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Temperature-independent arrest in female reproduction in a tropical fruit fly (Diptera: Tephritidae)

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Abstract

Polyphagous tropical fruit flies of the genus *Bactrocera* are generally assumed to undergo continuous breeding on the basis that hosts and temperature are not limiting. However, in their endemic monsoonal rainforest habitats, breeding hosts are not always available, and repeatable seasonal population depression for *Bactrocera* species has been documented. This has led to a recent hypothesis that some species in the genus may undergo seasonal reproductive arrest during the year. Working with outdoor-maintained mixed-sex colonies at a subtropical site, we documented changes in *Bactrocera tryoni* (Froggatt) female reproductive status and fecundity over time, with an emphasis on the period from May to August (winter), when population numbers in the field decline and then rebuild. Based on dissection, female flies emerging in mid-May did not contain mature eggs in the ovaries until mid-July, while sperm in the spermathecae was not observed until early August. Based on day degree accumulation and normal development, sexual maturation should have occurred by mid-June; that it did not provides evidence for delayed sexual development acting independently of ambient temperature. Fecundity was greatly suppressed in July compared to egg production in spring and summer, and mating was again delayed. Flies surviving from May through to September laid 70% of the egg load of new-generation spring flies emerging and had a similar egg fertility, showing large reproductive potential of 'old' flies. The results support a hypothesis for a seasonal break in breeding by *B. tryoni* that is not solely temperature related.

KEYWORDS

Bactrocera, breeding, diapause, fecundity, overwintering, populations, reproductive physiology

INTRODUCTION

Bactrocera Macquart (Diptera: Tephritidae) is a very large genus of frugivorous fly species (>600) endemic to the old-world monsoonal rainforests of Southeast Asia, the Western Pacific and Australia (Drew 2004; Drew & Romig 2013, 2020). Several species, such as *B. dorsalis* (Hendel), *B. carambolae* Drew & Hancock, *B. zonata* (Saunders) and *B. tryoni* (Froggatt), are horticultural pests of global or regional significance (Clarke 2019). Breeding and development of *Bactrocera* species is generally considered continuous so long as hosts and cold temperatures are not limiting (Baker et al. 2019; Michel et al. 2021; Yonow et al. 2004). Many of the pest *Bactrocera* species are polyphagous (Clarke 2017); thus, host availability is not thought to be limiting, although the fruiting of crops such as mango and guava is commonly linked to peaks in local population abundance (Susanto et al. 2022; Vayssières et al. 2014).

The assumption that hosts are not limiting breeding or development of the polyphagous *Bactrocera* ignores the biology of their endemic monsoonal rainforests, in which strong seasonality occurs due to the annual wet and dry season cycle (Bach 2002; Wolda 1978). This has led many tropical insects to develop diapause and quiescence

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mechanisms to survive periods when feeding and breeding hosts are not available (Denlinger 1986). In Australia, the primary pest fruit fly species *Bactrocera tryoni* (Froggatt) is commonly rare in traps from May through to August (Drew, Zalucki, & Hooper 1984; Lloyd et al. 2010; Yonow et al. 2004), corresponding to the first two-thirds of the northern dry season when ripe fruits are rare in the rainforest (Streatfield 2009). The evolutionary habitat of the Australian *Bactrocera* is the east coast rainforests (Starkie et al. 2024). *Bactrocera tryoni* are not only found in high abundance in rainforest environments (Ryan et al. 2025) but also demonstrate a seasonality closely aligned with the fruiting of rainforests (Clarke, Leach, & Measham 2022). Clarke, Leach, and Measham (2022) have argued that there is both direct and circumstantial evidence to support a hypothesis that, like many other tropical insects, *B. tryoni* may undergo an adult reproductive diapause/quiescence to survive the dry-season break in host availability and that the behaviour continues to be exhibited in human-modified systems where hosts are not limiting.

While significant work has been done on the seasonal phenology (Clarke et al. 2019; Fletcher 1979; Muthuthantri et al. 2010; Yonow et al. 2004) and reproductive physiology of *B. tryoni* (Fay & Meats 1983; Meats & Fay 1976; Meats & Khoo 1976; Tasnin et al. 2021b; Yap, Fanson, & Taylor 2015), interpreting the work is confounded by the almost complete temporal overlap between the southern hemisphere monsoonal dry season and the southern hemisphere autumn–winter months. Early *B. tryoni* researchers were all based in temperate Australia and explained a repeatable, seasonally observed decline in fly numbers and delayed adult sexual development corresponding with cool winter conditions (Fletcher 1975, 1986, 1989; Pritchard 1970). However, Merkel et al. (2019) and Tasnin et al. (2021a), working in subtropical Australia, recognised that *B. tryoni* populations still decline and appear to have a break in breeding during the autumn and winter months followed by a spring emergence peak, despite the seasonally cooler temperatures not falling below those predicted to impact development and reproduction (Pritchard 1970). Other workers based in the Australian tropics have also recorded the *B. tryoni* ‘winter’ decline (Drew, Zalucki, & Hooper 1984; Lloyd et al. 2010; Subramaniam et al. 2011), despite bioclimatic models predicting seven to nine generations of *B. tryoni* per year in tropical and subtropical parts of its range where temperature is not considered limiting (Meats 1981; Yonow & Sutherst 1998).

Two hypotheses therefore exist to explain the ‘winter’ decline in *B. tryoni* numbers seen in Australia. The first is that it is a direct response to cooler ambient conditions as proposed by Bateman and Sonleitner (1967), Pritchard (1970) and Fletcher (1975). The second is that *B. tryoni* has a reproductive physiology that includes an endogenously programmed, seasonal arrest in breeding that acts independently of ambient temperature (Clarke, Leach, & Measham 2022; Tasnin et al. 2021a). To test these alternate hypotheses, observations on *B. tryoni* female maturation and egg load were carried out similar to those reported for temperate Australia, but instead at a subtropical location. Specifically, experiments were conducted examining (i) ovarian development and mating status of females from an outdoor *B. tryoni* population emerging in mid-May to look for evidence of delays in maturation and mating within the context of day degree (DD) accumulation; (ii) the ability of those individuals to survive from May through to August and then still be capable of laying eggs to contribute to the emerging spring generation; and (iii) the egg load production of young individuals of four successive generations to compare seasonality of fecundity. The May–August period was chosen as the period when flies are rare in traps (Muthuthantri et al. 2010), and for which temperature cannot adequately capture population dynamics (Yonow et al. 2004).

We predicted that if the *B. tryoni* reproductive arrest reported in temperate Australia was due only to cooler winter conditions, then we would see no evidence of this in our subtropical site, as DD accumulation would be sufficient to allow maturation to occur with minimal delay. However, if the delay was an endogenously programmed mechanism for reproductive arrest acting independently of temperature, then we predicted that a breeding break of multiple months would still occur at our warmer site.

MATERIAL AND METHODS

General methodology

Two experiments were conducted. The first experiment tracked the reproductive fate of a single generation of *B. tryoni* females, maintained in sheltered outdoor cages, from mid-May (emergence) to late August. The second experiment similarly used outdoor-maintained flies but compared female fecundity and mating of 3- and 5-week-old flies of four successive generations at different times of the year (midwinter [MW], early spring [ES], late spring, summer). In both experiments, the reproductive development of flies was assessed through ovarian and spermathecal dissections, and fecundity was assessed using apple domes (described below) to collect eggs. Data for the first experiment are interpreted in the context of DD accumulation to determine if changes in reproductive capacity observed are linked to changes in ambient temperature or are acting independently of it. We note that the seasonal terms of winter, spring and so forth are used throughout this paper for the convenience of transmitting easily understood information. However, moving forward, we believe this usage is inappropriate, and we come back to this point in Section 4.

Colony maintenance

Approximately 15 kg of infested guava were collected from a guava orchard at the Redlands Research Facility, Cleveland QLD (27°31′29″ S, 153°15′02″ E) on 18 February 2021. At this site, guava is the last major fruit fly host crop before autumn and winter. Guava fruits were placed on vermiculite in 20-L ventilated containers at the facility. Approximately 2600 adults emerged from the fruit and became the parental population used to establish experimental colonies. Colony cages of approximately 5000 (32.5 cm × 77 cm × 32.5 cm) and 1500 (32 × 32 × 32 cm) individual flies were kept in a sheltered position under cover, such that they were exposed to natural light, temperature and humidity conditions but were protected from rain and a prevailing easterly breeze. Adult colonies were of mixed sex (approximately 50:50 male:female) and were provided with sugar, water and yeast hydrolysate protein ad libitum. Eggs were collected weekly from the parental generation using apple domes. Apple domes were made from an apple sliced across the middle with all flesh removed, leaving the skin only. Fifty pinholes were made in the dome. The dome was attached to a Petri dish using melted wax, and a twist wire was attached to assist in hanging the apple dome from the ceiling of the cage. Eggs were laid into the dome and could be washed out with sterile water onto filter paper for collection and transfer. Larval rearing also occurred in sheltered, outdoor conditions with the subsequent larvae reared on carrot-based rearing media (Heather & Cochran 1985). Experiments then began with the F1 adult generation.

Weather data and DD calculations

Temperature data were obtained from the Australian Bureau of Meteorology (bom.gov.au/climate/data) for the weather station closest to the research facility (140007, Redland Alexandra Hills, QLD), approximately 2.5 km away. DD analysis followed Pritchard (1970) and Fletcher (1975), with the DD requirements for female emergence to 50% of a population having mature eggs being 64.1 DDs, the development zero (DZ) being 13.5°C and the calculation of the DDs experienced for a given day being DD/day = ([maximum daily temp + minimum daily temp]/2) − DZ. Accumulated DDs are calculated from the last day of the adult emergence period and so represent the minimum number of DDs that could have been experienced by the experimental cohort.

Experiment 1: Reproductive physiology of overwintering females

The reproductive physiology of the same generation of overwintering females was assessed from May to August 2021. Approximately 1000 mixed-sex F1-generation flies of the same age (flies from eggs collected within a 24-h period) were set up in two large cages (dome-shaped cages with a base of 60 × 60 cm, height 60 cm) on 20 May 2021. Flies were provided with water, sugar and yeast hydrolysate ad libitum but were not provided with apple domes or fruit. Ten females were randomly sampled from across these two cages for dissection at fortnightly intervals, from 4 weeks of age through to 14 weeks based on known fecundity peaks in laboratory settings (Tasnin et al. 2021b).

After being chilled, individual females were dissected under a dissecting microscope, with each ovary and spermatheca placed in separate saline drops on a microscope slide and photographed. The mating status was determined by observing the presence or absence of sperm in the spermathecae, while the maturation status was determined by observing the presence or absence of mature eggs in the ovaries and the number of mature eggs counted (Drew 1969; Raghu, Halcoop, & Drew 2003). The mating status, presence of mature eggs in the ovary and number of mature eggs (Anderson & Lyford 1965) were recorded for each female.

In addition to fortnightly dissections, an assessment of the reproductive capacity of these flies when 16 weeks old was carried out to determine whether these then-very-old females could lay sufficient eggs to meaningfully contribute to building the spring population. Twenty female and 20 male 16-week-old flies were placed in each of the three cages (32 × 32 × 32 cm), and fecundity assessments were made on five consecutive days during the second week of September 2021. Cages were placed in a temperature-controlled glasshouse (temperature set at 26 ± 1°C) during the period of egg collection to minimise variation due to daily or seasonal (pertinent to Experiment 2, see next) changes in outdoor temperature and weather conditions, but the experimental flies were maintained outdoors between assessments. The cages were transferred to the glasshouse 30 min prior to the start of the assessments (09:30 h) for acclimatisation and placed back outdoors at the end. Once in the glasshouse, apple domes were placed in each cage at 10:00 h and removed at 13:30 h to match the known peak oviposition period (Ero, Hamacek, & Clarke 2011). Apple domes were then taken to a laboratory, where eggs were removed from each apple dome using a fine paint brush and transferred to black filter paper placed on a damp Wettex® sponge in a Petri dish. Eggs removed from each apple dome were counted and then held under ambient laboratory conditions for 48 h before the hatch rate was assessed.

To compare the results with the reproductive potential of younger females, three-week-old F2-generation females of the parental stock were assessed simultaneously, using the same method. These flies had emerged after winter from the earliest eggs laid by the F1 generation and were also maintained outdoors undercover.

Experiment 2: Reproductive capacity of females at different times of the year

The reproductive potential of 3- and 5-week-old females (generations F1–F5) was assessed across different

TABLE 1 Dates of trials assessing *Bactrocera tryoni* sexual maturity and fecundity across four seasonal periods in South East Queensland, Australia. Accumulated day degrees (DDs), based on a developmental zero of 13.5°C, are calculated from the last day of the adult emergence period and so represent the least number of days degrees that could have been experienced by the experimental cohort.

Season	Fly age (weeks)	Trial no.	Generation	Emergence date	Start of fecundity trial [accumulated DDs]	Dissection date [accumulated DDs]
Early winter						
	3	1	F1	07–10/5/2021	31/05/2021 [80.8]	04/06/2021 [95.1]
	3	2	F1	13–18/5/2021	07/06/2021 [66.7]	09/06/2021 [69.9]
	5	1	F1	07–10/5/2021	14/06/2021 [108.1]	16/06/2021 [114.2]
	5	2	F1	13–18/5/2021	21/06/2021 [91.05]	23/06/2021 [96.4]
Early spring						
	3	1	F2	26/07/2021–03/08/2021	23/08/2021 [66.8]	25/08/2021 [72.0]
	3	2	F2	06–13/08/2021	06/09/2021 [92.2]	13/09/2021 [123.4]
	5	1	F2	26/07/2021–03/08/2021	06/09/2021 [119.2]	10/09/2021 [133.6]
	5	2	F2	06–13/08/2021	20/09/2021 [154.3]	22/09/2021 [164.3]
Late spring/early summer						
	3	1	F3	26/10/2021–01/11/2021	22/11/2021 [180.4]	24/11/2021 [198.7]
	3	2	F4	02–09/11/2021	29/11/2021 [186.7]	01/12/2021 [204.7]
	5	1	F3	26/10/2021–01/11/2021	06/12/2021 [315.6]	09/12/2021 [346.2]
	5	2	F4	02–09/11/2021	13/12/2021 [323.3]	17/12/2021 [362.6]
Late summer						
	3	1	F5	11–17/01/2021	07/02/2022 [231.6]	07/02/2022 [231.6]
	3	2	F5	01–07/02/2022	28/02/2022 [207.6]	03/03/2022 [238.7]
	5	1	F5	11–17/01/2021	21/02/2022 [367.8]	[a]
	5	2	F5	[a]	[a]	[a]

[a] Insufficient females to conduct assessments.

seasons: MW, ES, late spring/early summer (LSES) and late summer (LS) (Table 1). Two fecundity assessment trials, conducted as for Experiment 1, were performed for each fly age and season, with accumulated DDs recorded. Additionally, for each season, 20 females not given an apple dome in which to oviposit were dissected and scored for maturation status (presence of mature eggs) and mating status, as described for Experiment 1.

Data analysis

A generalised additive model (GAM) using Bernoulli distribution and logit link function was run on maturation status and mating status using R Studio (R Version 4.2.2) to estimate the effect of age and time of year on young female fly reproductive physiology. The interaction between day of the year (Julian day) and age (two-level factor: 3 and 5 weeks) was specified using tensor product smooth (te) and cyclic p spline (cp). The estimation method was restricted maximum likelihood (REML). A similar model was run using Tweedie family for the number of mature eggs in the female ovary and eggs laid by the females as response variables. The models testing reproductive physiology of overwintering females' maturation (carrying mature eggs), mating status and number of eggs in the ovary used a similar model structure but with Julian day as the only explanatory variable. The number and hatch rate of eggs produced by 16-week-old overwintered females and 3-week-old spring-emerged females were compared using analysis of variance (ANOVA), with the daily counts treated as sub-samples.

RESULTS

Experiment 1: Reproductive physiology of overwintering females

The probability of female flies containing mature eggs in the ovaries or being mated through the cooler 'winter' period was significantly affected by the time of year ($z = 3.96$, $P < 0.001$, and $z = 3.29$, $P < 0.01$, respectively). None of the dissected flies contained any mature eggs in the ovary until 8 weeks of age, while at 12 weeks of age, mature eggs were recorded in all dissected females. Evidence of having mated (presence of sperm in the spermathecae) was not found until flies were 12 weeks of age (Table 2). The number of mature eggs in the ovary was also significantly affected by the time of year, with egg load increasing from July through August (edf $= 2.893$, $F = 56.107$, $P < 0.001$) (Figure 1).

Sixteen-week-old 'overwintered' female flies produced 96.9 ± 7.07 eggs/20 flies. This was significantly fewer eggs than produced by 3-week-old spring-emerged females (136.7 ± 17.29 eggs/20 flies) ($F = 18.30$; $P < 0.05$). However, the hatch rate of eggs of older 'overwintered' females (56.2% ± 7.83) was not significantly different from those of spring-emerged females (40.0% ± 5.49) ($F = 2.87$; $P > 0.05$).

Experiment 2: Reproductive capacity of females at different times of the year

The number of eggs laid differed significantly between 3- and 5-week-old flies ($t = -4.328$, $P < 0.001$). The number of eggs laid by both 3- and 5-week-old flies was also significantly affected by the time of year (edf $= 5.725$, $F = 82.04$, $P < 0.001$ and edf $= 5.494$, $F = 60.71$, $P < 0.001$, respectively). The average number of eggs produced per 20 females was low in trials performed in June for both 3-week-old flies (3.9 ± 1.22 eggs/20 females) and 5-week-old flies (14.9 ± 2.54 eggs/20 females). This increased during spring, with fecundity in 5-week-old females peaking in September (157.7 ± 9.10 eggs/20 females), and fecundity in 3-week-old females peaking in late November/early December (224.1 ± 9.70 eggs/20 females). The fecundity of both 3- and 5-week-old flies (179.1 ± 11.05 and 90.2 ± 9.07, respectively) declined in January/February (Figure 2).

Female dissections detected no effect of age (3- or 5-week-old) on the number of flies containing mature eggs ($z = 0.178$, $P = 0.859$), number of mated flies ($z = 1.072$, $P = 0.284$) or number of mature eggs in the ovary ($z = 1.584$, $P = 0.114$). However, time of year had a significant effect on all three parameters (Table 3), generally increasing from a low in June to a peak in November/December. Combining results for the 3- and 5-week-old flies, the mean number of mature eggs in females was very low in June 2021 (6.52 ± 1.33), increasing in August/September (25.61 ± 2.51), reaching a peak in November/December 2021 (36.30 ± 3.88) before declining again in

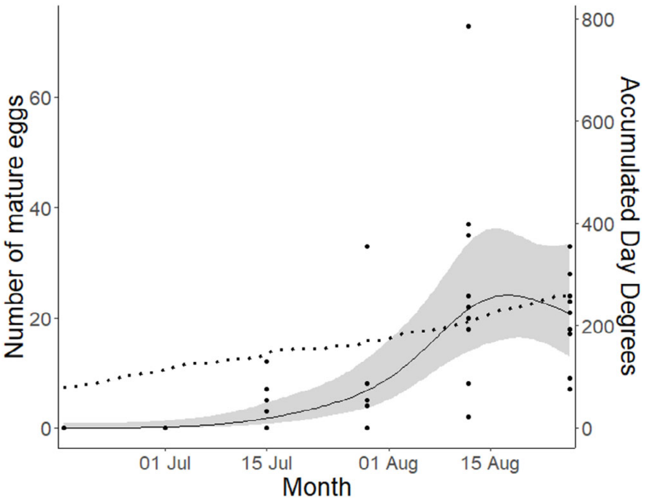

FIGURE 1 Number of mature eggs in the ovaries of female *Bactrocera tryoni* every 2 weeks from mid-June (4-week-old flies) to late August (14-week-old flies) in South East Queensland, Australia, with accumulated day degrees based on a developmental zero of 13.5°C (black dotted line). The fitted values on the response scale show 95% confidence interval (±2 * SE).

TABLE 2 Number of mature and mated *Bactrocera tryoni* females from 10 flies dissected every 2 weeks from mid-June to late August in South East Queensland, Australia.

Fly age (weeks)	Dissection date	DDs accumulated	Number of females with mature eggs	Number of mated females
4	16/6/21	74.85	0	0
6	30/6/21	110.7	0	0
8	14/7/21	139.5	4	0
10	28/7/21	163.4	4	0
12	11/8/21	203.2	10	7
14	25/8/21	257.6	10	7

Abbreviation: DD, day degree.

February/March 2022 (22.65 ± 3.52) (Figure 3). The proportion of females containing sperm in the spermathecae was the lowest in July 2021 (~1%), increasing in August/September (~49% mated), reaching a peak in November/December (75%), before reducing slightly in February/March 2022 (65%) (Figure 4).

DISCUSSION

The reproductive potential of female *B. tryoni* showed substantial seasonal variation at the subtropical study site. In Experiment 1, flies emerging in mid-May (early winter) failed to develop any mature eggs until mid-July and also failed to show evidence of mating until the first half of August. This was despite the 64 DDs required for 50% of a population to become sexually mature (Pritchard 1970) being accumulated before the first dissections in mid-June. The larger data set of Experiment 2 supported Experiment 1, with a highly reduced fecundity of females in June and the probability of mating not increasing until August. These data align with the reduction in *B. tryoni* adults seen during that same period in subtropical Australia (Lloyd et al. 2010; Muthuthantri et al. 2010). Further, females that survived from autumn through to the following spring, by which time they were 4 months old, laid greater than 70% of the egg load of young flies. Under normal development, these females should not have reached this age before dying, let alone be capable of laying large egg batches. Under laboratory conditions, nearly all female *B. tryoni* have ceased egg laying at ~11 weeks, with fecundity markedly declining after only 3 weeks (Tasnin et al. 2021b). Occurring at a subtropical site where temperature was not limiting, both the delay in maturation and mating and the longevity and fecundity of very old flies suggest an endogenous

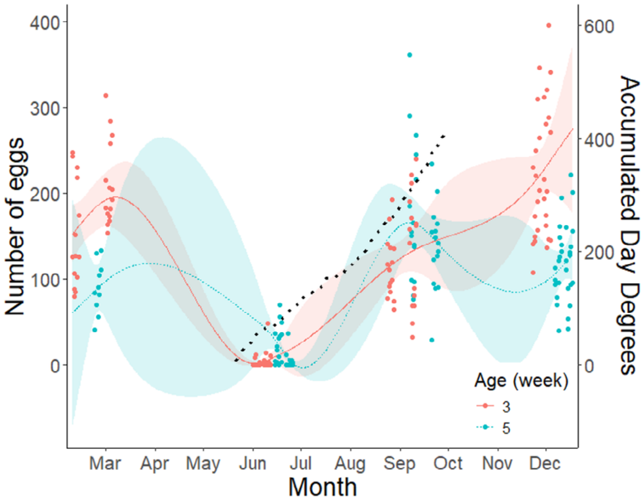

FIGURE 2 The number of eggs laid by 20 female *Bactrocera tryoni* at 3 weeks (red) and 5 weeks (blue) of age at different times of the year in South East Queensland, Australia, with accumulated day degrees (DDs) based on a developmental zero of 13.5°C (black dotted line). The fitted values on the response scale show 95% confidence interval (±2 * SE). The accumulated DDs shown cover the period where the hypothesised reproductive shutdown is thought to occur: 64.1 DDs are required for sexual maturation under normal development (Pritchard 1970).

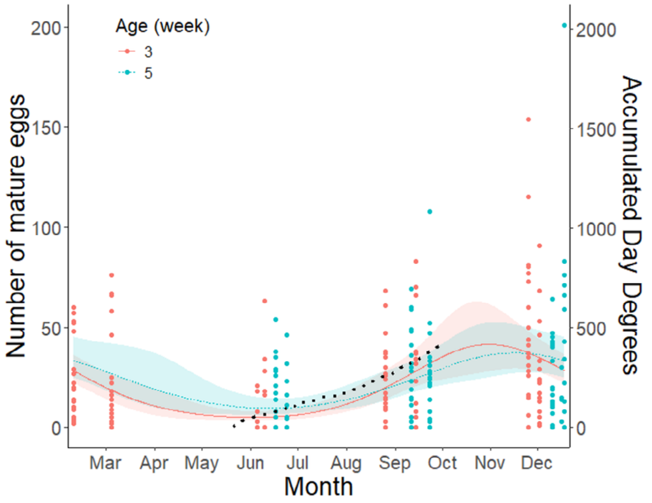

FIGURE 3 The number of mature eggs in the ovaries of *Bactrocera tryoni* at 3 weeks (red) and 5 weeks (blue) of age at different times of the year in South East Queensland, Australia, with accumulated day degrees (DDs) based on a developmental zero of 13.5°C (black dotted line). The fitted values on the response scale show 95% confidence interval (±2 * SE). Twenty-four females of each age class were dissected in June, 20 in each age class in August/September and November/December, and 20 three-week-old flies only in February/March. The accumulated DDs shown cover the period where the hypothesised reproductive shutdown is thought to occur: 64.1 DDs are required for sexual maturation under normal development (Pritchard 1970).

TABLE 3 Effect of time of year on reproductive physiology of 3- and 5-week-old female *Bactrocera tryoni* in South East Queensland, Australia.

Parameter	Fly age (weeks)	edf	Test statistic	*P* value
Maturation status	3	3.250	$X^2 = 53.31$	$P < 0.001$
	5	1.714	$X^2 = 27.04$	$P < 0.001$
Mating status	3	3.052	$X^2 = 27.61$	$P < 0.001$
	5	2.044	$X^2 = 28.58$	$P < 0.001$
Number of mature eggs	3	2.450	$F = 13.23$	$P < 0.001$
	5	1.899	$F = 7.13$	$P < 0.001$

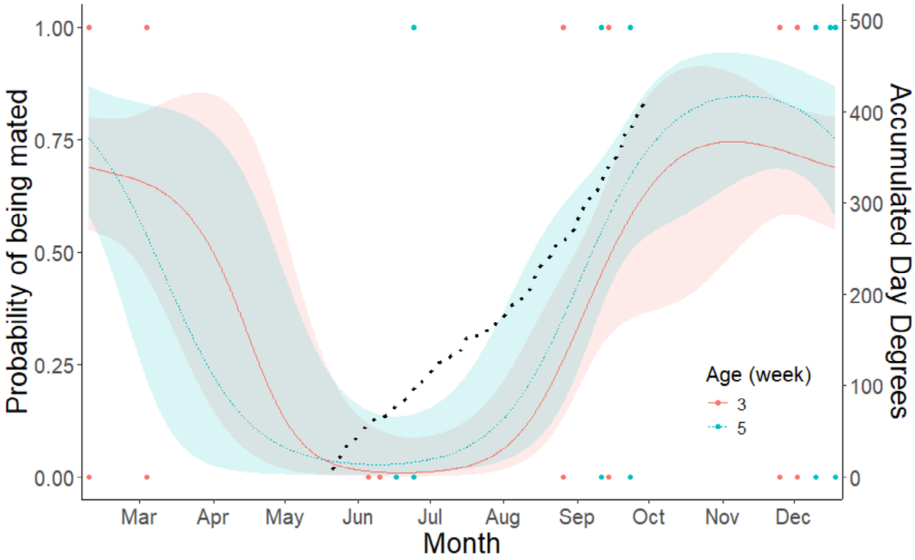

FIGURE 4 The probability of mating, based on presence of sperm in the spermatheca, of *Bactrocera tryoni* at 3 weeks (red) and 5 weeks (blue) of age at different times of the year in South East Queensland, Australia, with accumulated day degrees (DDs) based on a developmental zero of 13.5°C (black dotted line). The fitted values on the response scale show 95% confidence interval (±2 * SE). Twenty-four females of each age class were dissected in June, 20 in each age class in August/September and November/December, and 20 three-week-old flies only in February/March. The accumulated DDs shown cover the period where the hypothesised reproductive shutdown is thought to occur: 64.1 DDs are required for sexual maturation under normal development (Pritchard 1970).

mechanism causing an arrestment of *B. tryoni* reproduction, rather than a simple cool-season response to ambient temperatures as originally thought (Bateman & Sonleitner 1967; Fletcher 1974; Pritchard 1970). These points are developed further below.

Similarity of subtropical versus temperate patterns—Exogenous versus endogenous drivers

Our results, finding a reproductive arrest running from May to August, are very similar to those reported from the vicinity of Wilton, New South Wales (34°15′ S 150°41′ E, approximately 800 km south of our study site) in the 1960s and 1970s. Bateman and Sonleitner (1967), Pritchard (1970), Sonleitner (1973) and Fletcher (1975) all reported a non-reproductive period of *B. tryoni* from April to September, as well as the ability of adult flies to survive that period. Similarly, the exit from the reproductive arrest reported by Pritchard (1970) and Fletcher (1975) follows a very similar pattern to our results, although occurring approximately 2 weeks later. Fletcher noted the first maturation of female ovaries in late July, while Pritchard reported the first mature eggs on the 2 September and the first mating in mid-August. We report the first mature eggs in the first half of July and the first mating in early August. While Pritchard (1970) and Fletcher (1975) explained the phenological patterns they observed with respect to cool winter temperatures, both these authors and Bateman and Sonleitner (1967) explicitly noted that temperatures in April and May should not have been limiting for *B. tryoni* development and maturation. Pritchard and Fletcher again noted that their temperature-based models failed to accurately predict the switch back to reproductive activity, as their models predicted local ambient temperatures should still be too cool during August. Yonow et al. (2004) encountered the same problems around May and August when trying to model *B. tryoni* seasonal population phenology in temperate Australia using temperature, while temperature also failed to explain observed patterns of *B. tryoni* activity/populations in tropical and subtropical Queensland (Merkel et al. 2019; Muthuthantri et al. 2010). Given that the *B. tryoni* female reproductive arrest and maturation patterns in our data are nearly identical to those reported by Pritchard and Fletcher, despite substantial differences in ambient temperature, and given the inadequacy of temperature alone to fully explain the observations in both sites, the reproductive arrest appears to be primarily endogenously rather than exogenously driven. However, our slightly earlier dates for flies exiting the reproductive arrest than those reported by Fletcher and Pritchard indicate that temperature, or another locally acting exogenous mechanism, may impact the end of the reproductive arrest. This is presumably due to the existence of a quiescence phase when the insect can respond to environmental stimuli. Better understanding of the reproductive physiology in line with the molecular processes influenced by environmental stimuli (Denlinger 1986; Gill, Goyal, & Chahil 2017) may elicit an endogenous mechanism.

Reproduction of old flies in spring—Field evidence for reverse actuarial ageing?

Experiment 1 showed that female flies 4 months of age were able to lay at a rate of 72% that of 3-week old females with a similar hatch rate. Under normal laboratory rearing conditions, these very old females would either be dead or, if alive, incapable of laying eggs (Tasnin et al. 2021b). Clarke, Leach, and Measham (2022) raised the paradox of how very old females are able to 'kick-start' a new spring generation and suggested reverse actuarial ageing, identified in *B. tryoni* females by Yap, Fanson, and Taylor (2015), as the solution. Yap, Fanson, and Taylor (2015) showed that female *B. tryoni* deprived of protein (required for sexual maturation) and mates for 30 days, subsequently had the longevity and fecundity of 10-day-old flies (i.e., old flies became physiologically young again) after being supplied with those resources. Clarke, Leach, and Measham (2022) proposed that this might be happening with the overwintering females; that is, they remained sexually immature and unmated during the reproductive arrest period, but with maturation and mating in August, they became physiologically young again.

Fletcher (1986) adds support to this interpretation, reporting that 'At the end of winter, females need to feed on proteinaceous material, mature their eggs and mate before they can start infesting the spring fruit'. This description almost exactly mirrors the experimental conditions imposed by Yap, Fanson, and Taylor (2015) to trigger reverse actuarial ageing in *B. tryoni* females.

While our flies were maintained in mixed-sex cultures and provided with protein ad libitum, direct evidence from spermathecal dissection is that females do not mate until August. If reverse actuarial ageing is part of their reproductive process, they would not have fed on protein during this period, but this remains to be investigated. As we did not compare the longevity of our newly matured aged females with that of young flies, we have not fully demonstrated evidence for reverse actuarial ageing in the field.

'Overwintering'—Time to ditch the term for Bactrocera

The population decline of *B. tryoni* seen during the middle months of the southern-hemisphere year is routinely referred to as overwintering (Clarke et al. 2019). We now feel this term is misleading, as it infers a temperature-related explanation that we do not think is occurring. Using cooler winter conditions to explain a decline in reproduction is not just restricted to *B. tryoni* but has also been applied to *B. dorsalis* (Bess & Haramoto 1961; Haramoto & Bess 1970) and may be equally misleading (Clarke, Leach, & Measham 2022).

Moving forward, we feel it better to use the terms 'period of low populations', 'period of population increase', 'period of high populations' and 'period of population decline'. These terms are relative, will likely be regionally specific and are also somewhat verbose—none of which are ideal. However, until we know more about the changing reproductive physiology in Australian *Bactrocera* species, these terms impose no tacit assumptions about population drivers, as do terms such as overwintering, spring increase and autumn decline.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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REFERENCES

Anderson, D.T. & Lyford, G.C. (1965) Oogenesis in *Dacus tryoni* (Frogg.) (Diptera: Trypetidae). *Australian Journal of Zoology*, 13(3), 423–436. Available from: https://doi.org/10.1071/ZO9650423

Bach, C.S. (2002) Phenological patterns in monsoon rainforests in the Northern Territory, Australia. *Austral Ecology*, 27(5), 477–489. Available from: https://doi.org/10.1046/j.1442-9993.2002.01209.x

Baker, R, Gilioli, G, Behring, C Candiani, D., Gogin, A., Kaluski, T. et al (2019) *Bactrocera dorsalis* pest report to support ranking of EU candidate priority pests. pp.44. European Food Safety Authority.

Bateman, M.A. & Sonleitner, F.J. (1967) The ecology of a natural population of the Queensland fruit fly, *Dacus tryoni* I. The parameters of the pupal and adult populations during a single season. *Australian Journal of Zoology*, 15(2), 303–335. Available from: https://doi.org/10.1071/ZO9670303

Bess, H.A. & Haramoto, F.H. (1961) Contributions to the biology and ecology of the Oriental fruit fly, *Dacus dorsalis* Hendel (Diptera: Tephritidae), in Hawaii. Hawaii Agricultural Experiment Station Technical Bulletin No. 44, University of Hawaii, Honolulu, Hawaii.

Clarke, A.R. (2017) Why so many polyphagous fruit flies (Diptera: Tephritidae)? A further contribution to the 'generalism' debate. *Biological Journal of the Linnean Society*, 120, 245–257.

Clarke, A.R. (2019) *Biology and Management of Bactrocera and Related Fruit Flies*. Wallingford, UK: CAB International.

Clarke, A.R., Leach, P. & Measham, P.F. (2022) The fallacy of year-round breeding in polyphagous tropical fruit flies (Diptera: Tephritidae): evidence for a seasonal reproductive arrestment in *Bactrocera* species. *Insects*, 13(10), 882. Available from: https://doi.org/10.3390/insects13100882

Clarke, A.R., Merkel, K., Hulthen, A.D. & Schwarzmueller, F. (2019) *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) overwintering: an overview. *Austral Entomology*, 58(1), 3–8. Available from: https://doi.org/10.1111/aen.12369

Denlinger, D.L. (1986) Dormancy in tropical insects. *Annual Review of Entomology*, 31(1), 239–264. Available from: https://doi.org/10.1146/annurev.en.31.010186.001323

Drew, R.A.I. (1969) Morphology of the reproductive system of *Strumeta tryoni* (Froggatt) (Diptera: Trypetidae) with a method of distinguishing sexually mature adult males. *Australian Journal of Entomology*, 8(1), 21–32. Available from: https://doi.org/10.1111/j.1440-6055.1969.tb00729.x

Drew, R.A.I. (2004) Biogeography and speciation in the Dacini (Diptera: Tephritidae: Dacinae). *Bishop Museum Bulletin in Entomology*, 12, 165–178.

Drew, R.A.I. & Romig, M.C. (2013) *Tropical fruit flies of South-East Asia (Tephritidae: Dacinae)*. Wallingford, U.K.: CAB International.

Drew, R.A.I. & Romig, M.C. (2020) *The fruit Fly Fauna (Diptera: Tephritidae: Dacinae) of Papua New Guinea, Indonesian Papua, Associated Islands and Bougainville*. Wallingford, UK: CAB International.

Drew, R.A.I., Zalucki, M.P. & Hooper, G. (1984) Ecological studies of eastern Australian fruit flies (Diptera: Tephritidae) in their endemic habitat. I. Temporal variation in abundance. *Oecologia*, 64(2), 267–272. Available from: https://doi.org/10.1007/BF00376881

Ero, M.M., Hamacek, E. & Clarke, A.R. (2011) Foraging behaviours of *Diachasmimorpha kraussii* (Fullaway) (Hymenoptera: Braconidae) and its host *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) in a nectarine (*Prunus persica* (L.) Batsch var. nectarina (Aiton) maxim) orchard. *Australian Journal of Entomology*, 50, 234–240.

Fay, H.A.C. & Meats, A. (1983) The influence of age, ambient-temperature, thermal history and mating history on mating frequency in males of the Queensland fruit fly, *Dacus tryoni*. *Entomologia Experimentalis et Applicata*, 34(3), 273–276. Available from: https://doi.org/10.1111/j.1570-7458.1983.tb03333.x.*****

Fletcher, B.S. (1974) The ecology of a natural population of the Queensland fruit fly, *Dacus tryoni* VI. Seasonal changes in fruit fly numbers in the areas surrounding the orchard. *Australian Journal of Zoology*, 22(3), 353–363. Available from: https://doi.org/10.1071/ZO9740353

Fletcher, B.S. (1975) Temperature-regulated changes in the ovaries of overwintering females of the Queensland fruit fly, *Dacus tryoni*. *Australian Journal of Zoology*, 23(1), 91–102. Available from: https://doi.org/10.1071/ZO9750091

Fletcher, B.S. (1979) The overwintering survival of adults of the Queensland fruit fly, *Dacus tryoni*, under natural conditions. *Australian Journal of Zoology*, 27(3), 403–411. Available from: https://doi.org/10.1071/ZO9790403

Fletcher, B.S. (1986) The overwintering strategy of the Queensland fruit fly, *Dacus tryoni*. In: Economopoulos, A.P. (Ed.) *Fruit flies: proceedings of the second international symposium*. Colymbari, Crete, Greece: Elsevier Science Publications, pp. 375–382.

Fletcher, B.S. (1989) Temperature—development rate relationships of immature stages and adults of tephritid fruit flies. In: Robinson, A.-S. & Hooper, G. (Eds.) *Fruit flies their biology, natural enemies and control*. Amsterdam: Elsevier, pp. 273–289.

Gill, H.K., Goyal, G. & Chahil, G. (2017) Insect diapause: a review. *Journal of Agricultural Science and Technology*, 7, 454–473.

Haramoto, F.H. & Bess, H.A. (1970) Recent studies on the abundance of the Oriental and Mediterranean fruit flies and the status of their parasites. *Proceedings of the Hawaiian Entomological Society*, 20, 551–566.

Heather, N.W. & Cochran, R.J. (1985) Dacus tryoni. In: Singh, P. & Moore, R.F. (Eds.) *Handbook of insect rearing*. Amsterdam: Elsevier Science Publishers B.V., pp. 41–48.

Lloyd, A.C., Hamacek, E.L., Kopittke, R.A., Peek, T., Wyatt, P.M., Neale, C.J., et al. (2010) Area-wide management of fruit flies (Diptera: Tephritidae) in the central Burnett district of Queensland, Australia. *Crop Protection*, 29(5), 462–469. Available from: https://doi.org/10.1016/j.cropro.2009.11.003

Meats, A. (1981) The bioclimatic potential of the Queensland fruit fly, *Dacus tryoni*, in Australia. In: Littlejohn, M.J. & Ladiges, P.Y. (Eds.) *Ecological gradients and boundaries: proceedings of the ecological Society of Australia*, Vol. 11, pp. 151–161.

Meats, A. & Fay, H.A.C. (1976) The effect of acclimation on mating frequency and mating competitiveness in the Queensland fruit fly, *Dacus tryoni*, in optimal and cool mating regimes. *Physiological Entomology*, 1(3), 207–212. Available from: https://doi.org/10.1111/j.1365-3032.1976.tb00962.x

Meats, A. & Khoo, K.C. (1976) The dynamics of ovarian maturation and oocyte resorption in the Queensland fruit fly, *Dacus tryoni*, in daily rhythmic and constant temperature regimes. *Physiological Entomology*, 1(3), 213–221. Available from: https://doi.org/10.1111/j.1365-3032.1976.tb00963.x

Merkel, K., Schwarzmueller, F., Hulthen, A.D., Schellhorn, N., Williams, D. & Clarke, A.R. (2019) Temperature effects on "overwintering" phenology of a polyphagous, tropical fruit fly (Tephritidae) at the subtropical/temperate interface. *Journal of Applied Entomology*, 143(7), 754–765. Available from: https://doi.org/10.1111/jen.12645

Michel, A., Fiaboe, K.K.M., Kekeunou, S., Nanga, S.N., Kuate, A.F., Tonnang, H.E.Z., et al. (2021) Temperature-based phenology model to predict the development, survival, and reproduction of the oriental fruit fly *Bactrocera dorsalis*. *Journal of Thermal Biology*, 97, 102877.

Muthuthantri, S., Maelzer, D., Zalucki, M.P. & Clarke, A.R. (2010) The seasonal phenology of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) in Queensland. *Australian Journal of Entomology*, 49(3), 221–233. Available from: https://doi.org/10.1111/j.1440-6055.2010.00759.x

Pritchard, G. (1970) The ecology of a natural population of Queensland fruit fly, *Dacus tryoni* III. The maturation of female flies in relation to temperature. *Australian Journal of Zoology*, 18(1), 77–89. Available from: https://doi.org/10.1071/ZO9700077

Raghu, S., Halcoop, P. & Drew, R.A.I. (2003) Apodeme and ovarian development as predictors of physiological status in *Bactrocera cacuminata* (Hering) (Diptera: Tephritidae). *Australian Journal of Entomology*, 42(3), 281–286. Available from: https://doi.org/10.1046/j.1440-6055.2003.00364.x

Ryan, J.L., Clarke, A.R., Piper, A.M., Fuller, S. & Prentis, P.J. (2025) Gene flow and abundance of a tropical fruit fly in a horticultural landscape mosaic in eastern Australia is limited by cleared grazing land and area-wide management. *Evolutionary Applications*, 18(4), e70097. Available from: https://doi.org/10.1111/eva.70097

Sonleitner, F.J. (1973) Mark–recapture estimates of overwintering survival of the Queensland fruit fly, *Dacus tryoni*, in field cages. *Population Ecology*, 14(2), 188–208. Available from: https://doi.org/10.1007/BF02518843

Starkie, M.L., Cameron, S.L., Krosch, M.N., Sweet, A.D. & Clarke, A.R. (2024) Biogeographic influences on the evolution and historical dispersal of the Australo-Pacific Dacini fruit flies (Tephritidae: Dacinae). *Zoologica Scripta*, 53(1), 87–97. Available from: https://doi.org/10.1111/zsc.12631

Streatfield C. (2009) Demography and population genetic structure of *Uromys caudimaculatus*. Unpublished PhD thesis, Queensland University of Technology, Brisbane, Australia

Subramaniam, S, Jackson, K, Lloyd, A, Rosemary, K, Hamacek, E & Kreymborg, D. (2011) Alternative fruit fly control and market access for capsicums and tomatoes: a system approach for tomato and capsicum production in Bowen. Final report HAL Project VG06028. Agri-Science Queensland; Department of Employment, Economic Development and Innovation.

Susanto, A., Permana, A.D., Subahar, T.S., Soesilohadi, R.C.H., Leksono, A.S. & Fernandes, A.A.R. (2022) Population dynamics and projections of fruit flies *Bactrocera dorsalis* and *B. carambolae* in Indonesian mango plantation. *Agriculture and Natural Resources*, 56, 169–179.

Tasnin, S.M., Bode, M., Merkel, K. & Clarke, A.R. (2021a) A polyphagous, tropical insect herbivore shows strong seasonality in age-structure and longevity despite temperature and hosts not being limiting. *Scientific Reports*, 11, 11410.

Tasnin, S.M., Kay, B.J., Peek, T., Merkel, K. & Clarke, A.R. (2021b) Age-related changes in reproductive potential of Queensland fruit fly. *Journal of Insect Physiology*, 131, 104245.

Vayssières, J.-F., Sinzogan, A., Adandonon, A., Rey, J.Y., Dieng, E.O., Camara, K., et al. (2014) Annual population dynamics of mango fruit flies (Diptera: Tephritidae) in West Africa: socio-economic aspects, host phenology and implications for management. *Fruits*, 69(3), 207–222. Available from: https://doi.org/10.1051/fruits/2014011

Wolda, H. (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology*, 47(2), 369–381. Available from: https://doi.org/10.2307/3789

Yap, S., Fanson, B.G. & Taylor, P.W. (2015) Mating reverses actuarial aging in female Queensland fruit flies. *PLoS ONE*, 10(7), e0132486. Available from: https://doi.org/10.1371/journal.pone.0132486

Yonow, T. & Sutherst, R.W. (1998) The geographical distribution of the Queensland fruit fly, *Bactrocera* (Dacus) *tryoni*, in relation to climate. *Australian Journal of Agricultural Research*, 49(6), 935–953. Available from: https://doi.org/10.1071/A97152

Yonow, T., Zalucki, M.P., Sutherst, R.W., Dominiak, B.C., Maywald, G.F., Maelzer, D.A., et al. (2004) Modelling the population dynamics of the Queensland fruit fly, *Bactrocera* (Dacus) *tryoni*: a cohort-based approach incorporating the effects of weather. *Ecological Modelling*, 173(1), 9–30. Available from: https://doi.org/10.1016/S0304-3800(03)00306-5

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