METHODS

3.2.1 Study organisms and environmental conditions

The relationship between oviposition preference and offspring performance of *B. cucumis* was studied using mature fruits from Cucurbitaceae, Passifloraceae and Solanaceae. Cucurbitaceae fruit species used included cucumber, *Cucumis sativus* L.; zucchini, *Cucurbita pepo* L. and yellow button squash, *Cucurbita pepo* L. while those of Passifloraceae and Solanaceae included passionfruit, *Passiflora edulis* Sims, and tomato (var. ‘Grosse Lisse’), *Solanum lycopersicum* L. respectively. Fruits from Rosaceae, Myrtaceae, Solanaceae and Cucurbitaceae were used for the study that involved *B. tryoni*. Rosaceae fruits used included apple, *Malus domestica* Borkh; plum, *Prunus domestica* L. and pear, *Pyrus communis* L., while those of Myrtaceae, Solanaceae and Cucurbitaceae included guava, *Psidium guajava* L.; tomato (var. ‘Grosse Lisse’) and zucchini respectively. These plants were selected based on their phylogenetic relationship to the known primary hosts (i.e., Cucurbitaceae for *B. cucumis*, and Myrtaceae and Rosaceae for *B. tryoni*) (Judd et al. 2002, Angiosperm Phylogeny Group 2003), and also based on the reported cases of primary and alternate hosts of these two fly species (May 1957, Allwood and Angeles 1979, Smith et al. 1988, Hancock et al. 2000).

All studies were undertaken in the laboratory at controlled temperature and humidity of 26 ± 1 °C and 65 ± 10 % respectively. Adult flies used in this study were from
laboratory-reared colonies that were ninth and second generations removed from the wild, for *B. cucumis* and *B. tryoni* respectively. Fruits used in this study were sourced from organic farms to ensure freedom from agricultural chemicals.

### 3.2.2 Experimental protocol

The study was conducted at three plant taxonomic levels mentioned above and for each of the levels, both choice and no-choice experimental protocols were used for the oviposition preference studies. Measures of oviposition preference included pre-oviposition time period, oviposition time period and proportion of total eggs laid per fruit. My hypothesis was that if a fly species ranked one host higher than another, it would (i) accept the highly ranked host more quickly than other hosts for oviposition (i.e., shorter pre-oviposition time period), (ii) oviposit into the higher ranked host for a longer period of time, and (iii) deposit a proportionately greater number of eggs into the higher ranked host (Singer 1982, Papaj and Rausher 1983, Miller and Stickler 1984, Singer et al. 1992, Barton-Browne and Withers 2002). Additional choice studies the measured relative host preferences of the two fly species were also conducted. Measures of host preference for these studies included, relative number of fruit visitations, proportion of visits that resulted in oviposition attempts (curling of abdomen inwards and extending ovipositor at right angle to the fruit surface), and proportion of oviposition attempts that resulted in an oviposition event (penetration of fruit surface with the ovipositor) on each fruit. These preference measurements help identify where host discrimination occurred during the oviposition process (i.e., from visiting the host through to egg deposition).

Offspring performance studies were done with *B. cucumis* and *B. tryoni* to investigate the effect of each host species on the different life stages. The measures of offspring performance were proportion of eggs that hatched into larvae, proportion of eggs that became pupae, and proportion of eggs that became adults. In addition, a fitness index (*rl*) was calculated as a measure of the overall fitness for flies that emerged from each host species where \( rl = lx.mx/(tl+tp) \), and \( lx \) is the percentage pupation, \( mx \) is the mean pupal mass, \( tl \) is the larval duration, and \( tp \) is the pupal duration (Jallow and Zalucki 2003).
A total of twelve experiments were undertaken in this study. Experiments 1-4 investigated the relationship between oviposition preference and offspring performance for *B. cucumis* and *B. tryoni* on fruit species across different plant families (primary and alternate hosts) while experiments 5-8 investigated that on fruit species within their respective primary host plant family. The preference-performance relationship of *B. cucumis* and *B. tryoni* on plant variety within their primary host plant species was investigated in experiments 9-12.

### 3.2.3 Experiment 1: Oviposition preference of *B. cucumis* across different plant families

#### No-choice study

A single fruit of zucchini, tomato or passionfruit were placed separately in a 30 x 30 x 30cm cage. This was repeated with fifteen cages which consisted of five cages per fruit species. A single, once-mated, gravid, 16 days old female fly with no prior oviposition experience was placed in each cage at 0830h and the pre-oviposition and oviposition time periods were recorded for each fruit in each cage. When the oviposition event was accomplished, both the fruit and the fly were replaced with fresh fruit of the same species and a new fly from the same cohort. If no oviposition event occurred within the 2 hours, both the fly and fruit were removed and replaced with fresh fruit of the same species and a new fly. The observations were terminated at 1230h and each oviposited fruit and the respective fly were dissected. Experiments were done between 0830-1230h each day because preliminary observations showed a decrease in oviposition activity after 1230h. The proportion of total eggs laid was calculated by dividing the number of eggs deposited into the fruit by the sum of eggs laid and those that remained in the ovaries of the fly. The same experiment was repeated the following day except that 17 days old females from the same cohort were used.

#### Choice study

(i) Pre-oviposition time, oviposition time and proportion of eggs laid/ fruit species

These experiments were similar to the no-choice study except that the host fruits of each species were placed in the same 60 x 60 x 60cm cage (~ 30cm apart), and repeated in each of six cages. The fruit positions in the cages were randomized to eliminate positional effects. Pre-oviposition time period, oviposition time period and
proportion of total eggs laid were recorded. These experiments were conducted over two days using 19 and 20 days old flies from the same cohorts as those used in the no-choice experiments.

(ii) Fruit visitation, oviposition attempts and oviposition events/ fruit species
These experiments were similar to the first choice experiments (i) except that oviposition preference was measured by the number of fly visitations on each fruit, proportion of visitations that resulted in oviposition attempts, and the proportion of oviposition attempts that resulted in oviposition events. A single visitation to a fruit species was recorded each time a fly landed on a fruit. Similarly, a single oviposition attempt was recorded each time a fly made an oviposition attempt during a visit. If a fly departed and returned to the same fruit species; a second visit was recorded and a second oviposition attempt was recorded if one was made. Observations were terminated at the end of an oviposition event for each cage. Fruits recorded from cages where an oviposition event had occurred were dissected and checked for egg deposition.

3.2.4 Experiment 2: Offspring performance of B. cucumis across different plant families
Eggs of B. cucumis were collected by placing egging domes made from zucchini, tomato and passionfruit in a cage with 16-18 days old flies for 30 minutes. The flies used for egg collection were from the same cohort as those used in the preference study (Experiment 1), but were separated from those used in Experiment 1 on the third day after emergence. Ten eggs were removed from the domes of each fruit species and placed into each of ten fruits of the same fruit species (i.e., eggs from a zucchini dome were placed into zucchini fruits) using a fine tip paintbrush (960 N0. 2 China). The number of eggs per fruit was based on the lowest fruit weight to ensure that developing larvae had sufficient food (> 2g) to complete development. Individual fruits were placed on fine gauze on a piece of metal mesh covering the open top of a plastic container. The gauze ensured that no larvae drowned in the fluids from the decomposing fruit. The plastic containers holding the fruits were placed separately on sterile sawdust inside a larger container and were sealed with ventilated lid. After the first day of egg incubation, each fruit was observed at 2 hour intervals and the number of hatched eggs and time of egg-hatch was recorded.
The larval development period in each fruit and proportion of survival to pupae stage was recorded. When pupation began, the sawdust in each container was sieved daily until no more pupae were recovered. Pupae recovered each day from each fruit were counted, weighed, and placed separately on sterilized sawdust in a clear plastic container with a ventilated lid. Emerged flies were sexed and counted daily, and the proportion of eggs that survived to pupae and adulthood, and the pupal development period were recorded.

3.2.5 Experiment 3: Oviposition preference of *B. tryoni* across different plant families

The experimental procedures, and the data collected were similar to Experiment 1 except that *B. tryoni* was used instead of *B. cucumis*. The fruit species used in this study were guava, apple, tomato and zucchini.

3.2.6 Experiment 4: Offspring performance of *B. tryoni* cross different plant families

The experimental procedures, and the data collected were similar to Experiment 2, except the fruit species used were same as those used in Experiment 3 (guava, apple, tomato and zucchini) and the fruit fly species was *B. tryoni*. Each fruit was inoculated with 15 eggs from 16-20 days old *B. tryoni* colony that was kept separated from those flies used for the oviposition preference study in Experiment 3.

3.2.7 Experiment 5: Oviposition preference of *B. cucumis* within Cucurbitaceae

The experimental procedures, and the data collected were similar to Experiment 1, except that fruit species from the same plant family (Cucurbitaceae) were used. The fruit species used were cucumber, zucchini and yellow button squash.

3.2.8 Experiment 6: Offspring performance of *B. cucumis* within Cucurbitaceae

The experimental procedures, and the data collected were similar to Experiment 2, except that the fruit species used were cucumber, zucchini and yellow button squash, as in Experiment 5.
3.2.9 Experiment 7: Oviposition preference of B. tryoni within Rosaceae
The experimental procedures, and the data collected were similar to Experiment 1. However, fruits used in this study included apple, plum and pear (primary host of B. tryoni). Second generation 16-20 days old B. tryoni females were used in this study.

3.2.10 Experiment 8: Offspring performance of B. tryoni within Rosaceae
The experimental procedures, and the data collected were similar to Experiment 2. Fruit species used in Experiment 7 (apple, plum and pear) were used in this study and each fruit was inoculated with 15 eggs from 16-20 days old colony of B. tryoni.

3.2.11 Experiment 9: Oviposition preference of B. cucumis within cucumber varieties
All experimental procedures and the data collected were similar to Experiment 1. However, fruits used in this study were different cucumber varieties which included ‘Green’, ‘Lebanese’ and ‘Continental’. Sixth generation 20-23 days old B. cucumis females with no prior oviposition experience were used in this study.

3.2.12 Experiment 10: Offspring performance of B. cucumis within cucumber varieties
The experimental procedures and the data collected were similar to Experiment 2. The cucumber varieties used in Experiment 9 (‘Green’, ‘Lebanese’ and ‘Continental’) were used in this study and each fruit was inoculated with 15 eggs collected from a 24 day old colony of B. cucumis.

3.2.13 Experiment 11: Oviposition preference of B. tryoni within apple varieties
The experimental procedures and the data collected were similar to Experiment 1. However, fruits used in this study were different apple varieties which included ‘Red Delicious’, ‘Golden Delicious’ and ‘Granny Smith’. Sixth generation 20-23 days old B. tryoni females were used in this study.

3.2.14 Experiment 12: Offspring performance of B. tryoni within apple varieties
The experimental procedures and the data collected were similar to Experiment 2. Apple varieties used in Experiment 11 (‘Red Delicious’, ‘Golden Delicious’, and
‘Granny Smith’) were used in this study and each fruit was inoculated with 15 eggs collected from a 24 days old colony of B. tryoni.

3.2.15 Fruit traits influencing host use patterns of the two Bactrocera species

Two physical fruit traits, fruit size and pericarp toughness, were investigated to determine their roles in influencing the observed patterns of oviposition preference and host use. Fruit size was measured as the volume (mL) of water displaced when fruits were placed in water. Immediately after each of the above choice experiments was terminated, fruits from the cages in which the fly either oviposited or made oviposition attempts were placed individually in a known volume of water in a measuring cylinder. The amount of water displaced by the fruit was recorded as the volume of fruit. This was done for all the different fruit species used with both fly species.

Ten fruits of each species were randomly selected from the cohort of fruits used for the preference-performance study for both fly species to measure pericarp toughness. Pericarp toughness was measured as the force (Newton, N) required to penetrate the pericarp using a computerized Shimadzu Autograph penetrometer (AGS-H 500N model, Shimadzu Cooperation, Japan). Each fruit was placed on a plate directly below a 1.5mm diameter probe and the probe was allowed to descend and penetrated the fruit pericarp to 2cm depth at a speed of 10mm/minute. Each fruit was penetrated at three randomly selected sites and the mean reading of these three sites was recorded as the pericarp toughness of each fruit.

3.2.16 Statistical analyses

Statistical analyses were done using SPSS 11.5 for Windows (SPSS Inc, 2002). Data were subjected to one-way analysis of variance (ANOVA) or a t-test, with host species as the factor. Prior to parametric tests, all data were checked for normality, and homogeneity of variance was tested using Levene’s test. Where the assumptions of the ANOVA were violated, in spite of standard transformations, the non-parametric equivalent of ANOVA, Kruskal-Wallis test, was used instead. When a significant difference was detected by the ANOVA, Tukey’s HSD test or a Games-Howell test (when variance was heterogenous) was used for post-hoc, pair-wise comparisons of
means, after applying a Bonferroni correction. Any data recorded as proportions were arcsine-square root transformed prior to analysis and back-transformed for graphical presentation. A chi-square test was used to test for differences in fruit visitations, oviposition attempts and oviposition events on each fruit species.

3.3 RESULTS

Since the preference experiments for the within and across plant families were carried out over four days (using flies that were 16 and 17 days old for the no-choice and 19 and 20 days old for the choice studies), an analysis of variance was done to verify if there was a difference in the egg load of female flies used on the different days. The analysis showed that there was no significant difference in egg load \((F_{3,25} = 0.601, P = 0.621)\) and therefore data from the two day observations for the no-choice experiments were combined together for subsequent analyses and so were those for the choice experiments.

3.3.1 Experiment 1: Oviposition preference of \textit{B. cucumis} across different plant families

(i) Pre-oviposition time, oviposition time and proportion of eggs laid/fruit species

When fruits from different plant families (zucchini, passionfruit and tomato) were offered simultaneously to \textit{B. cucumis} in the choice study, there was no difference in preference with respect to the pre-oviposition time period \((F_{2,13} = 0.631, P = 0.548)\), oviposition time period \((F_{2,13} = 0.225, P = 0.802)\) or proportion of total eggs laid \((F_{2,13} = 1.429, P = 0.275)\). Although, there was no difference in the proportion of total eggs laid, only 22\% of the total number of oviposition events on passionfruit resulted in egg deposition, while eggs were deposited in all oviposition events on zucchini and tomato. When these three fruits were offered separately to \textit{B. cucumis} in the no-choice experiments, there were significant differences in the oviposition time period \((F_{2,10} = 5.812, P = 0.021)\) and the proportion of eggs laid between each fruit species \((F_{2,10} = 7.173, P = 0.012)\), but there was no significant difference in the pre-oviposition time period \((F_{2,10} = 0.413, P = 0.673)\) (Figure 3.1). Post-hoc tests showed that a greater amount of time was spent ovipositing in zucchini than in tomato while the time spent ovipositing on passionfruit did not differ from either of these two fruits. Egg deposition was only observed in zucchini (Figure 3.1).
Figure 3.1. Oviposition preference of *Bactrocera cucumis* (French) for zucchini, passionfruit, and tomato in a no-choice study with respect to pre-oviposition time period (*n* = 14), oviposition time period (*n* = 14) and proportion of eggs laid in a single oviposition event (*n* = 14). Bars are means + standard error. Bars with the same letter within a given preference ranking parameter are not significantly different from each other.

(ii) Fruit visitations, oviposition attempts and oviposition events/ fruit species

There was a significant difference in the number of visits each fruit received (*χ²* = 22.211, d.f. = 2, *P* < 0.001), where passionfruit and tomato received more visits than zucchini (Table 3.1). However, all visits to zucchini, and three-quarters of visits to passionfruit resulted in oviposition attempts, compared to a quarter of visits on tomato (Table 3.1). *B. cucumis* successfully oviposited in zucchini more often in its first visit than passionfruit which resulted in the lower number of fruit visitation to zucchini. There was no oviposition event recorded in tomato (Table 3.1). Eggs were laid only in zucchini but not in passionfruit even though penetration of the pericarp was recorded in passionfruit (Table 3.1).
Table 3.1. Number of visits made by *Bactrocera cucumis* (French) on zucchini, passionfruit and tomato and the proportion that engaged in oviposition attempts and oviposition events in a choice scenario.

<table>
<thead>
<tr>
<th>Fruit species</th>
<th>Cumulative number of visits</th>
<th>Proportion (%) of cumulative visits resulting in an oviposition attempt</th>
<th>Proportion (%) of cumulative oviposition attempts resulting in an oviposition event</th>
<th>Egg deposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zucchini</td>
<td>5</td>
<td>100</td>
<td>80</td>
<td>✓</td>
</tr>
<tr>
<td>Passionfruit</td>
<td>34</td>
<td>77</td>
<td>31</td>
<td>×</td>
</tr>
<tr>
<td>Tomato</td>
<td>18</td>
<td>28</td>
<td>0</td>
<td>×</td>
</tr>
</tbody>
</table>

3.3.2 Experiment 2: Offspring performance of *B. cucumis* across different plant families

Growth and survival of all life stages (% egg hatch through to adult emergence) were observed in each of the fruits. A Kruskal-Wallis test showed that there was a significant difference in the number of eggs that survived to larvae ($H = 10.495$, d.f. = 2, $P = 0.005$), pupae ($H = 22.461$, d.f. = 2, $P < 0.001$) and adults ($H = 22.249$, d.f. = 2, $P < 0.001$). Zucchini sustained a higher proportion of eggs that developed to larvae (100%), pupae (97 ± 4.83%) and adults (88 ± 9.19%) and this was followed by tomato with 92 ± 7.89% of eggs that developed into larvae, 60 ± 38.01 % into pupae and 53 ± 33.68% into adults (mean ± SD). Only one fruit out of the ten passionfruit yielded seven pupae that never developed into adults. Consequently, no analysis was done for passionfruit, but the data were still used for graphical representation (Figure 3.2). The fitness of *B. cucumis* was significantly higher on zucchini as compared to tomato ($t_{17} = 2.939$, $P = 0.016$) but was distinctively lower on passionfruit than that from zucchini and tomato (Figure 3.2).
Figure 3.2. Fitness index of *Bactrocera cucumis* (French) as a consequence of using zucchini, tomato and passionfruit. Bars are means ± standard error. Bars with the same letter are not significantly different from each other according to a *t*-test.

Preference-performance relationship of *B. cucumis* across different plant families
The three oviposition preference parameters were positively but non-significantly correlated with fitness index (pre-oviposition time period \( r = 0.85, P = 0.177 \), oviposition time period \( r = 0.666, P = 0.268 \) and proportion of total eggs laid \( r = 0.824, P = 0.192 \)). The lack of significance may be caused by the use of only three fruit species which resulted in low degrees of freedom to evaluate significance.

3.3.3 Experiment 3: Oviposition preference of *B. tryoni* across plant families
(i) Pre-oviposition time, oviposition time and proportion of eggs laid/ fruit species
A one-way ANOVA revealed that there was no significant difference in the pre-oviposition time period \( (F_{3,37} = 1.063, P = 0.377) \), oviposition time period \( (F_{3,37} = 1.521, P = 0.225) \) or the proportion of total eggs laid \( (F_{3,37} = 0.667, P = 0.577) \) by *B. tryoni* on guava, apple, tomato and zucchini in the no-choice situation (Figure 3.3). A similar oviposition preference ranking was also observed under the choice
experiments where $B. \textit{tryoni}$ equally preferred each fruit species with respect to the pre-oviposition time period ($F_{3,28} = 1.591, P = 0.214$), oviposition time period ($F_{3,28} = 2.030, P = 0.132$) and the proportion of total eggs laid ($F_{3,28} = 0.944, P = 0.432$).

**Figure 3.3.** Oviposition preference of $Bactrocera \textit{tryoni}$ (Froggatt) for guava, apple, tomato and zucchini in a no-choice study with respect to pre-oviposition time period ($n = 38$), oviposition time period ($n = 38$) and proportion of eggs laid in a single oviposition event ($n = 38$). Bars are means + standard error. Bars with the same letter for a given preference ranking parameter are not significantly different from each other.

(ii) Fruit visitations, oviposition attempts and oviposition events/ fruit species

A chi-square test showed that there was a significant difference in the number of visits ($\chi^2 = 12.271, \text{d.f.} = 3, P = 0.007$) made by $B. \textit{tryoni}$ between guava, apple, tomato and zucchini and the proportion of oviposition attempts that resulted in an oviposition event ($\chi^2 = 88.136, \text{d.f.} = 3, P < 0.001$) (Table 3.2). In contrast, there was no
significant difference in the proportion of total visits that resulted in oviposition attempts \( (\chi^2 = 7.126, \text{ d.f.} = 3, P = 0.068) \) between the fruit species. All fruit species presented to the flies had eggs deposited into them (Table 3.2). The lower number of visits and higher proportion of oviposition events on zucchini indicated that most of the flies that visited zucchini engaged in an oviposition event during their first visit.

**Table 3.2.** Number of visits made by *Bactrocera tryoni* (Froggatt) on guava, apple, tomato and zucchini and the proportion that engaged in oviposition attempts and oviposition events in a choice scenario.

<table>
<thead>
<tr>
<th>Fruit species</th>
<th>Cumulative number of visits</th>
<th>Proportion (%) of cumulative visits resulting in an oviposition attempt</th>
<th>Proportion (%) of cumulative oviposition attempts resulting in an oviposition event</th>
<th>Egg deposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guava</td>
<td>28</td>
<td>64.3</td>
<td>61.6</td>
<td>Yes (✓)</td>
</tr>
<tr>
<td>Apple</td>
<td>29</td>
<td>48.3</td>
<td>21.4</td>
<td>Yes (✓)</td>
</tr>
<tr>
<td>Tomato</td>
<td>19</td>
<td>63.2</td>
<td>8.3</td>
<td>Yes (✓)</td>
</tr>
<tr>
<td>Zucchini</td>
<td>9</td>
<td>77.8</td>
<td>85.7</td>
<td>Yes (✓)</td>
</tr>
</tbody>
</table>

**3.3.4 Experiment 4: Offspring performance of *B. tryoni* across plant families**

There was no significant difference in the proportion of eggs that survived to larvae \( (F_{3,36} = 1.068, P = 0.375) \) between guava, apple, tomato and zucchini, but there were significant differences between these fruits in the proportions that survived to pupae \( (F_{3,36} = 20.088, P < 0.001) \) and adults \( (F_{3,36} = 25.012, P < 0.001) \). Post-hoc tests showed that the proportion of eggs that survived to pupae and adults was high in apple and significantly different to that from tomato, but the proportion from guava did not differ from that of apple and tomato. Zucchini produced a significantly lower number of pupae and adults of *B. tryoni* as compared to the other three fruits.

There was a significant difference in the overall fitness of flies that developed in guava, apple, tomato and zucchini \( (\text{ANOVA}, F_{3,34} = 12.388, P < 0.001) \). Post-hoc comparisons revealed that the fitness of *B. tryoni* that developed from zucchini was significantly lower than those from the other three fruits. There was no significant difference in the fitness of offspring from guava, tomato and apple (Figure 3.4).
Figure 3.4. Fitness index of *Bactrocera tryoni* (Froggatt) as a consequence of using guava, apple, pear, tomato and zucchini. Bars are means + standard error. Bars with the same letter are not significantly different from each other.

Preference-performance relationship of *B. tryoni* across different plant families
The correlations between each of the three measures of oviposition preference (pre-oviposition time, oviposition time and % eggs laid) and offspring performance (fitness index) were weak and not statistically significant. The association of fitness with pre-oviposition time was negative ($r = -0.132$, $P = 0.434$), while it was positive with oviposition time ($r = 0.056$, $P = 0.472$) and proportion of eggs laid ($r = 0.613$, $P = 0.194$).

3.3.5 Experiment 5: Oviposition preference of *B. cucumis* within Cucurbitaceae
(i) Pre-oviposition time, oviposition time and proportion of eggs laid/ fruit species
A one-way ANOVA for the no-choice study showed that there was no difference in the pre-oviposition time period ($F_{2,20} = 0.173$, $P = 0.842$) of *B. cucumis* between fruits. However, there was a significant difference in oviposition time period ($F_{2,20} = 6.914$, $P = 0.005$) and proportion of eggs laid ($F_{2,20} = 5.932$, $P = 0.009$) between cucumber, zucchini and squash. Tukey’s HSD test revealed that the amount of time spent ovipositing in zucchini was significantly greater than in cucumber. Oviposition
duration on squash did not differ from the other two fruits (Figure 3.5). Post-hoc comparison also showed that the differences in proportion of eggs laid in the three fruits were similar to the relationship observed in terms of oviposition time period (Figure 3.5). When fruits were offered simultaneously in the choice study, *B. cucumis* equally accepted each fruit species and did not show any preference ranking with respect to its pre-oviposition time period ($F_{2,17} = 0.034$, $P = 0.967$), oviposition time period ($F_{2,17} = 0.519$, $P = 0.588$) or proportion of eggs laid ($F_{2,17} = 2.583$, $P = 0.105$).

![Oviposition preference of Bactrocera cucumis (French) for Cucurbitaceae fruit species with respect to the pre-oviposition time period ($n = 23$), oviposition time period ($n = 23$) and proportion of total eggs laid ($n = 23$) during a single oviposition event in a no-choice scenario. Bars are means ± standard error. Bars with the same letter within a given preference ranking parameter are not significantly different from each other.](image)

**Figure 3.5.** Oviposition preference of *Bactrocera cucumis* (French) for Cucurbitaceae fruit species with respect to the pre-oviposition time period ($n = 23$), oviposition time period ($n = 23$) and proportion of total eggs laid ($n = 23$) during a single oviposition event in a no-choice scenario. Bars are means ± standard error. Bars with the same letter within a given preference ranking parameter are not significantly different from each other.

(ii) Fruit visitations, oviposition attempts and oviposition events/fruit species

There was no difference in the number of visits each fruit received ($\chi^2 = 0.5$, d.f. = 2, $P = 0.778$) or in the proportion of oviposition attempts on each fruit ($\chi^2 = 4.545$, d.f. =
2, \( P = 0.103 \) (Table 3.3). However, the proportion of oviposition attempts that resulted in an oviposition event differed significantly among fruits (\( \chi^2 = 25.126, \text{d.f.} = 2, P < 0.001 \)). A greater proportion of oviposition events were observed in zucchini and squash than in cucumber. Oviposition events in all three fruit species resulted in egg deposition (Table 3.3).

Table 3.3. Number of visits made by *Bactrocera cucumis* (French) on zucchini, cucumber and squash and the proportion that resulted in oviposition attempts and oviposition events in a choice scenario.

<table>
<thead>
<tr>
<th>Cucurbitaceae fruit species</th>
<th>Cumulative number of visits</th>
<th>Proportion (%) of cumulative visits resulting in an oviposition attempt</th>
<th>Proportion (%) of cumulative oviposition attempts resulting in an oviposition event</th>
<th>Egg deposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zucchini</td>
<td>6</td>
<td>100</td>
<td>83.3</td>
<td>Yes (✓)</td>
</tr>
<tr>
<td>Squash</td>
<td>6</td>
<td>100</td>
<td>83.3</td>
<td>Yes (✓)</td>
</tr>
<tr>
<td>Cucumber</td>
<td>4</td>
<td>75</td>
<td>33.3</td>
<td></td>
</tr>
</tbody>
</table>

3.3.6 Experiment 6: Offspring performance of *B. cucumis* within Cucurbitaceae

There was no significant difference in the proportion of eggs that hatched into larvae (\( F_{2,27} = 0.500, P = 0.612 \)) between zucchini, squash and cucumber, but there was a significant difference in the proportion of eggs that survived through to pupae (\( F_{2,27} = 24.002, P < 0.001 \)) and adult (\( F_{2,27} = 11.849, P < 0.001 \)). The proportion of eggs from zucchini and squash that survived to pupae or adult did not differ, but was greater than those that developed from cucumber.

The fitness index of *B. cucumis* differed significantly across the three cucurbit species (ANOVA, \( F_{2,24} = 29.101, P < 0.001 \)). Post-hoc comparisons (Tukey’s HSD) revealed that the fitness of *B. cucumis* on zucchini and squash did not differ significantly from each other, but was significantly higher than that on cucumber (Figure 3.6).
Preference-performance relationship of *B. cucumis* within Cucurbitaceae

Correlation coefficients between each of the three measures of oviposition preference (pre-oviposition time, oviposition time and % eggs laid) and offspring performance (fitness index) were large but not statistically significant. The association of fitness with pre-oviposition time was negative \( r = -0.652, P = 0.274 \), while it was positive with oviposition time \( r = 0.686, P = 0.259 \) and proportion of eggs laid \( r = 0.726, P = 0.241 \). The lack of significance may be a reflection of the fact that only three fruit species were included in this study resulting in low degrees of freedom to evaluate significance.
3.3.7 Experiment 7: Oviposition preference of *B. tryoni* within Rosaceae

(i) Pre-oviposition time, oviposition time and proportion of eggs laid/ fruit species

When fruits within Rosaceae (apple, plum, pear) were exposed to *B. tryoni* in the no-choice experiments, *B. tryoni* equally preferred each fruit species with respect to its pre-oviposition time period (ANOVA, $F_{2,35} = 0.420$, $P = 0.660$), oviposition time period (ANOVA, $F_{2,35} = 0.355$, $P = 0.704$) and the proportion of total eggs that it deposited in each fruit species (ANOVA, $F_{2,35} = 2.037$, $P = 0.146$) (Figure 3.7). However, when apple, plum and pear were exposed simultaneously in the choice experiments, *B. tryoni* visited and oviposited in apple and plum, but did not visit or oviposit in pear. A $t$-test comparison in the preference ranking of *B. tryoni* between apple and plum showed that there was no difference in pre-oviposition time period ($t_{29} = 1.354$, $P = 0.186$), oviposition time period ($t_{29} = 1.423$, $P = 0.165$) and proportion of total eggs laid ($t_{29} = 0.712$, $P = 0.482$) between these two fruits.

![Mean pre-oviposition & oviposition time period (min) and Mean proportion of total eggs laid (%)](image)

**Figure 3.7.** Oviposition preference of *Bactrocera tryoni* (Froggatt) with respect to the pre-oviposition time period ($n = 38$), oviposition time period ($n = 38$) and proportion of total eggs laid ($n = 38$) for fruits within Rosaceae family in a no-choice scenario. Bars are means + standard error. Bars with the same letter within a given preference ranking parameter are not significantly different from each other.
(ii) Fruit visitations, oviposition attempts and oviposition events/ fruit species

The oviposition behaviour of *B. tryoni* on apple, pear, and plum in a choice experiment showed that there was no significant difference in the number of visits ($\chi^2 = 0.145, \text{d.f.} = 2, P = 0.930$) and the proportion of fruit visitations that resulted in oviposition attempts ($\chi^2 = 1.946, \text{d.f.} = 2, P = 0.378$) on the three fruit species. However, a significant difference was detected in the proportion of oviposition attempts that resulted in an oviposition event ($\chi^2 = 10.198, \text{d.f.} = 2, P = 0.006$) where plum received more oviposition events than apple and pear. All fruits that received oviposition events had eggs deposited into them (Table 3.4).

**Table 3.4.** Number of visits made by *Bactrocera tryoni* (Froggatt) on Rosaceae fruit species and the proportion that engaged in oviposition attempts and oviposition events in a choice scenario.

<table>
<thead>
<tr>
<th>Rosaceae fruit species</th>
<th>Cumulative number of visits</th>
<th>Proportion (%) of cumulative visits resulting in an oviposition attempt</th>
<th>Proportion (%) of cumulative oviposition attempts resulting in an oviposition event</th>
<th>Egg deposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple</td>
<td>19</td>
<td>84.2</td>
<td>62.5</td>
<td>Yes (✓)</td>
</tr>
<tr>
<td>Pear</td>
<td>19</td>
<td>68.4</td>
<td>69.2</td>
<td>Yes (✓)</td>
</tr>
<tr>
<td>Plum</td>
<td>17</td>
<td>70.6</td>
<td>100</td>
<td>Yes (✓)</td>
</tr>
</tbody>
</table>

3.3.8 Experiment 8: Offspring performance of *B. tryoni* within Rosaceae

A one-way ANOVA on the survival and development of the various life history stages of *B. tryoni* as a consequence of using apple, pear and plum showed that the performance of the offspring from these fruits differed across various life history stages among the fruits. There was no significant difference in the proportion of eggs that survived to larvae ($F_{2,27} = 1.292, P = 0.291$), but a significant difference was detected in the proportion of eggs that survived to pupae ($F_{2,27} = 15.733, P < 0.001$) and adult ($F_{2,27} = 12.957, P < 0.001$) between the three fruit species. The proportion of eggs that survived to pupae was similar in apple and pear but was significantly higher than plum which yielded a lower number of pupae (Tukey’s HSD test). The same relationship was observed between the fruits for the proportion of eggs becoming adults.
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The fitness index of *B. tryoni* that used apple and pear was high and did not differ from each other. In contrast, the fitness of the offspring that used plum was significantly lower than those from apple but did not differ from those which used pear (ANOVA, $F_{2,24} = 7.122$, $P = 0.004$, Figure 3.8).

![Fitness index of Bactrocera tryoni (Froggatt) as a consequence of using apple, pear and plum. Bars are means ± standard error. Bars with the same letter are not significantly different from each other.](image)

**Figure 3.8.** Fitness index of *Bactrocera tryoni* (Froggatt) as a consequence of using apple, pear and plum. Bars are means ± standard error. Bars with the same letter are not significantly different from each other.

**Preference-performance relationship of B. tryoni within Rosaceae**

The three measures of oviposition preference (pre-oviposition time period, oviposition time period and % eggs laid) in the no-choice scenario and offspring performance (fitness index) showed that offspring performance had a strong and statistically significant correlation with pre-oviposition time period ($r = -0.985$, $P = 0.008$) and oviposition time period ($r = 0.938$, $P = 0.031$). However, there was a weak non-significant correlation between proportion of eggs laid and offspring performance ($r = -0.153$, $P = 0.423$). The association of offspring performance with pre-oviposition time period and proportion of eggs laid was negative while that with oviposition time period was positive.
3.3.9 Experiment 9: Oviposition preference of *B. cucumis* within cucumber varieties

(i) Pre-oviposition time, oviposition time & proportion of eggs laid/ cucumber variety

In a no-choice experiments, *B. cucumis* showed no significant difference in its pre-oviposition time period (ANOVA, $F_{2,26} = 2.024, P = 0.152$) between the three cucumber varieties. However, there were significant differences in oviposition time period ($F_{2,26} = 4.272, P = 0.025$) and proportion of total eggs laid ($F_{2,26} = 6.592, P = 0.005$) between the three varieties. Tukey’s HSD post-hoc comparison at $\alpha = 0.05$ revealed that the time spend ovipositing in the ‘Lebanese’ cucumber variety was longer and not significantly different to that on the ‘Continental’ cucumber, but was significantly different to ‘Green’ cucumber which had the lowest mean oviposition time period. ‘Continental’ and ‘Green’ cucumber varieties did not differ from each other in their mean oviposition time periods (Figure 3.9). There was no significant difference in the proportion of eggs laid by *B. cucumis* in ‘Lebanese’ and ‘Continental’ cucumber varieties, but both varieties received significantly higher proportion of eggs than ‘Green’ cucumber (Figure 3.9).

When the three cucumber varieties were simultaneously exposed to *B. cucumis* in the choice experiments, there was no significant difference in oviposition preference with respect to pre-oviposition time period ($H = 0.936, \text{ d.f.} = 2, P = 0.626$) and oviposition time period ($H = 4.823, \text{ d.f.} = 2, P = 0.090$), but a significant difference was detected in the proportion of total eggs laid into the fruits ($H = 14.548, \text{ d.f.} = 2, P = 0.001$). ‘Green’ cucumber received $8.53 \pm 8.532$ % of the total eggs deposited into it while the ‘Lebanese’ and ‘Continental’ varieties received $66.06 \pm 8.851$ % and $91.03 \pm 8.974$ % respectively (mean ± S.E).
Figure 3.9. Oviposition preference of *Bactrocera cucumis* (French) between three cucumber varieties in a no-choice scenario with respect to pre-oviposition time period (*n* = 29), oviposition time period (*n* = 29) and proportion of total eggs laid in a single oviposition event (*n* = 29). Bars are means + standard errors. Bars with the same letter within a given preference ranking parameter are not significantly different to each other.

(ii) Fruit visitations, oviposition attempts and oviposition event/ cucumber variety

A chi-square analysis showed that there was no significant difference in the frequency of visitations (*χ²* = 4.455, d.f. = 2, *P* = 0.108) made by *B. cucumis* to each cucumber variety and the proportion of visits that resulted in oviposition attempts (*χ²* = 1.016, d.f. = 2, *P* = 0.602) on each variety. However, a significant difference was detected in the proportion of oviposition attempts that resulted in oviposition events (*χ²* = 11.510, d.f. = 2, *P* = 0.003). The ‘Green’ cucumber variety received fewer oviposition events than the other two varieties (Table 3.5). Although eggs were deposited in each variety, only 12.5% of the total ‘Green’ cucumber fruits that received oviposition events had eggs deposited into them, while all fruits of the ‘Lebanese’ and ‘Continental’ cucumber varieties that received oviposition events had eggs deposited into them (Table 3.5).
Table 3.5. Number of visits made by *Bactrocera cucumis* (French) on three cucumber varieties and the proportion that resulted in oviposition attempts and oviposition events in a choice scenario.

<table>
<thead>
<tr>
<th>Cucumber variety</th>
<th>Cumulative number of visits</th>
<th>Proportion (%) of cumulative visits resulting in an oviposition attempt</th>
<th>Proportion (%) of cumulative oviposition attempts resulting in an oviposition event</th>
<th>Egg deposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green cucumber</td>
<td>30</td>
<td>83.33</td>
<td>32.00</td>
<td>✓</td>
</tr>
<tr>
<td>Lebanese cucumber</td>
<td>19</td>
<td>89.47</td>
<td>64.71</td>
<td>✓</td>
</tr>
<tr>
<td>Continental cucumber</td>
<td>17</td>
<td>76.47</td>
<td>46.15</td>
<td>✓</td>
</tr>
</tbody>
</table>

3.3.10 Experiment 10: Offspring performance of *B. cucumis* within cucumber varieties

There was no significant difference in the overall fitness index of *B. cucumis* between the three cucumber varieties (ANOVA, $F_{2,13} = 0.762$, $P = 0.486$) (Figure 3.10). Similarly, no significant differences were observed for the proportion of eggs that successfully developed into larvae (Kruskal-Wallis, $H = 1.701$, d.f. = 2, $P = 0.427$), pupae (ANOVA, $F_{2,13} = 0.129$, $P = 0.880$) and adult (ANOVA, $F_{2,13} = 0.384$, $P = 0.689$) between the cucumber varieties.
Figure 3.10. Fitness index of the offspring of *Bactrocera cucumis* (French) from ‘Green’, ‘Lebanese’ and ‘Continental’ cucumber varieties. Bars are means ± standard error. Bars with the same letter are not significantly different from each other.

3.3.11 Experiment 11: Oviposition preference of *B. tryoni* within apple varieties

(i) Pre-oviposition time, oviposition time, proportion of eggs laid/ apple variety

A one-way ANOVA revealed that *B. tryoni* showed no significant difference in its oviposition preference for the three apple varieties with regard to pre-oviposition time period ($F_{2,29} = 0.645$, $P = 0.532$), oviposition time period ($F_{2,29} = 0.907$, $P = 0.415$) and proportion of total eggs laid ($F_{2,29} = 1.204$, $P = 0.314$) in the no-choice experiments (Figure 3.11). Similar oviposition behaviour was also observed in the choice experiments where a Kruskal-Wallis test detected no significant differences in the pre-oviposition time period ($H = 3.121$, d.f. = 2, $P = 0.210$), oviposition time period ($H = 0.719$, d.f. = 2, $P = 0.698$) and proportion of total eggs laid ($H = 1.431$, d.f. = 2, $P = 0.489$) between the three apple varieties.
Figure 3.11. Oviposition preference of *Bactrocera tryoni* (Froggatt) between three apple varieties in a no-choice scenario with respect to pre-oviposition time period \((n = 32)\), oviposition time period \((n = 32)\) and proportion of total eggs laid in a single oviposition event \((n = 32)\). Bars are means ± standard errors. Bars with the same letter within a given preference ranking parameter are not significantly different to each other.

(ii) Fruit visitations, oviposition attempts and oviposition events/ apple variety

A chi-square Goodness of Fit test revealed that there was a significant difference in the number of visits \((\chi^2 = 11.740, \text{d.f.} = 2, P = 0.003)\) made by *B. tryoni* to the different apple varieties. The ‘Red Delicious’ variety received more visits than ‘Golden Delicious’ and ‘Granny Smith’ varieties (Table 3.6). There was no significant difference in the proportion of visits that resulted in an oviposition attempt \((\chi^2 = 0.451, \text{d.f.} = 2, P = 0.798)\) between the apple varieties, but a significant difference was detected in the proportion of oviposition attempts that resulted in oviposition events \((\chi^2 = 12.111, \text{d.f.} = 2, P = 0.002)\). The ‘Granny Smith’ variety received fewer
oviposition events than the ‘Red’ and ‘Golden Delicious’ varieties (Table 3.6). Despite these differences, all fruits from the three apple varieties that received oviposition events had eggs deposited into them.

**Table 3.6.** Number of visits made by *Bactrocera tryoni* (Froggatt) on three apple varieties and the proportion that resulted in oviposition attempts and oviposition events in a choice scenario.

<table>
<thead>
<tr>
<th>Apple variety</th>
<th>Cumulative number of visits</th>
<th>Proportion (%) of cumulative visits resulting in an oviposition attempt</th>
<th>Proportion (%) of cumulative oviposition attempts resulting in an oviposition event</th>
<th>Egg deposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red Delicious</td>
<td>151</td>
<td>58.29</td>
<td>22.73</td>
<td>✓</td>
</tr>
<tr>
<td>Golden Delicious</td>
<td>104</td>
<td>54.81</td>
<td>24.56</td>
<td>✓</td>
</tr>
<tr>
<td>Granny Smith</td>
<td>106</td>
<td>50.94</td>
<td>5.56</td>
<td>✓</td>
</tr>
</tbody>
</table>

**3.3.12 Experiment 12: Offspring performance of *B. tryoni* within apple varieties**

The non-parametric Kruskal-Wallis test revealed that there was no significant difference in the proportion of eggs of *B. tryoni* that hatched into larvae (*H = 0.535, d.f. = 2, P = 0.765*) and the proportion that further developed into pupae (*H = 1.808, d.f. = 2, P = 0.405*) and adults (*H = 1.771, d.f. = 2, P = 0.413*) between the three apple varieties. However, there was a significant difference in the overall fitness index of *B. tryoni* from the three apple varieties (ANOVA, *F*<sub>2,24</sub> = 5.121, *P* = 0.014). Post-hoc comparison (Tukey’s HSD, α = 0.05) showed that the ‘Granny Smith’ apple variety provided offspring with a lower fitness index than those from ‘Red’ and ‘Golden Delicious’ varieties (Figure 3.12).
Figure 3.12. Fitness index of *Bactrocera tryoni* (Froggatt) as a consequence of using ‘Red Delicious’, ‘Golden Delicious’ and ‘Granny Smith’ apple varieties. Bars are means ± standard error. Bars with the same letter are not significantly different from each other.

### 3.3.13 Fruit traits affecting host use of *B. cucumis*

There was a significant difference in the sizes (volume) of fruits used by *B. cucumis* cross different plant families (Kruskal-Wallis, $H = 31.35$, d.f. $= 2$, $P < 0.001$). Passionfruit ($142 ± 24.23$ mL) was intermediate in size between tomato ($90 ± 18.4$ mL), and zucchini ($198.57 ± 36.13$ mL) which was the largest of the three fruit species. The sizes of fruits used for the within family (Cucurbitaceae) study were also significantly different from each other (Kruskal-Wallis, $H = 23.33$, d.f. $= 2$, $P < 0.001$). Cucumber ($320 ± 84.55$ mL) was the largest followed by zucchini ($212.73 ± 11.04$ mL), while squash ($158.18 ± 48.75$ mL) was the smallest of the three (mean ± SD). However, a non-parametric Kruskal-Wallis test showed that there was no significant difference in the mean volume of the three cucumber varieties used in experiments 9-10 ($H = 3.527$, d.f. $= 2$, $P = 0.171$).
A one-way ANOVA showed that there was a significant difference in the pericarp toughness of fruits across different plant families \( (F_{2,27} = 216.32, \ P < 0.001) \). Pericarps of zucchini \( (4.3 \pm 0.19 \text{ N}) \) and tomato \( (4.87 \pm 0.45 \text{ N}) \) were less tough than that of passionfruit \( (12.42 \pm 1.62 \text{ N}) \). A significant difference was also detected in the pericarp toughness of zucchini, cucumber and squash used in the within family (Cucurbitaceae) study \( (F_{2,27} = 140.5, \ P < 0.001) \). Pericarp toughness of all three fruits differed significantly from one another (Games-Howell test) where cucumber \( (8.6 \pm 0.98 \text{ N}) \) possessed the tougher pericarp followed by squash \( (4.85 \pm 0.41 \text{ N}) \) and zucchini \( (4.3 \pm 0.19 \text{ N}) \) (mean ± SD). Similarly, a one-way analysis of variance detected a significant difference in pericarp toughness \( (F_{2,27} = 72.958, \ P < 0.001) \) between the three cucumber varieties used at the plant variety level. Tukey’s post-hoc comparisons revealed that pericarp toughness between these cucumber varieties were different from each other. The ‘Green’ cucumber variety had the toughest pericarp followed by that of the ‘Lebanese’ variety. ‘Continental’ variety had the softest pericarp.

### 3.3.14 Fruit traits affecting host use of B. tryoni

A one-way analysis of variance detected a significant difference in the size of fruits used by B. tryoni across different plant families \( (F_{3,36} = 181.375, \ P < 0.001) \). Apple and zucchini were similar in size but larger than tomato, and guava was the smallest (Games-Howell test). A Kruskal-Wallis test also detected significant differences in the size of apple, plum and pear used in the within plant family (Rosaceae) study \( (H = 24.684, \ d.f. = 2, \ P < 0.001) \). Apple \( (106 \pm 9.66 \text{ mL}) \) was larger than plum \( (86 \pm 5.16 \text{ mL}) \), but was smaller in size when compared to pear \( (186 \pm 29.14 \text{ mL}) \) (mean ± SD). The three apple varieties used for the within plant variety study did significantly differ in size \( (\text{ANOVA, } F_{2,27} = 17.715, \ P < 0.001) \). Post-hoc comparison showed that the ‘Red Delicious’ and ‘Granny Smith’ varieties did not differ in size between each other, but were significantly larger in size to the ‘Golden Delicious’ variety.

There was a significant difference in pericarp toughness of guava, apple, tomato and zucchini used by B. tryoni across the different plant families \( (F_{3,25} = 77.941, \ P < 0.001) \). Post-hoc comparisons showed that apple was the toughest, while guava had the softest pericarp of the four fruits. Tomato did not differ in pericarp toughness from...
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apple and zucchini, while zucchini differed significantly from apple and guava. Similarly, the pericarp toughness of the fruits used in the within family (apple, plum, pear) study was also significantly different from each other (ANOVA, $F_{2,19} = 28.213$, $P < 0.001$). Post-hoc comparisons showed that apple had a tougher pericarp than plum and pear, while the pericarp of the two latter fruits did not significantly differ from each other (Tukey’s HSD test). Furthermore, a one-way analysis of variance revealed that there was significant difference in pericarp toughness ($F_{2,27} = 24.140$, $P < 0.001$) of the three apple varieties used for the within plant variety study. Tukey’s post-hoc test, after Bonferroni correction, revealed that the ‘Granny Smith’ variety possessed a tougher pericarp than the ‘Red’ and ‘Golden Delicious’ varieties.

3.4 DISCUSSION

I investigated host choice and host use patterns in this study to explore whether there were any differences between a specialist (B. cucumis) and a generalist (B. tryoni) tephritid. In particular I was interested in testing whether the position of these species at different points along the host use continuum conformed to the predictions of the preference-performance hypothesis (Kennedy 1965, Thompson 1988a, Abrahamson and Weis 1997). The results of the various tests with the two tephritid species showed interesting deviations from the predictions of the preference-performance hypothesis with respect to host choice and host use of B. tryoni, in contrast to that of B. cucumis. The oligophagous B. cucumis demonstrated an ability to discriminate fruits across different families, within same family and among variety within species. However, patterns of host ranking and host use followed the predictions of the preference-performance hypothesis only at the within plant family (Cucurbitaceae) level. This oligophagous B. cucumis chose hosts in a hierarchical rank order (Courtney et al. 1989) and preferentially used the fruit species that provided high offspring performance. The highly preferred zucchini and squash fruits yielded offspring with higher fitness, while the least preferred cucumber fruits produced offspring with low fitness (Figures 3.5, 3.6). Conversely, when plants from different plant families and varieties within species were encountered by B. cucumis, the physiological and/ or behavioural factors may have played a significant role in its host choice and use patterns rather than that proposed by the preference-performance hypothesis. For
example, the fact that eggs were not deposited in passionfruit and tomato after penetrating the pericarp of these fruits (Figure 3.1, Table 3.1) indicated that *B. cucumis* had the ability to assess the suitability of the fruit’s physical and chemical environment for egg and larval development.

Host choice and host use are distinctly different phases along the oviposition process (i.e., from host finding to host acceptance and then to host use by way of egg deposition or larval feeding). Although eggs were not deposited by *B. cucumis* in tomato after pericarp penetration occurred (Figure 3.1, Table 3.1), greater than 50% of larvae successfully developed into pupae when tomatoes were artificially inoculated with eggs. The lack of egg deposition into passionfruit and tomato following pericarp penetration indicates that the host discrimination behaviour of *B. cucumis* is stronger at a later phase in the oviposition process (i.e., after ovipositor penetration). This behaviour may suggest that specialised receptors on the ovipositor could be responsible for recognising cues from an appropriate host. Species in Cucurbitaceae may have some shared fruit traits that elicit egg deposition by *B. cucumis*, thereby resulting in the restricted host range of this species. What these specific traits are, warrant further investigation, as reported cases of incidental use of non-Cucurbitaceae hosts by *B. cucumis* (Smith et al. 1988, Allwood et al. 1999, Hancock et al. 2000) may potentially be explained by these traits being present in these alternate fruit species.

Another plausible mechanism for the restricted host use of *B. cucumis* would be its physiological status. Egg-load of an insect species plays a crucial role in its host choice and host use patterns, particularly in phytophagous insects, by either widening or restricting its host range (Courtney et al. 1989). Egg-limited insects are thought to exhibit stronger host discrimination behaviour resulting in a narrow host use pattern (Courtney et al. 1989, Larsson and Ekborn 1995, West and Cunningham 2002). The oligophagous *B. cucumis* has fewer ovarioles and eggs compared to the polyphagous *B. tryoni* (Fitt 1990) and may possess an oviposition strategy that minimizes the risk of placing eggs in unsuitable hosts (Kennedy 1965, Jaenike 1978a) thereby resulting in using only restricted, suitable hosts of Cucurbitaceae.

When *B. tryoni* was exposed to fruit species across different plant families in both the choice and no-choice scenario, it showed similar preference ranking of plants from
both their primary (guava, apple) and alternative (tomato, zucchini) hosts but had varying levels of offspring performance on these fruits (Figures 3.3, 3.4). A similar oviposition behaviour was also executed when B. tryoni encountered plant varieties (apple varieties) of the same species (Figure 3.11, 3.12). This indicated that the host choice and host use patterns observed may be a result of intricate behavioural/physiological associations between the fly and its larval host rather than just due to an optimization of the preference-performance relationship. From a behavioural perspective, polyphagous tephritid species respond positively to a wider set of host plant volatiles and visual stimuli than oligophagous species (Diaz-Fleischer et al. 2000). Several studies have shown that the polyphagous B. tryoni possesses the ability to positively respond to various plant cues (Pritchard 1969, Fletcher and Watson 1974, Eisemann and Rice 1985, 1992). Studies on other polyphagous tephritids such as A. suspensa (Nigg et al. 1994), C. capitata (Light et al. 1992, Warthen et al. 1997) and B. dorsalis (Light and Jang 1987) showed that these species also exhibit positive responses to a broader range of chemical compounds from ripening host fruits. In contrast, the response of the monophagous B. oleae was restricted to two related terpenes from ripening olive fruits (Scarpati et al. 1993). The results from this study suggested that the polyphagous B. tryoni was able to accept plants that have similar cues to those of its primary host, resulting in apparently wider host range. This behaviour was clearly demonstrated by the indiscriminate preference of B. tryoni for the three apple varieties with similar chemical cues and for plants across different families.

In contrast to B. cucumis, the polyphagous B. tryoni, showed no clear preference ranking for plant species within its primary host family (Rosaceae) when each plant species was encountered separately in a no-choice study (Figure 3.7). However, when apple, plum and pear were exposed simultaneously, B. tryoni preferentially used apple and plum compared to pear which was not even visited. This indicated that even when fruits deemed to be equivalent hosts are simultaneously exposed to B. tryoni, it exhibits a host ranking behaviour; a similar behaviour to that demonstrated by other polyphagous fruit fly species (Clarke et al. 2001). However, the host ranking patterns of B. tryoni do not necessarily correlate to offspring performance (see Experiment 8 under Results). Singer (1971), Tabashnik et al. (1981) and Courtney & Forsberg (1988) all reported similar host ranking behaviour for other putative generalist
phystophasous insects. When the polyphagous *B. jarvisi* simultaneously encountered its primary (*P. careya*) and alternate hosts, it highly ranked *P. careya* over the alternate hosts. However, *B. jarvisi* lost its host ranking behaviour in the absence of its primary host (Fitt 1986a); a similar behaviour to that demonstrated by *B. tryoni* in the no-choice tests. The loss of host ranking behaviour in the no-choice situation may reflect the ability of polyphagous species to use secondary or incidental hosts when primary hosts are not present.

Generalist phytophagous insects typically possess greater fecundity and phenotypic plasticity in traits associated with host selection and larval feeding response (Michaud 1990). Such characteristics may be a prerequisite to maintenance of polyphagy as offspring fitness will then be maximised on average when fecundity is partitioned among various hosts so as to spread the risk of a lower fitness return on one host (Levins and MacArthur 1969, Jaenike 1978a, Courtney 1982, Michaud 1990). Since *B. tryoni* has a higher fecundity than *B. cucumis* (Fitt 1990), it may be time-limited rather than egg-limited, and this may have resulted in its broader host use pattern in order to maximize fitness (Jaenike 1978a, b, Courtney et al. 1989, Mayhew 1997).

After arriving at a prospective oviposition site, female fruit flies used a variety of cues to determine whether the site is acceptable for oviposition. Some of these cues included the exterior fruit characteristics such as surface texture, pericarp toughness and the internal chemical composition and physical structure of the fruit (Pritchard 1969, Greany et al. 1983, Eisemann and Rice 1985, 1989, Katsoyannos 1989, Fletcher and Prokopy 1991). Although not all the fruit characteristics were tested, the results from the oviposition behaviour experiments and the corresponding fruit toughness measures revealed that pericarp toughness could play a key role in host use by tephritid females. For example, the high proportion of oviposition events during the first oviposition attempt on either zucchini or squash (Table 3.3) was possibly facilitated by the lower level of force required to penetrate the softer pericarp compared to cucumber with a tougher pericarp. Similarly, passionfruit with a tougher pericarp received few oviposition events despite the higher proportion of oviposition attempts by *B. cucumis* (Table 3.1). Such influence of pericarp toughness in host use was also evident in the oviposition behaviour of the polyphagous *B. tryoni*, where apple with a tough pericarp received a lower proportion of oviposition events than
guava and zucchini with softer pericarp, despite the similar proportion of oviposition attempts on these fruits (Table 3.2).

Pericarp toughness and surface texture in relation to the strength, length and shape of the aculeus as well as chemical fruit properties are possible factors of major importance in egg deposition by tephritids (Diaz-Fleischer et al. 2000). Once a fly accepts a fruit as a potential host, it explores the fruit surface before attempting to oviposit. In some species (e.g., *B. tryoni*, *B. cucurbitae*, *B. dorsalis*), it has been suggested that such exploration behaviour is performed to locate favourable oviposition sites such as holes made by previously oviposited females or breaks in the skin (Newell and Haramoto 1968, Pritchard 1969, Prokopy and Koyama 1982). However, if the preferred fruit surface is found to be too smooth, oily or tough, the fly may depart the fruit as it can neither grip nor penetrate the fruit tissue for egg deposition (e.g., Pritchard 1969, Balagawi et al. 2005, Dhillon et al. 2005). Plant stimuli such as colour, shape, size, volatiles and chemical compounds simultaneously or sequentially affect the oviposition decision of the female (Thorsteinson 1960, Kennedy 1965, Prokopy and Owens 1983, Jones 1991), and visual cues (e.g., size and shape) are more relevant for long distance orientation to the host plant (Moericke et al. 1975, Katsoyannos 1989, Fletcher and Prokopy 1991). This could be one reason why this laboratory study did not detect any influence of fruit size (a visual cue) in host choice and use by the two fly species.

Although pericarp toughness was similar in both tomato and zucchini, very few *B. cucumis* females engaged in oviposition attempts on tomato and none of these attempts resulted in an oviposition event (Table 3.1). This behaviour indicated that the chemical properties of tomato may have been responsible for inhibiting ovipositor penetration and egg deposition into tomato rather than pericarp toughness. For example, α-tomatine in fruits of *Lycopersicon* spp. have been reported to confer resistance to *Helicoverpa zea* (Boddie) and *Spodoptera exigua* (Hubner) in using tomato fruit for oviposition (Juvik and Stevens 1982, Kennedy 2003). Perhaps these same chemicals may confer resistance to tephritid oviposition as well. Although the fly ovipositor may overcome the physical fruit barriers and bore into the fruit, chemical compounds in the fruit such as glucose, fructose, sodium chloride and
calcium chloride may either stimulate or inhibit egg deposition (Girolami et al. 1981, Greany et al. 1983, Eisemann and Rice 1985). Influences of such physio-chemical fruit traits on tephritid flies have recently been demonstrated with *B. cucurbitae*, where the rate of infestation was positively correlated to moisture but negatively correlated with fruit toughness, ascorbic acid and potassium content (Dhillon et al. 2005). In addition to the internal chemical environment of the fruit, the role of fruit volatiles in host preference and host use also needs to be considered (e.g., Eisemann and Rice 1992). Each of the fruit species used in this study had some unique volatiles, hydrocarbons and oils (S. Balagawi, unpublished data). The role of these volatiles in dacine oviposition is unknown and needs further investigation.

In conclusion, it should be noted that host preference and host use are two distinct phases along the oviposition process. The oviposition behaviour of the two species discussed above indicates that a high host plant visitation rate by the insect species and even higher number of oviposition attempts on a plant species does not necessarily result in a high incidence of host use. The insect has to first overcome both the physical and chemical post-alighting fruit traits before it deposits eggs into the plant for subsequent larval use and development (Futuyma 1983b, Jones 1991). It is therefore not accurate to assume host use (utilization) by phytophagous insects based on host visitation and/or oviposition attempts. In addition, the level of egg deposition and/or larval infestation needs to be investigated (see Singer 1983 for definition of preference and host use). The preference-performance hypothesis may have some heuristic basis in evaluating patterns of host use by some group of phytophagous insects. However, the findings of my studies clearly demonstrated the importance of identifying the physiological and behavioural mechanisms that impact host preference and host use patterns of tephritids, which may be more indicative of their behaviour in nature.
CHAPTER 4: LIFE HISTORY AND DEMOGRAPHY OF BACTROCERA CUCUMIS (FRENCH) AND BACTROCERA TRYONI (FROGGATT) – A FUNCTION OF HOST USE
4.1 INTRODUCTION

Demographic studies of insects generally include four population aspects: size (the number of insects in the population), distribution (the arrangement of the population in the habitat at a given time), structure (the distribution of the population among its sex and age groupings), and change (the growth and decline of the population) (Shryock et al. 1976, Carey 1993, Price 1997). The fourth aspect of change in population growth is referred to as the population dynamics that results from fluctuations in both the biotic and abiotic factors to which the organism is exposed (Thomas 1976, Berryman 1996). Insect’s life history traits such as fecundity, survival to reproductive age and age at first reproduction, are equally important in determining population dynamics and the fitness of the insect, but factors influencing these life history traits are not understood for most insect species (Nylin 2001). Development time and reproductive patterns determine how populations respond to environmental fluctuations (Tammaru and Haukioja 1996, Nylin 2001).

In phytophagous insects, the life history traits may not only be important in determining population dynamics and fitness, but can also play a role in determining the host use patterns. For example, insects with short generation time and higher fecundity (r-selected species) tend to use a wide host range whereas those with lower fecundity and longer generation time (k-selected species) specialize on a narrow host range (Singer 1971, Courtney and Forsberg 1988, Courtney et al. 1989, Larsson and Ekbom 1995, Nomakuchi et al. 2001, West and Cunningham 2002). Conversely, physical and chemical composition of the host used may affect the life history traits, which in turn affect the population dynamics and fitness of phytophagous insects (Leather 1994, Awmack and Leather 2002). Elucidating the interactions between host use, life history traits and population dynamics of phytophagous insects is useful for understanding the mechanisms shaping their host range.

In this study, I tested the effects of selected primary and alternate hosts on the life history and population dynamics of B. cucumis and B. tryoni. Since these two species are pest species of commercial crops, it is important to elucidate which life history stage is the most critical stage to their demography and population growth. This stage could then be targeted for management intervention. To aid this, I used the life-history
information to develop demographic models that could be used to predict the population dynamics of these tephritid species, and identify possible pest management strategies with respect to their host use patterns.

4.2 MATERIALS AND METHODS

Eggs were collected from colonies of *B. cucumis* and *B. tryoni* reared under controlled laboratory conditions at 26 ± 1 °C and 65 ± 10 % relative humidity. The flies were considered ideal for this study because they had been reared upon the same pumpkin diet (*B. cucumis*) and carrot diet (*B. tryoni*) for tenth and fifth generations respectively, thus reducing intra-population genetic variability. All flies were fed with sugar, water (soaked in sponge) and protein (autolyzed yeast) resources upon emergence.

4.2.1 Life history studies for *B. cucumis*

**Egg collection and inoculation**

Ten organically grown fruits of pumpkin, cucumber, squash, zucchini, guava, passionfruit and tomato were washed and a 1cm deep insertion was made on each fruit with a sterile scalpel blade. Pumpkin, cucumber, squash and zucchini were identified as primary hosts while guava, passionfruit and tomato were identified as alternate hosts. Eggs of *B. cucumis* were collected by placing egging domes made from each fruit species in a cage with mated mature flies for 30 minutes. Groups of ten eggs were removed from the domes of each fruit species and placed into the ten fruits of the respective fruit species (i.e., eggs from zucchini dome were placed into zucchini fruits) using a soft, clean, fine paintbrush (960 No. 2 China). The number of eggs inoculated (10 eggs) was based on the lowest fruit weight of all the fruits and this ensured that each developing larva had sufficient quantity of diet (> 2g/larva) to complete development.

Each fruit was placed on fine gauze on top of a piece of metal mesh covering the open top of a plastic container. The gauze ensured that no larvae drowned in the fluid collected from the rotting fruit inside the container. The plastic container holding the fruit was placed on sterile sawdust inside a larger container and sealed with a
ventilated lid. Each fruit was maintained separately. After the first day of egg incubation, each fruit was checked every 2 hours and the number of hatched eggs and time of egg hatch recorded for each fruit.

**Pupae and adult fly handling**

After five days of incubation, sawdust from each fruit sample was sieved daily to ascertain pupation. The information on proportion of larval survival and developmental period were then calculated using the survival and developmental period data of the egg and pupal stages for each fruit. The pupae recovered each day from each fruit were counted, weighed and placed on sterile, moist sawdust in a separate, clear container with a ventilated lid. Flies that emerged from each fruit were counted and sexed daily and transferred to a smaller cage (30cm x 20cm x 20cm) and fed sugar, water and yeast autolysate protein (MP Biomedicals, LLC, Aurora, Ohio, USA). Pupal survival (%) and development time were calculated and flies that emerged from each fruit species were placed in separate cages.

Each cage was observed daily at dusk and a total of 21 once mated male and 21 once mated female flies from a population of a single fruit species were placed into 6 different cages (30cm x 20cm x 20cm). This consisted of three female cages with seven once mated females in each cage, and three male cages with seven once mated males in each cage. The above procedure was repeated for the fly populations from each fruit species. All flies had access to water, crystalline sugar and yeast autolysate protein at all times and these food resources were replaced at 10-day intervals.

**Adult survivorship and fecundity**

Flies from each of the above cages were used to measure the survivorship (male & female) and fecundity (female) of populations reared from the different fruits. Female flies from each cage were always exposed to an egging device (see below for description) that was placed in the cage at 0800 hours and removed at 1630 hours the following day. The number of eggs laid by the females and daily number of dead flies from both male and female cages were recorded. Data on survivorship and fecundity were collected for the entire lifespan of the male and female flies in each of the cages.
The egging device used in this study was prepared using Bacteriological Agar No.1 (Oxoid LTD, Basingstoke, Hampshire, England), fresh concentrated juice from each respective fruit and water. Seven grams of agar was added to 300mL of tap water in a beaker and heated on a Magnetic heater-stirrer (CH2093-001, Industrial Equipment & Control, Australia). Using a magnetic rod, the solution was mixed until the agar dissolved and a clear solution was formed. The heater was turned off and 15mL of fruit juice added and stirred for 30 seconds. Before the agar mixture turned solid, it was poured into 5cm diameter disposable Petri dishes and left to cool and solidify. A piece of circular gauze (2mm x 1.5mm mesh size, 5cm diameter) was placed on each of the solid agar surfaces to help provide a textured surface to facilitate oviposition.

### 4.2.2 Life history studies for B. tryoni

The procedures used for B. tryoni were similar to those described for B. cucumis above. The only difference was in the fruit species used as primary and alternate hosts for B. tryoni. The primary hosts used for B. tryoni were guava, apple var. ‘Red Delicious’, pear and plum, while tomato var. ‘Grosse Lisse’ and zucchini were used as alternate hosts.

### 4.2.3 Life table and demographic analysis

The fundamental step in determining population parameters is to first construct a life table. The life table provides the population parameters such as survival and fecundity of a certain population with respective to attributes such as age or the stage of the organism. Life tables and summary statistics were constructed for B. cucumis and B. tryoni. A population projection matrix (stage-structured Lefkovitch matrix) (Lefkovitch 1965) was constructed based on the life-table data and summary statistics (see Ebert 1999 page 128). The matrix was of the form

\[
A = \begin{pmatrix}
  s_1 & f_2 & f_3 & \cdots & f_n \\
  g_1 & s_2 & 0 & \cdots & 0 \\
  0 & g_2 & s_3 & \cdots & 0 \\
  \vdots & \vdots & \vdots & \ddots & \vdots \\
  0 & 0 & \cdots & g_{n-1} & s_n
\end{pmatrix}
\]
Chapter 4. Demography of B. cucumis & B. tryoni – a function of host use

This matrix describes the number of offspring born to each age/stage class as well as the proportion of individuals that survive and remain in the same class and those that survive and enter the next age/stage class. It is sometimes referred to as the transition probability where “fₓ” is fecundity, “sₓ” is the probability of staying in the same class and “gₓ” is the probability of transferring to the next class (Ebert 1999). The advantage of constructing a population matrix is that it could be used to test how sensitive the population growth rate is to variations in the probability of survival rates and fecundity at various stages by simulating changes in these population parameters. Simulating the same proportional change for each stage by keeping all other age/stages constant enables a comparison of the relative effect of the different age/stages on the population intrinsic growth rate, r (Crouse et al. 1987).

Since the age of the pre-adult fruit fly stages (e.g., larvae) were difficult to identify, stage-based life tables and population matrices were developed for populations of B. cucumis and B. tryoni from the different fruits and were analysed using PopTools (Hood 2005) to determine the population parameters. The population parameters between fruits used by one fly species were analysed using chi-square test for goodness of fit, while any comparison made between the two fly species was analysed by an independent sample t-test.

The following formulae were used to compute the different matrix elements.

Survival rate of entire stage (lₓ) = lₓ+∆ₓ/ lₓ
Survival rate per day (p) = \(\sqrt{\frac{\text{number of days}}{(lₓ+∆ₓ/ lₓ)}}\)
Fraction leaving = 1/ days in the stage
Fraction staying = 1 - fraction leaving
Probability of transferring (gₓ) = fraction leaving \times survival rate per day
Probability of staying (sₓ) = fraction staying \times survival rate per day
Fecundity per stage (fₓ) = (total eggs/ reproductive days) \times survival rate of eggs

The key demography parameters investigated were stable stage distribution (cₓ), reproductive value (vₓ), net reproductive rate (Rₒ), generation time (T), finite rate of increase (λ) and intrinsic rate of increase (r). The relationship between Rₒ, T and r is
that, \( r = (\ln R_0/T) \) (see Ebert 1999 page 15). The intrinsic rate of increase \( r \) is the rate of natural increase in a close population that has been subject to age-specific or stage-specific fertility and mortality. If \( r \) remains constant over a long time period, then the population tends to converge to a stable population distribution \((c_x)\). The reproductive value \((v_x)\) provides a measure of the present and future contribution of a female of certain age to the rate of \( r \) while the net reproductive rate \((R_0)\) is the net growth rate per generation. However, in species with overlapping generations (e.g., \( B. cucumis \) and \( B. tryoni \)), \( R_0 \) is also the expected lifetime reproduction of a newborn female. Generation time \((T)\) is the length of time from one cohort of newborn to the next cohort of newborn (Pressat 1985, Caswell 1989, Carey 1993, Ebert 1999).

The technique of population projection by post multiplying the matrix elements with the population vector is used to forecast the state of the future population (Crouse et al. 1987). In the output of the matrix the dominant eigenvalue \( \lambda \) (finite rate of increase) is equal to \( e^r \) where \( r \) is the intrinsic rate of increase of the initial population \( N_0 \) in a given time period \( t \) as illustrated by the population equation \( N_t = N_0 e^{rt} \). This implies that if \( \lambda = e^r = 1 \), then \( r = 0 \), and the population remains stable. If \( r > 0 \), that is \( \lambda > 1 \), the population increases with time and the larger the value of \( r \) or \( \lambda \), the more rapid is the increase in the population (Crouse et al. 1987). A stable population distribution often occurs in a constant environment where the proportion of individuals in the different stage class of a population tends to grow towards stable stage distribution. The elements of the right eigenvector in the projection matrix output represent the stable stage distribution \((c_x)\) of the population while the elements of left eigenvector represents the reproductive value \((v_x)\) for each corresponding stage (Caswell 1989).

4.3 RESULTS

4.3.1 Egg, Larval & Pupal survivorship

There was a distinct difference in the survivorship of the pre-adult stages of \( B. cucumis \) between the primary (Cucurbitaceae) and alternate plant species and the difference was highly significant at the host feeding larval stage \( (\chi^2 = 150.989, \text{ d.f.} = \ldots) \).
6, $P < 0.001$). Guava and passionfruit from the alternate host had a high proportion of larval mortality while mortality from tomato fruit was similar to that of pumpkin fruit which belonged to the primary host plant family (Tables 4.1, 4.2). Although there was lower larval mortality from Cucurbitaceae species, there was a significant difference ($\chi^2 = 89.713$, d.f. = 3, $P < 0.001$) within plants of this primary host plant family. Offsprings from cucumber had the highest larval and pupal mortality, while squash and zucchini provided offspring with the lowest larval and pupal mortality. Larval mortality in pumpkin was intermediate between cucumber and either squash or zucchini (Tables 4.1, 4.2). Offsprings from squash and zucchini had the lowest mortality in the larval stage, whereas all the other fruits had the highest pre-adult mortality in the larval stage.

In contrast to $B. cucumis$, $B. tryoni$ sustained the highest mortality at the larval stage in both the primary and alternate host fruits it used (Table 4.3) and a significant difference in larval mortality was observed between the primary and alternate hosts ($\chi^2 = 36.038$, d.f. = 5, $P < 0.001$). A significant difference in larval mortality was also noticed within fruits of primary ($\chi^2 = 19.987$, d.f. = 3, $P = 0.002$) and alternate ($\chi^2 = 4.431$, d.f. = 1, $P = 0.035$) hosts. Apart from plum, larvae had a lower mortality in the other fruits from the primary plant families (Myrtaceae and Rosaceae) than the alternate host plants (tomato and zucchini) (Tables 4.3, 4.4). The mortality in the egg and pupal stages of $B. tryoni$ were low and similar in all the fruit species accept for zucchini which had the highest pupal mortality (Tables 4.3, 4.4).

The overall larval mortality of $B. cucumis$ reared from its primary hosts and tomato was low (26.12 ± 23.69%) while that of $B. tryoni$ reared from its primary hosts and tomato was twice (58.84 ± 17.61%) that of $B. cucumis$ (mean ± SD) (Tables 4.1, 4.3). There was no variation in the egg period of $B. cucumis$ between the different fruit species, while some variations between fruits were observed in the larval and pupal periods. Similar trend was also observed in duration of the pre-adult growth period of $B. tryoni$ across plant species, but the number of days lived in each of the pre-adult stages by $B. tryoni$ was longer than that of $B. cucumis$ (Tables 4.1, 4.3).
Table 4.1. Stage-based life table for *Bactrocera cucumis* (French) reared from different fruits in the laboratory at 26 ± 1 °C and 65 ± 10 % relative humidity.

<table>
<thead>
<tr>
<th>Fruit</th>
<th>Stage</th>
<th>Number of days lived per stage (x)</th>
<th>Fecundity (eggs per female/ stage) (Mₐ)</th>
<th>Number at beginning of stage (Nₐ)</th>
<th>Proportion at beginning of stage (Lₑ)</th>
<th>Number dying at stage x (dₑ)</th>
<th>Percent of stage dying</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pumpkin</td>
<td>E</td>
<td>1.19</td>
<td>0.00</td>
<td>100.00</td>
<td>1.00</td>
<td>8.00</td>
<td>8.00</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>7.45</td>
<td>0.00</td>
<td>92.00</td>
<td>0.92</td>
<td>33.00</td>
<td>35.87</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>11.97</td>
<td>0.00</td>
<td>59.00</td>
<td>0.59</td>
<td>7.00</td>
<td>11.86</td>
</tr>
<tr>
<td></td>
<td>A₁</td>
<td>8.00</td>
<td>0.00</td>
<td>52.00</td>
<td>0.52</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>A₂</td>
<td>184.00</td>
<td>158.84</td>
<td>52.00</td>
<td>0.52</td>
<td>29.71</td>
<td>57.14</td>
</tr>
<tr>
<td></td>
<td>A₃</td>
<td>112.00</td>
<td>0.00</td>
<td>22.29</td>
<td>0.22</td>
<td>22.29</td>
<td>100.00</td>
</tr>
<tr>
<td>Cucumber</td>
<td>E</td>
<td>1.21</td>
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<td>100.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>11.58</td>
<td>0.00</td>
<td>99.00</td>
<td>0.99</td>
<td>56.00</td>
<td>56.57</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>10.39</td>
<td>0.00</td>
<td>43.00</td>
<td>0.43</td>
<td>10.00</td>
<td>23.26</td>
</tr>
<tr>
<td></td>
<td>A₁</td>
<td>6.00</td>
<td>0.00</td>
<td>33.00</td>
<td>0.33</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
<td></td>
<td>A₂</td>
<td>246.00</td>
<td>233.53</td>
<td>33.00</td>
<td>0.33</td>
<td>24.00</td>
<td>72.73</td>
</tr>
<tr>
<td></td>
<td>A₃</td>
<td>80.00</td>
<td>0.00</td>
<td>9.43</td>
<td>0.09</td>
<td>9.00</td>
<td>95.45</td>
</tr>
<tr>
<td>Squash</td>
<td>E</td>
<td>1.21</td>
<td>0.00</td>
<td>100.00</td>
<td>1.00</td>
<td>3.00</td>
<td>3.00</td>
</tr>
<tr>
<td></td>
<td>L</td>
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<td>97.00</td>
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<td>0.56</td>
<td>55.93</td>
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<td>Zucchini</td>
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<td>2.00</td>
<td>2.00</td>
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<tr>
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<td>0.31</td>
<td>31.43</td>
<td>100.00</td>
</tr>
<tr>
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<td>E</td>
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<td>0.00</td>
<td>100.00</td>
<td>1.00</td>
<td>9.00</td>
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</tr>
<tr>
<td></td>
<td>L</td>
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<td>0.00</td>
<td>91.00</td>
<td>0.91</td>
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<td>34.07</td>
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</tr>
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</table>

E=Egg; L=Larvae; P=Pupae; A₁= Pre-reproductive adults; A₂ = Reproductive adults; A₃ = Post-reproductive adults
Asterisk (*) = pupae did not develop into adult hence could not verify pupal period
Dash (-) = offspring did not reach the adult pre-reproductive, reproductive and/ or post-reproductive life stages
Table 4.2. Stage-based summary statistics for *Bactrocera cucumis* (French) reared from different fruits in the laboratory at 26 ± 1 °C and 65 ± 10 % relative humidity. Summary statistics for passionfruit and guava fruits were excluded due to non-completion of the pupal or adult stage classes.

<table>
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<tr>
<th>Fruit</th>
<th>Stage</th>
<th>Days in stage</th>
<th>Survival of entire stage (E)</th>
<th>Survival rate per day (p)</th>
<th>Fraction leaving</th>
<th>Fraction staying</th>
<th>Probability of transferring (g)</th>
<th>Probability of staying (s)</th>
<th>Fecundity (f)</th>
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</table>

E=Egg; L=Larvae; P=Pupae; A1=Pre-reproductive adults; A2=Reproductive adults; A3=Post-reproductive adults
Table 4.3. Stage-based life table for *Bactrocera tryoni* (Froggatt) reared from different fruits in the laboratory at 26 ± 1 °C and 65 ± 10 % relative humidity.

<table>
<thead>
<tr>
<th>Fruit</th>
<th>Stage</th>
<th>Number of days lived per stage (x)</th>
<th>Fecundity (eggs per female/ stage) (Mₓ)</th>
<th>Number at beginning of stage (N₀)</th>
<th>Proportion at beginning of stage (lₓ)</th>
<th>Number dying at age x (dₓ)</th>
<th>Percent of stage dying</th>
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</table>

E=Egg; L=Larvae; P=Pupae; A1= Pre-reproductive adults; A2 = Reproductive adults; A3 = Post-reproductive adults
Dash (-) = flies did not reach the adult reproductive and post-reproductive life stages
### 4.3.2 Adult survivorship and fecundity

A chi-square test showed that there was a significant difference in the proportion of adult *B. cucumis* that emerged from the different fruits ($\chi^2 = 158.293, \text{d.f.} = 6, P < 0.001$). All fruit species of the primary host plant family (Cucurbitaceae) yielded a high number of adults, while only tomato from the alternate host plant family (Solanaceae) yielded an adult fly population similar to that of the Cucurbitaceae plant species (Table 4.1). However, there was a significant difference in adult emergence
even within the Cucurbitaceae plant species ($\chi^2 = 33.938$, d.f. = 3, $P = < 0.001$). More adult *B. cucumis* emerged from squash and zucchini as compared to cucumber and pumpkin fruits. This was mainly due to the higher larval survivorship on squash and zucchini as compared to the latter two larval food resources. Guava (Myrtaceae) yielded only eight adult flies while passionfruit (Passifloraceae) did not yield any (Table 4.1). Adult survivorship of *B. tryoni* was less than 50% of the total eggs inoculated and survivorship was significantly different across both primary and alternate hosts ($\chi^2 = 54.354$, d.f. = 5, $P < 0.001$). Adult emergence from primary hosts ranged between 31-47 percent except for plum which provided lower adult survivorship similar to that from the alternate hosts (Tables 4.3, 4.4).

The adult pre-reproductive period was not significantly different between flies from fruits used by *B. cucumis* ($\chi^2 = 1.095$, d.f. = 4, $P = 0.895$) and *B. tryoni* ($\chi^2 = 1.404$, d.f. = 4, $P = 0.843$). However, there were significant differences in the reproductive period of *B. cucumis* ($\chi^2 = 21.078$, d.f. = 4, $P = 0.003$) and *B. tryoni* ($\chi^2 = 25.872$, d.f. = 4, $P = 0.001$) that emerged from their respective primary hosts and tomato (Tables 4.2, 4.4). The oligophagous *B. cucumis* females that emerged from the primary hosts had a longer reproductive period and produced more eggs than those from the alternate host, tomato (Table 4.2) and, hence, showed a significantly strong positive correlation ($r = 0.906$, n = 5, $P = 0.034$) between reproductive period and fecundity. In contrast, there was no significant correlation ($r = 0.429$, n = 5, $P = 0.471$) between fecundity and reproductive period among *B. tryoni* that emerged from the primary and alternate hosts. Female *B. tryoni* from the alternate tomato host had the second longest reproductive period with lowest fecundity in comparison to flies from the primary hosts which had the longest (pear) and shortest (guava & plum) reproductive period but higher fecundity (Table 4.4).

There was a significant difference in the mean overall lifespan of female flies of *B. cucumis* and *B. tryoni* that emerged from their respective primary hosts and tomato ($t_{9} = 3.323$, $P = 0.01$). Females of *B. cucumis* survived for a longer time period (35.4 ± 1.8 weeks) than females of *B. tryoni* (28 ± 4.6 weeks) (mean ± SD) (Figures 4.1, 4.2). The mean weekly survivorship of female *B. cucumis* from the different fruits did not differ (Figure 4.1), however, a considerable difference was seen in the female survivorship of *B. tryoni* where those from guava fruit had the lowest survivorship
while those from tomato maintained a high percent survivorship during most of their survival period (Figure 4.2).

**Figure 4.1.** Mean weekly survivorship of female *Bactrocera cucumis* (French) reared from different fruits. Symbols are means.

**Figure 4.2.** Mean weekly survivorship of female *Bactrocera tryoni* (Froggatt) reared from different fruits. Symbols are means.
The fecundity of *B. cucumis* \((117.45 \pm 76.69)\) from the primary hosts and tomato was significantly lower than that of *B. tryoni* \((365.75 \pm 122.99)\) from its primary hosts and tomato (mean ± SD). Furthermore, a distinct difference was observed in the pattern of egg distribution over time. While *B. cucumis* tended to lay lower, but evenly distributed number of eggs each day, over a 30 week period (Figure 4.3), female *B. tryoni* from the different fruits laid a higher number of their eggs in their first 11 weeks of survival (Figure 4.4).

**Figure 4.3.** Number of eggs laid by a female *Bactrocera cucumis* (French) reared from the different fruits in a single day of each week. Symbols are means.
Figure 4.4. Number of eggs laid by a female *Bactrocera tryoni* (Froggatt) reared from the different fruits in a single day of each week. Symbols are means.

While there was a similar mean weekly survivorship of female *B. cucumis* from the different fruits (Figure 4.1), a noticeable difference was observed in male survivorship where the males from pumpkin fruit had a lower percent survivorship compared to those from the other fruits (Figure 4.5). Difference in male survivorship was also observed for *B. tryoni* where males from plum fruit had the highest percent survivorship per week compared to those from apple which had the lowest survivorship (Figure 4.6).
Figure 4.5. Mean weekly survivorship of male *Bactrocera cucumis* (French) reared from different fruits. Symbols are means.

Figure 4.6. Mean weekly survivorship of male *Bactrocera tryoni* (Froggatt) reared from different fruits. Symbols are means.
The male fly populations of both *B. cucumis* and *B. tryoni* reared from the respective primary and alternate hosts tended to live longer than the females (Figures 4.1, 4.2, 4.5, 4.6). This may have been due to the experimental design which allowed males to mate only once, hence, using less reproductive energy as compared to females, which continually use energy in egg production and deposition, resulting in a shorter life span. However, laboratory studies on other tephritid species where males mated multiple times, reported male longevity to exceed that of females (Shoukry and Hafez 1979, Carey et al. 1995, Papadopoulos et al. 2002).

### 4.3.3 Population projection matrix

The stage-based population projection matrix for *B. cucumis* reared from the different fruits is presented in Table 4.5, while Table 4.6 presents that for *B. tryoni*. The probability of *B. cucumis* populations that remained in the egg stage was always lower than the probability of eggs that hatched into the larval stage (Table 4.5), while it was the contrary for populations of *B. tryoni* (Table 4.5). However, in the later life stages, there was a higher probability of populations that remained in each stage and a lower probability of populations transferred to the next life stage, for both species.
Table 4.5. Stage-based population projection matrix of *Bactrocera cucumis* (French) reared from different fruits in the laboratory at 26 ± 1 °C and 65 ± 10 % relative humidity.

<table>
<thead>
<tr>
<th>Fruit</th>
<th>Stage</th>
<th>E</th>
<th>L</th>
<th>P</th>
<th>A1</th>
<th>A2</th>
<th>A3</th>
</tr>
</thead>
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<tr>
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<td>A3</td>
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<td>0.00000</td>
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<tr>
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</table>

E=Egg; L=Larvae; P=Pupae; A1= Pre-reproductive adults; A2 = Reproductive adults; A3 = Post-reproductive adults
Table 4.6. Stage-based population projection matrix of *Bactrocera tryoni* (Froggatt) reared from different fruits in the laboratory at 26 ± 1 °C and 65 ± 10 % relative humidity.

<table>
<thead>
<tr>
<th>Fruit</th>
<th>Stage</th>
<th>E</th>
<th>L</th>
<th>P</th>
<th>A1</th>
<th>A2</th>
<th>A3</th>
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<tr>
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</table>

E=Egg; L=Larvae; P=Pupae; A1= Pre-reproductive adults; A2 = Reproductive adults; A3 = Post-reproductive adults

4.3.4 Population parameters

The various population parameters of *B. cucumis* and *B. tryoni*, for the populations from the different fruits, with respect to the different stage classes are presented in Table 4.7 and Table 4.8 respectively. At equilibrium, most of the populations of *B. cucumis* and *B. tryoni* were in the larval stage while an insignificant number were in the post-reproductive stage (Tables 4.7, 4.8).

Not surprisingly, individuals in the adult reproductive stage possessed higher reproductive values in all populations of the two fly species from the different fruits.
and, contributed considerably to the present and future intrinsic growth rate $r$ of *B. cucumis* and *B. tryoni* (Tables 4.7, 4.8). There was no significant difference in the reproductive values at the reproductive stage for flies from the different fruits used by *B. cucumis* ($\chi^2 = 1.447$, d.f. = 4, $P = 0.836$) and *B. tryoni* ($\chi^2 = 0.645$, d.f. = 4, $P = 0.958$). Populations of *B. tryoni* possessed a higher reproductive value than that of *B. cucumis*. The reproductive values for each population of *B. cucumis* and *B. tryoni* were low at birth, then increased to a peak at the reproductive stage and gradually declined to zero at the post-reproductive stage (Tables 4.7, 4.8). This type of trend in reproductive values is typical of a natural population, where the low reproductive value at birth reflects the probability that a newborn individual would die before reproducing and the decline in reproductive value as age increases reflect the fact that reproductive rates decreases and mortality increases with age of adults (Caswell 1989).

Intrinsic growth rate $r$ differed considerably between populations of *B. cucumis* from the different fruits (Table 4.7). Populations from squash and zucchini had the highest growth and net reproductive rates with shorter generation time, and possessed the characteristics of a healthy population, while populations from tomato had the lowest growth rate and net reproductive rate, and longer generation times (Table 4.7). Although the generation times were similar for *B. cucumis* populations from the Cucurbitaceae fruit species ($\chi^2 = 0.286$, d.f. = 3, $P = 0.963$), there was a significant difference in the net reproductive rates ($\chi^2 = 48.116$, d.f. = 3, $P < 0.001$). Populations from zucchini and squash had similar net reproductive rates that were nearly three-fold higher than that from pumpkin and cucumber (Table 4.7).

The generation times of *B. tryoni* from the primary fruits and tomato were very similar (Table 4.8), but the net reproductive rate differed significantly ($\chi^2 = 16.125$, d.f. = 4, $P = 0.003$) between the fly populations from the different fruits. The polyphagous *B. tryoni* from tomato fruits had the lowest net reproductive rate while those from the primary fruits had higher net reproductive rates (Table 4.8). The overall generation time of *B. tryoni* from its primary fruits and tomato was significantly shorter than that for *B. cucumis* (Tables 4.7, 4.8).
Table 4.7. Stage-based population parameters of *Bactrocera cucumis* (French) reared from different fruits in the laboratory at 26 ± 1 °C and 65 ± 10 % relative humidity.

<table>
<thead>
<tr>
<th>Fruit</th>
<th>Stage</th>
<th>Stable stage distribution $c_x$</th>
<th>Reproductive value $v_x$</th>
<th>Dominant eigenvalue $\lambda$</th>
<th>Intrinsic rate of increase $r$</th>
<th>Net reproductive rate $R_0$</th>
<th>Generation time (days) $T$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pumpkin</td>
<td>E</td>
<td>0.12285</td>
<td>0.05328</td>
<td>1.08176</td>
<td>0.07859</td>
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</tr>
<tr>
<td></td>
<td>L</td>
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<td>0.06344</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P</td>
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<td>0.13350</td>
<td></td>
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</tr>
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<td></td>
<td></td>
<td></td>
</tr>
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<td>A3</td>
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<td>0.00000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cucumber</td>
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<td>1.08228</td>
<td>0.07907</td>
<td>35.21823</td>
<td>45.04084</td>
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<td>L</td>
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</tr>
<tr>
<td></td>
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<td></td>
<td>A2</td>
<td>0.12936</td>
<td>0.45727</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>A3</td>
<td>0.00466</td>
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<tr>
<td>Squash</td>
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<td>0.09900</td>
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<td>45.72400</td>
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<td>L</td>
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<td></td>
<td>P</td>
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<td>0.06816</td>
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<tr>
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<td>P</td>
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<td>Tomato</td>
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<td>1.05153</td>
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<td>0.09018</td>
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<tr>
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<td>0.01936</td>
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</tbody>
</table>

E=Egg; L=Larvae; P=Pupae; A1= Pre-reproductive adults; A2 = Reproductive adults; A3 = Post-reproductive adults
Table 4.8. Stage-based population parameters of *Bactrocera tryoni* (Froggatt) reared from different fruits in the laboratory at 26 ± 1°C and 65 ± 10% relative humidity.

<table>
<thead>
<tr>
<th>Fruit</th>
<th>Stage</th>
<th>Stable stage distribution $c_x$</th>
<th>Reproductive value $v_x$</th>
<th>Dominant eigenvalue $\lambda$</th>
<th>Intrinsic rate of increase, $r$</th>
<th>Net reproductive rate, $R_0$</th>
<th>Generation time, $T$ (days)</th>
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<td>Guava</td>
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<td>0.02776</td>
<td>1.095876</td>
<td>0.09155</td>
<td>31.62426</td>
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<td>L</td>
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<td></td>
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<tr>
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<td>P</td>
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</tr>
<tr>
<td>Apple</td>
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<td>0.02489</td>
<td>1.12323</td>
<td>0.11621</td>
<td>51.18329</td>
<td>33.86411</td>
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<td>0.00000</td>
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</tr>
<tr>
<td>Pear</td>
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<td>0.02665</td>
<td>1.09932</td>
<td>0.09469</td>
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<tr>
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<tr>
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<td>P</td>
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<td>0.00000</td>
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<tr>
<td>Plum</td>
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<td>0.02151</td>
<td>1.09756</td>
<td>0.09309</td>
<td>32.82356</td>
<td>37.50297</td>
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</tr>
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<td>Tomato</td>
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</tr>
</tbody>
</table>

E=Egg; L=Larvae; P=Pupae; A1= Pre-reproductive adults; A2 = Reproductive adults; A3 = Post-reproductive adults

4.3.5 Elasticity (proportional sensitivity)

Elasticity of a population illustrates the proportional sensitivity of the population growth rate to changes in the element of the population matrix. The proportional sensitivity of each population of *B. cucumis* and *B. tryoni* from the different fruits was strongest at the adult reproductive stage for both species, while lower elasticity was attained at the other stage classes (Figures 4.7, 4.8). This implied that population change at the adult reproductive stage strongly influenced the population growth rate of both fly species than changes in any other stage classes. Population changes in the
adult post-reproductive stage did not have any influence in the population growth rate of the two fly species.

Populations of *B. cucumis* and *B. tryoni* that developed from tomato fruit were highly sensitive to changes in the adult reproductive stage (Figures 4.7, 4.8). Populations of *B. cucumis* from zucchini and *B. tryoni* from apple were least sensitive to changes in adult reproductive stage relative to that of tomato (Figures 4.7, 4.8).

![Figure 4.7](image_url)

**Figure 4.7.** Elasticity (proportional sensitivity) of the population growth rate to changes in the probability of survival in the different stage classes and fecundity of reproductive adults for *Bactrocera cucumis* (French) reared from the different fruit species.
Figure 4.8. Elasticity (proportional sensitivity) of the population growth rate to changes in the probability of survival in the different stage classes and fecundity of reproductive adults for *Bactrocera tryoni* (Froggatt) reared from the different fruit species.

4.3.6 Population simulation

The oligophagus *B. cucumis* and polyphagous *B. tryoni* are major pest species that demand considerable effort in field pest management in order to decrease population sizes and reduce damage to fruit crops. In order to predict the level of population reduction required to achieve a minimal growth rate of the fly species, a 50% reduction in the probability of survival and fecundity was simulated for each stage of the two fly species, while keeping the other matrix components constant for all the populations from the different fruits. The changes in the intrinsic growth rate *r* of *B. cucumis* and *B. tryoni* are shown in Figures 4.9 and 4.10 respectively.
The intrinsic growth rates of both fly species were not sensitive to changes in the probability of survival at the adult post-reproductive stage class (Figures 4.7, 4.8) and, therefore, a 50% simulated reduction in the probability of survival of this stage class showed no change in the intrinsic growth rate of both fly species from each fruit (Figures 4.9, 4.10). However, the population growth rate of all populations of \textit{B. cucumis} and \textit{B. tryoni} responded strongly to 50% reduction in probability of survival of the adult reproductive stage class. In general, a 50% reduction in the probability of survivorship at the adult reproductive stage markedly reduces the population growth rate for \textit{B. cucumis} from its primary host and tomato, compared to those for \textit{B. tryoni} (Figures 4.9, 4.10).

![Figure 4.9](image_url)

**Figure 4.9.** Changes in the intrinsic growth rate $r$ of the populations of \textit{Bactrocera cucumis} (French) from the different fruits resulting from a 50% simulated decrease in fecundity and probability of survivorship of individual life stages. The dashed lines represent the initial $r$ values determined from the initial matrix of populations from each fruit species.
Figure 4.10. Changes in the intrinsic growth rate $r$ of the populations of *Bactrocera tryoni* (Froggatt) from the different fruits resulting from a 50% simulated decrease in fecundity and probability of survivorship of individual life stages. The dashed lines represent the initial $r$ values determined from the initial matrix of populations from each fruit species.
4.4 DISCUSSION

This study examined the demographic consequences of host use in an oligophagous and polyphagous fruit fly species. Oligophagous host use suggests that populations of the oligophagous *B. cucumis* should perform equally (i.e., its population dynamics should be similar) when using plants within Cucurbitaceae, but should perform relatively poorly on hosts outside this family. In contrast, the polyphagous host use of *B. tryoni* implies that populations of *B. tryoni* from different hosts should have similar population dynamics (Thorsteinson 1960, Ehrlich and Raven 1964, Wiklund 1975, Jaenike 1978a, Futuyma 1983a, Jermy 1984, Jaenike 1990, Schoonhoven et al. 1998a, Thompson 1998, Walter 2003).

As predicted by theory, *B. cucumis* did perform better on Cucurbitaceae hosts relative to Solanaceae, Passifloraceae and Myrtaceae. While passionfruit and guava could not sustain a population, tomato was able to sustain positive population growth, albeit much smaller than that on Cucurbitaceae hosts. Even within Cucurbitaceae hosts, there were differences in the relative performance of *B. cucumis*. Although all four hosts tested resulted in a positive population growth rate, squash and zucchini sustained far more rapid population growth than did pumpkin and cucumber. The polyphagous *B. tryoni* exhibited positive population growth across primary and alternate hosts as predicted by theory. However, there were distinct differences in suitability of the different hosts in which apple permitted rapid population growth and tomato permitted the slowest growth.

The difference in population dynamics of both fly species was mainly due to the differences in fecundity between the populations reared from the different hosts. Fecundity of *B. cucumis* was far lower for flies from tomato than on Cucurbitaceae hosts (Table 4.1), while *B. tryoni* from tomato also had lower fecundity than those from other hosts (Table 4.3). This resulted in a lower net reproductive rate and, hence, a lower population growth rate from tomato for both species (Tables 4.7, 4.8). The lack of egg deposition and lower offspring performance of *B. cucumis* on tomato may be due to its chemical fruit properties than to the physical fruit traits (Chapter 3).
Comparing the preference and performance of the oligophagous *B. cucumis* and polyphagous *B. tryoni* on different hosts (Chapter 3) to their demographic performance on those hosts identified in this study revealed some interesting patterns. *B. cucumis* had a high oviposition preference and showed strong larval performance on zucchini and squash (Chapter 3). These hosts were also the ones that enabled most rapid population growth in this demographic study (Table 4.7). Similarly, *B. cucumis* exhibited low preference for cucumber and tomato that provided poor larval performance (Chapter 3) and also were poor hosts from a demographic perspective. These results are in agreement with the predictions of the preference-performance hypothesis. These results suggest that in addition to larval survival, larval nutrition has effects that carry through into the reproductive performance of adults that emerged from those fruits, as has been documented in other tephritids (Kaspi et al. 2002).

The polyphagous *B. tryoni* showed some interesting departures from the predictions of the preference-performance hypothesis. The host that was the most preferred had the poorest larval performance, plum (Chapter 3), but sustained moderate demographic growth that was similar to that in pear (low preference, moderate larval performance; Chapter 3). Apple that was equally preferred for oviposition as plum, but elicited more moderate larval performance, had the highest demographic growth of *B. tryoni*. Hosts that may yield lower larval survival may still be superior from a demographic perspective as they may result in adults that are more fecund (compare fecundity of apple vs. plum in Table 4.6). Such relationship has also been reported for other polyphagous tephritid species (Krainacker et al. 1987).

In addition to the differences between populations of different fruits, the differences in the overall egg load, generation time and distribution patterns of eggs over time between the two species (Figures 4.3, 4.4) provided some explanation for the differences in their current host use patterns. The population parameters of high fecundity and shorter generation time of *B. tryoni* indicated that its host acceptance threshold would be lower than that of *B. cucumis* and, therefore, even lower ranked hosts could be used by *B. tryoni* resulting in wider host range. On the other hand, the lower fecundity and longer generation time of *B. cucumis* provided a higher host acceptance threshold and, therefore, high host discrimination occurred resulting in
specialized host use pattern. These physiological and time limitation factors which elucidate such host use patterns conforms to the ‘hierarchy threshold model’ (Singer 1971, Singer 1982, Courtney et al. 1989) and the ‘time-limitation hypothesis’ (Levins and MacArthur 1969, Jaenike 1978a, Wikelund 1981, Courtney 1982) postulated to explain host use and host choice mechanisms in phytophagous insects.

A variety of fruit fly pest management strategies such as protein bait sprays, sterile insect release and biological control through parasitoids, are used throughout the world. However, before any control strategy could be utilized, studies on the behaviour and ecology of the fly with respect to its host and the ever-changing environmental conditions must be known. Additionally, a basic understanding of the biology (life history) and physiology of the two fruit flies is needed in order to choose the most appropriate management strategy.

The life history transition that has the greatest impact on demography for both dacine species was the adult reproductive stage (Figures 4.7, 4.8). The survival of pre-reproductive adults was also among the three strongest influences on demography of $B. cucumis$ and $B. tryoni$ (Figures 4.7, 4.8). The nutritional requirements of adult tephritid fruit flies have been well studied in that the adult flies require a carbohydrate source for energy and water for survival (Christenson and Foote 1960, Bateman 1972, Tsitsipis 1989). In addition, flies require a proteinaceous resource in order to achieve sexual maturity and ovarian development (Hagen and Finney 1950, Steiner 1955). Based on these physiological requirements, the protein bait spray as a control option was developed targeting the pre-reproductive and early reproductive stages. This is currently one of the best control strategies used throughout the world. While physiological requirements of the female fly could have been the reason behind the use of protein bait sprays, my study provided a life history and population demographic basis for using protein bait applications that target pre-reproductive and reproductive stages. In addition, predators or pathogenic fungi may be used to target reproductively mature flies as a biological control method. Preliminary studies using this approach against other $Bactrocera$ species are in progress and have shown promise (Dr. A. Chinajariyawong-pers.comm.).
Another fruit fly control option has been the use of fruit fly parasitoids, especially species of the Family Braconidae (Purcell 1998). Although, parasitoids have been reported to decrease fruit fly populations (Newell and Haramoto 1968), they have not been able to reduce populations to a level low enough to lessen fruit damage below the economic threshold level (Vijaysegaran 1984, Wharton 1989, Aguiar-Menezes and Menezes 1997). The inability of parasitoids to provide economic control may be due to a number of reasons; 1) most larvae burrow deep into the fruit which makes it difficult for the parasitoids’ ovipositor to reach them (Nishida 1955), 2) the large time lag between the host fly reproductive period and that of the parasitoids makes it impossible for the parasitoids to use the host (Wong et al. 1984) and 3) fruit flies have a higher reproductive rate than the parasitoids, which makes it difficult for parasitoids to have an impact on the fruit fly populations (Debouzie 1989). While these factors provide some explanation, the results from my study indicated that there are significant life history traits that may provide further explanations. Since, most parasitoids target the egg and larvae stages (Wharton and Gilstrap 1983, Vijaysegaran 1984, Chinajariyawong et al. 2000, Stibick 2004), and my results showed that B. cucumis and B. tryoni were least sensitive to probability of egg and larval survival (Figures 4.7, 4.8), I suggest that any effort to reduce populations of B. cucumis and B. tryoni by use of egg or larval parasitoids would always result in minimal reduction of their population growth rate.

In addition to survival of reproductive and pre-reproductive adults, a third major influence on the demography of these species was pupal survival (Figures 4.7, 4.8). This suggests that parasitoids that kill the pupae could suppress populations of B. cucumis and B. tryoni. At present issues related to intra-guild predation may potentially limit the effective deployment of this method (Wang and Messing 2004). Augmentative releases of only the pupal parasitoids such as Dirhinus giffardii Silvestri, untimely may provide biological control of both these pest species, provided they pose low risk to non-target species. My data indicated that biological control efforts to manage dacine fruit flies should consider life-history consequences of host use when determining managing strategies for pest populations in fruit crops.
CHAPTER 5: GENERAL DISCUSSION

5.1 GENERAL DISCUSSION

Optimality theory in the form of the preference-performance hypothesis has been tested in most insect-plant systems, but has had varying level of success in explaining patterns of host use (Kouki 1993, Berdegué et al. 1998, Carr et al. 1998, Bruyn et al. 2002, Jallow and Zalucki 2003). In this thesis, I investigated the relevance of the preference-performance hypothesis in explaining the ecology of the oligophagous *B. cucumis* versus the polyphagous *B. tryoni*. Specifically, I enquired if the preference-performance hypothesis explains host use patterns of dacines species, and if so at which plant taxonomic level was this evident? If it does not explain host use, then what might be the other factors that determine host use of both the specialist and generalist Dacinae? I subsequently investigated the life history and demographic consequences of host-use patterns of these dacine species.

In accordance with optimality theory, I predicted that preference for hosts in *B. cucumis*, the relative specialist, to be strongly correlated with offspring performance on those hosts. In particular I expected that *B. cucumis* would use hosts within the Cucurbitaceae with equal efficiency. When Cucurbitaceous hosts were offered to *B. cucumis* with hosts from alternate families, I anticipated preference and performance to be significantly better in Cucurbitaceae. Host discrimination was exhibited by *B. cucumis* within Cucurbitaceae species and also among hosts across different families. While there were correlations between oviposition preference and offspring performance parameters, these were dependent on the parameter used, rather than a case of optimizing preference and performance. The observed patterns were more plausibly explained by behavioural and physiological factors. For example, while *B. cucumis* did not oviposit into tomato, it was not because of its lack of suitability for larval development; over 50% of eggs manually inoculated into tomato developed into pupae (Chapter 3). Even when *B. cucumis* could penetrate the pericarp of tomato, it did not deposit any eggs. This suggests that factors associated with the texture of the pericarp in relation to the act of oviposition, and the chemical environment perceived by the ovipositor are important in the oviposition decision by the female fly. These
factors may explain why *B. cucumis* exhibited host discrimination within the Cucurbitaceae and even among varieties of cucumber (Chapter 3).

For the generalist *B. tryoni*, based on the broad published host range, I anticipated that it would show equal preference across hosts in multiple families. This was not the case. As in previous evaluations of purportedly polyphagous species (Clarke et al. 2001), *B. tryoni* preferentially used certain host species even when equivalent hosts within its major host family (Rosaceae) were provided simultaneously. Even within a single species (apple), *B. tryoni* used ‘Red Delicious’ and ‘Golden Delicious’ varieties more efficiently than ‘Granny Smith’ variety. Again, host use did not appear to be a result of optimizing offspring performance (Chapters 3), and behavioural and physiological explanations seemed more plausible.

The physiological and behavioural factors associated with host-use behaviour (Table 1.1) provide clues as to what factors may best explain host use pattern in different dacine species. Insects are adapted to a set of cues that influence each step leading to host use (Walter 2003). Since insect traits were standardized across experiments by using flies from the same cohort and similar age classes, I investigated two physical plant traits in this regard (fruit size and pericarp toughness) to explain some of the host use patterns observed. Predictably, fruit size, a pre-alighting factor which may be a valuable long-distance cue for flies to locate hosts, did not explain the patterns seen in the laboratory-based experiments. Pericarp toughness, a post-alighting factor, however, was a good predictor of whether or not a fly could oviposit into a given fruit (Chapter 3). However, as evident from the absence of *B. cucumis* oviposition in tomato, despite penetration of the pericarp, several other post-alighting factors was also likely to be important.

In addition to the behavioural aspects of dacine-host plant relationships, life history parameters of tephritid species play a significant role in host use (Fitt 1990). The generalist *B. tryoni* possessed a higher fecundity and net reproductive rate, and shorter generation time while the specialist *B. cucumis* had a lower fecundity and net reproductive rate with a longer generation time (Chapter 4). While the demographic patterns of the oligophagous *B. cucumis* appeared to conform to optimality theory, *B. tryoni* showed some interesting departures from the predictions of the preference-
performance hypothesis (Chapter 4). For *B. tryoni* it was evident that hosts that may yield lower survival in terms of larval survival (i.e., offspring performance) may still be demographically suitable because of the enhanced reproductive performance of adults emerging from such fruit, hence, showing to the importance of quality of adult food resource as an important factor in the demography of this species.

Organizing demographic data and analysing them using population projection models also enabled me to identify critical stages that influence the demography of these two species across different host fruits. The population growth rates of both the oligophagous *B. cucumis* and polyphagous *B. tryoni* were highly sensitive to adult reproductive stage, indicating that influencing probability of survival at this life stage would be critical to managing these pest species (Chapter 4). This highlighted why protein-bait sprays are valuable in managing populations of these dacinines. Predators or pathogens that target the adult reproductive stage could also provide successful biological control of these pest fruit fly populations. In addition to survival of reproductive individuals, pupal survival was also important to the demography of these species. This suggests that biological control targeting this stage also may yield population suppression across different fruit production systems.

While this study sought to explore fundamental differences in host use patterns between specialist (oligophagous) and generalist (polyphagous) dacine fruit flies, the results indicated that greater attention needs to be paid to the underlying mechanisms that influence host choice and host use in understanding host-use patterns. Although lists based on rearing records (e.g., Allwood et al. 1999, Hancock et al. 2000) are valuable in understanding the potential host range of different dacine species, designation of host status of a plant or defining the host range exclusively from these tools may not be prudent (Clarke et al. 2001). Detailed investigations on physiological and behavioural adaptations influencing host use may be more valuable (Walter 2003, Rajapakse et al. 2006) both in understanding host use patterns to manage pests and in prioritising species for quarantine surveillance. This is a key gap in dacine biology.
5.2 Gaps in the knowledge

1) Relationship between ovipositor morphology and pericarp toughness

Pericarp toughness is one of the key factors that influences host use in dacine species, as has been demonstrated in this study (Chapter 3) and other recent studies (e.g., Dhillon et al. 2005). A key morphological adaptation that has enabled tephritids to use living plants or plant parts, unlike their ancestral counterparts, has been the evolution of a stronger aculeus to facilitate easier penetration into the tough surface of fruits and other plant parts (Diaz-Fleischer et al. 2000). As mentioned in Diaz-Fleischer et al. (2000), Jones (1989) reported that the morphology of the aculeus of tephritids, which is designed to penetrate living host tissues, is influenced by its host characteristics, such that species of flies utilising fruits with a thick cuticle have sharper pointed tips than those utilising fruits with a thin cuticle. Such studies relating aculeus morphology and host fruit traits have never been reported for dacine fruit flies.

2) Effect of chemical composition of fruits on host use

If the fly overcomes physical fruit traits so that the ovipositor penetrates the fruit surface, chemical compounds in the fruit may either stimulate or inhibit egg deposition and subsequent larval growth (e.g., Girolami et al. 1981, Greany et al. 1983, Eisemann and Rice 1985, Dhillon et al. 2005). The chemical composition of the fruits used by *B. cucumis* and *B. tryoni* did show some potential to affect the oviposition preference (*B. tryoni*) and oviposition performance (*B. cucumis*) of the two species in this study (Chapter 3). While some studies have demonstrated the influence of fruit volatiles on oviposition preference of *B. tryoni* (Fletcher and Watson 1974, Eisemann and Rice 1992), in-depth studies identifying the internal chemical compounds of fruits and their effect on offspring performance of *B. tryoni* have not been undertaken. Similarly, the effect of fruit volatiles and the chemical components of fruits in oviposition preference and offspring performance of *B. cucumis* require considerable research.

The use of the host plant may be related to the chemical cues that relate to primary adaptations of different dacine species. Therefore while several taxa may be used by a species, host use may be determined by a specific set of cues that elicit host acceptance; i.e., species may actually be quite specialised with respect to plant cues to
which they respond and host range may be a function of how broad or narrow these stimuli are distributed among fruits. For example, the polyphagous *Helicoverpa armigera* Hubner uses pigeon pea as its primary host because it possesses a higher concentrations of a broad spectrum of electrophysiological active chemicals than the less preferred hosts (Rajapakse et al. 2006).

3) **Factors influencing population dynamics of tephritids**

While this study investigated the influence of host species on the population dynamics of *B. cucumis* and *B. tryoni* (Chapter 4), it was a laboratory-based study and did not incorporate the effect of other factors such as weather, habitat structure or parasitoids. Similarly, most demography studies incorporating climatic factors have not included the effect of host species in their population models (e.g., Yonow et al. 2004). Demographic studies of the two dacine species incorporating all possible factors affecting their demography, is therefore essential in order to elucidate a realistic estimation of population growth rate and then develop an appropriate pest management strategy. While field-based estimations of demography may prove to be logistically very difficult, the next step towards building greater realism into these demographic models may be to conduct similar studies under field-cage environments.

4) **Use of parasitoids targeting reproductive adults and pupal life stages**

Causing mortality to life stages that have strong influences on population dynamics would be vital in managing pest populations of dacine species. As has been demonstrated in this study, changes in the probability of survival at the adult reproductive stage and pupal survival have more significant effect on the population growth rate than other life-history transitions (Chapter 4). Current biological pest management options for dacine fruit flies have been those involving parasitoids that target the egg and larvae stages, and these have not always resulted in adequate management of pest populations. The results generated from this study suggest that research on the role of predators or pathogens that target the adult reproductive stage may be necessary for successful population management of *B. tryoni* and *B. cucumis* through the use of biological agents. Pupal parasitoids used augmentatively may also yield greater population suppression in these dacines than parasitoids targeting other life-stages.
Addressing these key gaps could be fruitful avenues for subsequent studies.
REFERENCES


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APPENDIX

A. Other peer-reviewed Journal Publications


Appendix

B. Photographs used in the thesis

Photographs on the title page were taken from the world pest fruit fly poster published and compiled by Richard Piper from the Scientific Advisory Services. Photographs on title page of Chapter 5 are a composite of Steve Wilson, Richard Drew and the author while Figure 1.1 was extracted from Raghu (2002). All other photographs are by the author.