



# The seasonal phenology of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) in Queensland

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## Abstract

*Bactrocera tryoni* is a polyphagous fruit fly, originally endemic to tropical and subtropical coastal eastern Australia, but now also widely distributed in temperate eastern Australia. In temperate parts of its range, *B. tryoni* populations show distinct seasonal peaks driven by changing seasonal climates, especially changing temperature. In contrast to temperate areas, the seasonal phenology of *B. tryoni* in subtropical and tropical parts of its range is poorly documented and the role of climate unknown. Using a large, historical (1940s and 1950s) fruit fly trapping dataset, we present the seasonal phenology of *B. tryoni* at nine sites across Queensland for multiple (two to seven) years per site. We correlate monthly trap data for each site with monthly weather averages (temperature, rainfall and relative humidity) to investigate climatic influences. We also correlate observed population data with predicted population data generated by an existing *B. tryoni* population model. Supporting predictions from climate driven models, *B. tryoni* did show year-round breeding at most Queensland sites. However, contrary to predictions, there was a common pattern of a significant population decline in autumn and winter, followed by a rapid population increase in August and then one or more distinct peaks of abundance in spring and summer. Mean monthly fly abundance was significantly different across sites, but was not correlated with altitudinal, latitudinal or longitudinal gradients. There were very few significant correlations between monthly fly population size and weather variables (either for the corresponding month or for up to 3 months previously) for eight of the nine sites. For the southern site of Gatton fly population abundance was correlated with temperature. Results suggest that although climate factors may be influencing patterns of *B. tryoni* population abundance in southern subtropical Queensland, they are not explaining patterns of abundance in northern subtropical and tropical Queensland. In the discussion we focus on the role of other factors, particularly larval host plant availability, as likely drivers of *B. tryoni* abundance in tropical and subtropical parts of its range.

**Key words** Dacinae, population modelling, Queensland fruit fly, tropical fruit fly.

## INTRODUCTION

*Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) (Queensland fruit fly or Q-fly), is one of the most serious insect pests of horticulture in eastern Australia (Dominiak *et al.* 2003a). Eggs are laid directly into the host fruit where larvae develop before leaving the fruit to pupate in the soil. Losses caused by Q-fly are as a result of direct fruit losses, costs of field control, and the post-harvest treatment costs required for domestic or international market access.

Q-fly is endemic and widely distributed in tropical and subtropical eastern Australia (May 1963; Zalucki *et al.* 1984) and, with the exception of the ‘fruit fly free zone’ where active population suppression is maintained, is now also permanently

established in temperate NSW and parts of Victoria (Bateman 1967; Fletcher 1979; O’Loughlin *et al.* 1984). In temperate regions the fly is multivoltine, but shows distinct climate driven seasonality, with populations over-wintering as non-reproductive adults and then breeding in spring and summer (Bateman 1968; Fletcher 1975, 1979). The seasonal population patterns of *B. tryoni* in temperate areas are driven by temperature, rainfall and environmental moisture (Bateman 1968; Dominiak *et al.* 2003b), with temperature being the major environmental driver (Bateman 1968; Pritchard 1970; Fletcher 1975, 1979).

In contrast to the well-documented ecology of *B. tryoni* in temperate Australia, almost nothing is known about *B. tryoni*’s population ecology in the endemic parts of its range. In Stanthorpe, a high-altitude, cold-winter area, Cowley *et al.* (1990) recorded few or no fruit fly catches during winter months, a result that reflects a typical, temperate pattern. Marked seasonal changes in the population abundance of *B. tryoni* in

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other, less temperate parts of the state have also been recorded (Drew & Hooper 1983; Drew *et al.* 1984; Lloyd *et al.* 2007); however, and what influences these patterns is less clear. Drew *et al.* (1984) found that *B. tryoni* abundance was less limited by temperature and rainfall in the subtropics, but rather host availability and fly dispersion were thought to play more important roles. Similar interpretations have been made for *B. tryoni* in subtropical areas (Raghu *et al.* 2000) and for other tropical tephritids, for example, other *Bactrocera* spp. (Drew *et al.* 1984; Tan & Serit 1994) and *Anastrepha* spp. (Hurtado *et al.* 1995). Even in temperate areas, abundance of overwintering *B. tryoni* in orchard habitats is dependent on fruit availability (Sonleitner & Bateman 1963; Bateman 1968; Fletcher 1973, 1974). Existing population models for Q-fly (Yonow & Sutherst 1998; Yonow *et al.* 2004) indicate likely relative abundance if fruit is always available for breeding, but this is clearly not the case in orchard production systems, or in tropical rainforests where fruiting patterns are generally highly seasonal (Boulter *et al.* 2006).

Presented as part of his PhD, May (1961) carried out fruit fly trapping across multiple Queensland sites over multiple years in the 1940s and 1950s. Because of the untimely death of Alan May, this very large and valuable dataset was never published. Formally analysing this historical dataset for the first time, we present in this paper data on the population phenology of *B. tryoni* populations at nine Queensland sites. Specifically, we: (1) compare and contrast average annual population phenologies of *B. tryoni* at nine sites across Queensland, ranging from temperate Stanthorpe to tropical Cairns; and (2) investigate the role of abiotic variables (monthly average temperature, rainfall and relative humidity) in driving the large-scale phenological patterns observed. We further use the dataset to independently assess the applicability of a process-based, *B. tryoni* population model (Yonow *et al.* 2004)

to subtropical and tropical environments by determining the degree of correlation between observed population data and predicted data.

## MATERIALS AND METHODS

### Study sites

Nine Queensland sites are used in this paper, ranging from Stanthorpe in the south to Cairns in the north (Table 1). Across this range the sites vary significantly in their climate, with Stanthorpe having an essentially temperate climate (despite its subtropical location) with a very marked and cold winter, whereas Cairns is located in the wet tropics and has a true tropical monsoon climate. Depending on their location, sites in between are affected to a greater or lesser extent by contrasting temperate and tropical influences. As a historical dataset, it is important to keep in mind that the current usage of the land may not be what it was in the 1950s. For example, Sunnybank, now a suburb of Brisbane, was then a productive small-crop and orchard area, whereas tropical fruit production, now common in areas of the north and far-north, was rare.

### Data collection

Fly trapping was carried out by Allen May and colleagues of the (Queensland) Department of Primary Industries and Fisheries from 1944 to 1959. For any one location, fruit fly trapping was carried out for 2–7 years and could be carried out at one or more ‘trapping stations’ (Table 1). Ten traps were maintained at each trapping station and all trapping stations were located in fruit growing areas where traps were placed in host trees. Trapping was conducted using a liquid lure as described

**Table 1** Details of trapping sites as used by May (1961) and in this study

Location of trapping sites	Features of the trapping site	Climate	Trapping period	Number of trapping stations per site
Cairns (16°9'S, 145°7'E)	Regional orchard surrounded by commercial orchards and rain forests	Coastal, wet tropic	3 years (1952–1954)	2
Atherton (17°3'S, 145°5'E)	Urban citrus orchard surrounded by other fruit trees and rain forests	Subcoastal, tropical highlands	4 years (1955–1958)	1
Ayr (19°6'S, 147°4'E)	Urban mixed fruit orchards surrounded by eucalyptus forests	Coastal dry tropics	4 years (1950–1953)	2
Rockhampton (23°3'S, 150°5'E)	Semi urban citrus orchard and vegetable gardens surrounded by rainforests and eucalyptus forests and water course	Coastal, dry tropics	2 years (1955–1956)	1
Maryborough (25°5'S, 152°7'E)	Citrus orchard, no other fruits produced commercially at site	Coastal, subtropics	2 years (1957–1958)	1
Gatton (27°5'S, 152°7'E)	Fruit growing area (mainly citrus) surrounded by irrigated field crop	Coastal, subtropics	7 years (1950–1957)	1
Toowoomba (27°6'S, 151°9'E)	Mixed fruit growing area surrounded by exposed conditions with farms and grazing areas	Subtropical, winter-temperate influences	4 years (1950–1953)	2
Sunnybank (27°6'S, 153°E)	Urbanised areas having fruit trees and fruit gardens surrounded by eucalyptus forests	Coastal, subtropics	3 years (1952–1954)	3
Stanthorpe (28°6'S, 151°9'E)	Commercial deciduous fruit orchards	Warm-temperate	3 years (1954–1956)	4

by May and Caldwell (1944). This lure is formulated using pulped orange (10 ounces (=283 g)), ammonium carbonate (0.5 ounces (=14.2 g)) and rain water (1 pint (=0.57L)), held for 24 h in a closed container. The lure was used in McPhail traps after being diluted with water at 1:30 lure: water ratio. This formula attracts both male and female *B. tryoni*, in contrast to the male-specific lures that are more commonly used for contemporary monitoring.

Traps were hung permanently in host trees and serviced weekly. Trapped flies were examined under 5× magnification in 70% alcohol and identified for species, sex and then, following dissection, age group (teneral, non-gravid (females only), mature). Trap data are presented in May's (1961) thesis as stacked vertical columns (i.e. for each week the number of immature males, mature males, immature females, non-gravid females and mature females are stacked in a single column to represent the week's total catch). This column data were transcribed from the graphs into Excel spreadsheet format by DM.

### Data summation

Analyses or data presentations (see next section) were carried out using weekly or monthly data (i.e. summed weekly catches within a calendar month), depending on the analysis or presentation. Combining weekly data could hide potentially important weekly variation, for example, the result of short term weather variation, and for this reason correlations between weather and population were done on weekly data. However, presenting weekly data in graphs or figures can be visually overwhelming, without supplying significant additional information. For this reason, phenology curves are presented using monthly data. The reader is referred to May's (1961) thesis, held by The University of Queensland library, if they wish to view weekly phenology data.

### Inter-site comparisons of mean monthly *B. tryoni* abundance and phenology

Mean monthly catch was compared across the nine sites (using one-way ANOVA followed by a Tukey HSD post-hoc test) to look at broad changes in *B. tryoni* abundance across Queensland. Correlations between latitude, longitude and altitude and mean monthly catch per site were carried out to determine if variation in fly abundance between sites was related to geographic location of the site.

Seasonal phenologies across sites were compared through visual comparison of mean monthly population curves for total males and total females. Annual phenology graphs were generated using mature female, immature female and teneral (both sexes, May did not present separate teneral data for each sex) age classes after having converted monthly trap data for each age class to a proportion of the total annual catch for that age class. The data presented in these latter graphs are the mean monthly data for the site (as for male/female phenologies), but are presented without a measure of error. This is done for visual clarity and because only very broad-scale phenological

patterns are discussed, for which measures of error are largely unimportant.

### Comparison of trap catches with weather data

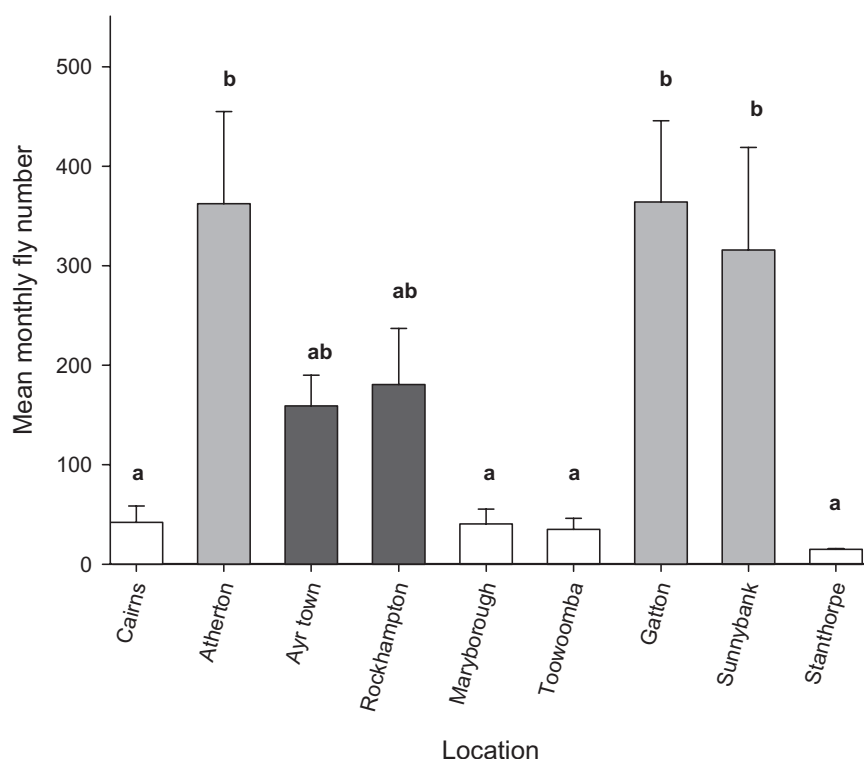
Relationships between weekly trap catches within a site and weather variables (mean weekly temperature, total rainfall, mean weekly relative humidity) were tested using multiple linear multiple regression analysis. Weather data corresponding to the trapping location and dates were obtained from the SILO Data Drill (<http://www.longpaddock.qld.gov.au/silo/>) and was site- and time-specific. In addition to the correlation between weather variables and trap catch in the same week, correlations were also done on weather variables lagged 4, 8 and 12 weeks before the trap catch, to test for weather effects on earlier life stages and/or generations.

### Comparison of observed data with model predicted data

Yonow *et al.* (2004) modelled Q-fly population dynamics using DYMEX®. DYMEX® is a process-based, modular modelling software package for the development of cohort-based, life-cycle models. Both internal (e.g. within a life cycle) and external (e.g. environmental) processes can be incorporated into a model, each affecting the different life stages within an organism's life cycle, so determining the survival, age and physiological status of individuals within a cohort (where a cohort is a group of individuals of a user-defined abundance and stage (e.g. 100 eggs; Maywald *et al.* 1999).

The main feature of Yonow *et al.*'s (2004) model of *B. tryoni* population dynamics is that the life stage properties are primarily regulated by climatic variables (i.e. temperature, rainfall, soil moisture, evaporation) and host fruit availability is held constant. The population phenologies thus generated represent the perceived influence of climate. Using climate to generate Q-fly phenologies is a valid assumption, at least for temperate parts of Australia, as temperature and rainfall are considered to drive the system in these regions (Bateman 1968; Meats 1981; O'Loughlin *et al.* 1984). Model validation runs by Yonow *et al.* using data from three temperate sites and regressing observed data against predicted data, produced significant  $R^2$  values of 0.16, 0.27 and 0.37 (d.f. =, respectively, 85, 60 and 114). Thus although the explanatory power of the model is relatively low (as recognised by the model authors), the model is still thought to capture the major features of Q-fly population dynamics. We used Yonow *et al.*'s model to predict the population dynamics of *B. tryoni* at our nine subtropical and tropical sites and compared the predicted results with the observed population data from May's thesis. We wished to determine if the pattern of Q-fly population dynamics in Queensland matched that observed in other states, as exemplified by the model.

The DYMEX model we used was as described and parameterised by Yonow *et al.* (2004). Two consecutive calendar years, beginning on 1 January, were used for the simulation run for each site. The years chosen for the simulations were



**Fig. 1.** Mean (+SE) monthly abundance of *Bactrocera tryoni* at nine sites in Queensland. Columns surmounted by the same letter are not significantly different at  $P = 0.05$ .

randomly selected within the years that each site was sampled. Because the model runs on daily time steps, corresponding daily meteorological data (daily average temperature, rain fall and daily average relative humidity) was obtained from the SILO Data Drill for each of the nine sites for the relevant years (Cairns 1952/1953, Atherton 1956/1957, Ayr 1952/1953, Rockhampton 1954/1955, Maryborough 1957/1958, Toowoomba 1951/1952, Gatton 1950/1951, Sunnybank 1952/1953, Stanthorpe 1954/1955). Initialisation values for the model runs were as used by Yonow *et al.* (2004). Correlations between predicted and observed data were done using weekly interval data.

## RESULTS

### Inter-site comparisons of *B. tryoni* abundance

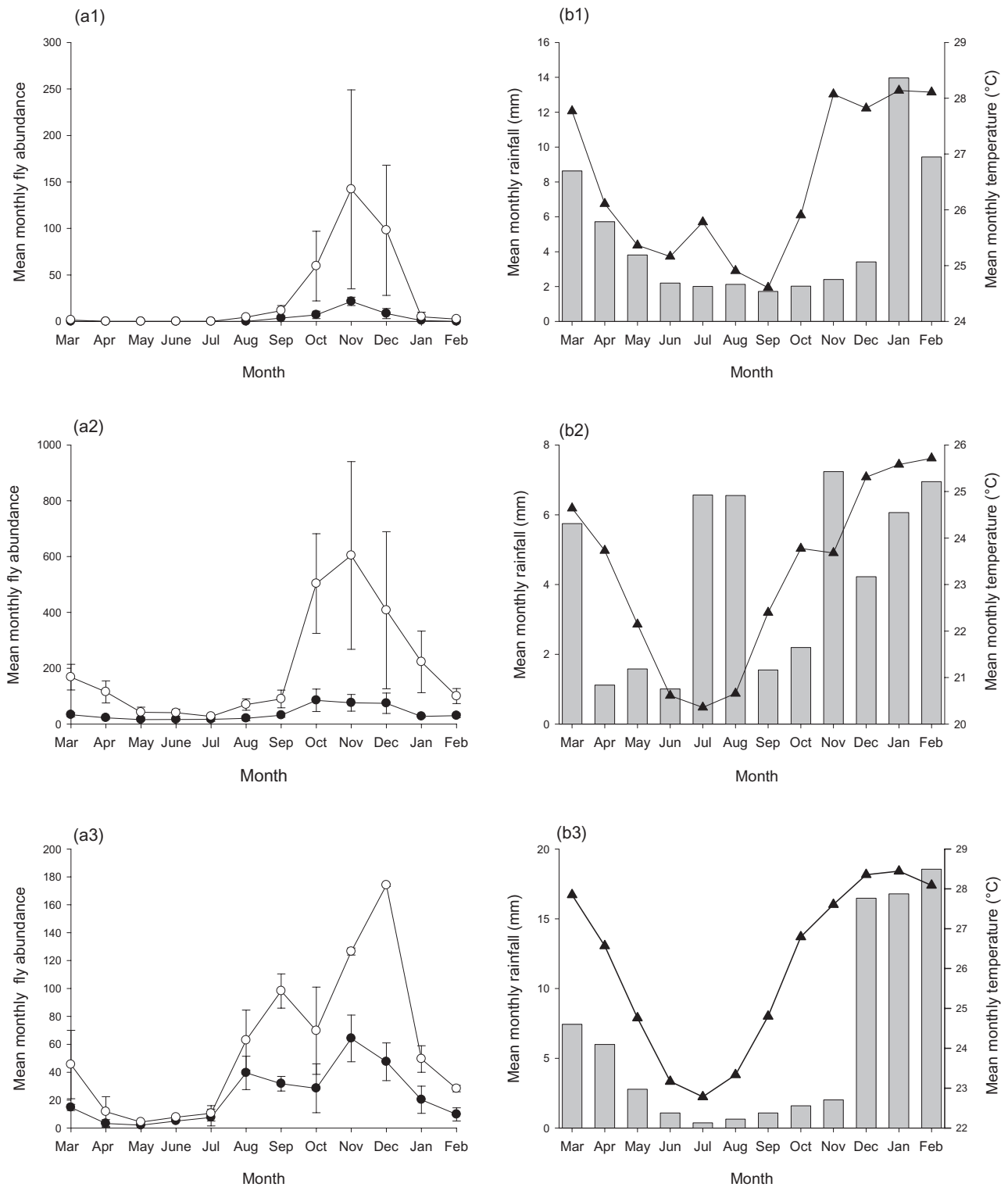
There was significant variation in mean monthly *B. tryoni* abundance across the nine sampling sites. There were no obvious patterns in the abundance between sites, with some neighbouring sites (e.g. Cairns and Atherton) having quite different abundance levels, and quite disjunct sites (e.g. Atherton and Gatton) having very similar levels (Fig. 1). There was no correlation between mean monthly abundance at a site and site latitude ( $r = 0.16$ ,  $P = 0.07$ ), longitude ( $r = 0.14$ ,  $P = 0.14$ ) or altitude ( $r = -0.05$ ,  $P = 0.60$ ).

### Seasonal abundance

*Bactrocera tryoni* populations were trapped throughout the year in six of the nine locations, but were not trapped for one

or more months in Cairns, Maryborough and Stanthorpe (Fig. 2). All sites showed distinct periods of high and low population abundance, with reproductive potential clearly not uniform throughout the year. Cairns, Atherton, Rockhampton and Toowoomba had a unimodal pattern of *B. tryoni* abundance, with a rapid rise in population numbers in mid- to late-spring, followed by an equally dramatic drop in numbers over summer leading into a period of low abundance in autumn and winter (this phenology pattern will be described as a 'type I' pattern for the remainder of the paper). Ayr, Maryborough and Sunnybank had two or more population peaks in the annual cycle (type II phenology pattern), with each again showing the rapid population increase in spring, which typified the type I pattern. Gatton and Stanthorpe (type III) showed less dramatic post-wintering population growth, with their populations increasing gradually during spring and summer to a late summer/early autumn peak, before declining again into winter.

Low abundance in many sites was represented by zero or near-zero values and these coincide with late autumn and winter months. The duration of the period of low abundance, however, was highly variable ranging from 3 to 4 months in some sites (e.g. Cairns, Atherton, Rockhampton, Maryborough, Toowoomba, Sunnybank and Stanthorpe) and as short as 1 month in others (Ayr and Gatton) (Fig. 2). Low abundance cannot be directly attributable to cold winter temperatures only, as even tropical sites (e.g. Cairns) showed such periods. The timing of the initiation of population increase following the period of low abundance differed between sites and ranged from July to September. There was no obvious latitudinal effect on the initiation of population increase as might be



**Fig. 2.** (a) Population phenology of male (closed circle) and female (open circle) *Bactrocera tryoni* across nine sites in Queensland, Australia, with (b) corresponding long-term temperature (closed triangle) and rainfall (vertical bar) averages for the same sites. 1 = Cairns, 2 = Atherton, 3 = Ayr, 4 = Maryborough, 5 = Rockhampton, 6 = Toowoomba, 7 = Gatton, 8 = Sunnybank, 9 = Stanthorpe. The number of year's data contributing to any one site is given in Table 1.

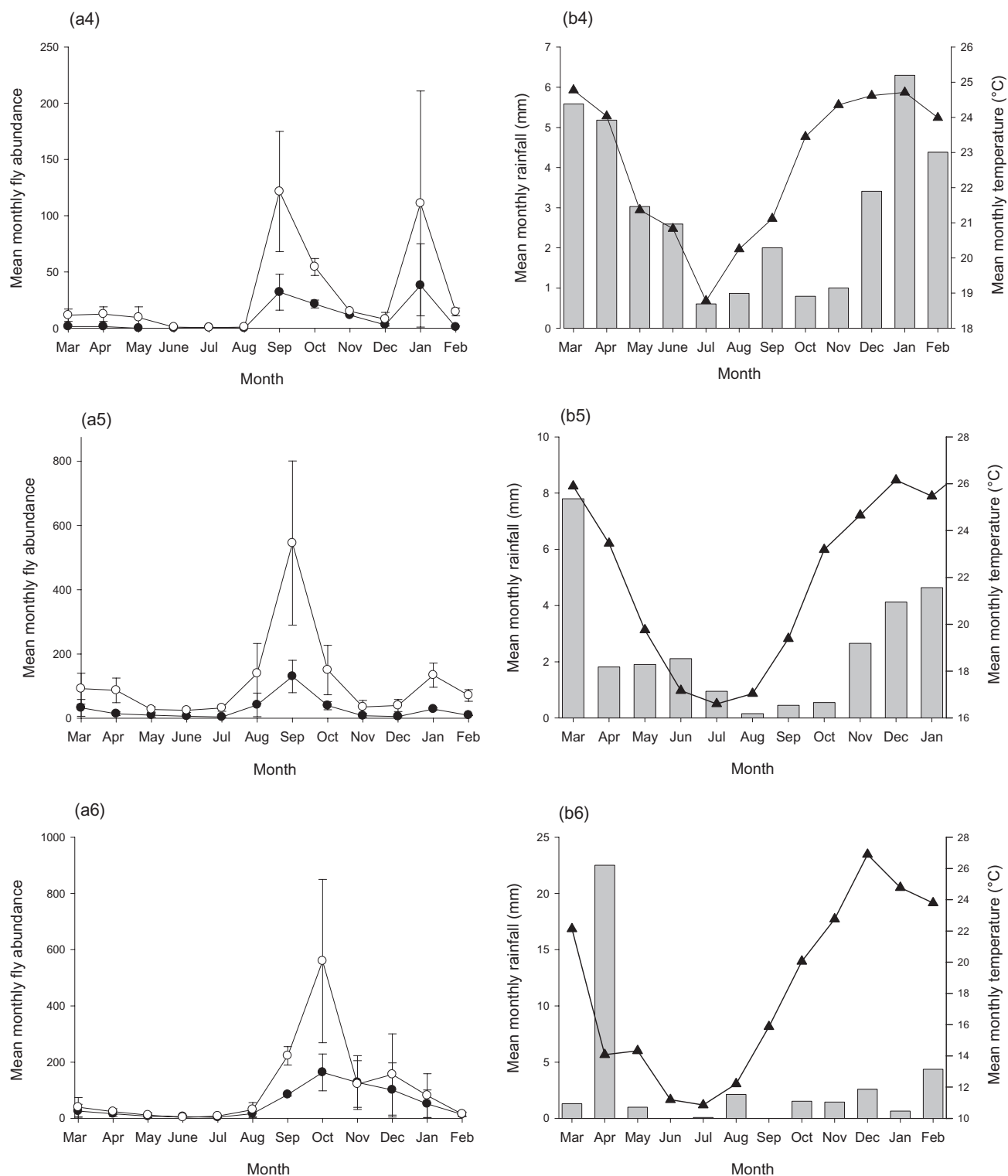


Fig. 2. Continued

expected if, for example, changing day length or similar was influencing the pattern.

### Female phenology

With the exception of Cairns, Stanthorpe and Toowoomba, all age groups (i.e. teneral, immature and gravid) of female *B.*

*tryoni* were collected at all times during the year at all sites, even when population numbers were very low (Fig. 3). Determining voltinism from the information in Figure 3 is difficult, but the presence of tenerals throughout the year at most sites is indicative of continual breeding (i.e. multivoltinism).



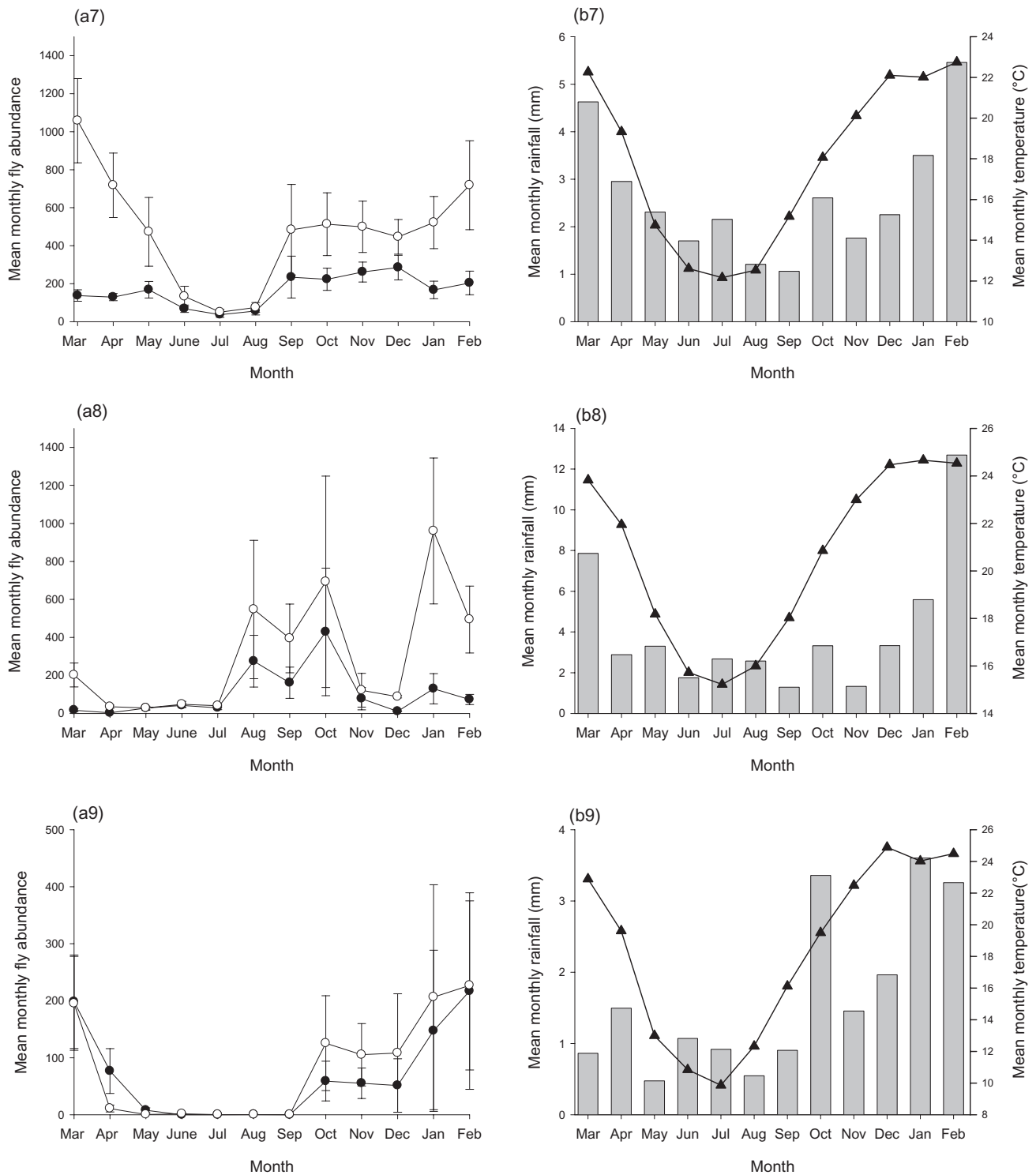
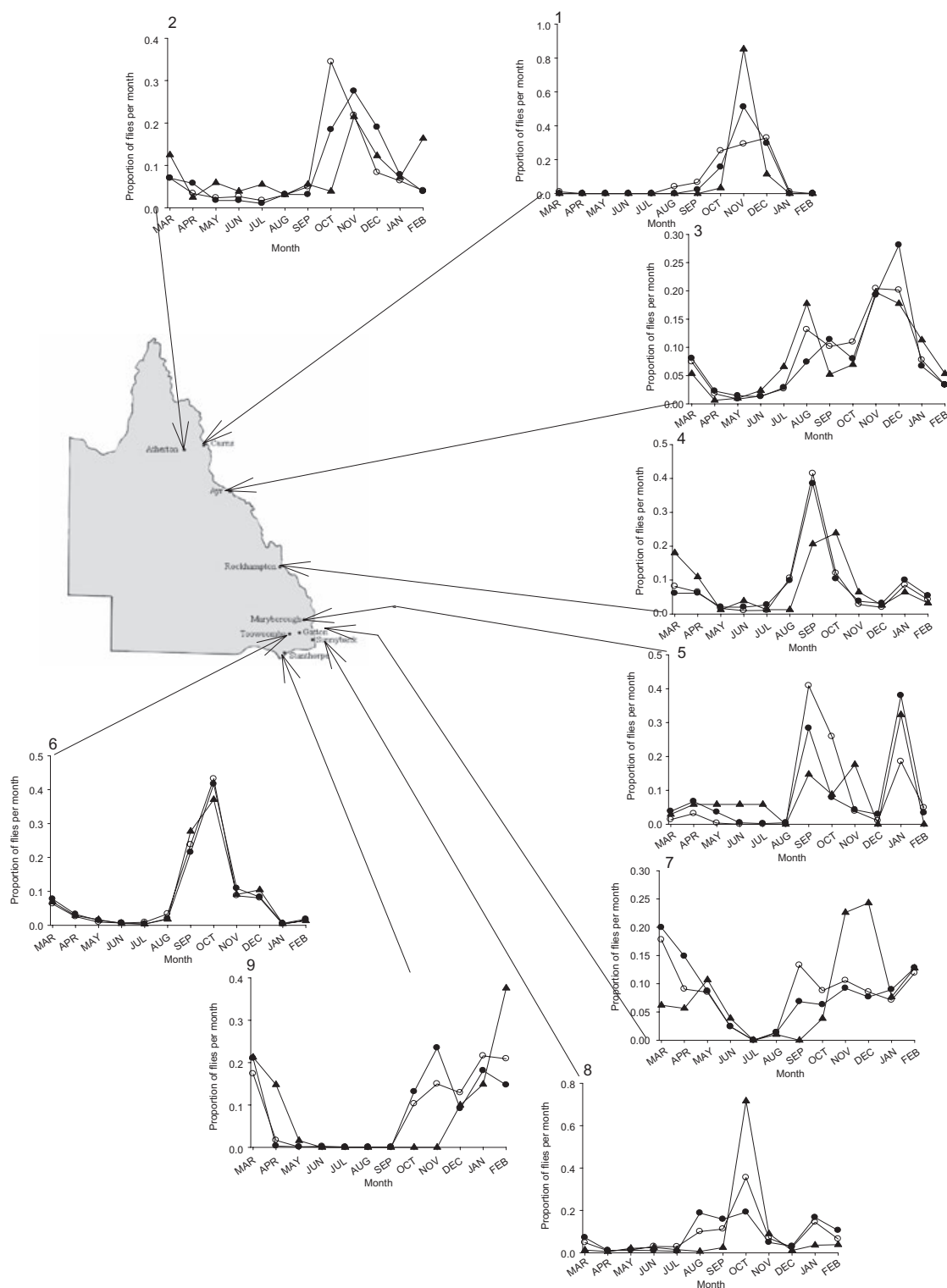


Fig. 2. Continued

The initial spring population, in nearly all cases, consists on non-gravid or gravid females – but not teneral. Non-gravid females appeared with or before gravid females in some sites (e.g. Stanthorpe, Cairns and Sunnybank) and thus we infer that flies during the period of low abundance (at least in the southern parts of Queensland) may resorb follicles, as is known to occur

in NSW (Pritchard 1970). That non-gravid females also appeared first in tropical Cairns suggests egg resorption may not only be driven by cold temperatures, but may also be moderated by other factors. We can also not dismiss the possibility that non-gravid females are from teneral that have dispersed/moved into the trapping location from another locality.



**Fig. 3.** Annual phenology of combined teneral male and female (closed triangle), non-gravid female (open circle) and gravid female (closed circle) *Bactrocera tryoni* populations in nine locations in Queensland. Within a graph, each plot presents the monthly proportional number of flies only of that age class, not the proportion of that age class as a proportion of all age classes combined. Thus the sum of proportions for the three age classes for any given month can exceed 1.

The teneral flies that build up rapidly in the spring are likely the F1 generation of the flies present during the period of low population abundance. The appearance of teneral flies in Toowoomba, Maryborough and Ayr occurs at the same time as the

appearance of gravid and non-gravid females in late winter. In contrast, F1 generation teneral flies appeared 1 or 2 months after the late-winter/spring emergence of flies in Rockhampton, Stanthorpe, Gatton and Atherton (Fig. 3). In the type I and



**Table 2** Results of linear multiple regression analysis for the relationship between weekly *Bactrocera tryoni* trap catch and three weather variables (weekly average temperature, rainfall, weekly average relative humidity) at nine sites in Queensland

Site	Years of correlation	Number of weeks	R <sup>2</sup>	F	P	Partial correlation coefficient		
						Temperature	Rainfall	Relative humidity
Cairns	1952–1953	96	0.29	12.5	<0.001	0.26	0.05	–0.37
Atherton	1956–1958	144	0.17	9.55	<0.001	0.20	0.13	–0.21
Ayr	1952–1954	144	0.19	9.50	<0.001	0.22	0.15	0.20
Rockhampton	1954–1955	96	0.01	0.37	0.70	–0.02	–0.07	–0.01
Maryborough	1957–1958	96	0.01	0.32	0.80	0.01	–0.07	–0.02
Sunnybank	1952–1954	144	0.01	0.81	0.48	0.07	0.03	0.06
Toowoomba	1951–1952	96	0.07	2.44	0.06	0.07	0.01	–0.10
Gatton	1950–1952	144	0.12	6.8	<0.001	0.32	–0.15	0.01
Stanthorpe	1954–1956	144	0.18	10.8	<0.001	0.38	–0.07	0.05

type II population phenology groups, the teneral flies built up very rapidly in the spring population. However, in the type III populations (particularly Stanthorpe), the increase in the teneral population is delayed in initiation and slower in build up.

### Population fluctuation and weather

Correlations between *B. tryoni* trap catch and weather variables were inconsistent across the state. Multiple linear regression analysis detected significant correlations between weather variables and weekly trap catch for the two most southern sites (Gatton and Stanthorpe) and the three most northern sites (Cairns, Atherton and Ayr), but not the four intermediate sites (Table 2). The partial correlation coefficient values for the significant southern and northern sites did not follow the same pattern. For the southern sites, temperature was clearly the most important variable within the multiple regression, with rainfall less important and negatively correlated with abundance: relative humidity was unimportant. For the northern sites, temperature and relative humidity were equally important and were positively and negatively correlated, respectively, with population abundance. Rainfall was positively correlated with abundance, but to a lesser extent than the other two variables. Correlations on time lagged weather data provided no additional insights as very few correlations were significant. Results of the time-lagged analysis are provided in Muthuthantri (2008).

### Fit with DYMEX model

Model predictions, as assessed through correlation between predicted and observed weekly data, were generally poor, particularly for the subtropical sites. Fly populations were predicted to breed continuously throughout the year in northern tropical sites (Cairns, Atherton, Ayr, Rockhampton) (Fig. 4), but only correlations for female flies in Cairns and Ayr, male flies in Cairns and teneral flies in Ayr were significant (Table 3). In the subtropical sites, the model predicted that continuous breeding populations should not occur throughout the year, with reproductive males and females going into an over-wintering stage during part, or all, of the winter months. Maryborough appears to be on the geographic boundary where

flies cease breeding in the winter months, with flies predicted to enter the over-wintering stage in 1957, but not 1958 (Fig. 4). Predictive power of the model was again weak for the southern sites, with only Stanthorpe showing consistent positive correlations between observed and predicted populations.

Unexpectedly, many sites showed negative correlations between observed and predicted data, which in two cases (Atherton and Sunnybank, female flies) were significant (i.e. model-predicted fly populations should be declining when actual populations were increasing, and vice versa). The negative correlations indicate that the model is obviously failing to capture key elements of the population dynamics of Q-fly in subtropical and tropical areas.

## DISCUSSION

Hurtado *et al.* (1995) consider that a minimum of 3–4 years of population data should be analysed to gain a proper representation of fruit fly population phenology in a given locality, especially if the year to year fluctuation is variable. Population data from seven of the nine sites in this study fulfil this requirement and we believe the dataset gives a valid overview of the population phenology of *B. tryoni* in Queensland. Changes in land use in the 50+ years since this data were collected means that a current worker could not, with confidence, use the data presented here for any given site, but broad phenological patterns, particularly with respect to interactions with climate variables, should still be relevant.

Previous studies have predicted that up to 15 generations per year of *B. tryoni* could potentially occur in northern parts of the fly's range (Meats 1981; Yonow & Sutherst 1998). These predictions have, however, been almost exclusively based on research undertaken in temperate Australia and assume abiotic conditions (particularly temperature) are the drivers of Q-fly population dynamics in all parts of its range. In contrast, the major results of this study are that the influence of abiotic weather variables are not consistent across the subtropics and tropics and at least one existing population model that is based largely on climate drivers (Yonow *et al.* 2004), has little predictive capacity for most Queensland sites (Table 3). This discussion focuses on the role of the abiotic variables (tem-

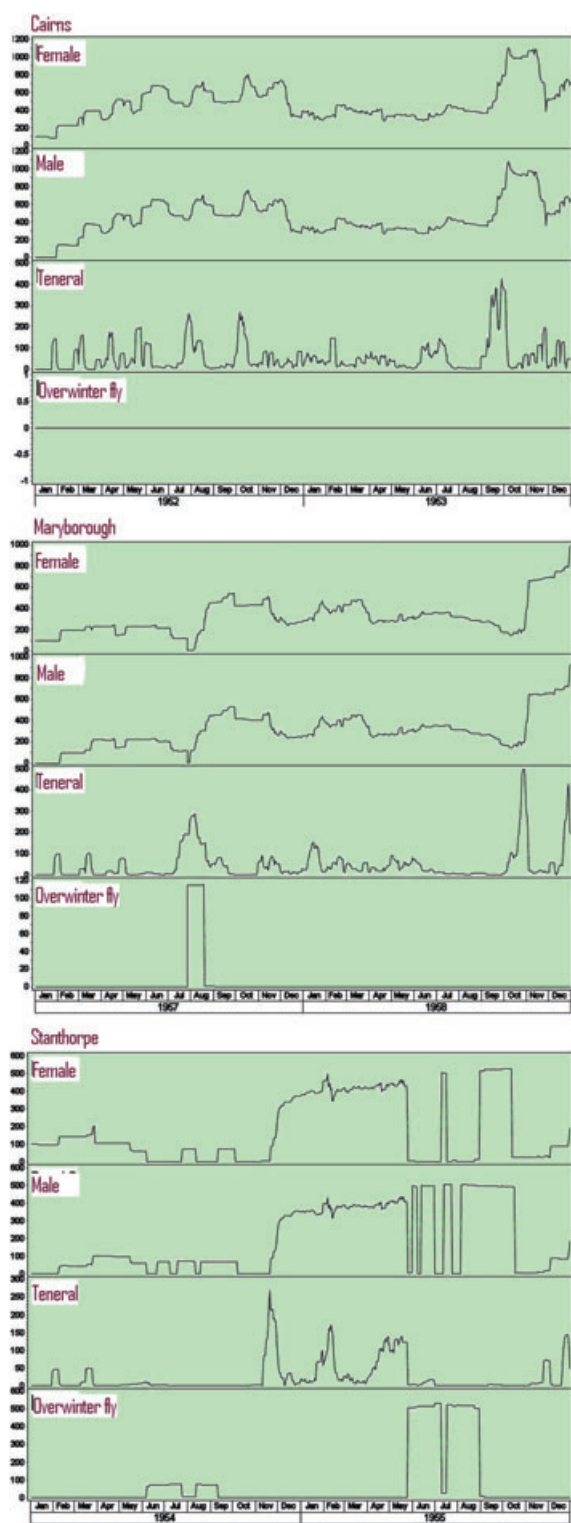


Fig. 4. Population phenology of *Bactrocera tryoni* at three Queensland sites as predicted by the *B. tryoni* population model of Yonow et al. (2004).

perature, rainfall and humidity) on *B. tryoni* population dynamics in tropical and subtropical parts of its range and then speculates on the possible role of unrecorded variables, particularly host fruit availability. We do not discuss the possible

role of natural enemies as these are thought to have only a very minor impact on *B. tryoni* populations (Snowball 1966; Waterhouse & Sands 2001).

### Impact of temperature on *B. tryoni* populations in subtropical Queensland

In temperate parts of Australia, *B. tryoni* breeding is curtailed in winter because of mean temperatures falling below thresholds required for ovarian maturation ( $13.5^{\circ}\text{C}$ ) (Pritchard 1970) and mating ( $16^{\circ}\text{C}$ ) (Meats & Fay 1976). However, for Queensland, only the most southern sites are likely to have cold temperature influenced breeding patterns. Ovarian maturation in *B. tryoni* is not driven solely by a minimum temperature threshold, but depends more on appropriate day degree accumulation (which itself is driven by the length and magnitude of the maximum and minimum daily temperatures) (Fletcher 1975; Meats & Khoo 1976). Mean monthly winter temperatures for most of the sites (Fig. 2) are around  $14\text{--}16^{\circ}\text{C}$  or higher (i.e. above threshold) and even if, during the coldest periods, favourable temperatures persist for sufficient time during the day such that ovarian maturation rate exceeds absorption rate (Meats & Khoo 1976), then ongoing egg laying is possible. This is seen even in southern sites such as Gatton and Sunnybank, where breeding (as evidenced by the presence of teneral flies) is almost continuous through the year, although significantly reduced in winter (Fig. 3). Only in Stanthorpe is breeding almost certainly curtailed for several months because of winter temperatures.

Although breeding is continuous or near-continuous at most sites, winter temperatures in the southern sites appear marginal for breeding (Gatton, Sunnybank, Toowoomba and Maryborough) (Fig. 2). Maryborough appears to be on the edge of this unfavourable range (Fig. 4), with teneral fly populations apparent during the colder months, even though the mean temperatures are marginally suitable for breeding and mating (Figs 2,3). Minimum temperatures at Maryborough during winter are well above those required for larval and pupal development and, so long as eggs are laid, the local population will continue to develop.

Survival of *B. tryoni* is terminated by continuous and prolonged (i.e. 5–7 days) exposure to subzero temperatures (Meats 1976; Fletcher 1979). However, low abundance of *B. tryoni* in temperate areas in winter need not be caused by low temperature induced mortality, but may be because flies migrate to winter refuge sites, such as forest (Fletcher 1979). For our study sites in Queensland, zero or subzero temperatures are rare, although overnight lows in this range do occur routinely during winter in Stanthorpe and occasionally also in Toowoomba. It is thus reasonable to assume that the low or zero population sizes exhibited in southern sites in June and July are not as a result of cold-induced mortality, but are more likely as a result of dispersal of flies to sheltering sites and a failure to collect them in traps, or alternatively the flies may not be physiologically responsive to the traps in cooler months because of temperature induced delays in sexual maturity.

**Table 3** Pearson correlation (*r*) values of *Bactrocera tryoni* observed weekly fly catches for nine Queensland sites with population levels predicted by the *B. tryoni* model of Yonow *et al.* (2004)

	Female (predicted) vs. female (observed)	Male (predicted) vs. male (observed)	Teneral (predicted) vs. Teneral (observed)
Cairns	<b>0.20 (<i>P</i> &lt; 0.05)</b>	<b>0.31 (<i>P</i> &lt; 0.01)</b>	−0.07 ( <i>P</i> = 0.4)
Atherton	−0.20 ( <i>P</i> < 0.05)	0.00 ( <i>P</i> = 0.9)	0.16 ( <i>P</i> = 0.1)
Ayr	<b>0.26 (<i>P</i> &lt; 0.01)</b>	0.16 ( <i>P</i> = 0.1)	<b>0.24 (<i>P</i> &lt; 0.05)</b>
Rockhampton	−0.09 ( <i>P</i> = 0.3)	−0.07 ( <i>P</i> = 0.4)	−0.03 ( <i>P</i> = 0.7)
Maryborough	0.13 ( <i>P</i> = 0.1)	<b>0.22 (<i>P</i> &lt; 0.05)</b>	−0.12 ( <i>P</i> = 0.2)
Sunnybank	−0.28 ( <i>P</i> < 0.05)	−0.1 ( <i>P</i> = 0.3)	−0.18 ( <i>P</i> = 0.07)
Toowoomba	−0.15 ( <i>P</i> = 0.1)	−0.05 ( <i>P</i> = 0.6)	−0.2 ( <i>P</i> < 0.05)
Gatton	<b>0.37 (<i>P</i> &lt; 0.01)</b>	0.04 ( <i>P</i> = 0.6)	−0.00 ( <i>P</i> = 0.9)
Stanthorpe	<b>0.27 (<i>P</i> &lt; 0.01)</b>	<b>0.25 (<i>P</i> &lt; 0.05)</b>	<b>0.29 (<i>P</i> &lt; 0.01)</b>

Values in bold font: significant at *P* = 0.05.

### Role of rainfall and humidity

Summer abundance of *B. tryoni* in temperate regions is strongly influenced by rainfall, possibly because pupal emergence is favoured by moisture availability in the air and in the soil (Bateman 1968). O'Loughlin (1964) observed that the fly population growth increases significantly in temperate areas if summer rainfall is above 170 mm per month, but such population growth does not occur if summer rainfall is below this level. Rainfall, however, had the lowest partial correlation coefficients for each of our nine sites (Table 2). Given this conflict between our data and that of Bateman and O'Loughlin, we suspect that in southern temperate areas (which have wet winters but dry summers) rainfall can be limiting to flies during summer, whereas in the tropics which have a spring/summer dominated rainfall pattern, no such limitation occurs. Relative humidity, but not rainfall, was negatively correlated with fly abundance in our two most northern sites and may be a reason why fly population decline during summer in the tropical north.

### Host availability

Data on fruit phenology were not collected by May (1961) and so we cannot formally test a link between fruit availability and fly phenology. Even indirect attempts to do this are confounded by the passage of time. Sunnybank, for example, was a major fruit production area in the 1950s, but is now simply part of Brisbane's urban sprawl and so it is difficult to determine what hosts may have been available. Nevertheless, in the absence of direct temperature, rainfall or humidity effects, ecological differences such as host availability and site conditions (e.g. surrounding rural, urban or forest habitats) are alternative explanatory variables of inter- and intra-site variation in total abundance and phenology patterns, as is the case for other fruit flies (Aluja *et al.* 1996; Leblanc & Allwood 1997; Leweniqila *et al.* 1997; Tora Vueti *et al.* 1997; Raghu *et al.* 2000; Raghu & Clarke 2001; Dominiak *et al.* 2006). In terms of total population abundance, the fact that both Sunnybank and Gatton were small crops producing areas in the 1950s (as Gatton still is), with the potential of supplying near year-round host availability for *B. tryoni*, may be an important reason why flies were so abundant at those sites (Fig. 1).

All sites north of Maryborough have year-round temperature conditions favourable for *B. tryoni*'s normal activities (e.g. mating, foraging and egg development) and flies should be able to successfully reproduce at these sites at all times of the year (Yonow & Sutherst 1998). However, populations at these sites show distinct fluctuations during the year which are generally not correlated to weather variables (Table 2). As an extreme example, *B. tryoni* was rare or absent in Cairns for half the year from January to July (Fig. 2), although the more common pattern across sites was for continuous breeding, but with distinct peaks of abundance. In the absence of climatic correlates to explain population variation, we assume these peaks and troughs are matched by, respectively, an availability or absence of hosts. For example, flowering and fruit set in northern tropical rainforests is highly seasonal and peaks around the beginning of the wet season in October/November (Boulter *et al.* 2006 and references therein). This fruiting peak is a likely driver of the dramatic peak of abundance of flies in Cairns, which in the 1950s would have been almost entirely generated through rainforest breeding. Out of the fruiting season, the absence of suitable host fruits may have caused flies to migrate away from Cairns, explaining the absence of flies at that site. Many other studies have demonstrated positive correlations between fruit fly abundance and host availability (Tan & Serit 1994; Hurtado *et al.* 1995; Aluja *et al.* 1996; Papadopoulos *et al.* 2001; Hong & Hui 2005).

### Implications for management

Data presented in this paper have important implications for both research and management. From a management perspective it is clear that it is no longer sufficient to simply say, or infer, that based on weather variables Q-fly is always abundant in its endemic range. Rather, the fly shows distinct seasonal depression in populations across the whole state and this offers promise as a component of market access discussions. A probable link between local fly abundance and local fruit availability also suggests that attempting area-wide population suppression through control of feral and non-commercial hosts, as well as commercial hosts, is probably justifiable. Both area-wide management and periods of low pest pressure have been used to gain access of South Burnett citrus into



interstate markets and should be pursued for other production areas.

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