

Temperature-Driven Dynamics of Development and Reproduction in *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae): Insights for Advanced Pest Management

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Abstract

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The oriental fruit fly, *Bactrocera dorsalis* (Hendel), is a highly invasive and adaptable agricultural pest, posing significant challenges across diverse ecological and climatic conditions. This study investigates the influence of temperature on the development, longevity, and fecundity of *B. dorsalis* based on the results of laboratory experiments. We analyzed the data using both linear and nonlinear modeling approaches to better understand the temperature-dependent biological characteristics of *B. dorsalis*. These models identify critical thermal thresholds and optimal temperature ranges for providing insights into key life history traits and population dynamics under changing environmental conditions. By integrating temperature-dependent models, this study highlights their potential to refine pest management strategies, including precise timing for interventions such as trap deployment, chemical applications, and sterile insect techniques (SIT). Moreover, these models provide a valuable framework for assessing the impacts of climate change on *B. dorsalis* phenology and geographic distribution, supporting the development of adaptive and sustainable pest management practices tailored to diverse agroecosystems.

Key words: *Bactrocera dorsalis*, Temperature-dependent traits, Population modeling, Pest management, Climate change.

INTRODUCTION

The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), is a highly invasive and polyphagous pest that poses substantial threats to global agriculture. It is known to attack over 500 plant species, including both cultivated and wild plants, highlighting its extensive adaptability and ecological plasticity. Among the 85 species in the *B. dorsalis* complex, the identification and differentiation of this species remain challenging due to its morphological and ecological similarities with closely related species such

as *B. papayae*, *B. philippinensis*, and *B. invadens* (Drew & Hancock 1994; Clarke *et al.* 2005; Leblanc *et al.* 2013; San Jose *et al.* 2013; Schutze *et al.* 2015). Its geographic range extends from the Asia-Pacific region to parts of Africa, further solidifying its status as a major agricultural pest (Stephens *et al.* 2007; De Villiers *et al.* 2016; Hassani *et al.* 2016).

The life cycle of *B. dorsalis* involves egg deposition into ripening fruit by adult females, where hatched larvae feed and cause significant economic losses. After feeding, larvae pupate in the soil. This species' development is directly

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influenced by environmental conditions, as it does not exhibit an obligatory diapause stage (Christenson & Foote 1960; Hardy 1973). Its rapid adaptation to new environments, coupled with high reproductive capacity, short generation time, and broad climatic tolerance, enables its successful establishment in diverse regions. Furthermore, human activities such as international trade in fruits and vegetables have facilitated its global spread (Leblanc *et al.* 2013; Sridhar *et al.* 2014; Hassani *et al.* 2016; Dong *et al.* 2022; Deschepper *et al.* 2023).

The invasiveness of *B. dorsalis* has been well-documented in various regions. In Taiwan, it was identified as a significant pest in 1912 (Hendel 1912), causing damage to over 20 economically important crops (Huang & Chi 2014). Similar infestations have been recorded in Japan, where eradication strategies such as methyl-eugenol attractants and insecticides achieved temporary success in the 1980s, though reinvasions remain a challenge (Koyama *et al.* 1984; Ohno *et al.* 2009; Otuka *et al.* 2019). In China, *B. dorsalis* has expanded its range into mid-China, though its spread is limited by overwintering constraints near 30°N latitude (Sridhar *et al.* 2014; Hong *et al.* 2015; Magarey *et al.* 2015; Jaffar *et al.* 2023). This ability to persist across diverse ecological and climatic contexts highlights the challenges of managing this species on a global scale.

Temperature plays a pivotal role in regulating the development, survival, and fecundity of *B. dorsalis*. While adults can forage over long distances- up to 38.6 km in some cases (Huang & Chi 2014)- temperature and host plant availability primarily dictate their establishment. Despite extensive research on stage-specific development, there remains a lack of comprehensive models addressing temperature-dependent development, adult longevity, and reproduction. Temperature-dependent oviposition models (OMs) have become essential tools for predicting egg-laying patterns and seasonal population dynamics across a range of insect pests (Baek *et al.* 2024; Lee *et al.* 2024; Sampaio *et al.* 2024). For *B. dorsalis*,

characterized by a distinct pre-oviposition period and prolonged adult lifespan, these models must account for daily temperature fluctuations affecting reproduction and survival. Recent advancements, including two-phase OMs that separately model the pre-oviposition and oviposition periods, have improved prediction accuracy under varying temperature conditions. Such models are invaluable for forecasting pest adaptations and optimizing management strategies, particularly in the context of climate change.

In this study, we aim to discuss two interrelated themes: the temperature-dependent development and the combined effects of temperature on longevity and fecundity in *B. dorsalis*. By integrating these two aspects, this review provides a comprehensive understanding of how temperature influences the life history traits and population dynamics of this pest species. The findings will inform the development of predictive models and facilitate the design of effective pest management strategies under diverse environmental conditions.

EXPERIMENTAL FRAMEWORK AND METHODOLOGIES FOR TEMPERATURE-DRIVEN LIFE CYCLE ANALYSIS OF *B. dorsalis*

Colony establishment and maintenance

Colonies of *B. dorsalis* were provided from the Taiwan Agricultural Research Institute (TARI). These colonies, maintained since 1996, were established from a wild population collected in Wufeng County, Taichung, Taiwan. Rearing followed established protocols (Huang & Chi 2014). Larvae were fed on a nutrient-rich artificial diet and provided with sawdust for pupation following the established rearing protocol. Larvae were reared on an artificial diet composed of 5 g of sodium benzoate (Sigma-Aldrich Co., Milan, Italy), 240 g of granulated sugar (Taiwan Sugar corporation, Tainan, Tai-

wan), 140 g of yeast (Vietnam- Taiwan Sugar Company Limited, T Hoa, Vietnam), 20 mL of HCl (Sigma-Aldrich Co., Wien, Austria), 480 g of wheat grain (purchased from a local store, Taichung, Taiwan), and 1,100 mL of water. The pupae were collected by sieving the sawdust. The pupae were moved to a 30 cm × 30 cm container where the adults emerged. The adults were fed an artificial diet composed of 200 g of Yeast Hydrolysate Enzymatic (MP Biomedicals, LLC., Illkirch-Graffenstaden, France), 40 g of granulated sugar, 10 mL of protein hydrolyzate (Alco Standard corporation, Valley Forge, PA), and 50 mL of water. Adults were then provided with a gelatinous mixture, containing water, 100 g of sugar, and 37.5 g of agar (Fei Kung Agar-Agar Co., Ltd, Tainan, Taiwan). Oviposition was induced using guava juice-coated cups (Samayoa *et al.* 2018). The relative humidity was 50–80%, temperature $25 \pm 1^\circ\text{C}$, and photoperiod 14 : 10 (L : D) for mass rearing of *B. dorsalis*.

Temperature-dependent developmental studies

Development rates of immature stages (egg, larva, and pupa) were assessed across eight constant temperatures (13.0 to 34.8°C). Newly deposited *B. dorsalis* eggs (< 3 h old) were collected from the cup by using distilled water. About 100 eggs were inoculated on 9 pieces of filter paper (1 cm × 1 cm), which were placed above a thin layer of artificial diet medium in Petri dishes (90 mm × 15 mm, Alpha Plus Scientific Corp., Taoyuan, Taiwan,). More than 1,000 eggs were placed in environmental chambers (Model A 414931206, Yuh Chuen Chiou Industry Co., Ltd., Kaohsiung, Taiwan) set at eight constant temperatures. Larvae and pupae were reared individually in a controlled environment, with daily observations to determine stage-specific developmental durations. Temperature and humidity (50–80%) in environmental chambers were rigorously maintained, with data used to calculate stage-specific developmental thresholds and rates.

Adult longevity and reproductive performance

One newly emerged (< 12 h) virgin female and two males were placed into a cage (10 cm × 15 cm × 10 cm) with a supply of the artificial diet and a 10% sugar- containing gel. A female with two males produces significantly more eggs than females with only one male (Huang & Chi 2014). Eighteen or twenty cages were treated at each temperature, but a few cages were excluded from the analysis when the female escaped from a cage during egg examination. A perforated plastic cup (diameter and height both 4 cm) with a cotton ball soaked in guava juice placed inside the cup was provided for the oviposition site. The number of eggs laid per female in the cup was recorded daily. The adult oviposition period (AOP) of each female was determined by the day from which the female first laid a significant number (> 5) of eggs consistently, as many females did not lay eggs consistently at 13.5°C, 16.7°C, and 34.9°C. Adult pre-oviposition period (APOP) was defined from adult emergence to AOP, and total pre-oviposition period (TPOP) was obtained by summing the APOP and immature development period examined in the previous study (Samayoa *et al.* 2018). Longevity of males and females was monitored under each temperature conditions to evaluate survival dynamics.

Modeling developmental and reproductive dynamics

Temperature-dependent development rates for all immature stages were analyzed using linear and nonlinear models (Campbell *et al.* 1974; Lobry *et al.* 1991; Rosso *et al.* 1993; Shi *et al.* 2011; Ratkowsky & Reddy 2017). Linear regression was employed to estimate the lower developmental threshold and thermal constant, while nonlinear models such as the Lobry-Rosso-Flandroids (LRF) and performance models captured the thermal responses more comprehensively.

For adults, longevity was modeled using a temperature-dependent survival function, where age-specific survival rates were normalized to physiological age (Curry & Feld-

man 1987). A modified Weibull distribution was used to describe survival probabilities, providing a flexible framework for predicting age-specific survival under varying temperatures. Fecundity patterns were modeled using the two-phase oviposition model, which integrates pre-oviposition and oviposition phases to describe reproductive dynamics comprehensively (Choi *et al.* 2020). The pre-oviposition phase accounts for reproductive maturation, while the oviposition phase predicts daily egg production based on age-specific cumulative oviposition rates. Fig. 1 illustrates the structure and simulation process of the two-phase

oviposition model, highlighting its separation into two distinct phases and the integration of physiological age-based predictions for fecundity and survival.

Temperature-dependent developmental models enabled the prediction of adult emergence patterns under fluctuating thermal conditions, providing a foundational framework for simulating population dynamics. The longevity and fecundity of adult *B. dorsalis* were incorporated into the simulation using age- and temperature-dependent models. Longevity was modeled using a Weibull function, normalized to physiological age, to describe survival

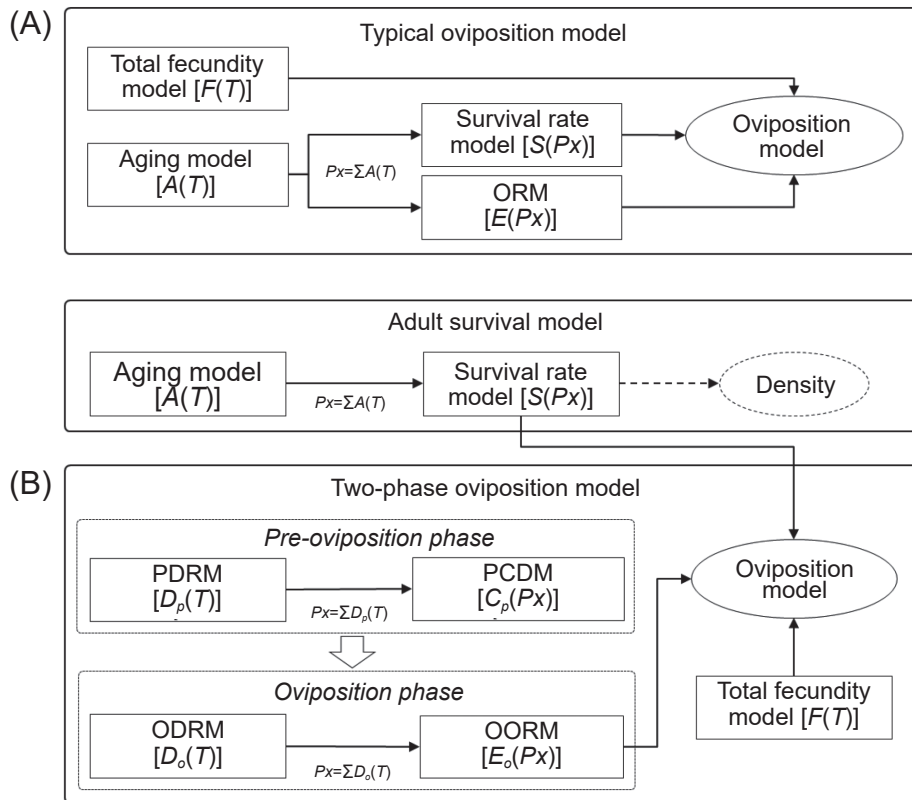


Fig. 1. Illustration of the model structure and simulation process for (A) the current oviposition model (OM) and (B) two-phase OM. (A) The current OM consists of three components; a fecundity model, a female survival rate model, and a cumulative oviposition rate model (ORM), all based on the physiological age (Px) derived from the female aging model. (B) The two-phase OM separates the process into two phases. The pre-oviposition phase applies to newly emerged females, where the completion of pre-oviposition is predicted using the pre-oviposition complete distribution model (PCDM) based on the physiological age derived from the pre-oviposition development rate model (PDRM). In the oviposition phase, the daily oviposition is predicted using an age-specific cumulative oviposition rate model (OORM), derived from the oviposition development rate model (ODRM). The daily egg production is calculated as the product of the daily egg proportion, fecundity model, and survival model.

probabilities under varying thermal conditions (Weibull 1951; Pinder *et al.* 1978). For fecundity, the two-phase oviposition model was employed to account for the pre-oviposition and oviposition phases. The pre-oviposition phase used a development rate function to predict the time required for reproductive maturation, while the oviposition phase employed a cumulative Weibull function to describe age-specific oviposition rates. Total fecundity per female was modeled using Brière's equation (Brière *et al.* 1999). These models allowed for precise simulation of daily egg production and reproductive contributions across different temperature regimes.

THERMAL EFFECTS ON THE LIFE CYCLE AND POPULATION DYNAMICS OF *B. dorsalis*

Developmental rates and thermal thresholds

Development occurred at temperatures ranging from 14.4 to 34.8°C. However, failure to progress beyond the egg and larval stages at 13°C and 14.4°C, respectively, highlights critical lower thermal thresholds for population establishment (Tables 1 and 2). These findings suggest limited sur-

vivability in cooler climates. For statistical comparisons among temperature treatments, one-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) tests ($P < 0.05$) were performed. Prior to these analyses, the assumptions of normality and homogeneity of variance were evaluated using the Shapiro-Wilk's test. Several traits- including developmental durations (egg, larva, pupa, and total immature)- exhibited significant departures from normality. These deviations are biologically interpretable, as holometabolous insects such as *B. dorsalis* often

Table 1. Development time, median, and hatchability of *Bactrocera dorsalis* eggs across various temperatures.

Temperature (°C)	No.	Development time (d)		Hatchability (%)
		Mean $\pm$ SE ^z	Median	
13.0	2,500	- ^y	-	0.0
14.4	2,500	7.6 $\pm$ 0.04 a	7.1	13.7
16.2	1,930	5.2 $\pm$ 0.04 b	4.9	5.9
19.5	2,000	3.0 $\pm$ 0.02 c	2.7	42.9
23.8	1,140	2.2 $\pm$ 0.02 d	1.8	24.4
27.7	2,300	1.9 $\pm$ 0.02 e	1.6	12.3
31.8	1,500	1.5 $\pm$ 0.00 f	1.3	27.6
34.8	1,230	2.0 $\pm$ 0.02 e	1.8	33.5

^z Means followed by the same letters in a column are not significantly different ($P < 0.05$, Tukey studentized range test).

^y Eggs did not hatch at temperature tested.

Table 2. Development time and survival of *Bactrocera dorsalis* larvae and pupae across temperature gradients.

Temperature (°C)	No. examined	Development time (Mean $\pm$ SE (Median), d) ^z			Survival (%)	
		Larva	Pupa	Larva to adult emergence	Pupation ^x	Adult emergence ^w
14.4	200	34.10 $\pm$ 1.09 a (34.5)	- ^y	-	9.5	0.0
16.2	200	19.80 $\pm$ 0.84 b (18.9)	29.60 $\pm$ 0.75 a (29.0)	53.10 $\pm$ 0.60 a (52.5)	69.5	60.0
19.5	200	12.70 $\pm$ 0.92 d (11.7)	17.30 $\pm$ 0.89 b (16.9)	32.90 $\pm$ 0.79 b (32.3)	83.5	75.5
23.8	200	9.30 $\pm$ 0.94 e (8.5)	11.20 $\pm$ 0.92 c (10.7)	22.20 $\pm$ 0.86 c (21.4)	86.5	75.0
27.7	200	8.30 $\pm$ 0.92 e (7.5)	9.20 $\pm$ 0.92 d (8.4)	18.60 $\pm$ 0.85 d (17.5)	65.5	54.0
31.8	200	8.10 $\pm$ 0.88 e (7.3)	7.80 $\pm$ 0.87 e (7.3)	16.90 $\pm$ 0.76 d (16.0)	76.0	42.0
34.8	200	15.30 $\pm$ 2.02 c (14.0)	7.00 $\pm$ 0.00 e (7.0)	23.70 $\pm$ 0.00 c (22.8)	2.0	0.1

^z Means followed by the same letters in a column are not significantly different, as determined by honestly significant difference (HSD) test at $P = 0.05$.

^y No pupa developed to the adult stage.

^x The percent survivorship from larva to pupal stage.

^w The percent survivorship from larva to adult emergence.

display synchronized developmental transitions under constant environmental conditions. This biological characteristic results in clustered distributions of developmental durations, which inherently deviate from the normal distribution assumption. To address these violations, we applied non-parametric Kruskal-Wallis tests as a robust alternative. The results confirmed significant temperature effects across all measured traits and were largely consistent with the parametric analyses. The convergence of these findings reinforces the robustness and reliability of our interpretation regarding the temperature-dependent developmental responses in *B. dorsalis*. Between 14.4°C and 31.8°C, development times for all life stages decreased significantly with increasing temperature: egg ($F_{6, 2693} = 7,986.4$, $P < 0.0001$), larval ($F_{6, 603} = 997.4$, $P < 0.0001$), pupal ($F_{5, 561} = 3,686.1$, $P < 0.0001$),

and larval to adult stages ($F_{5, 591} = 4,582.0$, $P < 0.0001$). Development duration decreased significantly between 14.4°C and 31.8°C, with eggs requiring 7.6 to 1.5 d and larval-to-adult stages requiring 53.1 to 16.9 d. Temperature is a key determinant of the development dynamics of *B. dorsalis*, with each life stage exhibiting distinct responses to thermal conditions. Understanding these dynamics is crucial for predicting population trends and implementing effective pest management strategies (Fig. 2). At temperatures exceeding 31.8°C, especially 34.8°C, survival rates declined sharply, indicating a critical upper thermal limit that could severely impact population persistence and geographic distribution. Lower developmental threshold (LDT) ranged from 9.4 to 10.3°C across life stages, with thermal requirements spanning 33.2–325.5 degree-days (DD) (Table 3).

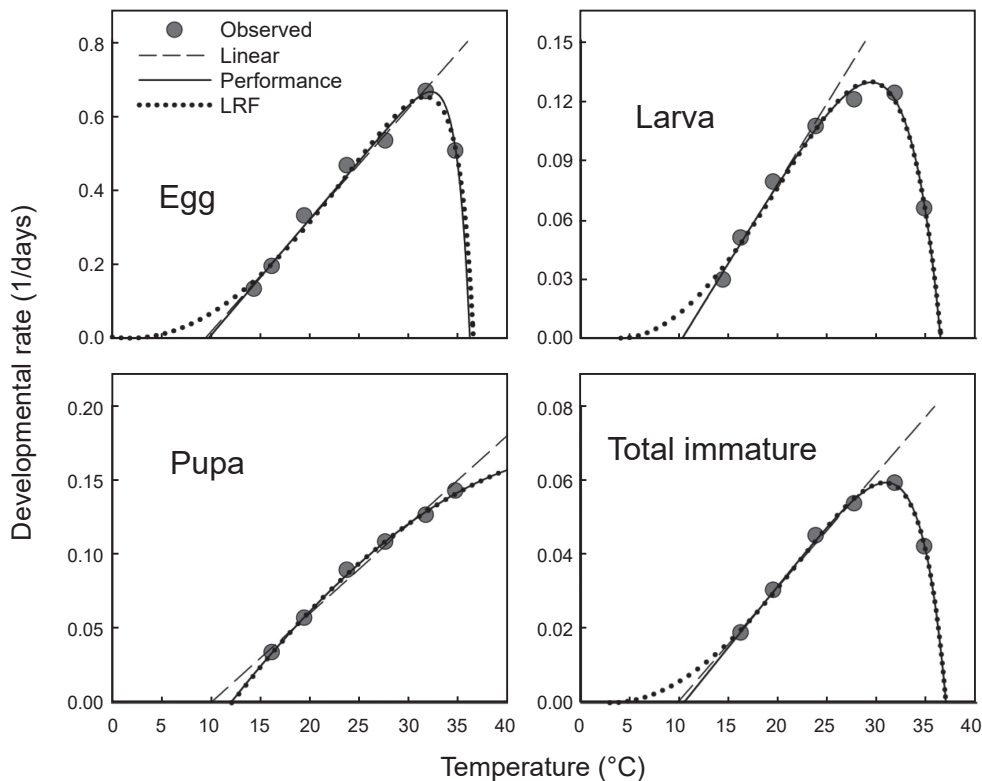


Fig. 2. Comparison of linear and nonlinear models (performance and LRF) fitted to the observed developmental rates (day^{-1}) across life stages (egg, larva, pupa, and total immature) of *Bactrocera dorsalis*. Red points represent observed data, and fitted curves highlight temperature-dependent trends for each stage.

Table 3. Developmental thresholds and thermal requirement for different life stages of *Bactrocera dorsalis*.

Stage ^z	Equation	r^2	Lower development threshold (°C)	Thermal constant (degree-day; DD)
Egg	$0.0301 X - 0.2837$	0.988	9.4	33.2
Larva	$0.0081 X - 0.0836$	0.987	10.3	123.1
Pupa	$0.0074 X - 0.0852$	0.986	10.0	166.5
Egg to pupa	$0.0033 X - 0.0344$	0.990	9.8	325.5

^z Egg: $F_{1,4} = 327.05$, $P < 0.0001$; Larva: $F_{1,2} = 143.76$, $P = 0.0069$; Pupa: $F_{1,2} = 216.60$, $P = 0.0006$; Egg to pupa: $F_{1,2} = 205.12$, $P = 0.0048$.

To evaluate the temperature-dependent development of *B. dorsalis*, we compared three candidate models: a linear regression model, Shi's two-phase performance model, and a logistic rate function. These models were applied to four developmental stages- egg, larva, pupa, and total immature- and their performance was evaluated using Akaike information criterion (AIC and AICc), Bayesian information criterion (BIC), and root mean square error (RMSE). Among the tested models, the performance model proposed by Shih consistently provided the best fit across most stages, particularly for total immature development, as indicated by its lowest AIC, BIC, and RMSE values. To further evaluate the predictive robustness of each model, we performed 10-fold cross-validation using the full dataset. The performance model demonstrated strong and consistent predictive accuracy across all developmental stages, either outperforming or equaling the linear and LRF models. Although the linear model occasionally yielded lower RMSE values, its inability to represent biologically meaningful nonlinearities- particularly near thermal limits- limited its ecological applicability. Taken together, the performance model offers the most balanced trade-off between statistical accuracy and biological interpretability under changing temperature conditions. In addition to model performance evaluation, the LRF model offered valuable insights into optimal developmental temperatures, estimating 31.7°C for eggs, 29.3°C for larvae, and 30.7°C for egg-to-adult emergence. These estimates help delineate the thermal tolerance ranges of *B. dorsalis* and inform assessments of its potential ecolog-

ical adaptability. The completion of developmental stages was further characterized using a two-parameter Weibull distribution, which effectively described the cumulative proportion of development across temperatures (Fig. 3). Simulations based on these models also visualized temperature-dependent adult emergence patterns, showing that 50% cumulative emergence occurred by day 18 under optimal conditions (29–32°C) (Fig. 4). These findings underscore the critical role of temperature in shaping the developmental dynamics and population phenology of *B. dorsalis*.

The longevity and fecundity of *B. dorsalis* adults were significantly influenced by temperature, with variations observed in lifespan, fecundity, and reproductive timing across different thermal conditions (Table 4). To further investigate these effects, we evaluated female and male longevity, fecundity, as well as the preoviposition (APOP) and oviposition (AOP) periods. Normality of the data was assessed using the Shapiro-Wilk test. While adult longevity and oviposition period generally satisfied the assumption, fecundity and preoviposition period deviated from normality in several temperature treatments. Given these deviations, particularly for fecundity and APOP, we applied non-parametric Kruskal-Wallis tests to examine temperature effects. All four traits showed significant variation across temperature treatments. Female longevity decreased from 116.8 d at 18.8°C to 22.4 d at 34.9°C, while male longevity followed a similar trend, declining from 113.0 d at 13.5°C to 30.9 d at 34.9°C. These trends highlight the temperature sensitivity of adult survival and its potential effects on population persistence

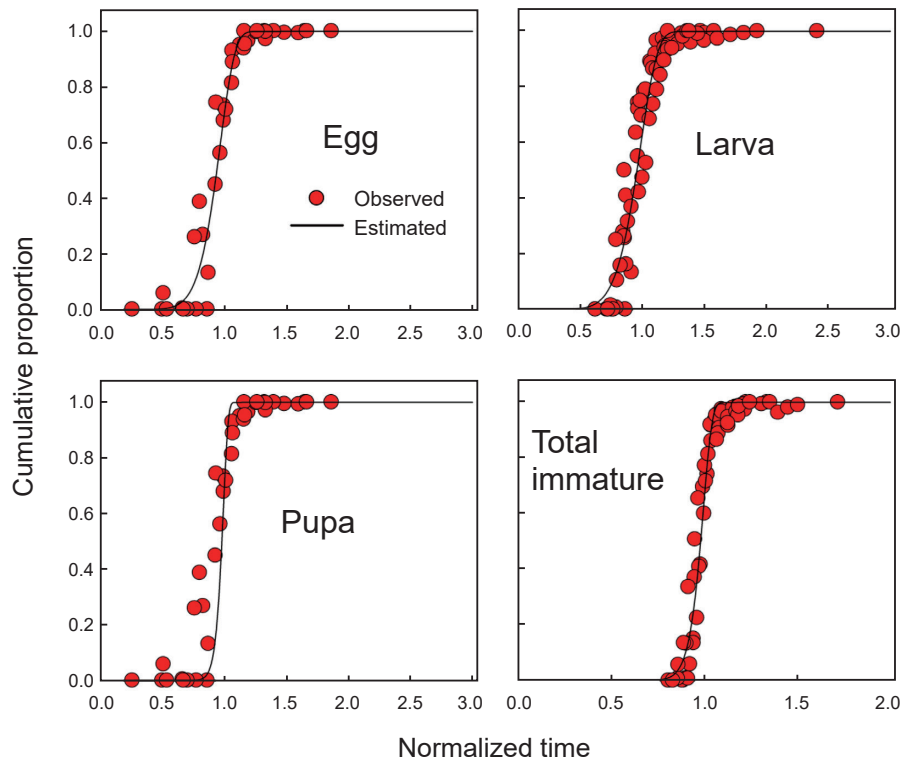


Fig. 3. Cumulative proportions of development completion for each stage of *Bactrocera dorsalis* (egg, larva, pupa, and total immature) as a function of normalized time (developmental time/mean developmental time). Solid lines represent fitted curves based on the two-parameter Weibull function, while red dots indicate observed data.

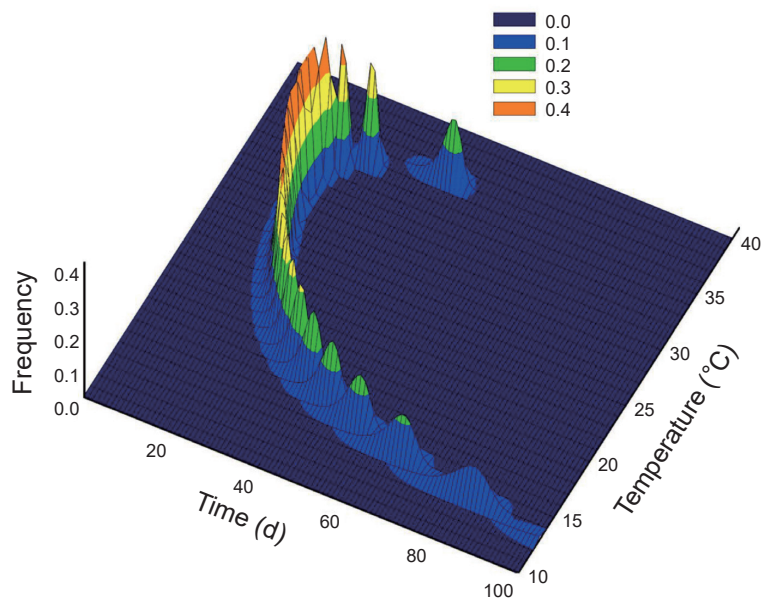


Fig. 4. Simulated adult emergence patterns of *Bactrocera dorsalis* under temperature-dependent conditions based on the performance model.

Table 4. Longevity (d) and fecundity of *Bactrocera dorsalis* adults across various constant temperatures.

Temperature (°C)	Female			Male	
	<i>n</i>	Longevity (Mean ± SE) ^z	Fecundity (Mean ± SE)	<i>n</i>	Longevity (Mean ± SE)
13.5	17	94.10 ± 10.72 (87.0) abc ^y	- ^x	24	113.00 ± 5.68 (122.3) a
16.7	20	53.50 ± 4.46 (54.5) cde	63.0 ± 22.5 c	21	51.40 ± 3.25 (53.8) cde
18.8	18	116.80 ± 7.45 (107.0) ab	922.0 ± 86.7 b	29	79.60 ± 6.35 (76.5) bc
23.5	20	78.50 ± 6.40 (71.0) bcd	1,545.0 ± 160.6 a	36	68.10 ± 4.03 (62.0) bcd
28.1	16	43.30 ± 4.33 (39.0) def	1,684.0 ± 131.9 a	30	43.30 ± 2.08 (44.0) def
32.0	17	42.10 ± 4.63 (37.8) def	958.0 ± 86.9 b	33	30.90 ± 1.79 (28.8) efg
34.9	17	22.40 ± 1.81 (21.5) ef	138.0 ± 34.2 c	34	19.00 ± 0.59 (19.0) fg

^z Standard error.^y Means followed by the same letters in a column are not significantly different, as determined by honestly significant difference (HSD) test at $P = 0.05$. Statistical results: female longevity ($F_{6, 118} = 27.69$, $P < 0.0001$), Fecundity ($F_{6, 118} = 55.57$, $P < 0.0001$) and male longevity ($F_{6, 200} = 68.96$, $P < 0.0001$).^x No eggs were laid by the female. Numbers in the parentheses represent the median longevity at each temperature.

under fluctuating climatic conditions. Fecundity peaked at 1,684 eggs per female at 28.1°C, suggesting an optimal temperature for reproduction. Beyond this range, fecundity declined sharply, likely due to thermal stress impairing reproductive physiology ($F_{6, 118} = 27.69$, $P < 0.0001$) (Fig. 5).

Reproductive timing metrics, including the APOP, AOP, and TPOP, also displayed strong temperature dependence. APOP decreased from 38.1 d at 16.7°C to 4.6 d at 32.0°C but increased slightly at 34.9°C. Conversely, AOP peaked at 103.1 d at 18.8°C and declined at both higher and lower temperatures (Table 5). The aging rates of adults increased linearly with temperature above 18.8°C, as modeled using a Weibull distribution. Females exhibited higher survival proportions than males across most temperatures (Fig. 6C and 6D). Thermal constants for female and male longevity were estimated as 507.1 DD and 433.4 DD, respectively (Table 6). Collectively, these findings highlight the profound impact of temperature on adult survival and reproductive performance in *B. dorsalis*. The identification of optimal and limiting temperature thresholds contributes to a better understanding of how temperature governs population persistence and reproductive success. Such insights are essential for developing pre-

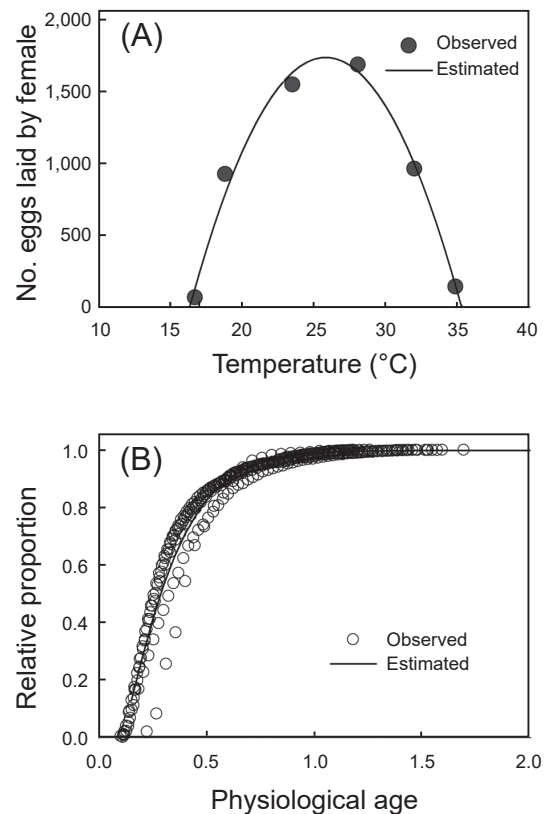
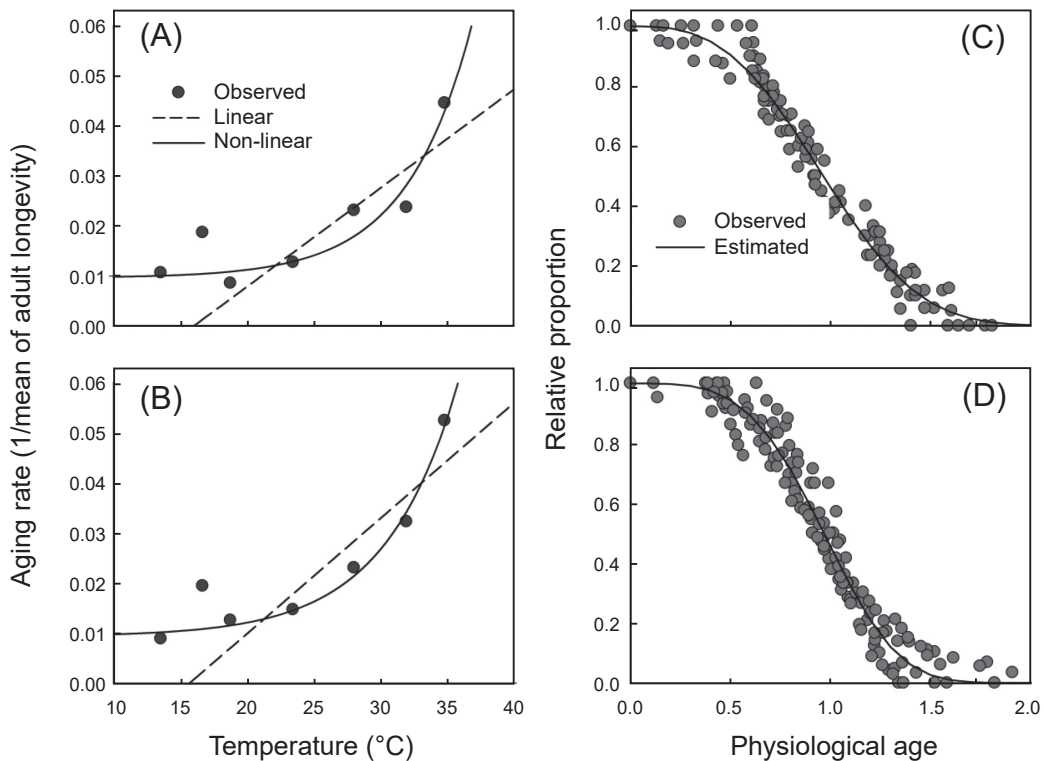


Fig. 5. (A) Fecundity of *Bactrocera dorsalis* females at various temperatures, fitted with a quadratic equation (solid line). (B) Cumulative oviposition probability distribution modeled using a three-parameter Weibull function for females after emergence.

Table 5. Adult pre-oviposition period (APOP) (d), adult oviposition period (AOP), and total pre-oviposition period (TPOP) of *Bactrocera dorsalis* at different temperatures.

Temperature (°C)	No. female oviposited ^z	APOP (Mean $\pm$ SE ^y)	AOP (Mean $\pm$ SE)	TPOP ^x
16.7	11	38.10 $\pm$ 3.06 a ^w	23.60 $\pm$ 4.27 c	91.2
18.8	17	16.20 $\pm$ 0.75 b	103.10 $\pm$ 7.20 a	49.1
23.5	20	9.00 $\pm$ 0.21 c	69.50 $\pm$ 6.46 b	31.1
28.1	16	5.40 $\pm$ 0.58 cd	37.80 $\pm$ 4.24 c	24.1
32.0	17	4.60 $\pm$ 0.15 d	37.50 $\pm$ 4.66 c	21.5
34.9	11	6.20 $\pm$ 0.50 cd	17.40 $\pm$ 1.55 c	29.9

^z Female consistently laid a significant number of eggs (> 5).^y Standard error.^x TPOP represents the sum of APOP and the immature development period, as reported in a previous study (Samayoa *et al.* 2018).^w Means with the same letters within a column are not significantly different, as determined by honestly significant difference (HSD) test at $P = 0.05$. Statistical results: APOP ($F_{5,86} = 130.25$, $P < 0.0001$) and AOP ($F_{5,86} = 32.09$, $P < 0.0001$).**Fig. 6.** Aging and survival rates of *Bactrocera dorsalis* adult females and males across various constant temperatures. (A, B) Aging rates (1/mean longevity) for females and males, respectively, fitted with a linear model (dashed line) and a nonlinear model (solid line). (C, D) Survival proportions for females and males, respectively, modeled using a two-parameter Weibull function based on physiological age.

dictive models and adaptive management strategies in the context of climate change.

Fig. 7 provides critical insights into the population dynamics of *B. dorsalis* under

varying thermal conditions and offers practical applications for pest management. The comparison between the current oviposition model and the two-phase oviposition model

Table 6. Low developmental threshold (LDT) and thermal constant (TC) for adult longevity, adult pre-oviposition period (APOP), adult oviposition period (AOP), and total pre-oviposition period (TPOP) of *Bactrocera dorsalis*.

Stage	Equation ^z	r^2	LDT (°C)	TC (degree-day; DD)
Male adult longevity	$0.0023 X - 0.0363$	0.84	15.7	433.4
Female adult longevity	$0.0020 X - 0.0316$	0.83	16.0	507.1
APOP	$0.0126 X - 0.1806$	0.99	14.3	79.2
AOP	$0.0014 X - 0.0175$	0.89	12.2	696.6
TPOP	$0.0023 X - 0.0241$	0.97	10.6	437.4

^z Linear regression analysis results: Male adult longevity ($F_{1,3} = 15.89$, $P = 0.0283$), Female adult longevity ($F_{1,3} = 15.02$, $P = 0.0304$), APOP ($F_{1,3} = 417.307$, $P = 0.00026$), AOP ($F_{1,2} = 20.5065$, $P = 0.04547$), and TPOP ($F_{1,3} = 96.5145$, $P = 0.00224$).

demonstrates that the latter offers a more nuanced understanding of temperature-driven reproductive performance, particularly under suboptimal or extreme temperatures. By accurately predicting daily egg production across a wide thermal range (10 to 40°C), the two-phase model highlights key thermal thresholds and optimal reproductive temperatures, such as the peak fecundity observed at 28°C. The findings shown in Fig. 7 provide a robust framework for understanding the thermal ecology of *B. dorsalis* and this knowledge can be translated into effective, sustainable, and climate-responsive pest control strategies. By combining these findings from Figs. 4 and 7, pest management strategies can be fine-tuned to effectively suppress populations while minimizing environmental impact. These models represent a significant step toward sustainable, climate-responsive pest management and contribute to broader ecological understanding of temperature-sensitive invasive species.

PRACTICAL APPLICATION OF TEMPERATURE-BASED MODELS IN PEST MANAGEMENT

The integration of temperature-dependent development and fecundity models offers a robust framework for understanding the population dynamics of *B. dorsalis*. These models enable precise predictions of life stage transitions, reproductive potential, and population fluctuations under changing thermal conditions. Leveraging these insights allows for optimized

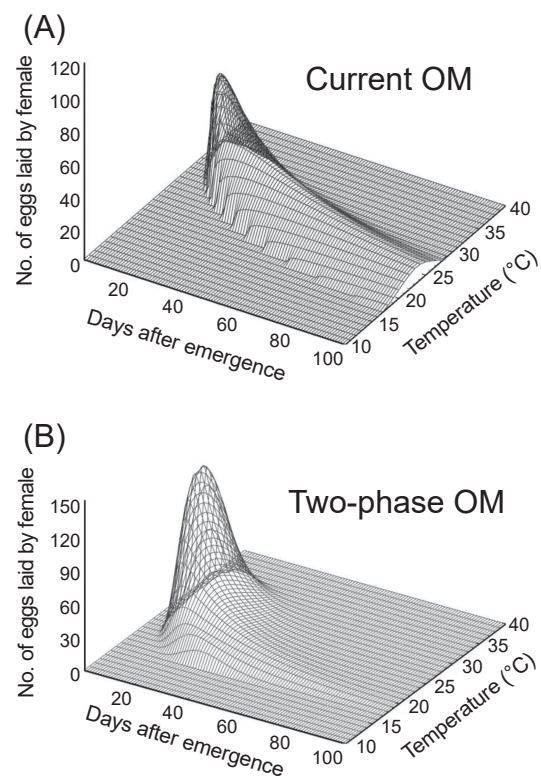


Fig. 7. Predicted daily egg production of *Bactrocera dorsalis* females using (A) the current oviposition model (OM) and (B) the two-phase OM across temperatures ranging from 10 to 40°C after adult emergence.

pest management strategies that minimize economic losses and environmental impacts.

Predicting seasonal population dynamics

One of the primary applications of integrated models is predicting the seasonal activity

patterns of *B. dorsalis*. By incorporating local temperature data into the model, researchers can estimate key developmental milestones, such as larval emergence, pupation, and adult emergence, which are critical timing control measures (Choudhary *et al.* 2025). For instance, in regions with significant temperature fluctuations, models can identify periods of rapid development or delayed emergence, enabling timely interventions. At optimal temperatures (25–30°C), *B. dorsalis* completes its life cycle rapidly, leading to population surges. Predicting these surges allows pest managers to implement preemptive measures, such as deploying traps or applying insecticides during peak activity periods.

Trap deployment and monitoring

Temperature-dependent models guide the strategic placement and timing of placing monitoring traps to control *B. dorsalis* populations. Traps baited with attractants like methyl eugenol effectively capture male flies. Model predictions of adult emergence can optimize trap deployment, ensuring maximum impact (Rincon *et al.* 2024). For instance, traps can be placed in vulnerable orchards before adult emergence during optimal spring temperatures. Early capture of males reduces mating success and population growth. Additionally, predictions of larval development times allow for targeted monitoring of high-risk areas to enhance the precision of pest control efforts. Integrating automated trapping systems with temperature-based models further improves management by predicting life stage transitions such as larval emergence and adult eclosion.

Timing of chemical applications

Chemical control remains a vital component of integrated pest management (IPM) for *B. dorsalis* (Wang *et al.* 2024). Integrated models optimize the timing of insecticide applications by targeting the most vulnerable life stages, such as newly emerged adults or early instar larvae. For instance, if a model predicts a sharp

increase in adult emergence within a week due to rising temperatures, insecticides can be applied during this period for maximum efficacy while minimizing non-target effects. Similarly, soil treatments can target pupal stages at their peak density, effectively reducing adult emergence rates.

Supporting sterile insect technique (SIT) programs

Sterile insect technique (SIT) relies on releasing sterile males to reduce wild population fertility (Shelly & Manoukis 2022). Integrated models enhance SIT by predicting peak reproductive periods, allowing for the strategic timing of sterile male releases. In tropical regions with year-round *B. dorsalis* activity, models can identify high reproductive potential periods, ensuring sterile males effectively compete with wild males. Furthermore, models can simulate the impact of different release densities and frequencies, optimizing SIT strategies for varying environmental conditions.

Assessing the impact of climate change

Climate change significantly affects *B. dorsalis* management by altering its geographic range and phenology (Qin *et al.* 2019; Cai *et al.* 2023). Integrated models can simulate how rising temperatures and shifting weather patterns influence population dynamics, supporting proactive management strategies. For instance, in regions not yet invaded by *B. dorsalis* but becoming climatically suitable, models can predict potential invasion risks, enabling early detection and monitoring. Conversely, in areas where temperatures may exceed the species' thermal limits, models can guide adaptive strategies, such as crop diversification or planting schedule adjustments.

Economic and environmental benefits

Applying integrated models reduces reliance on broad-spectrum insecticides, lowering costs and minimizing environmental impacts. By targeting specific life stages and optimizing intervention timing, these models enhance the efficiency and sustainability of pest man-

agement programs (Neta *et al.* 2021). Moreover, by incorporating temperature-dependent parameters, the models ensure that IPM strategies remain adaptable to local environmental conditions and resilient in the face of climate change.

CONCLUSION

The study of temperature-dependent traits, including development, longevity, and fecundity, in *B. dorsalis* provides critical insights into the species' biology and population dynamics. These findings underscore the pivotal role of temperature in shaping key life history traits, such as development rates, reproductive potential, and survival, which collectively influence population growth and geographic distribution.

Integrated modeling approaches, combining empirical data with mechanistic frameworks, are invaluable for understanding these complex interactions. Linear models provide essential metrics, such as LDTs and thermal constants, to estimate phenology and generation times. Meanwhile, nonlinear models, such as LRF and performance models, refine predictions by accounting for the effects of extreme temperatures, offering a more comprehensive understanding of *B. dorsalis* responses to its thermal environment.

The integration of development and fecundity models enhances the ability to simulate population dynamics in detail, paving the way for practical pest management applications. These models enable precise predictions of life stage transitions and reproductive patterns, optimizing interventions such as trap deployment and insecticide application. They also play a crucial role in advanced techniques like the SIT and in adapting pest management strategies that adapt to the challenges of climate change.

As global temperatures rise, adaptive and proactive pest management becomes increasingly critical (Jaffar *et al.* 2023). Integrated models offer a robust framework for predicting how climate change will impact *B. dorsalis* phenology and distribution, ensuring that the

continued effectiveness of management programs. Future research should aim to refine these models by incorporating additional environmental factors, such as humidity and photoperiod, and by developing region-specific adaptations to improve their utility.

In conclusion, the comprehensive study and modeling of temperature-dependent traits in *B. dorsalis* mark a significant step forward in sustainable pest management. By merging biological insights with advanced modeling techniques, researchers and practitioners can effectively address the challenges posed by this invasive species, safeguarding both agricultural productivity and ecological stability in a changing climate.

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溫度驅動動態對東方果實蠅 (*Bactrocera dorsalis* (Hendel)) (雙翅目：果實蠅科) 發育與繁殖之探討：蟲害進階管理的見解

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摘要

安晶駿、金廷恩、辛宗煥、黃毓斌。2025。溫度驅動動態對東方果實蠅 (*Bactrocera dorsalis* (Hendel)) (雙翅目：果實蠅科) 發育與繁殖之探討：蟲害進階管理的見解。台灣農業研究 74(3):249–264。

東方果實蠅 (*Bactrocera dorsalis* (Hendel)) 是一種入侵性與環境適應性極強的農業害蟲，在不同的生態與氣候條件都構成防檢疫上重大挑戰。本文將應用線性與非線性模式，論述溫度對東方果實蠅發育、壽命及繁殖力之影響。這些模式確立了其臨界發育閾值與最適發育溫度範圍，藉此瞭解不同環境條件下之生活史關鍵策略與其族群動態。本研究彙整相關溫度依變模式之數值特性，此特性可應用於改善蟲害管理策略之潛力，包括精準規劃防治時機，陷阱設置、化學藥劑施用及昆蟲不孕技術。此外，這些模式可提供生活史關鍵資料作為評估氣候變遷對東方果實蠅之物候學與地理分布的影響，藉此制定不同農業生態系統下適合的韌性策略與永續的害蟲管理。

關鍵詞：東方果實蠅、溫度依變特性、族群模式建置、蟲害管理、氣候變遷。

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