Effect of temperature on development and survival of immature stages of *Bactrocera invadens* (Diptera: Tephritidae)

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Abstract

The development and survival of immature stages of *Bactrocera invadens* Drew, Tsuruta and White (Dipt.: Tephritidae), a new invasive fruit fly pest in Africa, was studied in the laboratory at five constant temperatures of 15°C, 20°C, 25°C, 30°C and 35°C and photoperiod of L12:D12. The developmental time of eggs was 5.71 days at 15°C, decreasing to 1.24 days at 35°C. Larval development periods decreased from 35.95 days at 15°C to 6.64 days at 35°C. Pupal development at 15°C took 34.08 days while no adults emerged at 35°C, this being the most lethal temperature. The longest total development period occurred at 15°C (75.74 days) and was shortest at 30°C (17.76 days). The linear model provided a reliable fit of development rates vs. temperature for the immature stages. Lower developmental thresholds that were estimated from linear regression equations for the egg, larva and pupal stages were 8.8, 9.4 and 8.7, respectively. Total degree-day (DD) accumulation was estimated at 376 DD for development from egg to adult emergence. The highest adult survival given as the mean of emergence from a cohort of 50 eggs occurred at 20–30°C. At the egg stage, survivorship was highest at 20–30°C and at the larva and pupa stages, it was at 25°C. The practical implication of the findings is discussed in relation to mass rearing of *B. invadens* and understanding its biology and ecology.

Introduction

Tephritid fruit flies within the genus *Bactrocera* Macquart are recognized worldwide as among the most destructive insect pests of fruits and vegetables (White and Elson-Harris 1992; Clarke et al. 2005). They cause enormous damage to fruits through direct feeding by the developing larvae, and indirect losses are also associated with quarantine restrictions imposed by importing countries to prevent entry and establishment of unwanted fruit flies. Although the genus *Bactrocera* are known to be largely endemic to Asia and the Pacific, six species namely *Bactrocera cucurbitae* (Coquillett) (Dipt.: Tephritidae), *Bactrocera dorsalis* Hendel, *Bactrocera invadens* Drew, Tsuruta and White, *Bactrocera latifrons* (Hendel), *Bactrocera oleae* (Gmelin) and *Bactrocera zonata* (Saunders) have successfully invaded other regions of the world and have become established (White and Elson-Harris 1992; Quilici and Jeuffrault 2001; Clarke et al. 2005; Ekesi et al. 2006).

Bactrocera invadens was first detected at the Kenya coast in 2003 (Lux et al. 2003). This pest has now rapidly spread across most of the sub-Saharan African region and currently reported from 24 countries including the Comoros Island. It has been recovered from over 30 host plants species including cultivated and wild hosts although mango

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appears to be the most preferred cultivated plant (Drew et al. 2005; Vayssières et al. 2005; Ekesi et al. 2006; Mwatawala et al. 2006; Rwomushana et al. 2008). *Bactrocera invadens* is also rapidly displacing indigenous fruit fly species on mango. For example, in Kenya, 82% of the flies emerging from mango during 2003 season was *Ceratitis cosyra* and 18% was *B. invadens*. In 2004, 23% of the flies emerging from mango was *C. cosyra* and 76% was *B. invadens* (Ekesi et al., unpublished data). By 2005, 92% of the fruit flies emerging from mango were *B. invadens* (Ekesi et al. 2006). The insect like several other *Bactrocera* species is multivoltine and highly fecund, laying over 1000 eggs per female (Ekesi et al. 2006) and may partly be responsible for gradually displacing the native mango fruit fly species that lay just 300 eggs (Manrakhan and Lux 2006). Although the basic biological studies of *B. invadens* was reported by Ekesi et al. (2006) and artificial diet for mass rearing of the insect has been developed (Ekesi et al. 2007), thermal requirements of the insect have not been fully described.

Many biotic factors affect insect growth and development, and temperature is probably the single most important environmental factor affecting the development of poikilothermic organisms. Two fundamental thermal parameters that express how the rate of development of ectotherms depends on temperature are the lower threshold temperature for development (T_{min}: temperature below which no measurable development takes place) and the thermal constant, K [number of degree day (DD) above temperature T_{min} for completion of development] (Higley et al. 1986). These parameters reflect the process of heat accumulation and use the linear portion of the rate vs. temperature development curve (Higley et al. 1986; Hanula et al. 1987; Herrera et al. 2005). Temperatures have been reported to be the main abiotic factors affecting survival and development of many tephritid species (Fletcher 1987; Vargas et al. 1997; Brévault and Quilici 2000; Duyck and Quilici 2002). As no report exists on the effect of this important variable on *B. invadens*, this work aimed at studying the effects of different constant temperatures on the survival and development of the insect. This information will be relevant in the optimization of laboratory rearing conditions for mass rearing of the insect and its parasitoids, understanding temporal and geographical patterns of abundance and application of suppression methods, development of population models and understanding intra- and inter-specific relations of *B. invadens* with other native fruit fly species.

Materials and Methods

Insect culture

The initial stock culture of *B. invadens* originated from a natural population from infested mango fruits collected at a local market in Nairobi, Kenya, in 2003 and the larvae were subsequently reared on a yeast-carrot-based artificial diet (hereafter referred to as diet) in the laboratory. The colony has been maintained for more than 100 generations at the Animal Rearing and Containment Unit (ARCU) of the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya. Rearing conditions are maintained at 28 ± 1°C, 50 ± 8% relative humidity (RH) and photoperiod of L12:D12.

Egg collection

Eggs of *B. invadens* were collected from the stock colony by providing ripe mango dome (fruit skin that has the seed and pulp scooped out) to mature female flies. The domes were placed over a 9-cm diameter Petri dish lined with moistened filter paper. Domes were maintained in 30 cm × 30 cm × 30 cm perspex cage at 28 ± 1°C, 50 ± 8% RH. Each dome was pierced with an entomological pin (38 mm long, 0.3 mm diameter) to facilitate oviposition. Eggs were collected within 2 h of oviposition using a moistened fine camel's hair brush.

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Fifty eggs were counted and carefully lined on a rectangular piece of sterilized black cloth in a Petri dish and placed on top of 50 g of diet. The composition and insect performance on this diet is reported in Ekesi et al. (2007). The Petri dishes were immediately transferred to thermostatically controlled environmental chambers (MLR-153, Sanyo, Japan) set at five constant temperatures of 15°C, 20°C, 25°C, 30°C and 35°C (±1°C) and 50 ± 8% RH, 12:12 L:D photoperiod. Duration of egg stage was observed at 8-hourly intervals under a binocular microscope for determination of egg hatch.

At egg eclosion, Petri dish covers were removed and the dishes were separately transferred in to larger rectangular plastic rearing containers (7 cm × 7 cm × 5 cm) containing a thin layer (~0.5 cm) of moist sterilized sand at the bottom for pupation. The top of the plastic containers were screened with light cloth netting material for

ventilation. The containers were then maintained at the same constant temperature in the environmental chambers. Mature late third instar larvae leave the Petri dishes containing the artificial diets *ad libitum* and jump into the sand in the larger containers to pupate. After 7 days, the containers were observed for puparia and the puparia were thereafter separated from sand daily by sifting.

Puparia were held in smaller-ventilated transparent cylindrical plastic cages (5.5 cm × 12.5 cm) (J-12, GP plastics, Kenya) and maintained at the same five constant temperatures until eclosion. Records were kept of the duration and developmental rate of the different stages and mortality of egg, larvae and puparia. Developmental duration was estimated as the observed time when 50% of the stages either hatched, formed puparia or emerged as adult (Vargas et al. 1984). Stage-specific survival rates were determined by dividing the number of individuals alive at the end of each stage by the initial number (Vargas et al. 1984). The final number of emerged adults per 50 eggs was calculated as the product of survival rates in the different stages from egg to adult.

Temperature thresholds and thermal constants

Regression analysis was used to estimate lower development thresholds for egg, larvae and puparia (Liu et al. 1995; Liu and Meng 1999). To establish this relationship, the developmental time of individual life stages (i.e., the time required for 50% of individuals to complete a given biological stage) was determined at the series of constant temperatures and the developmental rate estimated (i.e., 100/developmental time) and then plotted against temperature (Brévault and Quilici 2000). In this model, the development rate $V(T) = a + bT$, where a and b are regression parameters fitted to the data of individual insects that develop to adult (Liu and Meng 1999). The lower development threshold t (i.e., the temperature at which the development rate is zero) was estimated by solving the regression equation for the x-intercept, which represented the estimate of the development threshold (Price 1984). The thermal constant (DD above the lower threshold required to complete development) was calculated by the formula $K = n(T - t)$, where K = thermal constant, n = duration of development (days), T = average temperature of the period (°C) and t = threshold temperature (°C), with the corresponding data of the five thermal levels, for each stage and for the stage development, averaging the corresponding data (Pruess 1983; Vargas et al. 1996; Urra and Apablaza 2005). The range of variation in developmental time for each immature stage was determined from the formula: r.v. = max. developmental time - min. developmental time. The coefficient of variation was calculated as c.v. = 100 × r.v./developmental time, for each stage (Brévault and Quilici 2000).

Data analyses

For each temperature, there were five replicates and each temperature was tested three times. Developmental time and survival rates were analyzed by a completely randomized block design, considering various replicates as multiple observations at each temperature. Prior to analysis, the developmental time data and percentages of survivorship were transformed [ln $(x + 1)$] and [Arcsin sqrt(x)], respectively, to meet the assumption of homogeneity. Standard ANOVA were then used to test the effect of the various treatments on development time and survival. Means were compared, where appropriate, by the Student Newman–Keuls (SNK) multiple range tests (P = 0.05) (SAS Institute Inc 2001).

Results

Effect of temperature on stage development

The time required for eggs to hatch ranged from 5.71 days at 15°C and decreased to 1.24 days at 35°C (F = 544.2, d.f. = 4, 15 P < 0.0001) (table 1). The highest range of variation (r.v.) for egg was at 15°C (F = 4.0, d.f. = 4, 15 P < 0.0001) (table 1). Mean coefficient of variation (c.v.) for egg development varied from 39% at 15°C to 86% at 35°C (F = 3.6, d.f. = 4, 15 P < 0.0001) (table 1). The linear regression model showed a strong positive linear relationship between temperature and egg development rate ($R^2 = 0.97$) (fig. 1a) with a lower development threshold of 8.8°C for this stage. The egg stage required 31 DD to complete development.

At larval stage, the trend was similar as with egg with development periods decreasing from 35.95 days at 15°C to 6.64 days at 35°C (F = 694.6, d.f. = 4, 15 P < 0.0001). Mean r.v. was highest (10.1 days) at 15°C, decreasing to 2 days at 20°C and fairly uniform across 25–35 days (F = 168.4, d.f. = 4, 15 P < 0.0001). The mean c.v. varied from 11% to 28% among the various temperatures tested (F = 9.4, d.f. = 4, 15 P < 0.0001). The linear regression between temperature and development rate for this stage was positive ($R^2 = 0.97$) (fig. 1b). *Bactrocera*

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Table 1 Mean developmental time (days ± SE), range of variation and coefficient of variation of immature stages of *B. invadens* at five constant temperatures

	Egg development			Larval development			Pupal development			
Temperature (°C)	Mean ± SE (days)	m.r.v. (days)	m.c.v. (%)	Mean ± SE (days)	m.r.v. (days)	m.c.v. (%)	Mean ± SE (days)	m.r.v. (days)	m.c.v. (%)	Total (days)
15	5.71 ± 0.04a	2.2a	38.5c	35.95 ± 0.34a	10.1a	28.1a	34.08 ± 0.37a	11.8a	34.6a	75.74
20	2.88 ± 0.04b	1.1b	38.1c	14.99 ± 0.17b	1.9b	12.7c	13.59 ± 0.19b	1.9b	13.9b	31.45
25	1.69 ± 0.02c	1.1b	65.1b	9.48 ± 0.18c	1.1c	11.6c	10.02 ± 0.09c	1.1c	11.0c	21.19
30	1.41 ± 0.02d	1.1b	78.0a	7.85 ± 0.02d	1.1c	14.0c	8.50 ± 0.07d	1.1c	12.9b	17.76
35	1.24 ± 0.03e	1.0b	80.6a	6.64 ± 0.08e	1.1c	16.6b	No emergence	–	–	–

m.r.v., mean range of variation [r.v. = max. (developmental time) - min. (developmental time), i.e., time lapse from the first to the last egg eclosion, from the first to the last larval pupation or from the first to the last adult emergence]; m.c.v., mean coefficient of variation [c.v. = (100 × r.v.)/developmental time). Means followed by different letters in the same column are significantly different (ANOVA and Student Newman–Keuls multiple range test, $P < 0.05$).

invadens required 168 DD above development threshold of 9.4°C to complete development from larval stage to the pupal stage.

Temperature had a significant effect on development of puparia ($F = 548.6$, d.f. = 4, 15 $P < 0.0001$). The longest duration occurred at 15°C (34.1 days) and it took 8.5 days to reach eclosion at 30°C. There was no eclosion at 35°C. As with the other stages, mean r.v. was highest at 15°C ($F = 391.9$, d.f. = 4, 15 $P < 0.0001$) and c.v. ranged from 11% to 35% across the temperatures ($F = 41.0$, d.f. = 4, 15 $P < 0.0001$). The linear regression between temperature and development rate for this stage was positive ($R^2 = 0.96$) (fig. 1c) with a lower development threshold of 8.7°C. The pupa required 178 DD for complete development. Total developmental duration was longest at 15°C (75.74 days) and shortest at 30°C (17.76 days) at the various temperatures that puparia eclosed.

Survival rates

Survival rates varied significantly relative to temperature for immature stage development (table 2). Overall, the highest survival given as the mean of adults emerging from an initial cohort of 50 eggs occurred at 20–30°C. At egg stage, survival ranged between 87% at 35°C and 95% at 20°C ($F = 2.5$, d.f. = 4, 15 $P = 0.0078$) but did not differ significantly between the temperatures tested. Survivorship at the larval stage ranged between 84% and 99% at 35°C and 25°C, respectively ($F = 2.8$, d.f. = 4, 15 $P < 0.0001$) but did not differ significantly between the upper and lower temperature limits tested and at 20°C. At the pupal stage, survival was 0% at 35°C and 96% at 25°C ($F = 34.0$, d.f. = 4, 15 $P < 0.0001$).

Discussion

The developmental time of immature stages of *B. invadens* was affected by temperature with the duration of each stage decreasing as temperature increased. The result is consistent with that of earlier workers who have reported similar trends with different species of Tephritid fruit flies (Carey et al. 1985; Vargas et al. 1996; Brévault and Quilici 2000; Duyck and Quilici 2002; Duyck et al. 2004). In our study, development prolonged at 15°C and 20°C in all developmental stages. Generally, the linear effect of temperature on development rate falls off at average daily temperatures than those experienced normally in the field (Howe 1967), implying that there is an intermediate 'optimum' temperature for development. In this study, optimum temperature for development was found to be between 25°C and 30°C. In *B. cucurbitae*, *B. dorsalis* and *B. oleae*, optimum temperatures for development have been reported to lie between 26°C and 30°C (Messenger and Flitters 1958; Tsitsipis 1980). Ekesi et al. (2006) have previously shown that *B. invadens* successfully completed development at 28°C which lie within the optimum range of 20–30°C reported in the present study. At 35°C, the duration of development for egg and larva was low and pupa suffered the highest mortality. This suggests that the upper developmental threshold for *B. invadens* lies between 30°C and 35°C. However, the damaging and irreversible effect of temperature of 35°C on development may be dependent on length of exposure. Indeed, conditions of high temperatures do not occur for extended periods of time during a given day. Indeed, all fruit fly developmental stages are sheltered from extremes of temperature [eggs and larvae in fruits and puparia occur in the soil under tree canopies

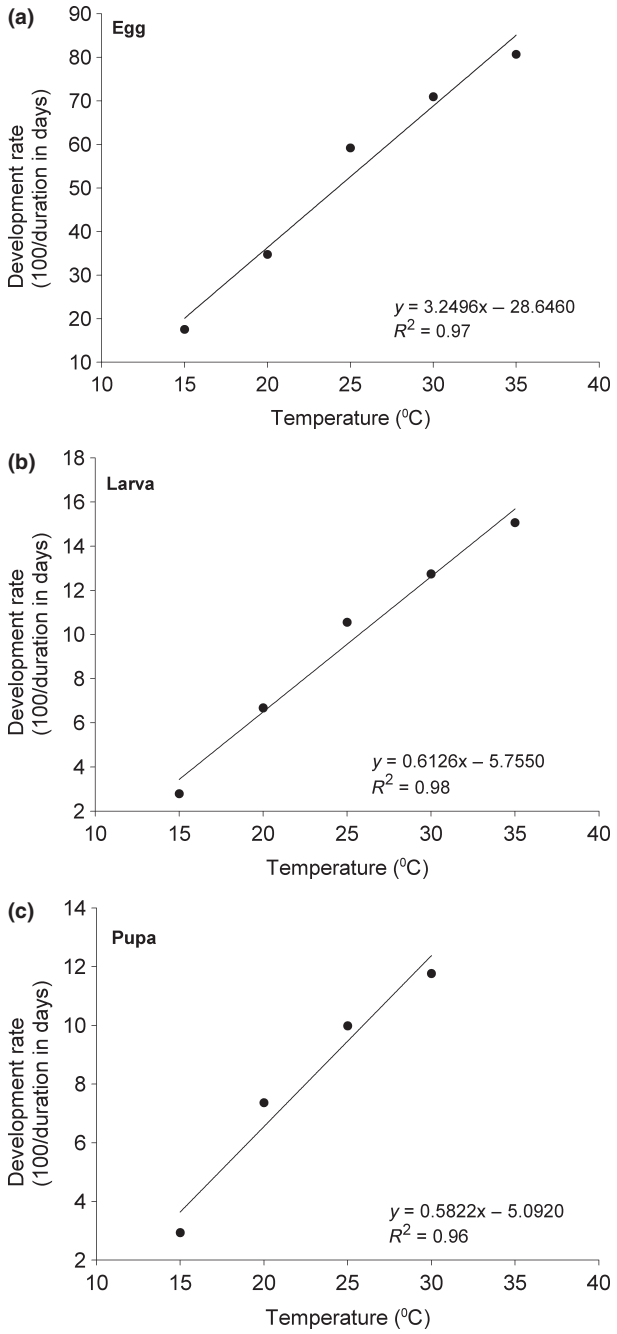

Fig. 1 Effect of constant temperature on development rates (100/duration in days) of different life stages of *B. invadens*: (a) egg; (b) larva; (c) pupa.

(Fletcher 1987)]. Therefore, extrapolation of these findings into field condition must be performed with caution.

The regressions were close to one, indicating a strong linearity of the model between 15°C and 35°C for egg and larvae and 15°C and 30°C for puparia. The linearity of this relationship was consistent with previous findings with Tephritidae (Vargas et al. 1996; Brévault and Quilici 2000; Duyck and Quilici 2002; Duyck et al. 2004). Because of the difficulties associated with data generation across the full range of temperatures, thermal constants or DD are often employed to account for differences in development rate because of temperature (Wagner et al. 1984). In this study, lower temperature threshold for *B. invadens* was 8.8°C, 9.4°C and 8.7°C for the egg, larva and puparium, respectively, with corresponding thermal constants of 31, 168 and 177 DD. In *B. zonata*, developmental thresholds for egg, larva and puparium were estimated to be 12.7°C, 12.6°C and 12.8°C with thermal constants of 25, 68 and 131 DD (Duyck et al. 2004). In *B. dorsalis*, Vargas et al. (1996) estimated lower temperature thresholds and thermal constants of 11.8°C, 5.6°C, 9.3°C and 21, 161, 176 DD for egg, larva and puparium, respectively. Our values are lower in comparison with those of *B. zonata* but within the range reported for *B. dorsalis*. This is perhaps not surprising given that *B. invadens* is believed to be a member of the *B. dorsalis* complex (Drew et al. 2005).

Bactrocera invadens has been described as a devastating quarantine pest (French 2005). In assessing the risk posed by this insect to horticultural industries outside its current range of distribution, one critical component should include determination of the likelihood of eggs hatching as commodities travel along pathways from the field to their final destination. Degree-days and developmental threshold become an important tool in such risk assessment (Sharpe et al. 1976; Thomas 1997). For example, in the event that any commodity is harvested soon after eggs of *B. invadens* are deposited in fruits, using the DD and lower temperatures established for this study, it implies that a 9.1 DD (egg DD + larva DD/2) is accumulated each day before egg hatch. It therefore means that untreated commodities with *B. invadens* eggs would need to be either utilized or destroyed within 8 days since it takes 31 DD for eggs to hatch. However, constant temperature studies underestimate developmental thresholds and actual thresholds tend to be lower than those obtained experimentally (Messenger 1964; Judd and McBrien 1994; Liu and Meng 1999). Degree-day models are also more accurate when temperatures fall within the lower and optimal development curve. The example given above must therefore be applied with caution also taking into account the protection from extremes of temperatures offered to the developmental stages by the commodities. However, the

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Table 2 Mean survivorship (% ± SE), pupae weight and adult characteristics of immature stages of *B. invadens* at five constant temperatures

Temperature (°C)	Mean ± SE (%)			
	Egg survival	Larval survival	Pupal survival	Mean adults/50 eggs
15	90.67 ± 1.83ab	83.54 ± 3.13b	72.16 ± 2.47b	27.01 ± 1.08b
20	94.80 ± 1.67a	90.29 ± 2.85ab	92.91 ± 3.79a	39.73 ± 2.17a
25	93.47 ± 1.44a	98.61 ± 0.57a	95.51 ± 1.30a	44.00 ± 0.90a
30	93.60 ± 1.48a	93.31 ± 1.70a	95.40 ± 0.90a	41.80 ± 1.38a
35	87.47 ± 1.58b	84.52 ± 3.18b	0.00 ± 0.00c	0.00 ± 0.00c

Means followed by different letters in the same column are significantly different (ANOVA and Student Newman–Keuls multiple range test, $P < 0.05$).

range of values obtained in this study should allow for more informed decision with respect to potential risk associated with *B. invadens* invasions and possible establishment.

Laboratory mass rearing of fruit flies are best carried out in controlled temperature conditions, and high survival rates coupled with short generation time are considered important criteria (Vargas et al. 1993; Kaspi et al. 2002). In our study, the survival rate for all development stages of *B. invadens* did not differ significantly between 20°C and 30°C. However, total developmental time was however highest at 20°C (31.5 days) compared with 25°C and 30°C (17.8–21.2 days). A suitable compromise between high survival rates and short developmental time would be to maintain the eggs, larvae and puparia at 25°C. Recent studies at *icipe* are also concentrating on mass rearing of *Fopius arisanus* (Sonan) for classical biological control of *B. invadens* (Mohamed et al., unpublished data), and our findings have direct bearing on parasitoids rearing for field releases. In this case, the strategy would be to allow for longer egg and larval duration of *B. invadens* for successful development of the parasitoids and a temperature of 20°C would therefore be appropriate since it delays onset of subsequent development stages while retaining high survivorship.

The extent to which an invasive species can extend its range or an existing species to respond to climate change is largely related to climatic factors such as temperature. Understanding the effect of temperature on survival of an insect which ultimately influences abundance and dispersal is fundamental to the study of insect ecology (Andrewartha and Birch 1954). In our study, survival of *B. invadens* was reduced at the temperature of 15°C. This may have probably contributed to limiting spread of the insect in highland areas of Kenya (Ekesi et al. 2006). In Australia, the bioclimatic potential of *Bactrocera tryoni* (Froggart) is related to thermal restrictions. Its altitude limits in the cooler southern parts are set by lethally low minimum winter temperatures (Meats 1981). In related thermotolerance studies with ours, there was no ovarian maturation of some adult tephritids reared at 15°C (Duyck and Quilici 2002; Duyck et al. 2004). We did not maintain our flies beyond emergence from puparia and cannot comment on the effect of low temperatures on ovarian maturation, but several morphotypes of *B. invadens* are known (Drew et al. 2005) and the possible existence of cold-hardening ecotypes of the insect cannot be ruled out. Huey et al. (1991) postulated that the relationship between development rate and temperature can be considered as the result of natural selection because this relationship changes when insects are exposed to different temperatures regimes for many generations. Gilbert and Raworth (1996) claimed that insects are selected for slow development in spring but fast development in summer. The entire physiological processes therefore have adaptive and ecological implications.

The data generated in this study offer valuable information on the development and survival of *B. invadens* under laboratory conditions and provide a basis for understanding the biology and ecology of the pest and development of control measures. Firstly, the data provides information that may be useful for optimizing environmental conditions necessary for mass rearing of *B. invadens*. The range of thermal parameters generated should help in the making of informed decisions regarding the quarantine risk associated with the insect. The data reported should also allow for development or improvement of models for better understanding of the bioclimatic potential of *B. invadens* and consequently its distributional limits and abundance. It is most likely that this information will become increasingly important as *B. invadens* continues to colonize new geographical areas.

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