



**Dispersal and mating  
behaviour of Queensland  
fruit fly, *Bactrocera tryoni*  
(Froggatt) (Diptera:  
Tephritidae): Implications  
for population  
establishment and control.**

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## **Declaration**

I hereby declare that the work contained in this thesis is my own and contains no materials previously written by another person, except where specifically acknowledged. I have not submitted a similar thesis at another university.

Christopher W. Weldon

September 2005

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## Preface

This thesis contains published works and works submitted for publication in peer-reviewed, scientific journals that are based on research undertaken at the University of Sydney towards the degree of Doctor of Philosophy. Inclusion of published material in a thesis is permitted by the regulations for the degree of Doctor of Philosophy at the University of Sydney. Consequently there is some redundancy within the thesis stemming from methodological repetition.

Where published material or material submitted for publication has been included as a Chapter, or part thereof, the reference for the publication follows the Chapter title. Reference to published material within the thesis will be cited as a Chapter number only.

This thesis is comprised of two major parts. Part I (Chapters 2 – 5) documents field and laboratory studies that were conducted to examine dispersal of male and female Queensland fruit flies, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae), including studies to assess techniques used to monitor dispersal. In Part II (Chapters 6 – 8) the mating behaviour of *B. tryoni* is explored in relation to density, sex ratio, and fly origin.

## Abstract

The Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae), a major pest of horticulture in eastern Australia, is a relatively poor coloniser of new habitat. This thesis examines behavioural properties that might limit the ability of *B. tryoni* to establish new populations. As the potential for *B. tryoni* to establish an outbreak population may be most directly limited by mechanisms associated with dispersal and mating behaviour, these two factors were the focus of this research project. The relevance of dispersal and mating behaviour for control of outbreak populations was assessed.

### Dispersal

#### ***(i) Dispersal patterns of males and females are not different.***

Dispersal of post-teneral male *B. tryoni* from a point within an orchard near Richmond, New South Wales, was monitored following temporally replicated releases. Application of sterile insect technique (SIT) requires knowledge of dispersal from a release point so that effective release rates can be determined. In addition, dispersal following introduction to new habitat can lead to low or negative population growth and an Allee effect. In Spring and Autumn, 2001 – 2003, three different strains of *B. tryoni* were released: (1) wild flies reared from infested fruit collected in the Sydney Basin; (2) a laboratory-reared strain with a colour mutation (*white marks*); and (3) sterile flies obtained by gamma-irradiation of a mass-reared strain. Dispersal was monitored using a grid of traps baited with the male attractant, cuelure. During the majority of releases, flies were mass-marked using a self-marking technique and fluorescent pigment powder to enable identification of recaptured flies. A preliminary study found that fluorescent pigment marks had no effect on adult survival and marks did not fade significantly in the laboratory over a period of five weeks after eclosion.

As cuelure repels inseminated sexually mature female *B. tryoni*, unbaited, coloured flat sticky traps, and black and yellow sticky sphere traps baited with a



food lure (protein autolysate solution) were used to supplement traps baited with cuelure. The effectiveness of these two sticky trap types was assessed, and recaptures used to compare patterns of dispersal from a release point by male and female *B. tryoni*. Fluorescent yellow (chartreuse), green, and clear unbaited flat sticky traps were relatively ineffective for monitoring dispersal of sterile male and female *B. tryoni*, recapturing only 0.1% of released sterile flies. Monitoring dispersal with sticky ball traps baited with protein autolysate solution was more successful, with yellow spheres and black spheres recapturing 1.7% and 1.5%, respectively. Trap colour had no effect on recaptures on flat sticky traps or sticky spheres. Equal recapture rates on yellow and black sticky sphere traps suggests that the odour of yeast autolysate solution was more important than colour for attraction of post-teneral flies to traps.

Using the results of recaptures on odoriferous black and yellow sticky sphere traps within one week of release, regression equations of male and female recaptures per trap were found to be similar (Figure 4-3). This is the first study to clearly indicate that post-teneral dispersal patterns of male and female *B. tryoni* released from a point do not differ, enabling the use of existing models to predict density of both sexes of *B. tryoni* following post-teneral dispersal.

***(ii) Males disperse further in Spring than in Autumn, but this is not temperature-related.***

Analysis of replicated recaptures in traps baited with cuelure revealed that dispersal of male *B. tryoni* in an orchard near Richmond, New South Wales, was higher in Spring than in Autumn (Figure 5-6). As the maximum daily temperature was significantly higher in Spring than in Autumn this result was unexpected, since earlier studies have found that *B. tryoni* disperse at the onset of cool weather in search of sheltered over-wintering sites. Dispersal of post-teneral *B. tryoni* may have been affected by habitat suitability; it was found that seasonal trends in dispersal could have been influenced by local habitat variables. Low mean dispersal distances in Autumn may be explained by the presence of fruiting hosts in the orchard, or the availability of resources required by over-wintering flies.

There was no significant correlation between temperature and mean dispersal distance, suggesting that higher rates of dispersal cannot be explained by temperature-related increases in activity. Recapture rate per trap was significantly negatively correlated with increasing daily maximum and average temperature. This may have consequences for detection of *B. tryoni* outbreaks in quarantine areas due to reduced cue lure trap efficiency.

***(iii) Maturity and source variation affect dispersal and response to cue lure.***

This research indicated that most male and female *B. tryoni* do not disperse far from a release point, suggesting that an invading propagule would not spread far in the first generation. However, there is considerable variation in flight capability among individuals. Comparison of wild, laboratory-reared *white marks*, and gamma-irradiated sterile male *B. tryoni* indicated that mean dispersal distance and redistribution patterns were not significantly affected by fly origin. Despite no difference in dispersal distance from the release point, recaptures of wild and sterile males per Lynfield trap baited with cue lure were highest within one week after release, whereas recaptures of *white marks* males per trap increased in the second week. This result may offer evidence to support the hypothesis that sterile male *B. tryoni* respond to cue lure at an earlier age. Rearing conditions used to produce large quantities of males for sterilisation by gamma-irradiation may select for earlier sexual maturity.

## **Mating Behaviour**

***(i) Density and sex ratio do not affect mating, except at low densities.***

Demographic stochasticity in the form of sex ratio fluctuations at low population density can lead to an observed Allee effect. The effect of local group density and sex ratio on mating behaviour and male mating success of a laboratory-adapted strain of *B. tryoni* was examined in laboratory cages. In the laboratory-adapted strain of *B. tryoni* used in this study, a group of one female and one male was sufficient for a good chance of mating success. The proportion of females mated and male mating success was not significantly affected by density or sex ratio, although variability in male mating success was higher at low density. This could

indicate that mating success of *B. tryoni* can be reduced when local group density is low owing to decreased frequency in encounters between males and females.

**(ii) Mass-reared males exhibit aberrant mating behaviour, but this does not reduce mating success.**

Strong artificial selection in mass-rearing facilities may lead to decreased competitiveness of sterile males released in SIT programs as a result of alteration or loss of ecological and behavioural traits required in the field. The effects of domestication and irradiation on the mating behaviour of males of *B. tryoni* were investigated by caging wild, mass-reared and sterile (mass-reared and gamma-irradiated) males with wild females. Mating behaviour of mass-reared males was different from that of wild males, but behaviour of wild and sterile males was similar. Mass-reared males were found to engage in mounting of other males much more frequently than wild and sterile males, and began calling significantly earlier before darkness. Male calling did not appear to be associated with female choice of mating partners, although this does not exclude the possibility that calling is a cue used by females to discriminate between mating partners. Conditions used to domesticate and rear large quantities of *B. tryoni* for SIT may select for an alternative male mating strategy, with mass-reared males calling earlier and exercising less discrimination between potential mating partners. Despite differences in behaviour of wild, mass-reared and sterile males, frequency of successful copulations and mating success were similar.

**(iii) Pheromone-calling by males was increased in larger aggregations but this did not result in significantly more female visits.**

Finally, large laboratory cages with artificial leks were used to investigate the importance in *B. tryoni* of male group size for female visitation at lek sites and initiation of male pheromone-calling. Calling propensity of male *B. tryoni* was increased by the presence of conspecific males. Females visited the largest lek more frequently than single males, but there was no correlation between lek size and female visitation. Female *B. tryoni* had a limited capacity to perceive a difference between the number of calling males; female visitation at leks was only weakly associated with male calling, suggesting that lek size and the number of

pheromone-calling males may not be the only factor important in locating mates in *B. tryoni*. The weak, but positive correlation between male calling and female visitation may indicate that passive attraction maintains lek-mating in *B. tryoni*.

Further studies are essential on mating behaviour of *B. tryoni*, including identification of male mating aggregations in the field, measurement of habitat variables associated with male aggregations, the influence of density on wild *B. tryoni* mating success, and the role of pheromone-calling, in order to optimise use of SIT for control of this pest.

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## ***GENERAL INTRODUCTION***

# **CHAPTER 1. General Introduction**

## **1.1. Queensland fruit fly: a widespread pest**

Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) is a polyphagous, multivoltine species endemic to rainforests in eastern Australia. The natural distribution of this species extended from tropical, far north Queensland, to warm temperate, coastal New South Wales (May 1963; Drew 1978; Yonow & Sutherst 1998). Cultivated fruits introduced to Australia following European settlement proved to be suitable hosts for oviposition and development of larvae, resulting in a marked expansion of the range of *B. tryoni* (May 1963; Drew 1978; Raghu *et al.* 2000). Gravid females oviposit in the fruits of over one hundred species of native and introduced plants, including citrus, stonefruits and apples (Anon. 1997; Hancock *et al.* 2000), making *B. tryoni* the most serious pest of horticulture in eastern Australia, as well as several Pacific Islands where it has become established following inadvertent introduction (Tychsen 1977).

Effective control of *B. tryoni* is only possible in areas marginal for survival of this species, and where populations are isolated from denser continuous populations by distances greater than the flight range of inseminated females (Andrewartha *et al.* 1967). The potential geographic distribution of *B. tryoni* populations is limited by temperature and rainfall. Temperature influences the number of generations per year (Meats 1981), time for maturation of oocytes, and resorption of oocytes after maturation (Fletcher 1975; Meats & Khoo 1976). The main limiting factor for survival of *B. tryoni* in marginal areas is rainfall, with suitability changing markedly between years (Bateman 1968; Meats 1981; Yonow & Sutherst 1998). Irrigation tends to remove the limiting effects of lack of moisture (Fletcher 1974b; Meats 1981; Yonow & Sutherst 1998). In 1994, a Fruit Fly Exclusion Zone (FFEZ) was established in important orange and grape-growing areas in south-eastern central Australia, encompassing irrigated agricultural land in New South Wales, South Australia and Victoria. Managed by



the Tri-State Fruit Fly Committee, the FFEZ is located in a region considered to be marginal for the survival of *B. tryoni* (Meats 1981; Yonow & Sutherst 1998). The FFEZ is designated by interstate and international trade agreements as having ‘area freedom’ from *B. tryoni* so that produce can be exported without post-harvest treatment for this species (Anon. 1997). Control of this species in Australia is an expensive exercise, with costs exceeding \$A125 million in 1991 (Yonow & Sutherst 1998). Potential losses in the absence of control, based on data collected in Adelaide, could be greater than 80%, representing a value exceeding \$A800 million (Sutherst *et al.* 2000).

Outbreaks of *B. tryoni* frequently occur in the FFEZ, with subsequent cost increases, and reduced market value and access. Outbreaks of *B. tryoni* in the FFEZ have been attributed to introduction of infested fruit by human activity, or the occurrence of persistent, undetected low-level populations in towns within and surrounding the FFEZ. Using microsatellite markers, genetically distinct populations have been identified in towns surrounding the FFEZ (Gilchrist 2004). Moreover, it has been shown that outbreaks of *B. tryoni* within the FFEZ have been sourced from these small, isolated, usually low-level populations (Gilchrist 2004). Small populations of *B. tryoni* may be introduced into quarantined zones isolated from endemic areas by human transportation of infested fruit (Bateman 1977; Dominiak *et al.* 2000a; Meats *et al.* 2003).

## **1.2. Establishment of populations**

Despite being regarded as a major pest, *B. tryoni* is a poor coloniser of habitat when population density is low (Bateman 1977). Recent examination of trap captures in quarantine areas normally free of *B. tryoni* between the years 1974 and 2000 indicates that 57% of low level incursions failed to establish an outbreak (Meats *et al.* 2003). Small founder populations of *B. tryoni* introduced into new areas are unlikely to become established due to a dispersal-mediated Allee effect. The Allee effect is a positive relationship between any component of individual

fitness and either numbers or density of conspecifics, leading to low or negative population growth rates (Stephens *et al.* 1999).

Past studies have acknowledged that the Allee effect is a major reason for the success of quarantined zones that are declared free of tephritid fruit flies (Bateman 1977; Meats 1998b; Meats *et al.* 2003). Modelling and empirical evidence indicate that a migration-mediated Allee effect can result if too few individuals remain to reproduce fast enough to sustain loss by emigration (Hopper & Roush 1993; Lewis & Kareiva 1993; Menendez *et al.* 2002). Sexually immature (post-teneral) adult *B. tryoni* exhibit a tendency to disperse away from the site of pupal emergence regardless of the suitability of the immediate habitat for survival and reproduction (Bateman & Sonleitner 1967; Fletcher 1973). Long-distance dispersal may increase the chance of encountering spatially and temporally distributed resources, such as oviposition and feeding sites, in areas where *B. tryoni* is endemic and exist at high density (Bateman & Sonleitner 1967; Fletcher 1973; Bateman 1977; Fletcher & Kapatos 1981; Drew & Hooper 1983; Zalucki *et al.* 1984). Where a small number of flies are introduced into areas marginal for survival, dispersal of post-teneral adults will lead to low density and, potentially, an inability to locate mates (Bateman 1977). A dispersal-mediated Allee effect is particularly likely if an organism exhibits high dispersal but poor mate-finding capability (Hopper & Roush 1993), or no adaptation of female preference to the restricted choice possibilities (Keitt *et al.* 2001; Møller & Legendre 2001; Bessa-Gomes *et al.* 2003). Sexually mature adult movement in *B. tryoni* is non-dispersive, involving local movements to search for food, mates and oviposition sites (Fletcher 1973), so the ability of males to form large leks and the opportunity for females to encounter them after the post-teneral dispersal phase is limited (Bateman 1977).

### 1.3. Mating behaviour

Relatively little is known about mating behaviour of wild *B. tryoni* as matings have rarely been observed in the field (Fletcher 1987). In the endemic range of *B. tryoni*, dense swarms of males have been observed (Bateman 1972). In a field cage, males from a laboratory-adapted strain form a ‘flying swarm’ that settles on upwind, outer branches of a tree to form a compact ‘settled swarm’, where males perch on leaves and commence rapid wing-vibration (Tychsen 1977). Wing-vibration, or calling, is associated with dispersion of a pheromone produced by an internal abdominal gland and exuded via the anus (N. Pike, unpublished data). Females approach calling males, and copulation rapidly ensues (Tychsen 1977). Recently it has been suggested that pheromones released by calling male *B. tryoni* only operate at small scales within a tree canopy to attract females and induce conspecific males to remain in the vicinity of the pheromone source (Pike & Meats 2003).

Although information on mating behaviour of *B. tryoni* in the wild is scarce, observations to date suggest that this species exhibits a lek mating system (Fletcher 1987). Leks are aggregations of displaying males that females attend primarily for the purpose of fertilization (Höglund & Alatalo 1995). Gametes are the only contribution of males to females in species that form leks (Bradbury 1981). Lekking behaviour has also been observed in the Oriental fruit fly, *Bactrocera dorsalis* (Coquillett) (Arakaki *et al.* 1984; Shelly & Kaneshiro 1991; Prokopy *et al.* 1996), and Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann) (Arita & Kaneshiro 1989; Shelly & Whittier 1994; Kaspi & Yuval 1999; Shelly 2000).

The lek mating system of *B. tryoni* may increase the incidence of an Allee effect in populations at low density. Lek size has been shown to be an important factor for visitation of females and success of males on leks in several insect species (Aspi & Hoffmann 1998; Jones & Quinnell 2002), including other

tephritid fruit flies (Shelly 2001). Similarly, male group size has been shown to facilitate male calling or courtship behaviour in tephritid fruit flies (Burk 1984; McDonald 1987). Consequently, individual mating behaviour may not be facilitated in low-density populations of *B. tryoni* due to a lack of interaction with conspecifics.

#### **1.4. Consequences for pest management**

Current management of *B. tryoni* incursions in quarantine zones in Australia is guided by the current Code of Practice (Anon. 1997). The Code of Practice outlines responses that are related to the number of flies trapped per fortnight in surveillance traps baited with the male attractant, cue lure. Surveillance trap spacing is related to the perceived risk of fruit fly occurrence: 0.4 km in urban areas, 1 km in production areas, and sparsely elsewhere. Trapping of two or more male *B. tryoni* in a given trap within two weeks triggers the setting of 16 supplementary male-lure traps and 16 traps that attract both males and females within a radius of 200 m. A search for larvae is also made within the array of supplementary traps. An outbreak is declared following trapping of five males within 1 km in a period of two weeks, or the trapping of one female, or detection of larvae. Identification of an outbreak results in suspension of area free status within a radius of 15 – 80 km, bait spraying for two weeks, followed by the release of sterile insects for 8 – 12 weeks. Recent analysis of infestation data by Meats *et al.* (2003) indicates that quarantine radii following declaration of an outbreak are unnecessarily large, and the Code is currently under review.

As highlighted by Meats *et al.* (2003) the hierarchy of responses prescribed in the Code of Practice are not based on a full assessment of risks. Suspension zone radii are not clearly related to the risk of mated female flies travelling a given distance (Meats *et al.* 2003). Within the Code there is an underlying assumption that female *B. tryoni* dispersal is the same as that of males. This assumption is despite an absence of studies to compare male and female

dispersal patterns. Fletcher (1973) found similar estimates of male and female *B. tryoni* remaining in an orchard at Wilton, New South Wales, after release as young adults, but it was not possible to determine whether these values reflected emigration from the orchard or mortality. Furthermore, detection of one female or finding a site with larvae in the absence of other trap captures may not warrant declaration of an outbreak and subsequent loss of area freedom, as density of the detected population may be too low for the population to persist, with subsequent failure to establish.

Sterile insect technique (SIT) is an important component in programs to control outbreaks of *B. tryoni* (James 1992; Horwood & Keenan 1994; Dominiak *et al.* 1998; Dominiak *et al.* 2000b; Dominiak *et al.* 2003). The aim of SIT is to reduce the growth rate of a target population to below unity by saturating wild females with released mass-reared, sterilised males. The suggested minimum release rate to achieve eradication of *B. tryoni* is 60,000 sterile males per km<sup>2</sup> per week (Meats 1996). To produce the large quantity of males required for SIT, laboratory domestication and mass-rearing are required. However, the laboratory environment imposes unnatural selection pressures to which a population will adapt, resulting in increased fitness in the new environment and enabling the laboratory population to persist (Iwahashi 1996; Matos *et al.* 2000). This strong selection may result in the alteration or loss of ecological and behavioural traits that are necessary for mass-reared males to remain competitive when released in the field (Saul & McCombs 1995; Iwahashi 1996; Dalby-Ball & Meats 2000a; Briceño & Eberhard 2002), which is further compounded by sterilisation (Shelly & Whittier 1996; Lux *et al.* 2002).

## **1.5. Aims**

This project aimed to examine behavioural characteristics of Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) that limit the potential of this species to establish new populations. In particular, dispersal and mating behaviour

were studied as mechanisms that may decrease the potential of *B. tryoni* introduced in low numbers to establish an outbreak population. The relevance of dispersal and mating behaviour for control of outbreak populations was also assessed.

### **1.5.1. Dispersal**

Within the broad aim of examining dispersal as a mechanism leading to low colonisation ability in *B. tryoni*, the aims of research described in Part I of this thesis were:

- To assess methods used to monitor dispersal of *B. tryoni*. Methods used to mark flies released during dispersal studies, and efficiency of traps used to monitor dispersal were examined.
- To monitor patterns of immature adult (post-teneral) dispersal in *B. tryoni* under field conditions. The influence of season and temperature on dispersal was assessed.
- To compare the dispersal ability of male and female *B. tryoni* in the field.
- To compare dispersal ability of wild, laboratory-reared, and gamma-irradiated (sterile) *B. tryoni* in the field, in order to assist control of *B. tryoni* using sterile insect technique.

### **1.5.2. Mating Behaviour**

Part II of this thesis addresses mating behaviour in *B. tryoni* at low density. The aims of the research described in Part II were:

- To observe and describe mating behaviour of wild *B. tryoni*.
- To determine if mating behaviour of *B. tryoni* is influenced by density and sex ratio.
- To determine if female visitation at male aggregations and male mating behaviour is influenced by male aggregation size.

- To compare mating behaviour of wild, mass-reared and gamma-irradiated (sterile) male *B. tryoni* to assist control of this species using sterile insect technique.