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Modelling the population dynamics of the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*: a cohort-based approach incorporating the effects of weather

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Abstract

Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni* (QFF) is arguably the most costly horticultural insect pest in Australia. Despite this, no model is available to describe its population dynamics and aid in its management. This paper describes a cohort-based model of the population dynamics of the Queensland fruit fly. The model is primarily driven by weather variables, and so can be used at any location where appropriate meteorological data are available.

In the model, the life cycle is divided into a number of discreet stages to allow physiological processes to be defined as accurately as possible. Eggs develop and hatch into larvae, which develop into pupae, which emerge as either teneral females or males. Both females and males can enter reproductive and over-wintering life stages, and there is a trapped male life stage to allow model predictions to be compared with trap catch data.

All development rates are temperature-dependent. Daily mortality rates are temperature-dependent, but may also be influenced by moisture, density of larvae in fruit, fruit suitability, and age. Eggs, larvae and pupae all have constant "establishment" mortalities, causing a defined proportion of individuals to die upon entering that life stage. Transfer from one immature stage to the next is based on physiological age. In the adult life stages, transfer between stages may require additional and/or alternative functions. Maximum fecundity is 1 400 eggs per female per day, and maximum daily oviposition rate is 80 eggs/female per day. The actual number of eggs laid by a female on any given day is restricted by temperature, density of larva in fruit, suitability of fruit for oviposition, and female activity. Activity of reproductive females and males, which affects reproduction and trapping, decreases with rainfall. Trapping of reproductive males is determined by activity, temperature and the proportion of males in the active population.

Limitations of the model are discussed. Despite these, the model provides a useful agreement with trap catch data, and allows key areas for future research to be identified. These critical gaps in the current state of knowledge exist despite over 50 years of research on this key pest. By explicitly attempting to model the population dynamics of this pest we have clearly identified

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the research areas that must be addressed before progress can be made in developing the model into an operational tool for the management of Queensland fruit fly.

Keywords: Agricultural and horticultural pest; Ecological model; Life cycle; Population dynamics; Population model; DYMEX

1. Introduction

The Queensland fruit fly (QFF) *Bactrocera* (*Dacus*) *tryoni* (Froggatt) (Diptera: Dacineae), is one of Australia's most economically important horticultural pests. It is a tropical to sub-tropical species, with a wide host range (Fletcher, 1987a, 1989; Meats, 1981). There has been an increasing incidence of outbreaks of QFF in the more temperate, economically valuable horticultural areas, such as the Murrumbidgee Irrigation Area, Sunraysia and Adelaide since 1987 (Horticultural Policy Council, 1991). The total cost of all fruit flies to Australia was estimated at US$100 million in 1995–1996 (Colquhoun, 1998).

Whilst the population dynamics of the olive fruit fly, *Dacus oleae* have been modelled to some extent (Comins and Fletcher, 1988; Fletcher and Comins, 1985), previous models of QFF have only addressed its geographical distribution (Meats, 1981; Yonow and Sutherst, 1998). Due to the pest status of this species a great deal of research has been undertaken into aspects of the biology and ecology of QFF with a view to improving its management. *A priori*, we would expect that sufficient information exists to model the population dynamics of QFF. We now describe a DYMEX™ (Maywald et al., 1999) model that was built to improve our understanding of QFF population dynamics and relative abundance, and in so doing, identify critical gaps in knowledge.

2. The model

The model describes the life cycle processes of the QFF in relation to climate. It is scaled to represent a population of flies on an "average" fruit on an "average" tree in an "average" orchard at a location that is characterised by its meteorological data. The model was built using DYMEX (Maywald et al., 1999), a process-based, modular modelling software package that contains a library of modules that can be incorporated into any new model.

DYMEX is based on the concept of cohorts within a life stage. Cohorts are created in each time step in which one or more individuals enter a life stage, and each cohort is tracked independently. Processes defined in the model, such as development and mortality, or transfer from one life stage to the next, act at the cohort level, not the life stage level. Cohorts have a number of properties, or state variables, some of which are pre-defined, while others may be defined by the user. These properties track particular processes, or attributes, within the life stage (e.g. number, age, stress accumulation, thermal accumulation) that drive other processes (e.g. mortality, activity) in the same or subsequent life stages. The concept of cohort properties provides an elegant mechanism to account for the range of responses to the different conditions experienced by members of a population. This allows the model to be more realistic than models based on probability distributions, transition matrices (e.g. the Leslie-matrix approach, and the use of Monte-Carlo simulations.

2.1. Timer

The DYMEX Timer module defines the time step of the model (a day in our model), tracks time of year, the number of days since the start of the simulation and the simulation date, so as to relate biological and management events to days or dates. Because our model runs on a daily time step, all rates described below are daily rates.

2.2. Meteorological data

The meteorological data module reads the climatic variables necessary to run the model from a file. Daily minimum and maximum air temperatures, rainfall and evaporation are used in the QFF model.

All temperatures used in the model are air temperatures, as these are widely available meteorological data. Thus, even though eggs and larvae occur in fruit

and pupae are in the soil, development and mortality of these instars are modelled using air temperatures. As the model represents an "average" fruit on an "average" tree in an "average" orchard, it is not necessary to distinguish between trees, fruits, or patches of ground that are more (or less) exposed to the sun and thus experience different overall temperature conditions.

2.3. Soil moisture

Two soil moisture modules are used to characterise the moisture levels at different soil depths. In the first instance, a single-layer soil moisture module is used to represent a soil profile with a depth of approximately 90 cm and an intermediate water-holding capacity, comparable to a loam soil. There are three parameters: maximum moisture storage, or water-holding capacity of the soil (default value of 100 mm), drainage rate (the proportion of water in the soil that is lost through drainage each time step, default value of 0), and an evapotranspiration coefficient. In the QFF model, the evapotranspiration coefficient is defined as a function of soil moisture. At a soil moisture of 0.55 or greater, the evapotranspiration rate is set to 0.84, below 0.55, the evapotranspiration rate decreases with decreasing soil moisture to reach zero when the permanent wilting point (0.1) is reached (Johns and Smith, 1975).

Values from this soil moisture module are used to determine daily mortality rates of adult flies due to desiccation. Flies are normally within the canopy of trees, and we assume that canopy moisture levels reflect the moisture available to the root system. As long as the soil moisture remains above the permanent wilting point of plants, normal transpiration occurs and the canopy environment remains favourable for fly survival.

A second soil moisture module (shallow soil moisture, SSM) characterises the top layer of soil, where pupae are found. Moisture levels in this upper soil layer were considered to be a better predictor of pupal mortality than either the air or the deeper soil moistures. The three parameters are set as follows: the maximum moisture storage is 15 mm, the drainage rate is 0, and the evapotranspiration coefficient is a constant of 0.84, the rate given by Johns and Smith (1975) for moisture loss in this layer.

2.4. Daily temperature cycle

A Circadian module calculates a set of 24 numbers representing the average temperature each hour of the day. The calculations are based on an hourly sine curve interpolation of the daily minimum and maximum temperatures. Unless stated otherwise, all temperature-dependent functions in the model are driven by the daily temperature cycle.

2.5. Location-specific variables

A number of location-specific variables must be defined to run the model. These are defined by the user:

- Area of Orchard, in hectares (defaults to 1),
- Number of fruit trees per hectare (defaults to 1),
- The number of fruits per tree (defaults to 100),
- Fruit suitability index for larval development (defaults to 1 for optimal suitability),
- Fruit acceptability index for oviposition (defaults to 1 for optimal acceptability),
- Amount of irrigation, as a proportion of open pan evaporation (defaults to 0 for no irrigation),
- Length of irrigation season, in days (defaults to 0 for no irrigation).

2.6. Event module

An event module defines the irrigation season, allowing irrigation to be commenced on any user-defined date and terminated after the length of time defined by the location-specific variable 'Length of Irrigation Season'.

2.7. Function modules

- An activity index (AI) is used to influence reproduction by females and trapping of reproductive males. The AI is zero on days with 40 mm or more of rainfall, and maximal (1) on days with no rainfall.

  AI = 1 − 0.025 (rainfall) for rainfall below 40 mm, and
  AI = 0 for rainfall of 40 mm or more.

- The sex ratio can be adjusted outside the life cycle, in the event that sex ratios at adult emergence

are biased. It is a simple parameter that may vary between 0.25 and 0.75, with a default value of 0.5, and represents the female proportion of the population. This value is used to determine the proportion of pupae that transfer to both the teneral female and teneral male life stages.

2.8. Equation and expression modules

Equation and expression modules are used to calculate additional variables required as input into model processes. Thus, on any one day:

- Rainfall with irrigation = [total evaporation] × [irrigation amount] × [irrigation season] + [rainfall],
- Male proportion of active population = [activity index] × ([total number of reproductive males]/([total number of reproductive males] + [total number of reproductive females])),
- Available fruit = [area of orchard] × [number of fruit trees per hectare] × [number of fruit per tree]. With the default values for each of the location-specific variables, this last expression has a value of 100.

2.9. Life cycle

The QFF life cycle has ten life stages: egg, larva, pupa, teneral female, reproductive female, over-wintering female, teneral male, reproductive male, over-wintering male and trapped male. Various functions

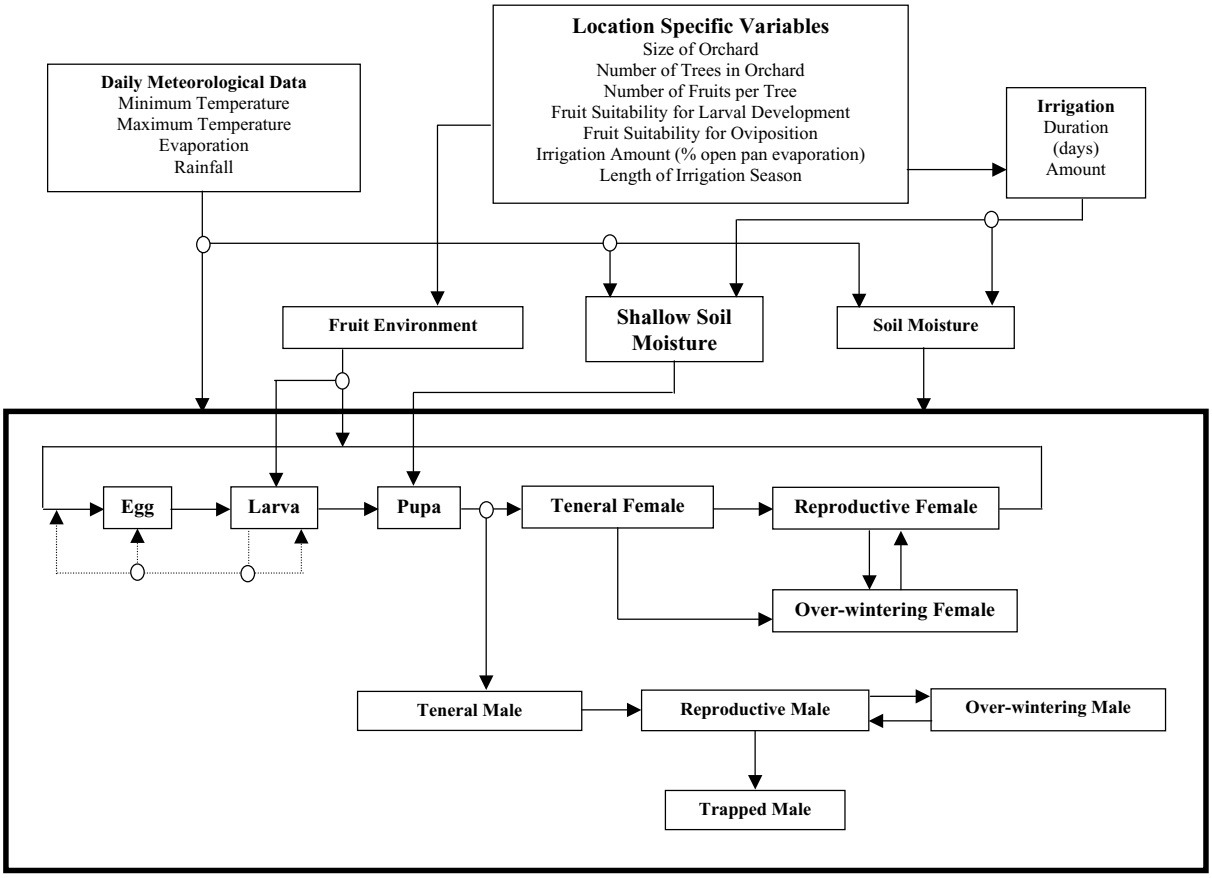

Fig. 1. Schematic diagram of Queensland fruit fly life cycle, and relationships with abiotic factors. Abiotic factors either influence the entire life cycle (e.g. meteorological data), or only certain aspects of the lifecycle (e.g. shallow soil moisture only affects pupae). The dotted lines linking larvae to egg-laying, eggs and larvae are larval density feedback loops upon these stages (see text for details).

describe development and mortality rates for each life stage and the transfer of individuals from one life stage to the next, as well as adult activity, fecundity and reproduction rates. Published data were used where possible to derive these functions. A schematic diagram of the life cycle and its relationships to environmental parameters is shown in Fig. 1.

3. Egg

3.1. Egg development rate

The development rate of eggs (E_d) is estimated from published data for temperatures up to 33 °C (Bateman, 1967; Fitt, 1984, 1990a; Meats, 1981; Myers, 1952; Pritchard, 1978):

$$E_d = 0.0382 \times T_c - 0.4229,$$

where T_c is the temperature in °C.

The regression has an R^2 value of 0.85 ($n = 13$) and indicates a lower egg development threshold of 11.1 °C.

3.2. Egg mortality rate

3.2.1. Egg establishment mortality—constant

Establishment mortality operates at the start of the life stage, causing a proportion of a cohort entering that life stage to die. Myers (1952), Barton Browne (1956) and Meats (1984) indicate that an average of 9% of eggs die at 25–27 °C, the temperatures most often used for laboratory cultures (Bateman, 1967, 1968; Fitt, 1984; Meats, 1981, 1984; Monro and Osborn, 1967). A constant establishment mortality of 9% is therefore used in the egg stage. All temperature-dependent daily mortality rates of eggs were adjusted by this amount prior to any calculations.

3.2.2. Egg establishment mortality due to larval density

A logistic function defines additional establishment mortality of eggs as a function of larval density:

$$f(L_n) = \frac{k1}{1 + \exp(-k3 \times (L_n - k2))},$$

where L_n is the average number of larvae per fruit, $k1$ is the asymptote (default = 1), $k2$ is the inflection point (default = 10), and, $k3$ is the slope (default = 0.5).

With the default values, this function gives a 50% establishment mortality of eggs (i.e. 50% of eggs laid on a given day die) at 10 larvae per fruit.

Total establishment mortality of eggs (E_{em}) is defined as

$$E_{em} = 1 - (1 - E_{cem}) \times (1 - E_{ldem}),$$

where E_{cem} is constant establishment mortality and E_{ldem} is establishment mortality due to larval density.

3.2.3. Egg mortality rate due to temperature

Daily mortality rates of eggs at high temperatures were derived from Myers (1952), Bateman (1967), Pritchard (1978), Meats (1981, 1984), and Fitt (1984, 1990a). At each temperature for which there were data, the mortality rate was calculated as $1 - S_D$, where $S_D = {S_T}^{1/D_D}$, S_D is the daily survival rate, expressed as a proportion, S_T is the total survival, expressed as a proportion, and D_D is the days to development.

Mortality rates at low temperatures were estimated. The only laboratory data available indicated that eggs kept at a constant 1 °C die in 10 days (Jessup, personal communication). Two linear equations define the daily mortality rate (E_{dm}) of eggs due to temperature:

$$E_{dm} = -0.0729 \times T_c + 0.1354 \text{ for temperatures below } 2\,^\circ\text{C}$$

and

$$E_{dm} = 0.1706 \times T_c - 5.4585 \text{ for temperatures above } 32\,^\circ\text{C}.$$

The regression equation defining mortality due to high temperature has an R^2 value of 0.92 ($n = 5$). The R^2 value for cold-induced mortality is meaningless, as the equation was estimated from only two data points.

3.3. Egg to larva transfer

All members of a cohort transfer to the larval stage when they have completed development (i.e. reached a physiological age of 1).

4. Larva

All larval instars are combined into a single life stage because there are no data available to adequately segregate the development and mortality functions for each instar.

4.1. Larval development rate

A linear function ($R^2 = 0.91$, $n = 11$) describes the rate of larval development (L_d) based on temperature (Bateman, 1967; Meats, 1981; Myers, 1952; O'Loughlin, 1964, 1975; Sonleitner and Bateman, 1963):

$$L_d = 0.0061 \times T_c - 0.0609.$$

The equation indicates a lower developmental threshold for larvae of 10 °C.

4.2. Larval mortality rate

4.2.1. Larval establishment mortality—constant

There is a constant establishment mortality of 15.3%, based on data at temperatures between 25 and 30 °C (Bateman, 1967; Meats, 1984). All other temperature-dependent mortality data for larvae were adjusted by this amount prior to any calculations.

4.2.2. Larval establishment mortality due to larval density

Fitt (1984) indicates that up to 80% of newly hatched larvae died when placed into fruits containing 2–3 days old larvae, but does not indicate the number of larvae present. Thus, as with eggs, additional establishment mortality is described by a logistic function dependent on larval density:

$$f(L_n) = \frac{k1}{1 + \exp(-k3 \times (L_n - k2))},$$

where L_n is the average number of larvae per fruit, $k1$ is the asymptote (default = 1), $k2$ is the inflection point (default = 18), and $k3$ is the slope (default = 2).

Due to a lack of data, parameters for this function were adjusted to result in 50% establishment mortality at an average density of 18 larvae per fruit.

Total establishment mortality of larvae (L_{em}) is defined as

$$L_{em} = 1 - (1 - L_{cem}) \times (1 - L_{ldem}),$$

where L_{cem} is the constant mortality and L_{ldem} is the mortality due to larval density.

4.2.3. Larval mortality due to temperature

Daily mortality rates of larvae were calculated using the same procedure as for eggs. The data used were from Myers (1952), Sonleitner and Bateman (1963), O'Loughlin (1964, 1975), Bateman (1967) and Meats (1981, 1984). Mortality at low temperatures (<1 °C) was estimated from laboratory data (Jessup, personal communication). A polynomial equation ($R^2 = 0.81$, $n = 13$) describes the mortality of larvae (L_{tdm}):

$$L_{tdm} = (0.0003 \times {T_c}^2) - (0.0105 \times T_c) + 0.1146.$$

4.2.4. Larval mortality due to larval density

To limit larval numbers to an acceptable range (20 larvae/fruit, Fitt, 1984), daily mortality of larvae is described with a logistic function dependent on their density:

$$f(L_n) = \frac{k1}{1 + \exp(-k3 \times (L_n - k2))},$$

where L_n is the average number of larvae per fruit, $k1$ is the asymptote (default = 0.5), $k2$ is the inflection point (default = 12), and $k3$ is the slope (default = 0.6).

4.2.5. Larval mortality due to fruit suitability

The suitability of fruit for larval development can affect the mortality rate of larvae. Fruit suitability is defined by the user as a constant between 0 and 1 (default of 1 for optimal). The resulting mortality rate (L_{fsdm}) is the complement of the fruit suitability index.

Total daily mortality of larvae (L_{dm}) is defined as

$$L_{dm} = 1 - (1 - L_{tdm}) \times (1 - L_{lddm}) \times (1 - L_{fsdm}),$$

where L_{tdm} is the mortality due to temperature, L_{lddm} is the mortality due to larval density and L_{fsdm} is the mortality due to fruit suitability.

4.3. Larva to pupa transfer

Surviving larvae transfer to the pupal stage when they have completed development.

5. Pupa

5.1. Pupal development rate

Development rates for pupae (P_d) were calculated from Myers (1952), Sonleitner and Bateman (1963), O'Loughlin (1964, 1975), Bateman and Sonleitner (1967), and Bateman (1967):

$$P_d = 0.0061 \times T_c - 0.068.$$

The lower threshold for development is calculated to be 11.2 °C, and the equation has an R^2 value of 0.97 ($n = 15$).

5.2. Pupal mortality rate

5.2.1. Pupal establishment mortality—constant

A constant establishment mortality of 22% was calculated from data collected between 20 and 30 °C (Bateman, 1967; Meats, 1984). All other temperature-dependent mortality data for pupae were adjusted by this amount prior to any calculations.

5.2.2. Pupal mortality due to temperature

Data from O'Loughlin (1964), Bateman and Sonleitner (1967), Bateman (1967) and Meats (1984) were used to calculate daily pupal mortality rates due to high temperatures. A linear regression was fitted to the data from 32 to 37.8 °C inclusive, ignoring a point from O'Loughlin (1964) (mortality rate of 1.0 at 32.2 °C) because it was derived at the excessively low RH of 28%. Mortality as a function of low temperatures was estimated from laboratory data (Jessup, personal communication). Two equations describe the rate of pupal mortality (P_{tdm}):

$$P_{tdm} = -0.025 \times T_c + 0.125 \text{ for temperatures below } 5\,^\circ\text{C}$$

and

$$P_{tdm} = 0.0457 \times T_c - 1.4192 \text{ for temperatures above } 31\,^\circ\text{C}.$$

The R^2 value for cold-induced mortality is meaningless, and the regression equation defining mortality due to high temperature has an R^2 value of 0.84 ($n = 3$).

5.2.3. Pupal mortality due to soil moisture

As pupae develop in the top layer of the soil, the moisture content of the upper soil layer was considered to be the best predictor of mortality. The SSM module was used to describe the effect of low and high soil moisture on pupal survival. Although several authors have alluded to soil moisture effects on pupal mortality in QFF (Dominiak et al., 2000b; Mavi and Dominiak, 1999) and in other fruit fly species (Bateman, 1972; Fitt, 1981), there were no data available and values were derived by a process of iteration to give plausible outcomes at the two model calibration sites of Coonamble and Dunedoo. The proportion of pupae dying (P_{smdm}) due to unsuitable SSM is described by a double quadratic function:

$$P_{smdm} = (0.5 - \text{SSM})^2 \text{ for SSM below } 0.5,$$

$$P_{smdm} = 5 \times (\text{SSM} - 0.9)^2 \text{ for SSM above } 0.9,$$

and

$$P_{smdm} = 0 \text{ for SSM between } 0.5 \text{ and } 0.9.$$

The total daily mortality of pupae (P_{dm}) is defined as

$$P_{dm} = 1 - (1 - P_{tdm}) \times (1 - P_{smdm}),$$

where P_{tdm} is the mortality due to temperature and P_{smdm} is the mortality due to soil moisture.

5.3. Pupa to teneral female and teneral male transfer

When a cohort of pupae has completed development, it transfers to either the teneral female or teneral male stage. The proportion that transfers to each of the teneral life stages is determined by the Sex Ratio (set externally, see Section 2.7).

6. Teneral female

This life stage includes the maturation process of non-reproductive females that emerge from the pupal life stage. Teneral females may become reproductive or enter an over-wintering stage, depending on the environmental conditions they experience.

6.1. Cohort property: days <18 °C

The exact environmental cues that result in adult flies seeking over-wintering sites are unknown, but teneral females (and other adult fly life stages) over-winter if they emerge late in autumn when temperatures are too cool for reproduction. A cohort property of 'Days below 18 °C' tracks the number of days when the maximum daily temperature is below 18 °C, and triggers over-wintering of cohorts that experience 5 consecutive days of temperatures of below 18 °C.

6.2. Cohort property: fly age

O'Loughlin (1964) and Bateman (1967) provide data on fly longevity. A cohort property of 'Fly Age' (FA) tracks the aging process (equivalent to a development process) across all female and male life stages. When an age of one is reached, mortality occurs (maximum longevity has been attained). O'Loughlin's (1964) data of 2 days' longevity at 32.2 °C, collected at 0% RH, were omitted from the analyses since mortality would have been caused by desiccation not temperature. A linear regression equation ($R^2 = 0.60$, $n = 49$) was fitted to all other data between 20 and 30 °C. A minimum rate of aging is set at 0.0027 (calculated to give maximum longevity of about 1 year, and equivalent to the rate predicted at 15 °C) to enforce aging at low temperatures. Without this imposed minimum rate, aging would not occur below 12.3 °C. No maximum rate is set, as high temperatures should result in earlier mortality. The daily aging increment is calculated as

$$\mathrm{FA} = 0.001 \times T_c - 0.0123 \text{ for temperatures above } 15\,^{\circ}\mathrm{C}$$

and

$$\mathrm{FA} = 0.0027 \text{ for temperatures below } 15\,^{\circ}\mathrm{C}.$$

6.3. Teneral female maturation (daily development rate)

Teneral females mature into reproductive females as a function of temperature. Sonleitner and Bateman (1963), O'Loughlin (1964), Pritchard (1970), Meats and Khoo (1976), Meats (1981, 1989), and Fletcher (1979, 1987a) provide information on the maturation process of teneral females. A linear regression ($R^2 = 0.88$, $n = 15$) was fitted to this data, to provide a maturation (or development) rate:

$$\mathrm{TF_d} = 0.0108 \times T_c - 0.133.$$

The lower temperature threshold for development is estimated to be 12.3 °C.

6.4. Teneral female mortality rate

Apart from the aging process (Fly Age) above, which results in death at the age of 1, there are no other data available on the mortality of teneral females. We assumed that flies would be more likely to die when temperatures were either excessively low or high (Meats, 1981), and when heavy rainfall (May, 1961) and excessive dryness occurred (Bateman, 1968). Soil moisture was used to measure dryness, on the basis that flies are generally found within the canopy of trees, which is usually a moister environment than the ambient air. We assume that canopy moisture levels reflect the moisture available to the root system, and that as long as the soil moisture remains above the permanent wilting point (~10% of the moisture holding capacity), normal transpiration occurs and the canopy environment remains favourable for fly survival. The default parameter values were estimated by fitting the model at Coonamble and Dunedoo.

6.4.1. Teneral female mortality due to temperature

$$A_{\mathrm{tdm}} = -0.07 \times T_c - 0.13 \text{ for temperatures below } -2\,^{\circ}\mathrm{C},$$

$$A_{\mathrm{tdm}} = 0.125 \times T_c - 4.5 \text{ for temperatures above } 36\,^{\circ}\mathrm{C},$$

and

$$A_{\mathrm{tdm}} = 0 \text{ for temperatures between } -2 \text{ and } 36\,^{\circ}\mathrm{C}.$$

6.4.2. Teneral female mortality due to rainfall

$$A_{\mathrm{rdm}} = 0.003 \times (\text{rainfall}) - 0.13 \text{ for rainfall above } 40 \text{ mm}$$

and

$$A_{\mathrm{rdm}} = 0 \text{ for rainfall of } 40 \text{ mm or less}.$$

6.4.3. Teneral female mortality due to soil moisture

$$A_{\text{smdm}} = 40 \times (\text{SM} - 0.1)^2 \text{ for soil moisture below } 0.1$$

and

$$A_{\text{smdm}} = 0 \text{ for soil moisture of } 0.1 \text{ or wetter.}$$

6.4.4. Teneral female mortality due to fly age

Teneral females that reach a Fly Age of one die.

The total daily mortality of teneral females (TF_{dm}) is defined as

$$\text{TF}_{\text{dm}} = 1 - (1 - A_{\text{tdm}}) \times (1 - A_{\text{rdm}}) \times (1 - A_{\text{smdm}}) \times (1 - A_{\text{adm}}),$$

where A_{tdm} is the mortality due to temperature, A_{rdm} is the mortality due to excessive rainfall, and A_{smdm} is the mortality due to soil moisture. A_{adm} is the mortality due to age.

6.5. Teneral female to reproductive female transfer

Teneral females transfer to the reproductive female stage when they have completed development.

6.6. Teneral female to over-wintering female transfer

Teneral females transfer to the over-wintering female stage when they have experienced 5 consecutive days of maximum temperatures below 18 °C.

7. Reproductive females

As with teneral flies, the model tracks fly age and the number of consecutive days with maximum temperatures below 18 °C that reproductive females experience.

7.1. Reproductive female mortality rate

Apart from the longevity data mentioned above for teneral females (Bateman, 1967), there are no other data available on mortality of reproductive females. Thus, daily mortality rates are defined by the same functions used for teneral females.

7.2. Reproduction

7.2.1. Fecundity

Fecundity refers to the potential number of offspring that a female can produce. As this is some quantity greater than 1000 eggs in a lifetime (Fitt, 1990b; Fletcher, 1989), we use a constant of 1400 eggs per female.

7.2.2. Egg production

The number of eggs that a female fly can lay daily depends on a number of factors.

7.2.2.1. Egg production: maximum number (EP_n). Females have fewer than 80 ovarioles and generally carry around 40–50 mature eggs when provided continuous access to fruit (Fitt, 1986). Bateman (1977) indicates that females lay 80 to over 100 eggs per week, or an average of 11 to over 14 eggs per day. However, females deprived of an oviposition site for several days may carry more than 80 mature eggs by storing them in the ovarioles (Fitt, 1986). Although fruit is presumed to be continuously available, since other factors (given below) will generally act to reduce the number of eggs laid per day, the model uses a default of 80 eggs/female per day ($\text{EP}_n = 80$).

7.2.2.2. Egg production restricted by fruit acceptability (EP_{fa}). The daily rate of egg production is a direct function of the attractiveness of fruit for oviposition, specified as the location-specific variable 'Fruit Acceptability for Oviposition'. The default value of 1 indicates optimally attractive fruit.

7.2.2.3. Egg production restricted by temperature (EP_t). Bateman (1967) provides evidence that oviposition is a function of temperature. A polynomial function, scaled from 0 to 1, describes the daily proportion of eggs (EP_t) laid as a function of temperature:

$$\text{EP}_t = \frac{(-0.11 \times T_c{}^2) + (5.61 \times T_c) - 67.86}{5.94}.$$

This equation effectively limits egg-laying to between 18.5 and 34 °C, with peak production around 26 °C. With only three data points available to fit the polynomial function, the R^2 value (1) is not meaningful.

7.2.2.4. Egg production restricted by activity index (EP_{AI}). Eggs are not laid on days of heavy rainfall (May, 1961). As a first approximation, an Activity Index was defined outside the life cycle (see Section 2.7), to determine the activity of adult flies as a function of rainfall. Only that proportion of females that are active can reproduce, and so the rate of egg production on days of 40 mm or more of rainfall is limited by the Activity Index.

7.2.2.5. Egg production restricted by larval density (EP_{ld}). Females prefer to oviposit in fruit that does not already contain larvae (Fitt, 1984). A complementary logistic function determines the proportion of eggs laid (EP_{ld}) when there are larvae present. The default parameters allow 50% of eggs to be laid when there are 12 larvae per fruit:

$$EP_{ld} = 1 - f(L_n),$$

where

$$f(L_n) = \frac{k1}{1 + \exp(-k3 \times (L_n - k2))},$$

L_n is the average number of larvae per fruit, $k1$ is the asymptote (default = 1), $k2$ is the inflection point (default = 12 larvae/fruit), and $k3$ is the slope at the inflection point (default = 0.6).

All of these functions are multiplied together to determine the daily number of eggs laid (EP) per female:

$$EP = (EP_n) \times (EP_{fa}) \times (EP_t) \times (EP_{AI}) \times (EP_{ld}),$$

where EP_n is the maximum number of eggs per day, EP_{fa} is the proportion of eggs determined by fruit acceptability, EP_t is the proportion of eggs determined by temperature, EP_{AI} is the proportion of eggs determined by female activity (based on rainfall), and EP_{ld} is the proportion of eggs determined by larval density.

Total eggs laid by individual females in a cohort are tallied and cannot exceed the maximum fecundity of 1400.

7.3. Reproductive female to over-wintering female transfer

Reproductive females transfer to over-wintering female life stage when they have experienced 5 consecutive days when the maximum temperature is below 18 °C.

8. Over-wintering female

8.1. Cohort property: days ≥18 °C

The environmental cues used to bring flies out of an over-wintering state into an active, reproductive state are as poorly defined as the cues used to induce over-wintering. A cohort property is used to track days where the maximum temperature reaches or exceeds 18 °C. To come out of over-wintering, flies must experience 4 consecutive days where the maximum temperature reaches or exceeds 18 °C.

8.2. Cohort property: fly age

Females transferring from the reproductive life stage continue to age at the same temperature-dependent rate as both teneral and reproductive females.

8.3. Over-wintering female maturation (development rate)

Ovarian maturation proceeds in over-wintering flies so long as temperatures are sufficiently warm (Fletcher, 1975, 1987b). A maturation process, identical to that in teneral females, is included in over-wintering females.

8.4. Over-wintering female mortality rate

As with other adult flies, apart from the longevity data mentioned above (Bateman, 1967; O'Loughlin, 1964), there are no other data available on mortality of over-wintering females. Daily mortality rates are defined by the same functions used previously for teneral and reproductive females, except that mortality due to high temperatures is omitted.

8.5. Over-wintering female to reproductive female transfer

Over-wintering females transfer to the reproductive life stage when they have experienced 4 consecutive days where the maximum temperature reaches 18 °C, and when maturation is complete. Transfer only occurs when both conditions are met.

9. Teneral male

All processes in the teneral male life stage are identical to those in the teneral female life stage.

10. Reproductive male

Similarly, most processes in the reproductive male life stage are identical to those in the reproductive female life stage, including the transfer to the over-wintering male life stage. However, the reproductive male life stage has no oviposition functions, and includes a process to define transfer of individuals to the trapped male life stage.

10.1. Reproductive male to trapped male transfer

This process is the product of three factors. The first is a direct function of the Activity Index (see Section 2.7), which determines the proportion of males in each cohort in this life stage that are active and can therefore be trapped.

The second is a linear function of the daily maximum temperature. Dominiak et al. (2000a,b) and MacFarlane et al. (1987) provide recapture rates of sterile male flies in different months of the year at three locations (Wagga Wagga and Lake Cargelligo in New South Wales and Wangaratta in Victoria). Average long-term monthly temperatures (maximum and minimum) for these locations were extracted from CLIMEX (Sutherst and Maywald, 1985; Sutherst et al., 1999) and the monthly recapture rates were plotted against the appropriate long-term average temperatures. The data suggest that trapping efficiency (as measured by recapture rates) varies with temperature, and an exponential function of the maximum temperature provides a good estimate ($R^2 = 0.78$, $n = 22$) of trap efficiency.

$$\mathrm{TE}_t = 0.0000003 \exp^{0.271 \times T_\mathrm{m}},$$

where T_m is the maximum daily temperature in °C.

The third factor is a linear function of the male proportion of the active, reproductive population (see Section 2.8). Different function shapes and parameters were tested, but the following linear function was the simplest and provided the best results (see Section 13.3):

$$\mathrm{TE}_\mathrm{mp} = 3.5 \times \mathrm{MP},$$

where MP is the male proportion of the active reproductive population.

Thus, total trap efficiency (TE), which determines for each cohort of reproductive males the proportion that transfers to the trapped male life stage, is calculated as

$$\mathrm{TE} = \mathrm{AI} \times \mathrm{TE}_t \times \mathrm{TE}_\mathrm{mp},$$

where AI is the activity index, TE_t is the temperature-dependent trapping efficiency and TE_mp is the trapping efficiency based on the proportion of males in the active population.

11. Over-wintering male

With one exception, the processes in the over-wintering male life stage are the same as those for the over-wintering female life stage. As there is no evidence to suggest that males that have over-wintered undergo another maturation period, over-wintering males revert to the reproductive male life stage (rather than the teneral male stage).

12. Trapped male

The trapped male life stage is a terminal life stage, reflecting the fact that males caught in traps are effectively removed from the population. The only process in this stage is mortality, which is artificially defined so that the number of males trapped each day can be tracked.

12.1. Trapped male daily mortality rate

Mortality of trapped males is defined as a function of chronological age. At the threshold age of 2 days, all males in a cohort die. An age of 2 (rather than 1) prevents flies from being killed on the same day that they are caught, and so prevents the model from returning a zero value for the number of flies on that day.

13. Simulation runs

13.1. Meteorological data

Daily meteorological data (minimum and maximum temperatures, rainfall and evaporation), from 1 January 1990 to 31 December 1999, were obtained from the SILO Data Drill (Jeffrey et al., 2001) for five locations in New South Wales: Coonamble, 30°56′S 148°23′E; Dunedoo, 32°02′S 149°22′E; Trangie, 32°04′S 147°59′E; Peak Hill, 32°47′S 148°11′E; and Geurie, 32°25′S 148°54′E).

13.2. Initialisation of model

A standard initialisation routine was applied to all simulations to ensure replication of results. Values used in the simulations are given in Table 1.

The runs include an irrigation component from mid-August to mid-April to improve the representation of the actual moisture conditions in orchards and in backyard gardens in towns, since landscape irrigation is a common feature in rural New South Wales, especially during the dry summers (Dominiak et al., 2000b; Mavi and Dominiak, 1999). According to the FAO (1977), adding irrigation equivalent to 70% of open pan evaporation prevents plant wilting by maintaining adequate soil moisture.

The QFF life cycle was initialised with a single introduction of 100 reproductive females and 100 reproductive males on 1 January 1991. For each location, the simulations ran from 1 January 1990 to 31 July 1998. The simulations were run for a year prior to the introduction of flies to ensure that the irrigation event was triggered and operating when flies were introduced. Running the simulations for some years prior to the period of interest (1996–1998) allowed fly populations to build up and stabilize.

Table 1
Initialisation values used in simulations

Model variable	Initialisation value
Location-specific variables	
Size of Orchard	1
Number of Trees in Orchard	1
Number of Fruit per Tree	100
Fruit Suitability for Larval Development	1 (optimal)
Fruit Suitability for Oviposition	1 (optimal)
Irrigation Amount (proportion of open pan evaporation)	0.7
Length of Irrigation Season, in days	243
Irrigation season event	Begins 14 August
Sex ratio	0.5
Soil moisture, initial store	0.5
Shallow soil Moisture, initial store	0.5

13.3. Model calibration and verification

The data from two sites, Coonamble and Dunedoo, were used to calibrate parameters of the model, particularly those for which we had little data. At Coonamble, 23 Lynfield traps (catching only male flies) were monitored weekly from 30 August 1996 until 30 April 1998. At Dunedoo, 6 Lynfield traps were monitored weekly from 5 April 1996 until 24 April 1998. The original data for both sites was marginally modified. For example, where it was obvious that traps had not been cleared the day after Christmas (no flies were recorded in any traps for that week) and the numbers of trapped flies were very large the following week (well over double the numbers in the following week), the number of flies caught in the second week was divided evenly over the 2 weeks.

Model output of the daily total number of trapped adult males was converted to total weekly trap catches, and then compared with trap catch data for the same week. Log-transformed values for both the predicted and observed values were used.

Through a process of iteration, values for those parameters for which there were no data (e.g. mortality of pupae due to soil moisture, activity of adult males, all density-dependent mortalities, trapping efficiency as a function of the male proportion of the active population) were manually adjusted to get the best fit to the trap catch data (Fig. 2). The R^2 from a linear regression of log values of predicted numbers on log values of observed numbers provided a measure of the goodness-of-fit of the model (Fig. 3). Whenever the value for an unknown parameter was adjusted, a measure of the goodness-of fit (R^2 value) was obtained to assess the impact of adjusting the parameter value. The model was deemed to be as complete as possible when further adjustments gave no improvement in fit. It was recognised that there were serious gaps in the understanding of some processes that no amount of adjustment would resolve (e.g. the impact of seasonal

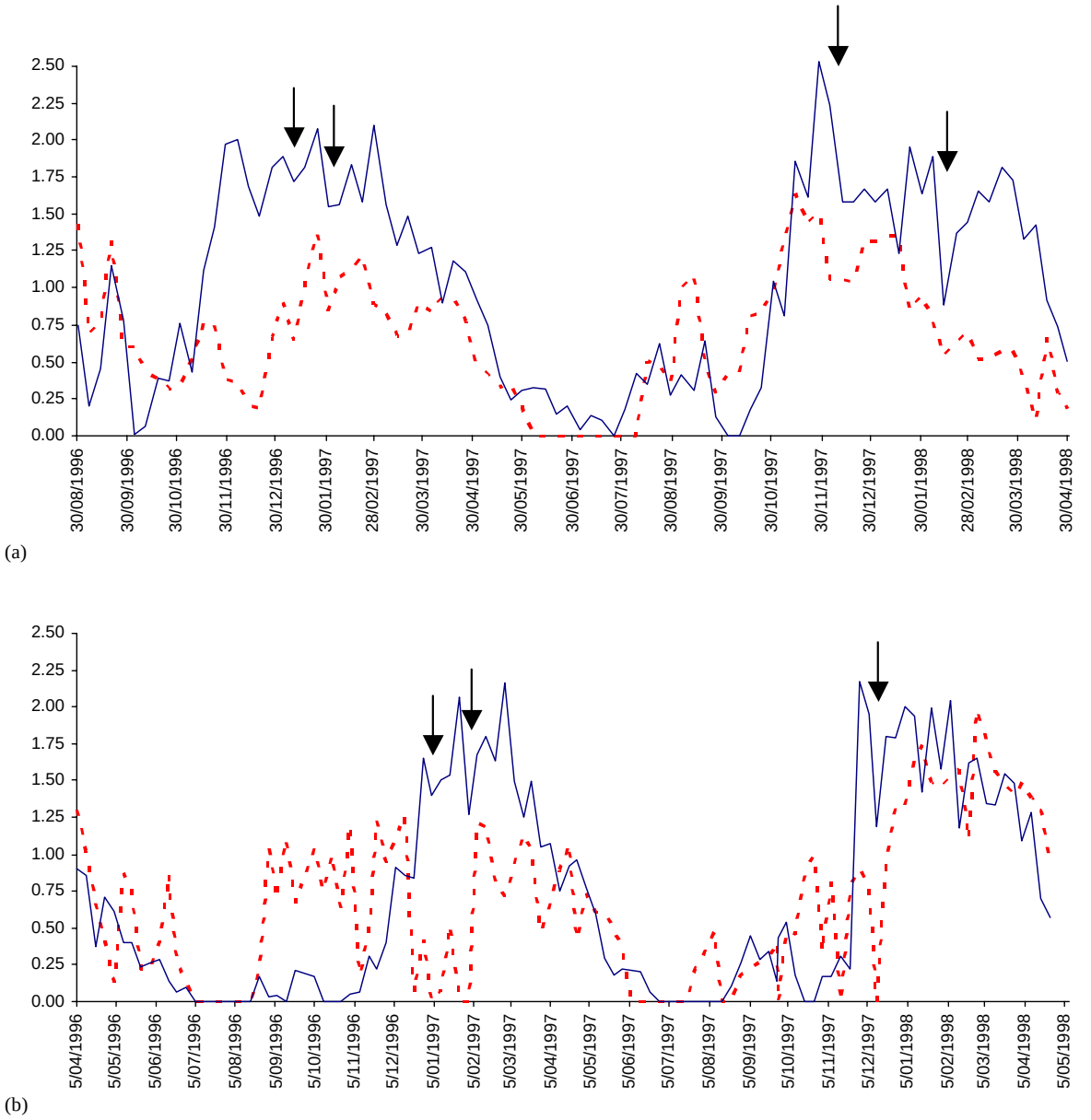

Fig. 2. Predicted and observed numbers of trapped males, using $\ln(x+1)$ values: (a) Coonamble; (b) Dunedoo. Solid lines are the predicted numbers of males caught in that week; dotted lines are the average values of all trap catches for that week. Arrows indicate periods where low trap catches coincide with hot weather.

availability and suitability of fruit types on phenology of fruit fly populations, and fly behaviour in different climatic conditions or physiological states).

At Coonamble, the R^2 value is 0.32 ($n = 88$), while at Dunedoo it is 0.28 ($n = 108$) (Fig. 3).

13.4. Model validation

The model was run at three additional sites for which Lynfield trap catches were available. At Trangie, 23 traps were monitored weekly from 23

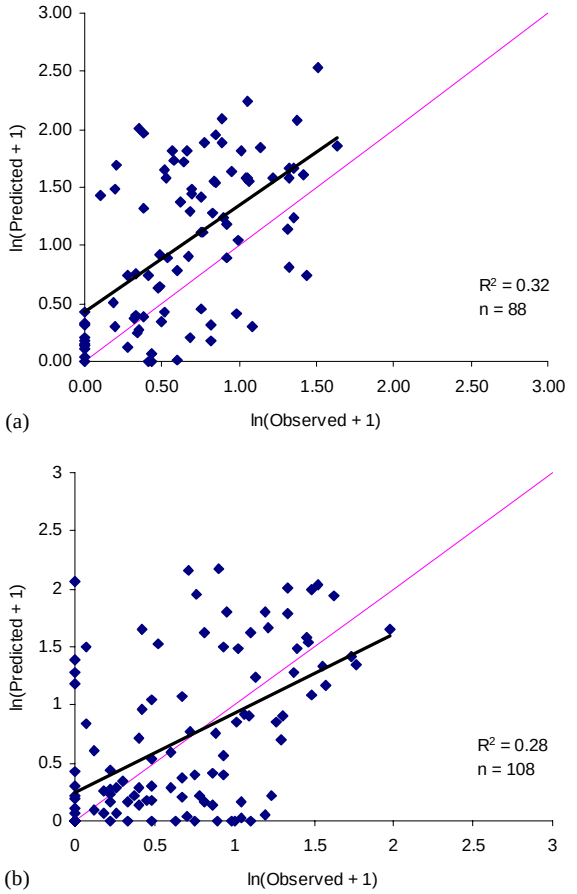

Fig. 3. Predicted numbers of trapped males plotted against observed numbers of trapped males: (a) Coonamble; (b) Dunedoo. Solid lines represent a regression of predicted vs. observed values, with the corresponding goodness of fit (R^2) value; dotted lines represent a perfect fit of the predictions to the observed catches.

February 1996 to 30 April 1998, at Peak Hill, 12 traps were monitored weekly from 6 September 1996 to 24 April 1998, and at Geurie, 4 traps were monitored weekly from 4 April 1996 to 30 May 1997.

Trangie was initially a control town, where no sterile males were released to control QFF populations. In 1996, Trangie became a low-level release site, with relatively few sterile males released weekly. From 13 September 1996, only 5000–6000 sterile males per km^2 were released weekly, and from 5 December 1997, 12,000 sterile males released weekly per km^2. It was thought that the low number of sterile males released had little impact on QFF population dynamics, so Trangie was included as a validation site, on the understanding that model predictions could be less reliable than elsewhere.

The results of the simulations at the three validation towns are shown in Fig. 4. While there are discrepancies between the predicted and observed numbers of flies caught in traps, the phenological patterns of the model are approximately correct, with flies active in the model at the correct times of the year.

Fig. 5 presents the goodness-of-fit of the model. The model has the worst fit at Trangie; almost entirely over predicting fly numbers which is not surprising, given that fly numbers would have been suppressed by the release of sterile males.

14. Discussion

Modelling stage-structured populations, where the physiological rate of aging is temperature-dependent, has a long tradition in insect ecology. Early models used a variant of the Leslie-matrix approach to model age structure, and solved the problem of moving individuals among stages by inventing arbitrary stages that evenly subdivided the life cycle, e.g. the quarter instar periods, or QUIPS, of Gutierrez et al. (1974). This time period became the basic time step for model operations, enabling movement of one stage to another during each time step. Matching to real time was determined by how many arbitrary life cycle steps occurred in, say, a day, when that day was made equivalent to the insect's physiological time scale, expressed, for example, in degree-days. Models were specifically written in some computer language (usually FORTRAN), parameterised for a particular example, and changing aging from a degree-days to some non-linear time scale required considerable reprogramming. Parameters had to be estimated for non-biologically realistic stages (e.g. QUIPS). Nevertheless, these "life-system models" had considerable success at integrating climate effects into insect population models and generating realistic comparisons between real population data on insect abundance and model output (e.g. Gilbert et al., 1976; Gutierrez, 1996). It was not easy to change these life system models or to estimate parameter values. Although the limitation of organisms all moving from one arbitrary stage to the next could be handled by non-progression

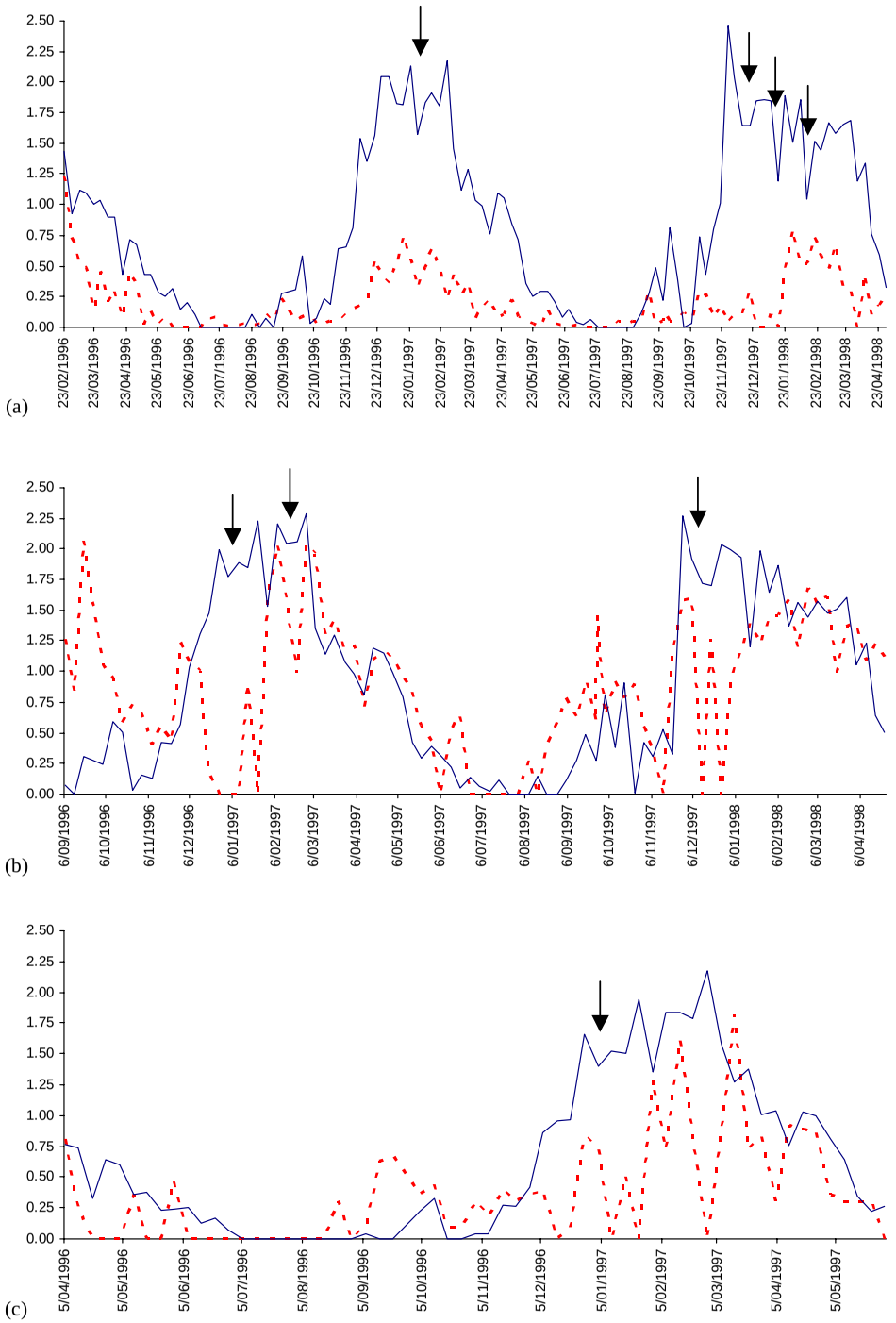

Fig. 4. Predicted and observed numbers of trapped males, using $\ln(x+1)$ values: (a) Trangie; (b) Peak Hill; and (c) Geurie. Solid lines are the predicted numbers of males caught in that week; dotted lines are the average values of all trap catches for that week. Arrows indicate periods where low trap catches coincide with hot weather.

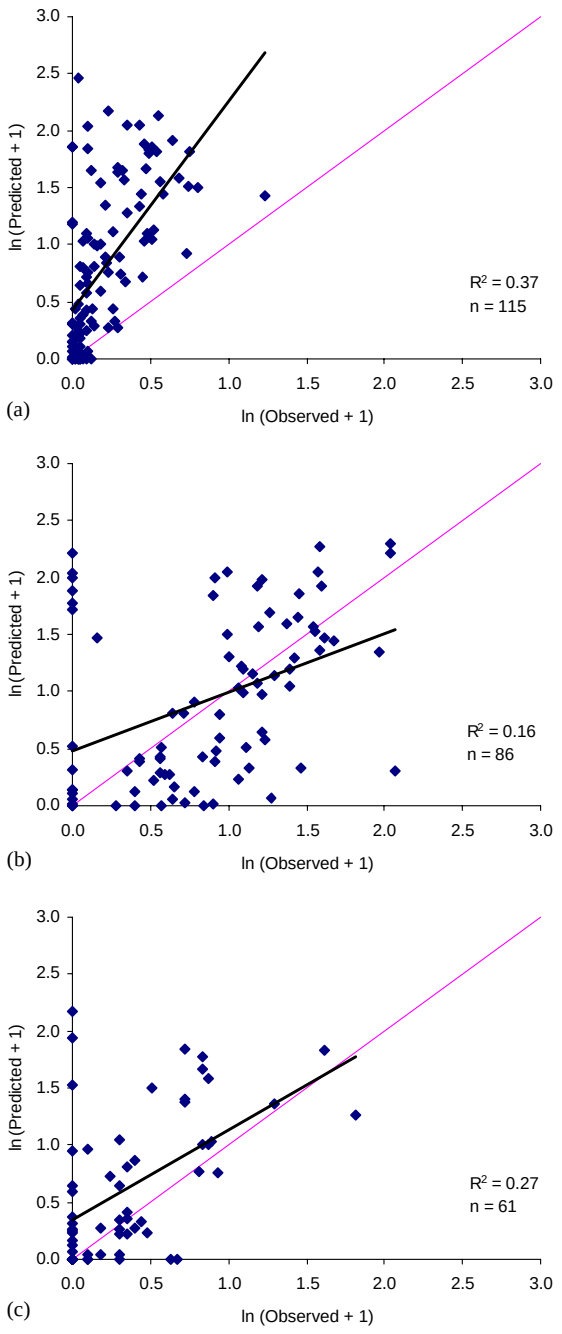

Fig. 5. Predicted numbers of trapped males plotted against observed numbers of trapped males: (a) Trangie; (b) Peak Hill; and (c) Geurie. Solid lines represent a regression of predicted vs. observed values, with the corresponding goodness of fit (R^2) value; dotted lines represent a perfect fit of the predictions to the observed catches.

probabilities, the models were not widely applied. These models belong to a general class of age structured population models (Caswell, 2000).

An elegant solution to modelling the dynamics of stage-based populations is the escalator-box car train algorithm (de Roos, 1977). A population is divided into cohorts, with the development of the average individual followed in each cohort. These are essentially book-keeping models. We use this book-keeping approach in our QFF model, but include a stage structured life cycle. Stages can be arbitrary or correspond to biologically meaningful units (e.g. instars). The stages recognised depend on the purpose of the modelling exercise and what information is available to compare to model output. Our model follows the development and abundance of cohorts within biologically meaningful stages (e.g. egg, larva, pupa, etc.). Cohorts are generated at each time step either by reproduction or development from a previous stage, which enables variable development to be included. This use of biologically relevant cohorts with variable development rates is a relatively new approach.

Another factor that distinguishes our model from previous work is the relative ease and speed with which the QFF model was constructed. The DYMEX modelling environment makes programming and coding unnecessary, therefore making population dynamics modelling more readily accessible to biologists and ecologists. A good graphic user interface, a library of modules, and the use of a specific formalism of lifestages and lifecycles means that largely by pointing and clicking, the *structure* of a model can be rapidly constructed (an hour for an experienced DYMEX modeller), and all relationships can readily be defined. Creating development rate equations, stage transition functions, mortality rates, and their generating process and links to the physical environment is straightforward. The only difficult part of building a model using DYMEX (or any population model for that matter) is parameterising the various functions and equations that are selected, i.e. mathematically defining the various life processes as a series of difference equations. However, because lifestages can be defined in biologically meaningful terms in DYMEX, parameter values are more readily estimated from experimental or observation data than the abstract stage transitions employed in some models (e.g. QUIPS).

The QFF model attempts to compare model output to real population data, as opposed to general caricatures of abundance. This has also been done recently by Choi and Ryoo (2003), who use a matrix model to compare predicted population estimates of *Paronychiurus kimi* (a soil Collembola) to field data, although they only provide field data for a single site.

Our model differs conceptually from that of Choi and Ryoo (2003) in two important respects. Firstly, Choi and Ryoo (2003) are able to compare model predictions directly with field measurements of population abundance, without the complications of a "baiting" function to sample adults that most likely includes variability in efficiency due to environmental factors (e.g. temperature), and population factors (e.g. the relative abundance of females). Secondly, because *P. kimi* populations can be sampled directly, Choi and Ryoo (2003) were able to initialise their model with the mean observed population abundance at the beginning of the simulation period, i.e. their model and validation data coincide at the beginning of the simulation. This minimised the potential for deviation (degrees of freedom) between the model and the field populations because of the lack of independence between matched pairs in each of the two time series. By contrast, the QFF model is initialised with an arbitrary population several years prior to the period of interest, minimising any initialisation artefacts, and maintaining the desirable independence between the simulation results and the validation datasets.

Another important facet of our model is that it is general for QFF, i.e. it is not site-specific, as we attempt to model the processes of development, reproduction, growth and mortality. As such, the model can be used for different locations given appropriate weather data.

The use of a cohort-based approach allowed us to model the population dynamics of QFF more realistically than was done in the only other phenological population dynamic model that exists for a fruit fly (*Dacus oleae*) (Fletcher and Comins, 1985). Natural variation in population processes in our model is driven by changing abiotic and biotic factors, whereas the *D. oleae* model relies solely on temperature and a Monte-Carlo approach to introduce some variability in the development rates.

Our model also differs from the *Dacus oleae* model (Fletcher and Comins, 1985) in that variables other than temperature drive population processes. Although most processes have a temperature component, many are affected by moisture and/or rainfall. Although we have had to estimate some parameters for which data were lacking, our model simulates the phenological pattern of QFF at the five locations reasonably well. Obvious deficiencies in the model are discussed below.

In the first instance, we recognise that the validation locations (Trangie, Peak Hill and Geurie) are climatically similar to the sites used to calibrate the model (Coonamble and Dunedoo). It would clearly be more meaningful to test the model in different climatic regions, e.g. tropical or Mediterranean. Although trap data have been published for Cairns in the tropics (May, 1961), there are currently no data available for evaporation during the period of this study. The appropriate meteorological data may become available in the near future (see http://www.nrm.qld.gov.au/silo) in which case this simulation will be possible.

There were adequate data available to fit the development functions of each of the life stages in relation to temperature. Thus, we have a high degree of confidence that the regression equations used to describe development rates are fairly robust, especially within the temperature range of 15–30 °C. However, there were virtually no data available at temperatures beyond these limits. The regressions indicate lower temperature thresholds for development (11.1 °C for eggs, 10 °C for larvae, 11.2 °C for pupae, and 12.3 °C for teneral females) that are consistent with published data (Fletcher, 1979, 1987a; Meats, 1989; Meats and Khoo, 1976; Monro and Osborn, 1967; Pritchard, 1970).

The data used to derive the aging function of adult flies were only collected at four temperatures: 20, 23 °C (a single point), 25, and 30 °C, and the regression analysis on these data indicates a lower threshold for aging of adult flies of 12.3 °C. However, over-wintering flies regularly experience temperatures lower than 12.3 °C, and must be subject to some degree of aging. For this reason we use a minimum aging rate of 0.0027, to provide a maximum longevity of just over 1 year (370 days). There is also a wide scatter in the data, and this regression is one of the poorer fits, with an R^2 value of only 0.60. Longevity data at temperatures beyond the narrow range of only 20–30 °C would be useful.

All of the development rates used are linear, with no cap on, or no reduction in, the rate of development

at high temperatures. This is for two reasons. Firstly, there are no data available with which to fit anything other than linear functions. So fitting any one of the many alternative non-linear functions is currently not an option. It is noteworthy that the *D. oleae* model suffers from the same lack of data (developmental data were not available at temperatures above about 35 °C) and that both linear and polynomial functions provided similar estimates of development for *D. oleae* (Fletcher and Comins, 1985).

Secondly, mortality rates of all stages are set sufficiently high that temperatures allowing for extremely rapid development will also result in high mortality. However, any additional information at temperatures greater than 30 °C would provide a better description of the phenology, and a different function type could easily be incorporated into our model to better describe development.

There is a paucity of data on the effects of high and low temperatures on mortality of all of the life stages. For cold-induced mortality, there was only data at 1 °C (Jessup, personal communication) for eggs, larvae and pupae. Other rates were estimated from field observations. For example, adult mortality was based on observations that several nights at low temperatures −3 to 5 °C) could severely reduce adult populations (Fletcher, 1975), although in general, over-wintering fly survival appears to be very good, as indicated by Fletcher (1979, 1987b) and the trap catch data (Figs. 2 and 3). Better information on the cold tolerance of QFF is necessary to determine if QFF has indeed acclimatised to the colder conditions in the southern regions of Australia (Meats, 1976) and to improve the model. Such information is crucial to any risk assessments regarding the potential of the fly to invade new areas via the importation of infested fruit.

Mortality at high temperatures was based on very few data points (eggs, larvae, and pupae) or was estimated from field observations (adults). Additional information would improve the reliability of the model in warm environments. It is not clear from the trap catch data in Figs. 2 and 4 whether hot weather results in mortality or whether it reduces fly activity. Examples of periods of low trap catches that coincide with periods of hot weather are marked by arrows in Figs. 2 and 4. In many cases the model predicts lower numbers of trapped flies as a result of increased mortality in hot weather, but the predicted fly numbers rebound far more quickly than do the trap catch data. Although we attempted in various ways to impose a reduction in activity due to high temperatures, we were unable to mimic these observed patterns of fly activity. To improve model predictions of flies caught in traps in the summer, it is essential to gain a better understanding of the nature of the impact of high temperatures on fly mortality, activity and response to traps.

The five simulations all point to the need to understand what causes fruit flies to over-winter. In the model, flies over-winter if they experience 5 consecutive days when the maximum temperature does not reach 18 °C, and they leave the over-wintering life stages when they experience 4 days in a row when the maximum temperature reaches or exceeds 18 °C. Although O'Loughlin et al. (1984) used a similar model to define the breeding season of QFF, this is unlikely to be a realistic process. We explored numerous mechanisms, including accumulating degree-days below various thresholds, accumulating insufficient warmth (i.e. degree-days of above various thresholds), and accumulating net cold (i.e. number of degree-days below a threshold temperature minus the number of degree-days above the same temperature threshold), but could find no mechanism that would work consistently at both Coonamble and Dunedoo. The various mechanisms tested indicate that over-wintering is not just temperature-dependent, but is probably linked to a variety of factors, including temperature, fruit availability and fruit suitability. Day length *per se* and a directional change in day length (e.g. shortening day length) are both unlikely cues, as over-wintering occurred at the beginning of July 1996 and at the beginning of June 1997 at Dunedoo (Fig. 2b). At the beginning of June, day length is still decreasing, while at the beginning of July it has begun to increase again. Until the mechanisms determining the onset and the ending of over-wintering are understood, it will be difficult to improve on the model predictions of fly numbers from about May to August.

The over-predicting bias of the model indicated in Figs. 3 and 5 (most points fall above the line of perfect fit) is partly due to the current inability to correctly describe both numbers of trapped flies in summer and over-wintering. At all sites except for Coonamble, there are instances in summer where no flies are recorded in traps, but the model predicts relatively high numbers of trapped male flies (Figs. 2b and 4a–c).

Similarly, at all sites the model predicts that males should be trapped in autumn and/or winter (the period from May to July), when no males were in fact caught (Figs. 2 and 4). Thus, until we can better define summer mortality and/or activity and over-wintering, the model will continue to be biased and will over-predict numbers of male flies caught in traps.

The influence of rainfall on the mortality and activity of adults, as well as on reproduction, has not been measured, although high rainfall reduces fly activity and the number of flies caught in traps (May, 1961). By reducing activity, high rainfall also presumably impacts on reproduction (egg laying) and on trap efficiency (inactive flies will not be flying into traps). The influence of rainfall on activity, mortality, and reproduction warrants investigation, particularly as QFF occurs in tropical regions that are often subject to heavy rainfall events.

All relationships between mortality and soil moisture were estimated from field observations. The soil environment directly affects pupae, yet there were no data available to indicate optimal, or even suitable, moisture conditions. Use of the SSM module provides for a more variable environment, and one that probably mimics reasonably well the conditions pupae experience. The Soil Moisture module represents moisture available to trees, thereby affecting the moisture conditions in fruit tree canopies, where flies are normally found. Because flies appear to prefer moister, riparian environments in New South Wales (Fletcher, 1974; MacFarlane et al., 1987; May, 1961), it was felt that soil moisture would indicate the moisture conditions experienced by flies better than open pan evaporation. Unfortunately, there were no data available to define these relationships. Given that moisture is probably one of the most important factors in determining fly survival, it is imperative that these relationships be examined.

Apart from constant establishment mortality, derived from mortality of the various life stages under optimal conditions, most mortality functions were largely estimated from limited evidence. We use larval density to drive establishment mortality of both eggs and larvae, as well as continuous daily mortality of larvae. Whilst this seems reasonable, these density-dependent relationships will be related to host fruit characteristics that are important, such as availability, size, type and condition (O'Loughlin, 1964). Larval competition not only impacts on development rates, but also on subsequent adult survival and fecundity (Comins and Fletcher, 1988). Changes in fruit type, quality and quantity over the course of the seasons are not included in the model, because there are insufficient data available on larval density relationships and host types, or on differential development and mortality rates in different fruit types. The seasonal availability of different fruit types will affect fly numbers (by impacting on development rates, survival and fecundity, either directly and/or via density feedback mechanisms), and could trigger over-wintering. This combination of host characteristics and density feedbacks could account for the over-prediction of numbers of trapped flies in summer and the delayed onset of over-wintering in most simulations (Figs. 2 and 4). Research in these areas would be very useful.

Finally, if a model is ever to come close to representing trap catches of adult males, it is essential to understand not only the factors that determine activity, but also any factors that influence the attractiveness of traps to male flies, and therefore trap efficiency. Fly activity in the model is only governed by rainfall, and trapping is a function of both temperature and the male proportion of the active population. As discussed earlier, it may be that high temperatures in summer also decrease activity.

An underlying problem in trying to compare our model predictions with the trap catch data is that the model is effectively trying to do two things at once. In the first instance, the model needs to accurately represent the overall population dynamics of QFF, and in the second instance, it must address the issue of what makes a trap attractive to males, since the traps only catch active, reproductively mature male flies. This is in contrast to other insect models, where predicted numbers can more readily be compared to observed field populations because the population sampling technique provides a direct measurement of population abundance (e.g. Choi and Ryoo, 2003). Defining trapping as a function of temperature and the male proportion of the active population greatly improved the model, but there are undoubtedly additional issues regarding both fly activity and trap attractiveness that we have been unable to address. If our understanding of the ecology of the QFF is to be substantially improved, an understanding of fly behaviour in terms of climatic conditions, physiological state,

and trap attractiveness under different conditions is critical.

It is therefore perhaps surprising that the model provides a reasonable description of the trap catch data—peaks and troughs in trapped male numbers are generally predicted at the right times. This is despite the fact that many functions could not be defined with quantitative data, and that we do not know the significance, in terms of population size, of a male fly caught in a trap. However, the overall degree of match between the model results and the trap data suggest that the underlying mechanisms driving the model are likely to be correct and fairly robust. In turn, this implies that additional research in the different areas outlined above is likely to significantly improve the model, as well as our understanding of fundamental issues in fruit fly population ecology. The key areas of research can be summarised as follows:

1. Clarifying the impact of low and high temperatures on the development and mortality of all life stages, and on the activity of adult flies,
2. Clarifying the impact of rainfall on activity and mortality of adult flies,
3. Defining the impact of soil moisture on the survival of pupae,
4. Identifying and defining the cues that trigger the onset and the termination of over-wintering (e.g. temperature, fruit type, availability and suitability),
5. Investigating the importance of different fruit types and their phenologies on the fruit fly population dynamics, and
6. Examining trap efficiency under different temperature, rainfall and sex ratio regimes.

In conclusion, we have been able to summarise the available data in a framework that allows us to better understand QFF population dynamics. The modelling process concurrently highlighted the critical gaps in our knowledge, which we have outlined as priority areas for future research. These issues are not difficult to address, and the new information would allow this model to be significantly enhanced, resulting in a tool that could be used to effectively manage QFF.

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