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SHORT COMMUNICATION

Survival and development of different life stages of *Bactrocera zonata* (Diptera: Tephritidae) reared at five constant temperatures compared to other fruit fly species

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Introduction

The peach fruit fly, *Bactrocera zonata* (Saunders) is one of the most harmful species of Tephritidae. It causes large amounts of damage in Asia (Butani, 1976; Butani & Verma, 1977; Agarwal *et al.*, 1999) and is a serious pest of peach *Prunus persica* (L.) Batsch (Rosaceae) and custard apple *Annona squamosa* L. (Annonaceae) in India (Butani, 1976; Grewal & Malhi, 1987), as well as guava *Psidium guajava* L. (Myrtaceae) and mango *Mangifera indica* L. (Anacardiaceae) in Pakistan (Syed *et al.*, 1970). It is a polyphagous species attacking some 40 species of fruit and vegetables (White & Elson-Harris, 1992) and has also been recorded from wild host plants of the families Euphorbiaceae, Lecythidaceae and Rhamnaceae (Syed *et al.*, 1970; Kapoor & Agarwal, 1983).

Bactrocera zonata is native from India where it was first recorded in Bengal (Kapoor, 1993). It is present in numerous countries of tropical Asia: India, Indonesia (Sumatra, Moluccas), Laos, Sri Lanka, Vietnam, Thailand (White & Elson-Harris, 1992), Burma, Nepal, Bangladesh, and probably all of south-east Asia (Kapoor, 1993). The species has been captured in traps in California (Carey & Dowell, 1989), from where it has been eradicated.

More recently, *B. zonata* has been recorded in Egypt, where it has spread throughout the country and where control measures have been recently initiated. As from 2000, monitoring and exclusion measures have been implemented in neighbouring countries (J.P. Cayol, International Atomic Energy Agency, personal communication). In view of its current distribution, *B. zonata* is an important threat to the whole Mediterranean area.

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In the Indian Ocean islands, this species was first recorded in the Mascarenes in 1986, on Mauritius (57°40′E, 20°10′S). Then, a few adults were detected each year from 1991 onward on Reunion Island (55°29′E, 21°53′S). Despite an eradication programme initiated in 2000–2001, populations have developed considerably and the species is now considered to be established on the island. Due to its large host range, this invasive species represents a new major threat to agriculture on Reunion Island.

Although this species is of economic importance, it has been poorly investigated except for a development study by Mohamed (2000). It therefore appeared useful to carry out a detailed study of the influence of temperature on *B. zonata* in our laboratory to compare results with previous studies using the same methodology conducted on three *Ceratitis* species (Diptera: Tephritidae) with which *B. zonata* is currently competing on Reunion Island (Duyck & Quilici, 2002).

The results should allow for a better understanding of the potential limits of the distribution of this species on Reunion Island and in other countries and for a comparison of its biological characteristics with that of related species. The results should also be most useful in optimizing the rearing conditions that are necessary for biological studies and control methods, such as releases of parasitoids for biocontrol or releases of sterile flies for eradication programmes.

Materials and methods

The study was conducted with a laboratory culture of *B. zonata* collected originally from Indian almond, *Terminalia catappa* L. (Combretaceae) on the north-western side of Reunion Island and reared on artificial diet in the laboratory for three consecutive generations. Laboratory rearing was

conducted at a constant temperature of 25±1°C with L12:D12 photoperiod under artificial light supplemented by natural light which is important for mating behaviour in this species (preliminary observations). *Bactrocera zonata* was reared on the same artificial diets as the ones developed by J. Etienne for *Ceratitis capitata* (Wiedemann) (Duyck & Quilici, 2002).

The time required for 50% of individuals to achieve development to a particular stage was determined at the following constant temperatures: 15, 20, 25, 30 and 35°C (±1°C). Experiments were conducted in environmental chambers (Luminincube II, Analis, Belgium; MLR-350, Sanyo, Japan) maintained under a L12:D12 photoperiod and 80 ± 10% relative humidity.

The methodology was identical to the one used for previous studies of tephritids in our laboratory (Brévault & Quilici, 2000; Duyck & Quilici, 2002) thus allowing a proper comparison with the species previously studied. For each stage studied, the individuals within a cohort were collected around the middle of the period between the first and the last individual reaching a specified instar. Each stage was studied using a randomized block design, assuming replicates as multiple observations at each temperature. The detailed methodology used for each stage and for data analysis has been described previously (Duyck & Quilici, 2002).

Results

Relationship between developmental time and temperature

The developmental times for eggs and pupae of *B. zonata* significantly decreased over the range of 15–30°C but not between 30 and 35°C ($F = 930.8$, df = 4, 15, $P < 0001$; $F = 58094.9$, df = 4, 15, $P < 0.0001$ for egg and pupal stages respectively). The duration of the larval stages also significantly shortened over the range of 15–25°C ($F = 859.4$, df = 4, 15, $P < 0.0001$) but not between 25 and 35°C (table 1).

The highest range of variation (r.v.) for all immature stages was at 15°C ($F = 22.5$, df = 4, 55, $P < 0.0001$), and then decreased or remained equal with increasing temperature. The coefficient of variation (c.v.) varied with temperature for egg and larval stages ($F = 86.6$, df = 4, 15, $P < 0.0001$ and $F = 6.1$, df = 4, 15, $P < 0.005$, respectively).

A linear regression model was established for the three immature stages over the range of 15–30°C (fig. 1), but not at higher temperatures. For egg, larval and pupal stages, a strong and positive relationship was observed between temperature and development rate ($R^2 = 0.99$, 0.98 and 0.99, respectively). Lower developmental thresholds for the egg, larval and pupal stages were 12.7, 12.6 and 12.8°C, respectively. The corresponding thermal constants were 24.8, 68.2 and 131.0 day degrees (DD), respectively.

As no ovarian maturation was observed at 15, 20 and 35°C, there were too few values to establish a linear regression model for this stage. However, the developmental time for ovarian maturation was significantly shorter at 30°C compared to 25°C ($F = 23.8$, df = 1, 4, $P < 0.01$).

Preimaginal survivorship

Survivorship varied significantly relative to temperature for all immature stages ($F = 20.3$, df = 4, 55, $P < 0.0001$) (table 2). The percentage of adults emerging from a cohort of 100 eggs (i.e. recovery rate) peaked at 70% at 25°C compared to 1% at 15°C.

Survivorship in the egg stage was highest at 25°C and decreased significantly at higher and lower temperatures ($F = 20.3$, df = 4, 15, $P < 0.0001$). Survivorship of larvae was highest over the range of 20–30°C and lowest at 15°C ($F = 65.9$, df = 4, 15, $P < 0.0005$) and a similar pattern was observed for pupae ($F = 11.0$, df 4, 15, $P < 0.0001$).

Over the whole range of temperatures, survivorship was significantly lower for eggs than for larvae or pupae ($F = 10.6$, df = 2, 57, $P < 0.0002$). The relatively high instantaneous mortality values at 15°C indicated that the high mortalities observed were not due only to the long duration of immature development at this temperature (table 2).

Discussion

The linearity of the relationship linking temperature to developmental time between 15 and 30°C for *B. zonata* was consistent with previous studies on the development of other species of Tephritidae (Messenger & Flitters, 1958; Vargas *et al.*, 1996; Brévault & Quilici, 2000; Duyck & Quilici, 2002). At 35°C, the developmental periods were similar to those at 30°C and mortality was higher than that at 30°C, which meant that the upper temperature threshold was close to that value. This phenomenon is consistent with other studies in

Table 1. Mean developmental time and range of variation of immature stages of *Bactrocera zonata* at five constant temperatures.

Temp. (°C)	Egg development			Larval development			Pupal development			Ovarian maturation	Total (days)
	Mean ± SD (hours)	m.r.v. (hours)	m.c.v. (%)	Mean ± SD (days)	m.r.v. (days)	m.c.v. (%)	Mean ± SD (days)	m.r.v. (days)	m.c.v. (%)	Mean ± SD (days)	
15	244 ± 13 *a*	45 *a*	18 *c*	30 ± 1.6 *a*	7 *a*	23 *ab*	53 ± 0.3 *a*	4 *a*	7 *a*	No maturation	_
20	83 ± 1 *b*	20 *b*	25 *b*	10 ± 0.1 *b*	1 *b*	11 *c*	20 ± 0.2 *b*	1 *b*	5 *a*	No maturation	_
25	49 ± 2 *c*	14 *b*	27 *b*	5 ± 0.5 *c*	1 *b*	12 *c*	10 ± 0.1 *c*	1 *b*	5 *a*	24 ± 3.4 *a*	41
30	34 ± 1 *d*	18 *b*	53 *a*	4 ± 0.1 *c*	1 *b*	15 *c*	8 ± 0.1 *d*	1 *b*	10 *a*	13 ± 1.5 *b*	27
35	37 ± 2 *d*	4 *c*	11 *d*	4 ± 0.2 *c*	1 *b*	23 *a*	8 ± 0.1 *d*	1 *b*	8 *a*	No maturation	_

n = 4 replicates for egg, larval and pupal development ; n = 3 replicates for ovarian maturation.
m.r.v., mean range of variation (r.v. = max[developmental time] – min[developmental time], i.e. the lapse of time 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, $P < 0.05$).

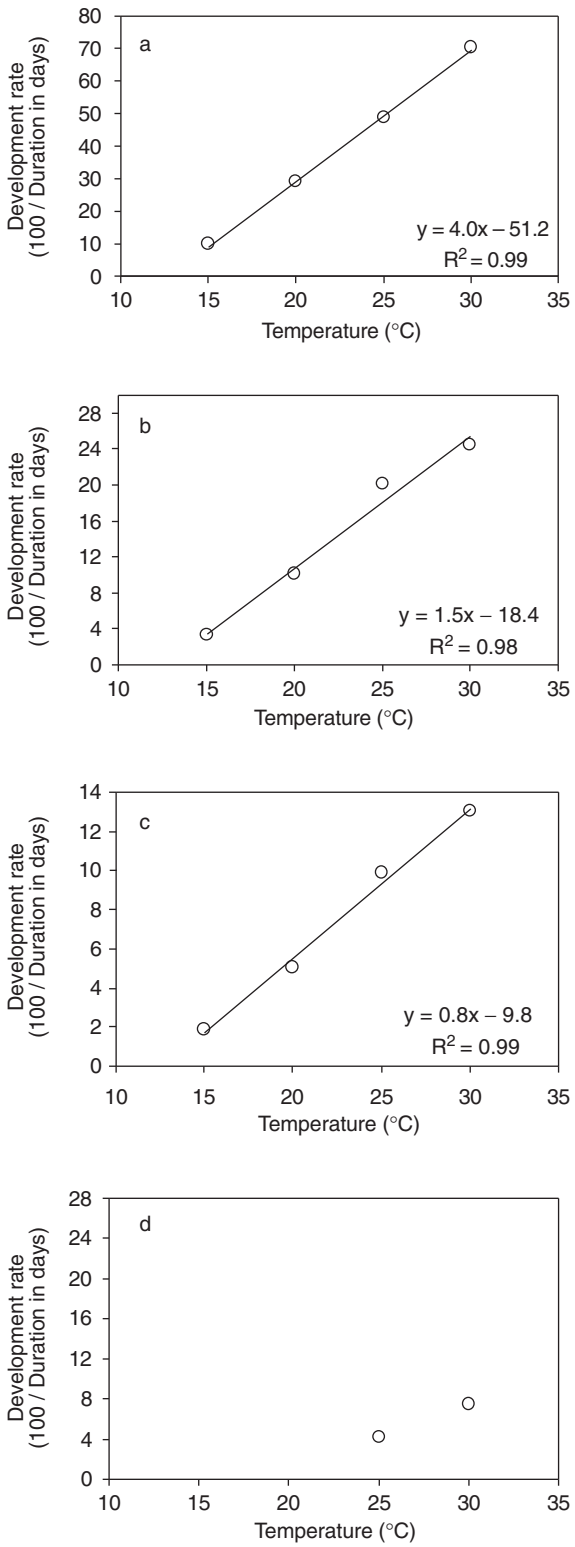

Fig. 1. Effect of constant temperatures on development rates (100 / duration in days) of different life stages of *Bactrocera zonata*, a) egg; b) larva; c) pupa; d) ovarian maturation of adult females.

which non-linear models fit better than linear models when approaching the temperature thresholds (Schoolfield *et al*., 1981; Wagner *et al*., 1984; Liu & Meng, 1999).

Mohamed (2000) calculated lower temperature thresholds of 10, 10 and 11.8°C for the egg, larval and pupal stages of *B. zonata* respectively, which were lower than those found in the present study. These differences may be explained by the strain used and by the type of food provided for the larvae, which was artificial diet compared to guava fruit used in the study of Mohamed (2000). Compared to the present results, the duration times found by Mohamed (2000) for the larval instars were shorter at low temperatures (e.g. 21 days vs. 30 days at 15°C) and longer at high temperatures (e.g. 7 days vs. 4 days at 35°C). Behavioural traits of cohorts at low temperatures, e.g. aggregation of larvae (Vargas *et al*., 1996) and nutritive value of food (Fernandes-Da-Silva & Zucoloto, 1993) may explain differences between the two studies. The higher larval survival observed in the present study compared to that recorded by Mohamed (2000) probably indicates that the artificial diet used is more suitable for larvae than guava fruits.

The threshold temperature for the egg stage of *B. zonata* was close to that of *Bactrocera dorsalis* (Hendel) reported by Vargas *et al*. (1997) whereas the threshold temperatures for the larval and the pupal stage were much higher than those of *B. dorsalis*.

During this study, ovarian maturation was obtained only over a very narrow range of temperature (25–30°C), as observed for *Ceratitis catoirii* Guérin-Mèneville (Duyck & Quilici, 2002). However, artificial laboratory conditions (constant temperatures, light intensity and photoperiod) during the present study may also have influenced the maturation of ovaries, as stated for other tephritid species by Tzanakakis & Koveos (1986).

Rearing conditions

The results obtained in this study show that the artificial diet previously developed for *C. capitata* is suitable for the development of larval instars of *B. zonata*. As a high degree of survival was observed for the larval stages at 25°C, this rearing diet can be considered favourable. The availability of a standardized artificial diet is useful for the regular production of flies for biological or behavioural studies in the laboratory and the development of a sterile insect technique (SIT) programme. However, before undertaking larger-scale rearing, it would be worth comparing the quality of the different diets developed for *B. zonata* by Qureshi *et al*. (1974) in Pakistan or by the Ministry of Agriculture on Mauritius (S. Permalloo and I. Seewooruthun, personal communication), or testing the diet used in Reunion Island for *Ceratitis rosa* Karsch (Duyck & Quilici, 2002) to determine the optimum ingredients.

A suitable compromise between short developmental time and a high survival would be to maintain the eggs, larvae and pupae at 30°C. This temperature should also be convenient for ovarian maturation of adult females but it would be necessary to verify that adult survival is not adversely affected at this temperature. However, adults could be maintained at a lower set temperature if required.

Geographical distribution

Bactrocera zonata shows higher low-temperature thresholds than those of the three *Ceratitis* species already

Table 2. Mean survivorship (%) and instantaneous mortality rate of immature stages of *Bactrocera zonata* at five constant temperatures (n = 4 replicates).

Temp. (°C)	Egg survival		Larval survival		Pupal survival		Emerged adults per 100 eggs
	Mean (%)	IM	Mean (%)	IM	Mean (%)	IM	
15	10 *c*	0.226	46 *c*	0.026	13 *d*	0.038	1
20	54 *b*	0.179	88 *ab*	0.013	96 *b*	0.002	46
25	71 *a*	0.165	98 *a*	0.004	100 *a*	0.000	70
30	58 *b*	0.378	89 *ab*	0.028	94 *b*	0.009	49
35	13 *c*	1.292	79 *b*	0.055	56 *c*	0.077	15

IM, instantaneous mortality rate (= – ln [survival] / developmental time).
Means followed by different letters in the same column are significantly different (ANOVA and Student Newman-Keuls multiple range test on Arcsin (Sqrt[X]), $P < 0.05$).

Table 3. (a) Temperature thresholds (*t*) and (b) thermal constants (*K*) of the different stages of *Ceratitis capitata*, *C. rosa* and *C. catoirii* according to Duyck & Quilici (2002) and *Bactrocera zonata* according to this study.

a

Stage	*C. capitata*	*C. rosa*	*C. catoirii*	*B. zonata*
	(°C)	(°C)	(°C)	(°C)
Egg	11.6	9.8	9.9	12.7
Larvae	10.2	3.1	8.9	12.6
Pupa	11.2	11.0	9.2	12.8
Ovarian maturation	8.9	8.0	–	–

b

Stage	*C. capitata*	*C. rosa*	*C. catoirii*	*B. zonata*
	(DD)	(DD)	(DD)	(DD)
Egg	28	35	35	25
Larvae	89	223	127	68
Pupa	143	147	194	131
Total (immature stages)	260	405	356	224
Ovarian maturation	90	138	–	–
Total	350	544	–	–

DD, day degrees.

present on Reunion Island (table 3). These higher developmental thresholds and the low survivorship of the different stages of *B. zonata* at 15°C should contribute to limit its spread in the highland areas of Reunion Island where *C. rosa* is the dominant species, (Duyck & Quilici, 2002). Moreover, the reduction in survivorship of the immature stages of *B. zonata* at 35°C is not as drastic as that observed for the *Ceratitis* species, indicating a preference for warm conditions (Duyck & Quilici, 2002). The developmental times are very short at high temperatures (4 days at 30 and 35°C) which confirms that this species is well adapted to hot climates and should thrive during the summer. *Bactrocera zonata* therefore represents a real threat to mango crops grown in the warmer, low altitude regions in the west of Reunion Island.

These results are consistent with current studies on tephritid populations dynamics on Reunion Island, in which *B. zonata* has not been found at altitudes higher than 900 m (unpublished results) while *C. rosa* is found readily at high altitudes (Etienne, 1982). However *B. zonata* is currently in the process of spreading and the limits of its altitudinal distribution have not yet been stabilized.

Even though temperature is the main factor influencing development, the influence of humidity would be worth studying, as this parameter is known to be important for pupal development of some tephritid species (Teruya, 1990). Also, biotic factors, and particularly interspecific competition, again adjusted by abiotic factors, can play a key role in determining the geographical distribution of tephritid species (Fitt, 1989) and deserve further study.

At a larger geographical scale, the results of this study indicate that the northern or southern latitudinal limits of *B. zonata* should not be as high as those of *C. capitata*. However, the population of *B. zonata* recently established in Egypt, not all that far from the northern limits of *C. capitata* in Corsica and southern France, in Europe, thrives well under a

Mediterranean climate and represents a major threat to neighbouring countries with similar climatic characteristics.

Invasions of new areas by *B. zonata* are most probably linked to the increase of international trade but may also be linked to global warming. Regarding its high temperature requirements, *B. zonata* may be particularly favoured by a warming up of the climate, thus making it a potentially important invasive pest for a growing number of areas around the world.

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