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Survival and development of different life stages of three *Ceratitis* spp. (Diptera: Tephritidae) reared at five constant temperatures

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Abstract

Fruit flies (Diptera: Tephritidae) are the most damaging pests on fruit crops on Réunion Island, near Madagascar. Survival and development of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), the Natal fruit fly, *C. rosa* Karsch and the Mascarenes fruit fly, *C. catoirii* Guérin-Mèneville were compared at five constant temperatures spanning 15 to 35°C. Durations of the immature stages of *C. capitata*, *C. rosa* and *C catoirii* ranged from 14.5–63.8, 18.8–65.7 and 16.8–65.8 days, respectively, at 30–15°C. The lower developmental threshold and thermal constant were calculated using the temperature summation model. The thermal constant for total development of the immature stages of *C. capitata*, *C. rosa* and *C. catoirii* were 260, 405 and 356 DD, respectively. Species differed mainly during the larval stages and ovarian maturation period, with smaller differences in the egg stage. *Ceratitis rosa* appeared to be better adapted to low temperatures than the two other species as it showed a lower larval developmental threshold of 3.1°C compared to 10.2°C for *C. capitata* and 8.9°C for *C. catoirii*. Overall, *C. catoirii* had a low survival rate within the range of temperatures studied. The different responses of the three *Ceratitis* species to various temperatures explain to some extent their distribution on the island. The results obtained will be used for optimizing laboratory rearing procedures and for constructing computer simulation models to predict fruit fly population dynamics.

Introduction

Fruit flies (Diptera : Tephritidae) cause serious damage on fruit and vegetable crops in most tropical countries (White & Elson-Harris, 1992). This applies to Réunion Island (55°29′ East and 21°53′ South, near Madagascar) where seven species of economic importance are present (Etienne, 1982), including three species of the genus *Ceratitis* that infest fruit crops: the Mediterranean fruit fly, *Ceratitis (Ceratitis) capitata* (Wiedemann), is abundant in dry areas; the Natal fruit fly, *Ceratitis (Pterandrus) rosa* Karsch, the most harmful species, is very polyphagous and widespread on the island from sea level to an altitude of 1500 m and *Ceratitis (Ceratitis) catoirii* Guérin-Mèneville, an endemic species from the Mascarenes, is found mostly in moist areas at low altitude on the windward side of the island.

While many references are available on the development of *C. capitata* from work conducted in various countries (Messenger & Flitters, 1958; Tassan *et al*., 1983; Crovetti *et al*., 1986; Delrio *et al*., 1986; Vargas *et al*., 1996), *C. rosa* has been poorly studied despite its economic importance in many African countries (Hancock, 1989). The biology of *C. catoirii* is apparently unknown. The relative importance of these species on Réunion Island may depend on inter-specific competition, affected by intrinsic (e.g. biotic potential of each species) or extrinsic (e.g. climate, presence and abundance of the host plants) factors. This study was designed to investigate the influence of temperature on developmental time and survivorship of the immature

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stages and ovarian maturation of female adults of these three species. Though data on the pre-imaginal development of the medfly *C. capitata* exist (Messenger & Flitters, 1958; Crovetti *et al.*, 1986; Delrio *et al.*, 1986; Vargas *et al.*, 1996), it was decided to carry out this study on the three species together, to allow comparison with previous studies and to harmonize methodology. The results should allow for a better understanding of the recorded distribution of the three species and will be useful for ongoing work on the modelling of fruit flies population dynamics on Réunion Island. The results should also be useful for optimizing the rearing conditions of each species in the laboratory.

Materials and methods

The study was conducted with laboratory cultures of fruit flies. The strains of *C. capitata* and *C. rosa* were started from samples of infested fruits collected on Réunion Island and larvae subsequently reared on artificial diet in the laboratory for more than 50 and *c.* 25 generations, respectively. The strain of *C. catoirii* was derived from stock collected from infested fruits of *Psidium cattleianum* Sabine (Myrtaceae) on the south-east side of the island, and reared on artificial diet in the laboratory for only four to six generations. Laboratory rearings were conducted at room temperature (mean monthly temperature ranging from 19.1 to 25.9°C during the year 2000).

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). Cohorts of insects were kept in environmental chambers (Luminincube II, Analis, Belgium; MLR-350, Sanyo, Japan) under conditions of L12:D12 photoperiod and 80 ± 10% relative humidity.

The methodology used was similar to the one developed for the study of the tomato fly *Neoceratitis cyanescens* (Bezzi) (Diptera: Tephritidae) by Brévault & Quilici (2000), using different cohorts of insects for each particular stage. For each stage studied, individuals comprising a cohort were collected around the middle of the period between the first and last individual reaching a specified instar. Each stage was studied using a randomized block design, assuming replicates as multiple observations at each temperature.

Egg stage

Eggs were collected from an artificial egg-laying device offered to a stock colony for a two-hour period. The device consisted of a red plastic funnel (13 cm diameter) with numerous small holes through which the females laid their eggs. A piece of orange fruit was placed inside the funnel so that its odour stimulated egg-laying. The duration of the egg stage was determined by transferring 100 randomly selected eggs (adhering to the inside of the funnel) onto a moist filter paper in a 9 cm diameter Petri dish using a fine brush. Eggs were observed at two-hourly intervals under a binocular microscope to determine the time and percentage of hatching.

Larval stage

Specific artificial diets (defined by Etienne (1973) and Etienne (unpublished)) were used for rearing *C. rosa* and *C. capitata*, respectively (table 1). For each species, two artificial diets were used, a solid one (referred to as no. 1) for eggs and young larvae and a liquid one (no. 2) added to a bran substrate for older larvae. *Ceratitis catoirii* was reared on the same artificial diets as *C. rosa*. One hundred neonate larvae (< 2 h) were carefully transferred to a plastic container (6 × 9 × 2 cm) lined with artificial diet no. 1 at the time when the majority of eggs had just hatched, in order to prevent possible selection of faster developing individuals. About two days later, the larvae were transferred to a box containing artificial diet no. 2 and bran, which was then placed inside a larger plastic container (25 × 12 × 8 cm), the bottom of which was covered by a layer of sand to allow pupation of mature larvae. For both artificial diets, the size of the boxes and the density of larvae resulted in excess food resources available to the larvae. The sand was kept dry for *C. capitata* and slightly wet for the two other species, as previous observations had indicated that a moderate level of moisture was favourable for pupation of these two species. Observations were made three times a day by sifting the sand in order to record the number of pupae.

Pupal stage

One hundred puparia (< 2 h) were randomly chosen at the time when the majority of larvae had just pupated, and

Table 1. Composition of the artificial diets for larvae of the three *Ceratitis* species studied (according to (Etienne, 1973) and Etienne (unpublished).

Ingredients	*C. capitata*		*C. rosa*/*C. catoirii*	
	Diet 1	Diet 2	Diet 1	Diet 2
Dehydrated carrot powder	56 g		50 g	12.5 g
Bewer's yeast	52 g	75 g	25 g	31.25 g
Sugar		150 g		50 g
Dehydrated potato	90 g			12.5 g
Water + Nipagine + Sodium benzoate	450 ml	500 ml	500 ml	500 ml
HCl at 1.65 %	20 ml	20 ml		15 ml
Agar			5 g	
Wheat germ				25 g

Diet 1, a solid diet for eggs and young larvae; diet 2, a liquid diet added to a bran substrate for older larvae.

then transferred into a plastic box, containing a moist piece of sponge (> 80% r.h.). Towards the end of the pupal stage, the number of newly emerged adults was recorded three times a day.

Ovarian maturation

When the majority of adult flies had emerged, 150 males and 150 females (age < 4 h) were confined in a transparent plastic cage (30 × 30 × 30 cm) aerated by meshed openings. Adult flies had free access to a diet of sugar and enzymatic yeast hydrolysate (ICN Biomedical, Aurora, USA) and a wet sponge as a water source. Ten females were dissected daily to check for the presence or the absence of mature eggs in their ovaries.

Temperature summation model

The approach adopted was based on the assumption that above a certain lower threshold for development, the temperature–development rate relationship is linear (Fletcher, 1989). Therefore, a constant number of heat units (usually expressed as day-degrees) above this threshold are required to complete development (Wagner *et al.*, 1984; Fletcher, 1989).

To establish this relationship, the development time of individual life stages (i.e. the time required for 50% of individuals to complete a given biological stage) was determined at a series of constant temperatures. Development rate (i.e. 100/developmental time) was plotted against temperature. The lower development threshold t (i.e. the temperature at which the development rate is zero) was then determined by extrapolation of the regression line back to the x-axis. The thermal constant K (i.e. the number of day-degrees above the lower threshold required to complete development) was calculated from the regression equation using the relationship $y = K / (x - t)$ (Fletcher, 1989).

The range of variation in developmental time (r.v. = max[developmental time] – min[developmental time], i.e. the lapse in time from hatching of the first to the last egg, from the first to the last larval pupation or from the first to the last adult emergence) was determined for each stage. The coefficient of variation was calculated as : c.v. = [100 × r.v.] / developmental time, for each instar.

Survival rate

Stage-specific survival rate was determined by dividing the number of individuals alive at the end of each stage by the initial number. Therefore, the final number of emerged adults per 100 eggs was calculated as the product of survival rates in the different stages from egg to adult stage. The instantaneous mortality rate (IM) was estimated as -ln [survival]/developmental time (Rijn *et al.*, 1995).

Data analyses

All development tests for immature stages were replicated four times. Ovarian maturation of females was determined using three replicates of ten females. Percentages of survivorship were transformed (Arcsin(Sqrt[x]) to stabilize the variance. Standard analysis of variance (ANOVA) was used to analyse developmental time or survival rate of the three species. Means were compared by Student Newman-Keuls multiple range tests ($P = 0.05$) (Statistica 99, Statsoft).

Results

Relationship between developmental rate and temperature for each species

A linear regression model between temperature and development or maturation rate was established for all three species of *Ceratitis* over the range of 15–30°C.

For *C. capitata*, a strong and positive linear relationship was observed between temperature and development and maturation rate ($R^2 > 0.92$) (fig. 1). Lower temperature thresholds for egg, larval and pupal stages, and ovarian maturation period were estimated as 11.6, 10.2, 11.2 and 8.9°C, respectively. The day degree (DD) requirements to complete the egg, larval and pupal stages, ovarian maturation, and total development were 28, 89, 143, 90 and 350 DD, respectively.

For *C. rosa*, a linear model was fitted between 15 and 30°C for the immature stages and between 20 and 30°C for ovarian maturation (fig. 2). Correlation coefficients were high for both egg and pupal stages and for ovarian maturation period ($R^2 \geqslant 0.98$) but lower for the entire larval stages ($R^2 = 0.88$). The lower developmental thresholds for the egg, larval and pupal stages and ovarian maturation period were calculated as 9.8, 3.1, 11.0 and 8.0°C, respectively. The corresponding thermal constants were 35, 223, 147, 138 and 544 DD, respectively.

The relationship between developmental rate of the immature stages of *C. catoirii* and temperature was strongly linear over the range of 15–30°C ($R^2 > 0.98$) (fig. 3). However, the linear model was not used for the ovarian maturation period because there were not enough data points to establish the relationship. The lower developmental thresholds for egg, larval and pupal stages were determined as 9.9, 8.9 and 9.2°C , respectively. The thermal constants were 35, 127, 194 and 356 DD for egg, larval, pupal stages, and total development of immature stages, respectively.

Preimaginal survivorship

Survivorship in the egg stage was significantly lower for *C. catoirii* than for either *C. capitata* or *C. rosa* over the range 15–25°C ($F = 47.2$, df = 2, 27, $P < 0.0001$) (table 2). *Ceratitis catoirii* also exhibited the highest instantaneous mortality during this stage among the three species. Highest egg mortality at 30°C was shown by *C. rosa*. At 35°C, none of the eggs of any of the species hatched.

Ceratitis capitata was the only species with larval stages surviving at 35°C despite a 95% mortality rate. At all tested temperatures, the survival rate of *C. capitata* larvae was higher or equal to that of the other two species ($F = 83.8$, df = 2, 45, $P < 0.0001$). The survivorship of *C. rosa* at 30°C was very low with a high instantaneous mortality. In this case, a significant amount of mortality was observed during the prepupal stage (on average 50 larvae popped out of the larval diet whereas the mean survival rate reached only 23%).

Mortality in the pupal stage reached 100% at 35°C for all three species. The survival rate of *C. catoirii* was significantly lower than that of *C. rosa* and *C. capitata* over the range 15–30°C ($F = 30.8$, df = 2, 36, $P < 0.0001$) though not

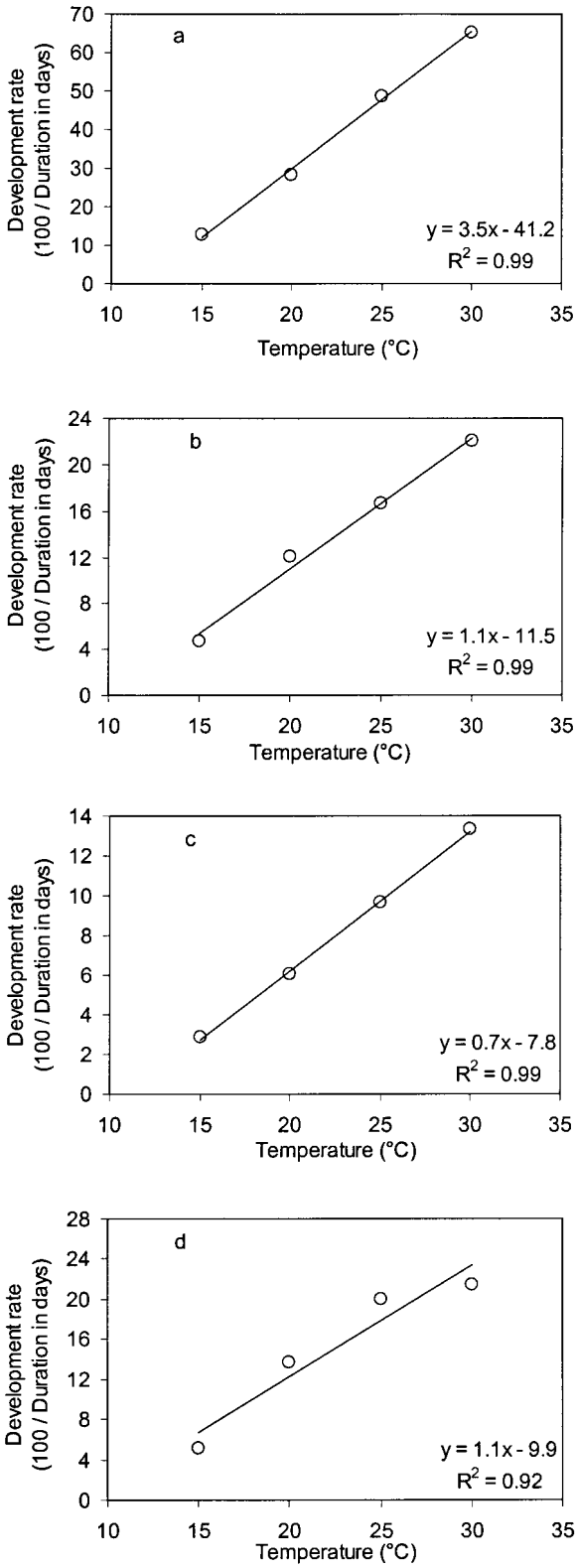

Fig. 1. Effect of constant temperatures on development rates (100/ duration in days) of different life stages of *Ceratitis capitata*: (a) egg; (b) larva; (c) pupa; (d) ovarian maturation of adult females.

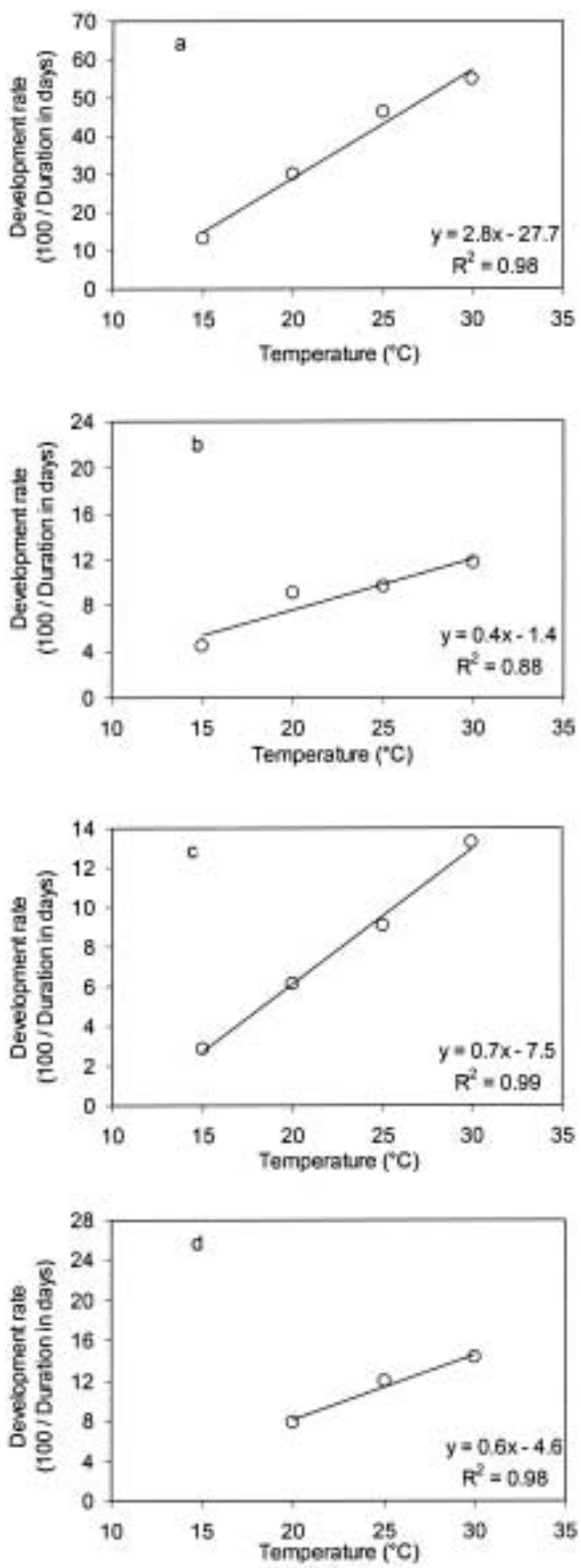

Fig. 2. Effect of constant temperatures on development rates (100/ duration in days) of different life stages of *Ceratitis rosa*: (a) egg; (b) larva; (c) pupa; (d) ovarian maturation of adult females.

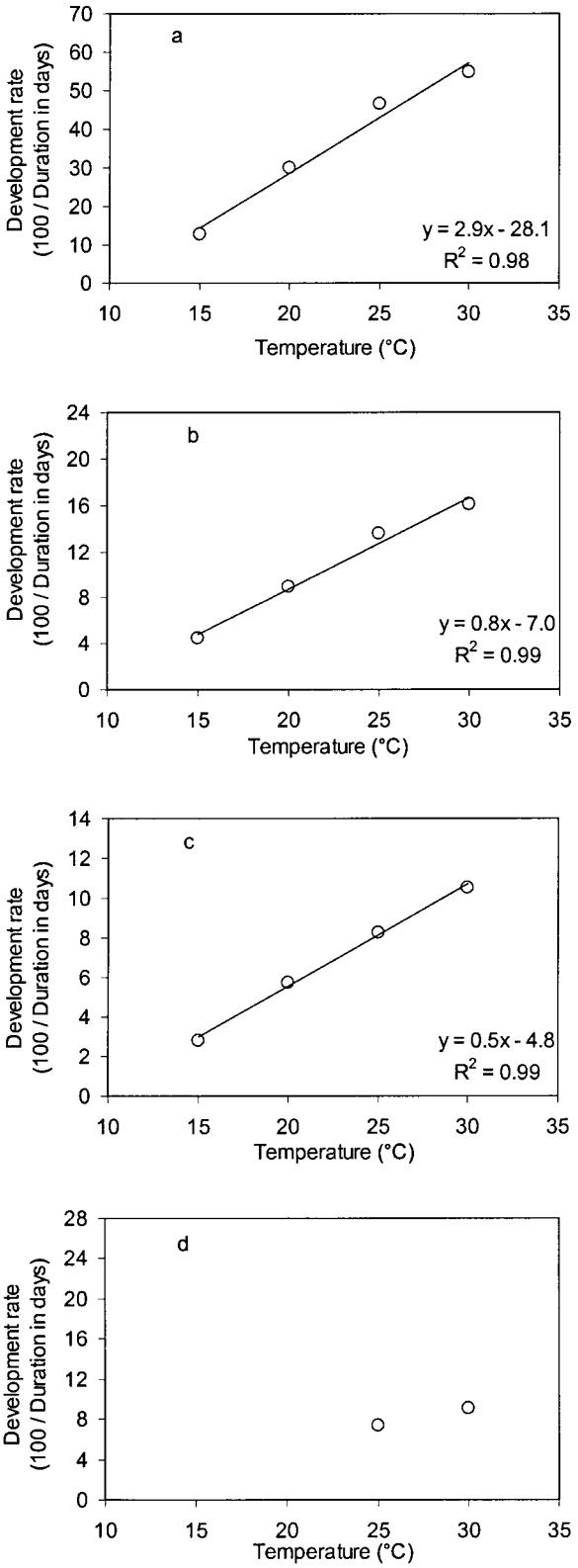

Fig. 3. Effect of constant temperatures on development rates (100/ duration in days) of different life stages of *Ceratitis catoirii*: (a) egg; (b) larva; (c) pupa; (d) ovarian maturation of adult females.

significantly different from that of *C. capitata* at 25°C. The survival rate of pupae was not significantly different between *C. rosa* and *C. capitata* at 15 and 20°C whereas at 25°C the survivorship of *C. rosa* was higher ($F = 8.6$, df = 2, 9, $P < 0.02$), and at 30°C definitely lower than that of *C. capitata* ($F = 53.0$, df = 2, 9, $P < 0.0005$). The highest instantaneous mortality rates were recorded for *C. catoirii* and *C. rosa* at 30°C.

Preimaginal developmental time

The duration of the egg stage varied significantly among species at each temperature except at 15°C (table 3). At 20°C, *C. capitata* exhibited an egg development period somewhat longer than that of *C. rosa* and *C. catoirii* ($F = 6.9$, df = 2, 9, $P < 0.02$) whereas at 25° and 30°C, the egg development period of *C. capitata* was shorter than that of the two other species ($F = 12.9$, df = 2, 9, $P < 0.005$; $F = 67.2$, df = 2, 9, $P < 0.0001$, respectively). The range of variation in developmental time (r.v.) did not differ among species except at 30°C, where the range of variation of *C. capitata* was lower than that of the two other species ($F = 4.5$, df = 2, 9, $P < 0.05$). The coefficient of variation (c.v.) did not vary either, except at 25°C where it was significantly lower for *C. rosa* ($F = 4.7$, df = 2,9, $P < 0.05$).

The larval developmental time of *C. capitata* was significantly shorter than that of the two other species over the range of 15–30°C ($F = 206.1$, df = 2, 36, $P < 0.0001$). At 15° and 20°C, the developmental time of *C. rosa* did not differ significantly from that of *C. catoirii* whereas at 25 and 30°C, *C. catoirii* showed faster larval development than *C. rosa* ($F = 296.8$, df = 2, 18, $P < 0.0001$). The range of variation of larval duration differed significantly among the three species at 25 and 30°C ($F = 676.4$, df = 2, 18, $P < 0.0001$): *C. rosa* had the greatest range of variation, while *C. capitata* had the smallest. The coefficient of variation was high for *C. catoirii* and *C. capitata* showing that the range of variation is important with respect to developmental time.

There was no significant difference in duration of the pupal stage of the three species at 15°C. By contrast, the pupal developmental time of *C. catoirii* was longer than that of *C. rosa* and *C. capitata* from 20 to 30°C ($F = 75.1$, df = 2, 27, $P < 0.0001$). The range of variation and its coefficient of variation were lower for *C. capitata* than for the two other species at 30°C ($F = 42.5$, df = 2, 9, $P < 0.001$; $F = 43.7$, df = 2, 9, $P < 0.001$, respectively).

Ovarian maturation duration

Maturation of eggs in *C. capitata*, *C. rosa* and *C. catoirii* was observed at 15–30°C, 20–30°C and 25–30°C, respectively (table 4). No maturation of eggs was observed in any species at 35°C. The developmental time for ovarian maturation was significantly different among the three species at each temperature within this range. Ovarian maturation of *C. capitata* was significantly faster than that of *C. rosa* at 20°C ($F = 15.1$, df = 1, 4, $P < 0.02$). *Ceratitis capitata* showed the shortest ovarian maturation period and *C. catoirii* the longest maturation period between 25° and 30 °C ($F = 54.9$, df = 2, 12, $P < 0.0001$).

Discussion

Physiological implications

High levels of survivorship of all stages of *C. capitata* were observed over the range 15–30°C consistent with

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

Stage	Species	15°C		20°C		25°C		30°C		35°C	
		Mean (%)	IM	Mean (%)	IM	Mean (%)	IM	Mean (%)	IM	Mean (%)	IM
Egg development	*C. capitata*	92 a	0.011	81 a	0.060	96 a	0.021	88 a	0.085	0 a	–
	C. rosa	88 a	0.017	80 a	0.067	91 a	0.044	74 b	0.167	0 a	–
	C. catoirii	68 b	0.049	67 b	0.120	60 b	0.236	83 a	0.105	0 a	–
Larval development	*C. capitata*	89 a	0.006	85 a	0.020	96 a	0.007	98 a	0.004	5 a	0.437
	C. rosa	69 b	0.017	54 b	0.056	87 b	0.013	23 c	0.172	0 b	–
	C. catoirii	54 b	0.028	77 a	0.023	66 c	0.057	64 b	0.072	0 b	–
Pupal development	*C. capitata*	84 a	0.005	95 a	0.003	79 b	0.023	79 a	0.031	0 a	–
	C. rosa	91 a	0.003	88 a	0.008	95 a	0.005	58 b	0.072	0 a	–
	C. catoirii	50 b	0.020	74 b	0.017	74 b	0.025	29 c	0.131	0 a	–

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

previous studies (Messenger & Flitters, 1958; Crovetti *et al*., 1986; Delrio *et al*., 1986; Vargas *et al*., 1996). Developmental time of *C. capitata* from egg to adult ranged from 16 to 64 days, between 30 and 15°C. These results for the immature stages are in general agreement with data from previous studies (Messenger & Flitters, 1958; Tassan *et al*., 1983; Crovetti *et al*., 1986; Delrio *et al*., 1986; Vargas *et al*., 1996).

Values for the temperature threshold and thermal constant were also consistent with previous studies, except for the period of larval development. In Hawaii, Vargas *et al*. (1996) found a lower temperature threshold of 5.2°C and a thermal constant of 139 DD for the larval stages of *C. capitata*, when using a linear model and working over a range of constant temperatures from 16 to 32°C, similar to the range used in our study. These important differences could result from the utilization of different rearing diets, the stock used, or from rearing conditions (e.g. larval density). These authors, however, recognized that the temperature threshold for larval development was probably underestimated in their study. The low value of this threshold in their study may have resulted from the behaviour of cohorts: larvae were observed crowding at the bottom of diet cups, probably to keep warm. Indeed, high densities of larvae in diet produce high levels of metabolic heat which can also affect developmental rate (Tanaka *et al*., 1972; Hooper, 1978). This behaviour was not observed in our study because of the low density of larvae used. Moreover, the threshold for egg plus larval stage calculated by Tassan *et al*. (1983) (t = 9.7°C) match our results. As the linear temperature summation model is less valid at extremes of temperature, it would be interesting to substantiate our data with further studies at lower temperatures, close to the developmental threshold, using non-linear models (Schoolfield *et al*., 1981; Wagner *et al*., 1984).

The lower developmental threshold for ovarian maturation of *C. capitata* has been estimated as 16.6°C by Tassan *et al*. (1983) compared to 8.1°C in our study. This difference may be due to laboratory adaptation of the strains tested or to different biological characteristics of *C. capitata* strains, as has been observed in other groups of insects (Lopez-Edwards *et al*., 1999).

No previous work has been published on the development of *C. rosa* at different temperatures. No immature stages of *C. rosa* were able to develop at 35°C and survivorship was low at 30°C. Mean larval development time and duration of ovarian maturation were significantly longer in *C. rosa* than *C. capitata* at all temperatures.

The biology of *C. catoirii* has not been studied before. The survivorship of this species was generally lower than that of *C. rosa* and *C. capitata* at the temperatures studied. The rearing diet used for *C. catoirii* in this study was developed originally for *C. rosa* and may not be optimal for this species. Lower survivorship rates of *C. catoirii* may be linked more to the dietary constraints factors than to intrinsic differences in survivorship abilities, though this rate is higher than that of *C. rosa* and that of *C. capitata* at certain given temperatures. It would be necessary to check the results obtained with *C. catoirii* on other artificial diets or on host fruits.

Linear regressions of developmental rate against temperature for all three species show that most of the correlation coefficients are close to one, indicating a strong linearity of the model between 15 and 30°C. The temperature summation model is thus a convenient means for estimating development times of these species over the range of temperatures studied. As the upper developmental thresholds have not been precisely investigated, it would be interesting to study development at temperatures ranging from 30 to 35°C in more detail to establish whether the species exhibit distinct temperature preferences.

In our study, the duration of ovarian maturation was used to assess the complete life cycle from egg-laying of one generation to egg-laying of the next one. However, Kasana & Aliniazee (1994), in their study on the effect of temperature on the pre-oviposition period of *Rhagoletis completa* Cresson (Diptera: Tephritidae), showed that numerous females never laid eggs despite the presence of mature eggs in their ovaries. If such a phenomenon should exist in the studied species, then the duration of their whole life-cycle would be underestimated in our study.

Comparisons of developmental times among the different species show that they differ mostly during the larval stages. As far as pre-imaginal development is concerned, *C. capitata* has a shorter life-cycle than the two other species within the range of temperatures studied. At 25°C for instance, the life-cycle of *C. capitata* (18 days) is three days shorter than that of *C. catoirii* and five days

Table 3. Mean developmental time and range of variation of immature stages of three *Ceratitis* species at five constant temperatures (n = 4 replicates).

Stage	Species	15°C			20°C			25°C			30°C			35°C		
		Mean ± sd	m.r.v.	m.c.v.	Mean ± sd	m.r.v.	m.c.v.	Mean ± sd	m.r.v.	m.c.v.	Mean ± sd	m.r.v.	m.c.v.	Mean ± sd	m.r.v.	m.c.v.
Egg development (hours)	*C. capitata*	187 ± 8 a	94 a	50 a	84 ± 3 a	51 a	61 a	49 ± 1 b	12 a	25 a	37 ± 1 b	13 b	37 a	No hatching		
	C. rosa	184 ± 9 a	90 a	49 a	80 ± 1 b	48 a	60 a	52 ± 1 a	10 a	19 b	44 ± 1 a	16 a	35 a	No hatching		
	C. catoirii	188 ± 7 a	99 b	53 a	80 ± 1 b	45 a	56 a	52 ± 1 a	14 a	26 a	44 ± 1 a	16 a	37 a	No hatching		
Larval development (days)	*C. capitata*	21 ± 0.4 b	5 a	24 a	8 ± 0.1 b	2 b	29 b	6 ± 0.1 c	2 c	27 c	5 ± 0.1 c	1 c	28 b	7 ± 0.4	2	31
	C. rosa	23 ± 0.6 a	7 a	29 a	11 ± 0.1 a	4 ab	38 ab	10 ± 0.6 a	8 a	77 a	9 ± 0.1 a	6 a	76 a	No pupation		
	C. catoirii	22 ± 0.6 a	5 a	23 a	11 ± 1.3 a	6 a	53 a	7 ± 0.4 b	4 b	52 b	6 ± 0.5 b	5 b	87 a	No pupation		
Pupal development (days)	*C. capitata*	35 ± 0.4 a	3 a	9 a	17 ± 0.6 b	3 a	16 a	10 ± 0.1 c	1 b	10 a	8 ± 0.1 b	1 c	7 c	No emergence		
	C. rosa	35 ± 0.6 a	4 a	10 a	16 ± 0.2 b	3 a	15 a	11 ± 0.2 b	2 ab	16 a	8 ± 0.1 b	2 a	31 a	No emergence		
	C. catoirii	36 ± 2.1 a	3 b	8 a	17 ± 0.1 a	4 a	20 a	12 ± 0.1 a	2 a	14 a	9 ± 0.1 a	1 b	15 b	No emergence		

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).
For a particular stage, means followed by different letters in the same column are significantly different (ANOVA and Student Newman-Keuls multiple range test, $P < 0.05$).

shorter than that of *C. rosa*. *Ceratitis catoirii* has a shorter pre-imaginal cycle than *C. rosa* at 25 and 30°C, while both species show a similar pre-imaginal development duration at 15 and 20°C. In addition, important differences in the duration of ovarian maturation were noticed between the three species.

Rearing conditions

The insects used were reared under laboratory conditions and thus might have behaved differently from individuals developing under more variable natural conditions. Whereas adults were reared all year round at room temperature (mean monthly temperatures ranging from 19.1 to 25.9°C during the year 2000), eggs, larvae and pupae were reared at a constant temperature of 25°C. This procedure may have resulted in a measure of selection for this temperature. This risk could be minimized by introducing 'wild caught' flies into the rearing cages, from time to time, but this may not always be effective, as sufficient mixing between the populations may prove difficult. On the other hand, Muniz (1987) found no significant differences in larval developmental times between a laboratory colony (reared for 19 years) and a field population of *C. capitata* studied at 26°C. As larval food composition can strongly influence larval development duration, it may be worthwhile to compare larval development on host fruits and artificial diet.

Geographic distribution

The high survival rates of *C. capitata* over a broad range of temperatures (15–30°C) may explain its wide distribution under different climatic zones (White & Elson-Harris, 1992). However, this species seems much more adapted to a Mediterranean rather than a tropical climate, where it prefers less rainy areas (Vargas *et al*., 1983; Harris & Lee, 1987). This could explain why it suffers from strong competition with *C. rosa* in the wetter areas on the windward side of Réunion Island (Normand *et al*., 2000). On mainland South Africa where both species also coexist, *C. rosa* indeed appears to be affected by a hot dry climate, such as in Western Cape Province, and is absent from many inland areas (Myburgh, 1961).

The presence of *C. rosa* in the highland areas of Réunion Island is not surprising as the minimum temperature thresholds for this species are lower than those of *C. capitata*, particularly during the larval stages. However, no ovarian maturation was observed in this species at 15°C even though the temperature threshold calculated for this stage was low (t = 5.9°C).

The lower survival of *C. catoirii* over the range of temperatures studied might explain the observed dominance of the other two species in interspecific competition in Réunion Island. *Ceratitis catoirii* is only present in low altitude areas on the island even though it has rather low temperature thresholds. It is possible that the lower temperatures experienced at medium and high altitudes may limit the reproductive success of this species, as it is unable to mature eggs at 15°C or even 20°C. As the rate of larval development and survival of egg and larval stages of *C. catoirii* are higher than those of *C. rosa* at 30°C, it might be expected that *C. catoirii* would be more competitive in the hotter coastal areas. Probably other components of the biotic potential of *C. rosa* may explain its dominance at low altitudes. However, the effects of temperature and

Table 4. Mean developmental time of ovarian maturation period of three *Ceratitis* species at five constant temperatures (n = 3 replicates).

Species	Mean developmental time ± sd (days)				
	15°C	20°C	25°C	30°C	35°C
C. capitata	20 ± 4.0	7 ± 0.6 b	5 ± 0.1 c	5 ± 0.6 c	No maturation
C. rosa	No maturation	13 ± 2.3 a	8 ± 1.5 b	7 ± 1.0 b	No maturation
C. catoirii	No maturation	No maturation	14 ± 0.6 a	11 ± 1.0 a	No maturation

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

interspecific competition do not fully explain why *C. catoirii* is more prevalent on the eastern wettest side of the island, where high humidity is probably favourable to this species. The lower diversity and abundance of host fruits utilized by *C. catoirii* on the western coast may be more important than temperature requirements in explaining its absence from this region of the island (Quilici & Jeuffrault, 2001).

Practical implications

Releases of parasitoids for biocontrol or releases of sterile flies for eradication programmes require regular, large scale production of mass-reared flies. Temperature plays a key role in the insect breeding process. These results should contribute to the improvement of rearing methods of the three species studied. A good compromise between achieving minimum developmental time and maximum survival rate should involve maintaining eggs and larvae of *C. capitata* and *C. catoirii* at 30°C and *C. rosa* at 25°C. A temperature of 25°C appears to be the most suitable for pupal development of the three species. However fluctuating temperatures may sometimes accelerate rearing procedures, in particular a lowering of temperature at night stimulates popping out (i.e. emergence) of *C. rosa* larvae from diet in readiness for pupariation (Myburgh, 1963; Etienne, 1973). The present work also provides information on the rearing of *C. catoirii* whose thermal requirements were unknown.

These data combined with results of other studies on trapping and population changes conducted on Réunion island over recent years, should be useful in the construction of computer simulation models of fruit fly population dynamics that will enable better monitoring and management of these important pests.

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