

## Age-Stage, Two-Sex Life Table of *Chrysodeixis chalcites* (Lepidoptera: Noctuidae) at Constant Temperatures on Semi-Synthetic Diet

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### Abstract

The golden twin-spot moth or tomato looper, *Chrysodeixis chalcites* (Esper), is a polyphagous and worldwide pest that causes important aesthetic damages to banana fruits in the Canary Islands. The life history parameters of *C. chalcites* were determined under laboratory conditions in base on the age-stage, two-sex life table at 15, 20, 25, 30, and 35°C, 65% relative humidity (RH), and a photoperiod of 16:8 (L:D) h, when it was reared on a semi-synthetic diet. The results show that *C. chalcites* was able to develop and survive from 15 to 30°C, but no development occurred at 35°C. Developmental threshold temperatures of the egg, larval, pupal, and total preoviposition stages were 10.42, 11.73, 11.22, and 9.42°C, respectively, and their effective accumulated temperatures were 58.31, 265.96, 118.57, and 562.39 degree-days, respectively. The adult longevity was reduced with increasing temperature, which ranged between 16.27 and 34.85 d for females and between 14.27 and 35.21 d for males. The highest values of net reproductive rate ( $R_0$ ) and fecundity were observed at 25°C, with 232.70 offspring and 1,224.74 eggs, respectively. Both the intrinsic rate of increase ( $r$ ) and finite rate of increase ( $\lambda$ ) increased significantly and mean generation time ( $T$ ) decreased significantly with increasing temperature. These results provide useful information that will allow predicting the impact of climate change on the distribution and population dynamics of *C. chalcites* and developing successful integrated management programs.

**Key words:** tomato looper, development, fecundity, population dynamic, climatic change

Temperature is considered, among climate-change elements, the most important abiotic factor directly affecting herbivorous insects (Bale et al. 2002). Several studies already showed that increased temperature may promote pest population growth, increase outbreak frequencies, and facilitate the geographic expansion of many pest species (Bale et al. 2002, Parmesan 2006, Lehmann et al. 2020), resulting in greater economic losses and reductions in food security (Sharma 2014). In this sense, the study of increased temperature effects on development and reproduction in agricultural pests is essential to predict population dynamics and develop sustainable and environment-friendly pest control strategies (Kroschel et al. 2013).

The golden twin-spot moth or tomato looper, *Chrysodeixis chalcites* (Esper) (Lepidoptera: Noctuidae) is a subtropical and extremely polyphagous species that causes severe damage in a large number of cultivated plants in many regions of Europe, the Mediterranean, the Middle East, and Africa (Cayrol 1972, Cabello et al. 1996, Polaszek

et al. 2012, CABI 2019). It has also been described as an invasive pest in tomato and green bean crops in Ontario, Canada (Murillo et al. 2013) and represents a new potential pathway of introduction in the United States (CPHST 2013). Currently, *C. chalcites* is one of the most important pests of banana crops in the Canary Islands, both in mesh-built greenhouses and in open fields (Fuentes et al. 2018), where its populations and damages have increased to a considerable level especially during the last decade (del Pino et al. 2011), possibly related to the elimination of some authorized insecticides (López-Cepero 2015), as well as the possible increased migration of this species linked to global climate change (Sparks et al. 2007). *Chrysodeixis chalcites* occurs throughout the banana production cycle and the larvae mainly attack the cigar leaf (the unfolding leaf) in young plants and developing fruits in adult plants (Vilardebo and Guérout 1964, del Pino et al. 2011), producing considerable external lesions that depreciate their commercial value (Perera and Molina

2007, del Pino et al. 2011). According to Fuentes et al. (2018), this pest can cause fruit damages estimated of up to 5.7% in commercial banana plantations when control measures are not effective.

Different studies have shown that the life cycle of *C. chalcites* is influenced strongly by climatic conditions and food composition (Bernal et al. 2018), being the development period of 28–29 d at 25°C on banana (Vilardebo and Guérout 1964). *Chrysodeixis chalcites* is a polyvoltine and migratory species and is present throughout the year in certain warm climate regions (Cayrol 1972, Cabello et al. 1996) with up to eight or nine generations per year in North Africa (Rashid et al. 1971, Harakly and Farag 1975). Immigrant specimens from North Africa or southern Europe have been regularly found in central and northern Europe in the late summer or autumn (Waring and Townsend 2003, Sparks et al. 2007, Collins et al. 2014), producing outbreaks both in open fields and protected crops, however, *C. chalcites* is unable to overwinter outdoors in these regions (Collins et al. 2014, CABI 2019). In the Canary Islands, *C. chalcites* is a resident species (Waring and Townsend 2003, del Pino 2011), frequently found throughout the year in coastal areas, where a Mediterranean-type climate is present (Fernández-Palacios and Nicholas 1995), with monthly average temperatures range from 16 to 24°C, and banana crops are developed (Galán-Sauco and Cabrera 2006).

Control of *C. chalcites* involves the repeated application of a limited number of authorized insecticides during the crop cycle (Hernández-Borges et al. 2009, del Pino et al. 2015), which may benefit the development of resistance (Broza and Sneh 1994, Horowitz et al. 1998), further reducing their effectiveness and increasing the production costs (Fuentes et al. 2018, Cakmak et al. 2019). However, inundative releases of the egg parasitoid *Trichogramma achaeae* Nagaraja and Nagarkatti (Hymenoptera: Trichogrammatidae) (Polaszek et al. 2012; del Pino et al. 2013, 2015), together the additional application of biological insecticides (*Bacillus thuringiensis* var. *kurstaki* and the nucleopolyhedrovirus of *C. chalcites*, ChchNPV) (Bernal et al. 2013, Simón et al. 2015, Fuentes et al. 2017) have been an important advance in the control of the pest in the Canary Islands. Therefore, practical application of biological control in association with other sustainable control techniques is the key for the integrated management of this pest (del Pino et al. 2015). The efficiency of these control methods depends on the treatment of pest populations at their most susceptible stages. Prediction of the *C. chalcites* development cycle would therefore greatly help in determining an optimal control schedule.

Understanding the survivorship and fecundity of the target pest under different environmental conditions is essential for the successful and effective application of any control strategy (Yang and Chi 2006). According to Li et al. (2015), life table studies are an effective tool that provide detailed data on the development time, survivorship and reproductive abilities of a pest population under different conditions. This knowledge is also required for predicting population dynamics (Chi and Su 2006), developing insect mass rearing systems (Chi and Getz 1988) and understanding how global warming and climate change can affect demographic processes and geographical distribution of a pest species (Gutierrez and Ponti 2014). With respect of lepidopteran pests as *C. chalcites* both males and females larvae eat and cause economic damages on the banana crops and, for this reason, it is essential to consider the influence of both sexes when studying their population dynamics. However, traditional female age-specific life table developed by different authors (Lewis 1942, Leslie 1945, Carey 1993) is exclusively focused on the females and pays no attention to the individual development rates, stage differentiation and males in a pest population. On the other hand, the age-stage, two-sex life table elaborated by Chi and

Liu (1985) and Chi (1988) include males and differences among individuals within each stage. In the last years, this class of life table has been utilized to characterize the population patterns of several insect pests (Gabre et al. 2005, Yang and Chi 2006, Yin et al. 2009, Bailey et al. 2010, Yin et al. 2010, Li et al. 2015), mites (Kavousi et al. 2009), and natural enemies (Chi and Yang 2003, Gabre et al. 2005, Yu et al. 2005, Chi and Su 2006, Huang and Chi 2012, Yu et al. 2013).

In the case of *C. chalcites*, the influence of temperature and diet on its development has been reported for several authors (Gaumont and Moreau 1961, Vilardebo and Guérout 1964, Rashid et al. 1971, Harakly and Farag 1975, Gasim and Younis 1989, Goodey 1991, Amate et al. 1998, Alami et al. 2014, Nouri-Ganbalani et al. 2015), but the influence of temperature on two-sex life tables have not been developed yet, as well as the determination of developmental threshold temperature and effective accumulated temperature values. Although such information is essential to predict its population dynamics and to develop management strategies under crop conditions. Therefore, the main objective of this study was to determine how an increase in rearing temperature may affect the development and survival of the immature stages of *C. chalcites*, as well as its reproductive parameters (e.g., adult survival, longevity, fecundity, and intrinsic rates of increase). This basic information will contribute to future studies regarding adequate phenological models for evaluation of pest management strategies and for population dynamics analysis, and it also may help to a better understanding of the effects of climate change on *C. chalcites* phenology.

## Material and Methods

### Insect Rearing

A laboratory colony of *C. chalcites* was established from natural populations originally collected on banana groves at Las Galletas (28° 01' 52" N, 16° 39' 32" W), Tenerife, Canary Islands, Spain. *Chrysodeixis chalcites* was reared following the methodology devised by Amate et al. (1998). First instar larvae were isolated in plastic vials (25 ml) and provided with a low-cost semi-synthetic diet composed by agar 20 g (Panreac Quimica S.L.U., Barcelona, Spain), powdered corn kernels 50 g (La Molineta, Tenerife, Spain), wheat germ 50 g (Casa Santiveri, Barcelona, Spain), brewer yeast 50 g (Casa Santiveri), ascorbic acid 4.5 g (Panreac Quimica S.L.U.), benzoic acid 1.8 g (Panreac Quimica S.L.U.), M-nipagine 1.8 g (Acofarma Distribución S.A., Barcelona, Spain), chloramphenicol 0.5 g (Panreac Quimica S.L.U.), vitamin additive 25 ml (S.P. Veterinaria, S.A., Tarragona, Spain), and distilled water 880 ml. This semi-synthetic diet has mainly been used to rear *C. chalcites* and other polyphagous lepidopteran species (Cabello et al. 1984; Amate et al. 1998, 2000). The use of this semi-synthetic diet provides the easiest manage and most consistent food source, and eliminates most problems involved with the production and maintenance of banana host plants, reducing the risks of contamination with entomopathogens (Cabello et al. 1984). Diet was replaced every 2 d and larvae were examined daily until the formation of the pupal chamber. Pupae were then sexed based on the morphological characteristics described by Goodey (1991) and kept individually in 25 ml plastic vials until adult emergence. Adult moths were transferred to cylindrical filter paper oviposition cages (14 cm high and 9 cm diameter) covered with Petri dishes and fed with a 10% honey solution supplied in a small cotton wick. The oviposition cages and cotton wick were replaced daily. Eggs were daily collected and deposited in plastic Petri dishes (9 cm diameter) until the emergence of the

neonate larvae. In both cases, breeding was completed in a climatic chamber at  $25 \pm 1^\circ\text{C}$ ,  $65 \pm 5\%$  relative humidity (RH) and a photoperiod of 16:8 (L:D) h.

### Development Time

The development of *C. chalcites* was studied at 15, 20, 25, 30, and  $35 \pm 1^\circ\text{C}$ , with a  $65 \pm 10\%$  RH and 16:8 (L:D) h photoperiod in climatic chambers. *Chrysodeixis chalcites* was reared for one generation at each temperature before to start the trials. Twenty pairs of moths were randomly chosen from the laboratory colony and confined inside cylindrical oviposition cages at the corresponding temperature. After 24 h, adults were removed and a minimum of 100 eggs (0–24 h old) were placed in plastic Petri dishes. Each isolated larvae represented a replicate. The eggs were daily examined, and the incubation period was registered. The neonate larvae hatched from eggs were individually isolated, using a camel hairbrush, in 25 ml plastic vials covered on the top with a mesh net for aeration and fed ad libitum with the semi-synthetic diet described above. The diet was replaced every 2 d. Larvae were daily examined to determine the survival and development time (molt) of every larval instar through the visual observation of the cephalic capsules, as well as the duration and survivorship of the pupal stage and the sex ratio of emerging adults.

### Oviposition Period, Fecundity, and Longevity

Moths less than 1 d old (<24 h) obtained in the development studies were paired (one female and one male) and introduced in oviposition cages, where they were daily monitored recording the preoviposition and oviposition periods, fecundity (number of eggs deposited per female) and adult longevity.

### Age-Stage, Two-Sex Life Table

The raw data on *C. chalcites* life history were analyzed based on the age-stage, two-sex life table theory (Chi and Liu 1985, Chi 1988), by means of the TWOSEX-MSChart software (Chi 2013). Life table parameters were calculated, including age-stage specific survival rate ( $s_{xj}$ ) (where  $x$  is age in days and  $j$  is stage), age-stage specific fecundity ( $f_{xj}$ ), age-specific survival rates ( $l_x$ ), age-specific fecundity ( $m_x$ ), as well as the intrinsic rate of increase ( $r$ ), finite rate of increase ( $\lambda$ ), gross reproductive rate ( $GRR$ ), net reproductive rate ( $R_0$ ) and mean generation time ( $T$ ).

The age-specific survival rate includes both male and female, and is calculated according to Chi and Liu (1985) as  $l_x = \sum_{j=1}^k s_{xj}$  and  $m_x = \frac{\sum_{j=1}^k s_{xj}f_{xj}}{\sum_{j=1}^k s_{xj}}$ , where  $k$  is the number of pest stages. The intrinsic rate of increase was calculated by the bisection method from the Eule–Lotka equation as  $\sum_{x=0}^{\omega} e^{-r(x+1)} l_x m_x = 1$ , with the age indexed from 0 to  $\omega$  (maximum age) (Goodman 1982). The  $GRR$  was determined as  $GRR = \sum m_x$ . The finite rate of increase ( $\lambda$ ) was measured as  $e^r$ . The  $R_0$  was estimated as  $R_0 = \sum_{x=0}^{\omega} \sum_{j=1}^k s_{xj}f_{xj}$ . The mean generation time ( $T$ ) is the time required for the pest population to increase to  $R_0$ -fold of its population size at the stable stage distribution (i.e.,  $e^{rT} = R_0$  or  $\lambda^T = R_0$ ), and was determined as  $T = (\ln R_0)/r$ .

### Statistical Analysis

Development time, fecundity, and adult longevity data under different temperature regimes were transformed to  $\log_{10}(x+1)$ , while emergence rate data were transformed to arcsine. All transformed data were analyzed by ANOVA test using the GLM procedure

and the average values were compared by Tukey's test ( $P = 0.05$ ) by means of the statistical software IBM SPSS Statistics Version 22 (IBM Corp. 2013). The life table parameters were calculated using the TWOSEX-MSChart software (Chi 2013) and the results were plotted with SigmaPlot Version 14.0 (Systat Software, Inc.). The bootstrap technique with 100,000 resamples (Efron and Tibshirani 1993), also included in the TWOSEX-MSChart software, was used to estimate the means, variances, and standard errors of the population parameters. A paired bootstrap test was used for statistical analysis. Finally, the thermal constant and lower threshold temperature for development were calculated according to the linear model described by Ikemoto and Takai (2000),  $DT = k + tD$ ; where  $DT$  is the product of development time in days ( $D$ ) and temperature ( $T$ ) in degrees Celsius ( $^\circ\text{C}$ ). The intercept,  $k$ , is the thermal constant in degree days ( $^\circ\text{d}$ ), and the slope,  $t$ , the lower development threshold in  $^\circ\text{C}$ . The parameters  $t$  and  $k$  were determined by linear regression.

## Results

### Development Time

*Chrysodeixis chalcites* successfully developed to adulthood at temperatures from  $15^\circ\text{C}$  to  $30^\circ\text{C}$  on semi-synthetic diet (Table 1), however, no development took place at the highest temperature tested ( $35^\circ\text{C}$ ) and egg hatching failed, indicating that  $35^\circ\text{C}$  exceeded the upper threshold. Statistical analysis manifested a significant influence of temperature on egg hatchability ( $F = 21.568$ ,  $df = 3$ ;  $P < 0.0001$ ) and incubation period ( $F = 24,575.72$ ;  $df = 3$ ;  $P < 0.0001$ ) of *C. chalcites*. The lowest temperatures (15 and  $20^\circ\text{C}$ ) caused a significant decrease in the egg hatchability when compared with the highest temperature levels (25 and  $30^\circ\text{C}$ ), lasting to  $12.74 \pm 0.05$  d at  $15^\circ\text{C}$  and decreasing to  $3.08 \pm 0.02$  d at  $30^\circ\text{C}$ . In addition, the temperature had a significant effect on the larval ( $F = 455.26$ ;  $df = 3$ ;  $P < 0.0001$ ) and pupal ( $F = 516.82$ ;  $df = 3$ ;  $P < 0.0001$ ) stages of *C. chalcites*. The larval developmental time varied from  $51.59 \pm 1.08$  d at  $15^\circ\text{C}$  to  $16.80 \pm 0.51$  d at  $30^\circ\text{C}$  (Table 1). According to the results, larval development of *C. chalcites* was completed in six instars at  $25^\circ\text{C}$ , but an extra larval stage (seventh) was observed in some larvae at 15 and  $20^\circ\text{C}$  that tends to prolong the life cycle, while other larvae no required more than five instars at  $30^\circ\text{C}$ . The pupal period varied from  $27.22 \pm 0.79$  d at  $15^\circ\text{C}$  to  $7.25 \pm 0.20$  d at  $30^\circ\text{C}$ . Mean total time of development significantly decreased with increasing temperature for both females ( $F = 715.43$ ;  $df = 3$ ;  $P < 0.0001$ ) and males ( $F = 1,165.86$ ;  $df = 3$ ;  $P < 0.0001$ ), and for all individuals combined ( $F = 1,785.64$ ;  $df = 3$ ;  $P < 0.0001$ ). Means total time of development ranged from  $27.27 \pm 0.58$  d at  $30^\circ\text{C}$  to  $91.81 \pm 0.77$  d at  $15^\circ\text{C}$ . There were no significant differences between male and female total time of development at all temperatures tested.

### Modeling Developmental Rates

Developmental rates of each immature life stage of *C. chalcites* fit the linear model suggested by Ikemoto and Takai (2000). The thermal constant ( $k$ ) and the lower thermal threshold ( $t$ ) values for the eggs were  $58.31 \pm 0.34$   $^\circ\text{d}$  and  $10.42 \pm 0.06^\circ\text{C}$  (mean values  $\pm$  SE) ( $r^2 = 0.956$ ;  $F = 27,825.73$ ;  $df = 1$ ;  $P < 0.001$ ), respectively. The thermal constant for the larvae was  $265.96 \pm 13.09$   $^\circ\text{d}$  and the lower thermal threshold  $11.73 \pm 0.44^\circ\text{C}$  (mean values  $\pm$  SE) ( $r^2 = 0.861$ ;  $F = 697.27$ ;  $df = 1$ ;  $P < 0.001$ ). The thermal constant for the pupae was  $118.57 \pm 3.39$   $^\circ\text{d}$  and the lower thermal threshold  $11.22 \pm 0.25^\circ\text{C}$  (mean values  $\pm$  SE) ( $r^2 = 0.946$ ;  $F = 1,974.79$ ;  $df = 1$ ;  $P < 0.001$ ). Finally, the thermal constant and the lower thermal threshold values for the total preoviposition period (TPOP) were

**Table 1.** Duration of the development (days) (mean  $\pm$  SE) of *Chrysodeixis chalcites* reared at different temperatures

Developmental stage	15°C		20°C		25°C		30°C	
	<i>n</i>	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE
Egg	114	12.74 $\pm$ 0.05a	140	5.06 $\pm$ 0.02b	783	4.08 $\pm$ 0.01c	245	3.08 $\pm$ 0.02d
First instar	76	7.91 $\pm$ 0.12a	102	5.35 $\pm$ 0.15b	78	3.33 $\pm$ 0.07c	82	2.70 $\pm$ 0.09d
Second instar	74	5.70 $\pm$ 0.17a	85	5.00 $\pm$ 0.27b	74	2.47 $\pm$ 0.08c	76	2.42 $\pm$ 0.10c
Third instar	74	6.24 $\pm$ 0.28a	78	4.99 $\pm$ 0.24b	69	2.45 $\pm$ 0.07c	75	2.32 $\pm$ 0.14c
Fourth instar	71	7.79 $\pm$ 0.31a	68	5.90 $\pm$ 0.34b	66	2.73 $\pm$ 0.10c	72	2.49 $\pm$ 0.11c
Fifth instar	65	9.83 $\pm$ 0.47a	63	6.57 $\pm$ 0.36b	55	2.75 $\pm$ 0.12d	64	3.75 $\pm$ 0.18c
Sixth instar	39	11.97 $\pm$ 0.50a	41	7.07 $\pm$ 0.45b	39	3.36 $\pm$ 0.15c	27	5.59 $\pm$ 0.30c
Seventh instar	4	9.50 $\pm$ 3.75a	10	9.60 $\pm$ 1.19b	-	-	-	-
Prepupa	27	4.52 $\pm$ 0.21a	37	1.70 $\pm$ 0.11b	36	1.00 $\pm$ 0.00c	54	1.00 $\pm$ 0.00c
Larva	27	51.59 $\pm$ 1.08a	37	36.03 $\pm$ 1.10b	36	17.42 $\pm$ 0.30c	54	16.80 $\pm$ 0.51c
Pupa	27	27.22 $\pm$ 0.79a	31	13.65 $\pm$ 0.43b	36	7.86 $\pm$ 0.13c	48	7.25 $\pm$ 0.20c
Preadult duration								
All	27	91.81 $\pm$ 0.77a	31	54.48 $\pm$ 0.72b	36	29.28 $\pm$ 0.67c	48	27.27 $\pm$ 0.58c
Female	13	90.08 $\pm$ 1.19a	18	54.28 $\pm$ 1.01b	19	29.05 $\pm$ 0.99c	22	27.14 $\pm$ 0.92c
Male	14	93.43 $\pm$ 0.97a	13	54.77 $\pm$ 1.01b	17	29.53 $\pm$ 0.88c	26	27.38 $\pm$ 0.71c
Egg hatchability (%)	-	50.74 $\pm$ 6.93b	-	46.67 $\pm$ 1.45b	-	94.05 $\pm$ 1.55a	-	84.34 $\pm$ 4.24a

Means followed by different letters in the same row are significantly different at  $P < 0.05$  (Tukey test).

**Table 2.** Adult longevity and reproductive parameters (mean  $\pm$  SE) of *Chrysodeixis chalcites* reared at different temperatures

Parameter	15°C		20°C		25°C		30°C	
	<i>n</i>	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE	<i>n</i>	Mean $\pm$ SE
Female longevity (d)	13	34.85 $\pm$ 1.57a	18	27.17 $\pm$ 0.93b	19	20.37 $\pm$ 0.31c	22	16.27 $\pm$ 0.47d
Male longevity (d)	14	35.21 $\pm$ 1.90a	13	20.69 $\pm$ 1.66b	17	14.71 $\pm$ 0.48c	26	14.27 $\pm$ 0.38c
APOP (d)	13	7.15 $\pm$ 0.56a	18	3.89 $\pm$ 0.44b	19	3.00 $\pm$ 0.11b	22	1.64 $\pm$ 0.22c
TPOP (d)	13	97.23 $\pm$ 1.09a	18	58.17 $\pm$ 1.71b	19	32.05 $\pm$ 0.46c	22	28.77 $\pm$ 0.72c
Oviposition period (d)	13	21.15 $\pm$ 1.62a	18	20.00 $\pm$ 1.28a	19	14.37 $\pm$ 0.30b	22	13.27 $\pm$ 0.57b
Fecundity (eggs per female)	13	556.38 $\pm$ 82.18b	18	464.22 $\pm$ 66.59b	19	1224.74 $\pm$ 55.71a	22	550.95 $\pm$ 48.23b

Means followed by different letters in the same row are significantly different at  $P < 0.05$  (Tukey test).

562.39  $\pm$  70.21 °d and 9.42  $\pm$  1.16°C (mean values  $\pm$  SE) ( $r^2 = 0.971$ ;  $F = 66.10$ ;  $df = 1$ ;  $P < 0.001$ ), respectively.

### Fertility

The effects of different temperatures on the adult longevity, preoviposition, and oviposition periods, and fecundity of *C. chalcites* are given in Table 2. The male and female adult longevity was significantly different between the temperatures studied. The highest female longevity was obtained at 15°C (34.85  $\pm$  1.57 d) and lowest at 30°C (16.27  $\pm$  0.47 d) ( $F = 94.346$ ;  $df = 3$ ;  $P < 0.0001$ ). The male longevity was also longest at 15°C (35.21  $\pm$  1.90 d) and shortest at 30°C (14.27  $\pm$  0.38 d) ( $F = 81.020$ ;  $df = 3$ ;  $P < 0.0001$ ). The total fecundity of *C. chalcites* was influenced by different constant temperatures ( $F = 34.821$ ;  $df = 3$ ;  $P < 0.0001$ ) and was highest at 25°C (1,224.74  $\pm$  55.71 eggs) and lowest at 20°C (464.22  $\pm$  66.59 eggs). The fecundity was greatly reduced at 15, 20, and 30°C. However, fecundity at 20°C was not significantly different from that at 15 or 30°C (Table 2). The adult preoviposition period (APOP) and TPOP of *C. chalcites* were significantly different for the tested temperatures ( $F = 42.693$ ;  $df = 3$ ;  $P < 0.0001$  for APOP and  $F = 753.63$ ;  $df = 3$ ;  $P < 0.0001$  for TPOP). The females developed at 30°C showed the shortest APOP and TPOP (1.64  $\pm$  0.22 and 28.77  $\pm$  0.72 d, respectively) in comparison to the other measured temperatures. The highest APOP and TPOP were detected

at 15°C (7.15  $\pm$  0.56 and 97.23  $\pm$  1.09 d, respectively). The oviposition period of *C. chalcites* was longer at 15°C (21.15  $\pm$  1.62 d) than at 20°C (20.00  $\pm$  1.28 d), 25°C (14.37  $\pm$  0.30 d), or 30°C (13.27  $\pm$  0.57 d).

### Age-Stage, Two-Sex Life Table

The population growth parameters of *C. chalcites* reared at different temperatures are shown in Table 3. The net reproductive rate ( $R_0$ ) was significantly different based on the rearing temperature. The highest value of  $R_0$  was observed at 25°C (232.70 offspring per individual) and the lowest at 20°C (59.69 offspring per individual). Furthermore, the GRR of *C. chalcites* was also significantly higher at 25°C (753.42 offspring per individual) compared with other temperatures. Temperature also had a significant influence in the intrinsic rate of increase ( $r$ ) and the finite rate of increase ( $\lambda$ ) values, recording the lowest at 15°C (0.0413 and 1.0422  $d^{-1}$ , respectively) and the highest at 25°C (0.1348 and 1.1442  $d^{-1}$ , respectively). Finally, the mean generation time ( $T$ ) ranged from 35.64 d at 30°C to 108.73 d at 15°C.

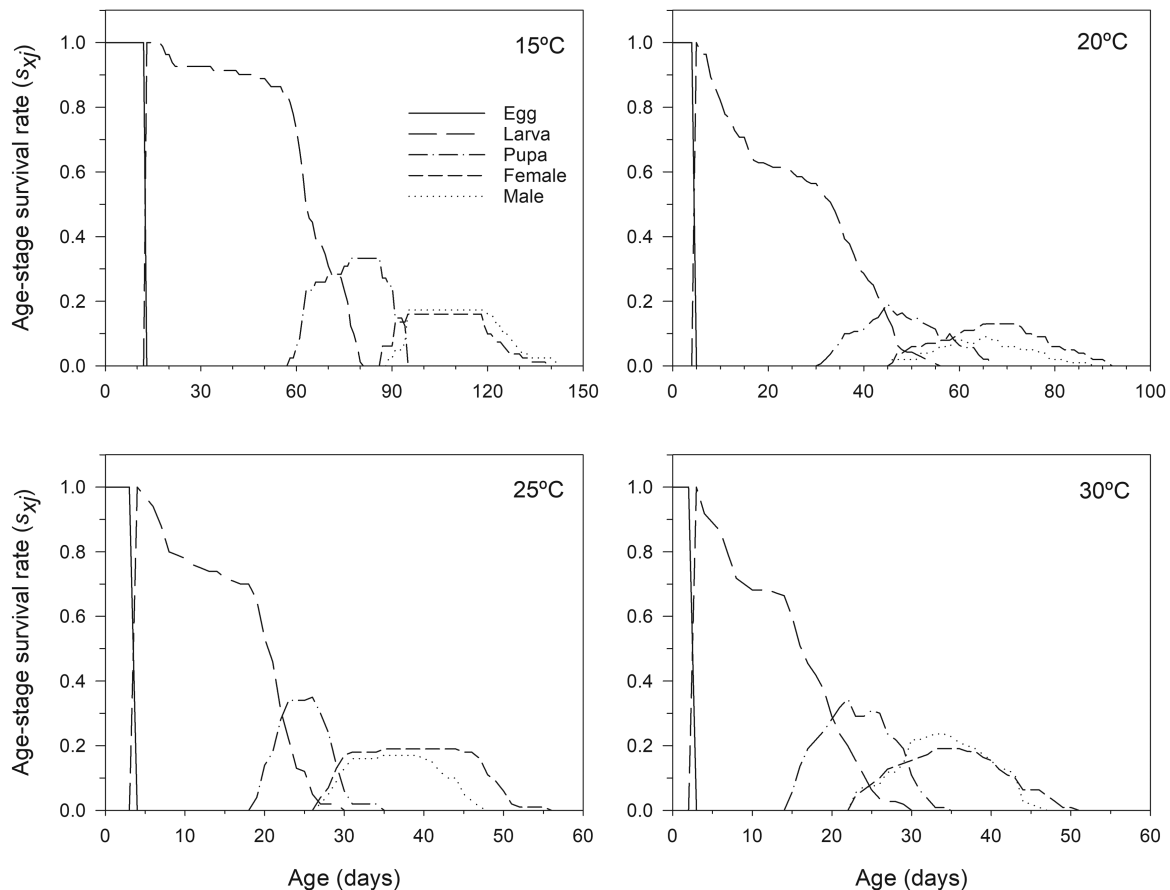
### Age-Stage Specific Survival Rate

The age-stage specific survival rate ( $s_{xj}$ ) of *C. chalcites* at the tested constant temperatures is shown in Fig. 1. It represents the probability that a newly hatched larva of *C. chalcites* will survive to

**Table 3.** Mean generation time ( $T$ ), net reproduction rate ( $R_0$ ), intrinsic rate of natural increase ( $r$ ), finite rate of increase ( $\lambda$ ), and  $GRR$  (mean  $\pm$  SE) of *Chrysodeixis chalcites* reared at different temperatures

Parameter	Temperature			
	15°C	20°C	25°C	30°C
$T$ (d)	108.73 $\pm$ 1.26a	68.24 $\pm$ 1.70b	40.43 $\pm$ 0.40c	35.64 $\pm$ 0.87d
$R_0$ (offspring)	89.29 $\pm$ 25.99b	59.69 $\pm$ 15.51b	232.70 $\pm$ 49.07a	110.19 $\pm$ 23.03b
$r$ ( $d^{-1}$ )	0.0413 $\pm$ 0.0029c	0.0599 $\pm$ 0.0042b	0.1348 $\pm$ 0.0060a	0.1319 $\pm$ 0.0076a
$\lambda$ ( $d^{-1}$ )	1.0422 $\pm$ 0.0031c	1.0617 $\pm$ 0.0044b	1.1442 $\pm$ 0.0064a	1.1411 $\pm$ 0.0086a
GRR (offspring)	294.00 $\pm$ 76.36b	405.66 $\pm$ 77.67b	753.42 $\pm$ 107.49a	418.19 $\pm$ 67.72b

Means in a row followed by different letters are significantly different at  $P < 0.05$  (Paired bootstrap test). SEs were estimated by bootstrapping (100,000 replications).

**Fig. 1.** Age-stage survival rate ( $s_{xj}$ ) of *Chrysodeixis chalcites* reared at 15, 20, 25, and 30°C, using the age-stage, two-sex life table.

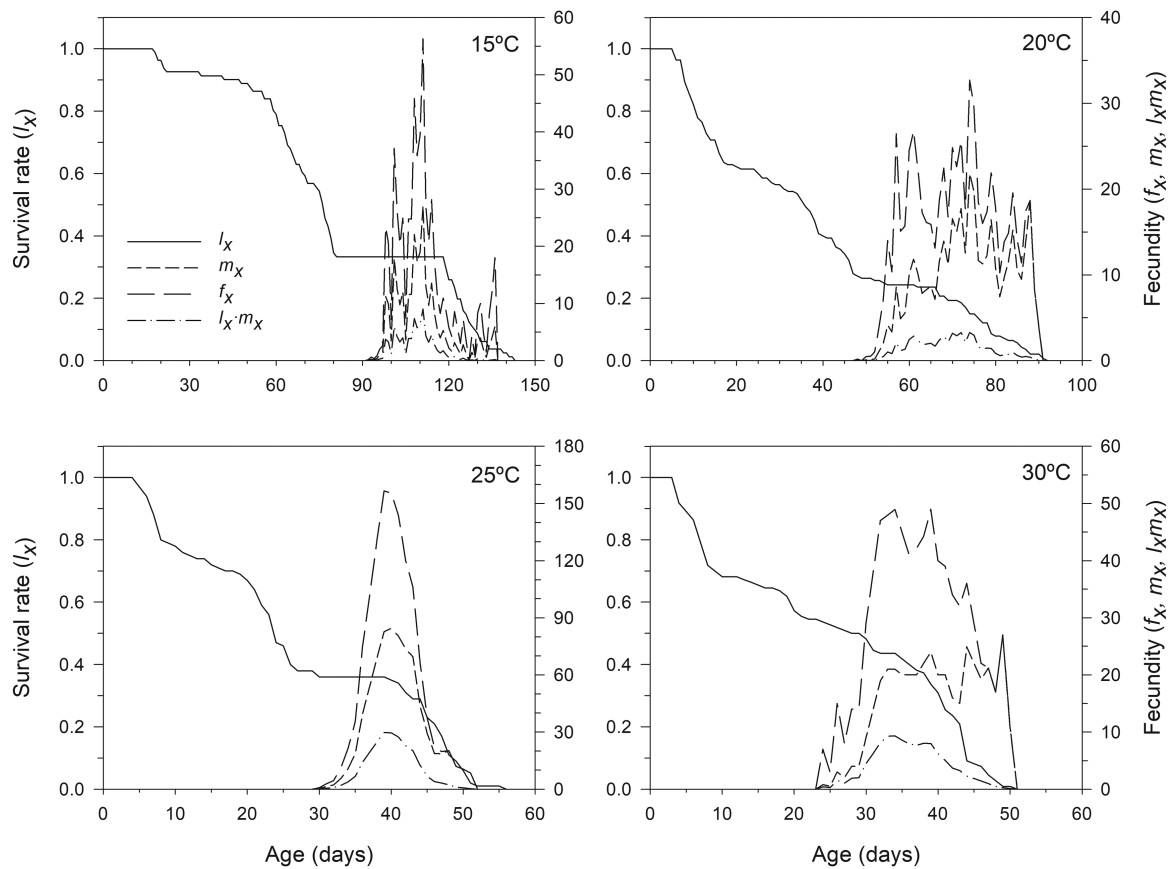
age  $x$  and develop to stage  $j$ , as well as the stage differentiation and survivorship of this species. Because of the different rates of development between the individuals and between the two sexes, there were significant overlaps among the different life stages in the survival curves. The egg survival rate was 1.0 at four temperatures tested. The probability that a neonate larva of *C. chalcites* reaches the pupal stage was 0.33, 0.26, 0.36, and 0.49 at 15, 20, 25, and 30°C, respectively. Finally, the pupal survival rates were 1.0, 0.84, 1.0, and 0.89 at 15, 20, 25, and 30°C, respectively.

#### Age-Specific Survival Rate, Age-Stage-Specific Fecundity, and Age-Specific Fecundity

The values for age-specific survival rate ( $l_x$ ), age-stage specific fecundity ( $f_{xj}$ ) and age-specific fecundity ( $m_x$ ) of *C. chalcites* are

illustrated in Fig. 2. They indicate that tomato looper can successfully survive and reproduce on semi-synthetic diet between 15 and 30°C. The age-specific survival rate ( $l_x$ ) indicates the probability that a newly hatched larva will survive to age  $x$  and is determined by joining all individuals of both sexes. However, the age-stage-specific fecundity ( $f_{xj}$ ) is the average number of offspring produced by *C. chalcites* individuals of the age  $x$  and stage  $j$  per day, and due to only females (the fourth stage) can produce offspring, there is only the single curve  $f$  (i.e., female). According to our results, first eggs were laid at the age of 92, 48, 30, and 24 d at 15, 20, 25, and 30°C respectively. The maximum daily fecundity (peak of  $f$  [i.e., female]) of *C. chalcites* over the above temperatures was 56.31, 32.71, 156.58, and 49.00 eggs, respectively, happening at the age of 111, 74, 39, and 34 d, respectively (Fig. 2).





**Fig. 2.** Age-specific survival rate ( $l_x$ ), age-stage specific fecundity ( $f_{xj}$ ), age-specific fecundity ( $m_x$ ) and age-specific maternity ( $l_x m_x$ ) of *Chrysodeixis chalcites* reared at 15, 20, 25, and 30°C, using the age-stage, two-sex life table.

### Life Expectancy

Figure 3 shows the age-stage-specific life expectancy ( $e_{xj}$ ) of *C. chalcites*, which estimates the time that an individual of age  $x$  and stage  $j$  is expected to live. According to our results, at 25°C a 27-d-old adult female will be alive on average another 22.42 d, while a 27-d-old adult male will be alive on average another 17.24 d. The maximum life expectancy of newborn *C. chalcites* was 83.73, 38.04, 27.71, and 26.26 d at 15, 20, 25, and 30°C, respectively.

### Reproductive Value

The curves of reproductive value ( $v_{xj}$ ) of *C. chalcites* are shown in Fig. 4. This parameter predicts the contribution of an individual from age  $x$  and stage  $j$  to the future population, and the reproductive value of a newborn ( $v_{01}$ ) is exactly the finite rate of increase (Fisher, 1930). Adult females of *C. chalcites* started to emerge from pupae at 27 d (Fig. 1) and commenced having offspring at 30 d at 25°C. The female reproductive value ( $v_{xj}$ ) significantly raised drastically to 365.10 at 98 d at 15°C, to 256.47 at 67 d at 20°C, to 685.02 at 37 d at 25°C, and to 271.28 at 31 d at 30°C. The reproductive value was highest at 25°C but lowest at 20°C, and it occurred earliest at 30°C but latest at 15°C.

### Discussion

According to Régnière et al. (2012), temperature is the most significant factor influencing growth and development of insects. The effects of temperature on insects are species specific. Development and reproduction occur within the range of upper and lower temperature

thresholds (Begon et al. 2006). Optimal environmental temperature allows rapid development and reproduction of insects, while temperatures above or below this range can have adverse effects (Bale et al. 2002, Régnière et al. 2012). Butterflies and moths show a sensitive reaction to the change of abiotic factors and have been considered as good indicator species in monitoring climate change (Kocsis and Hufnagel 2011). In this sense, various studies already showed that climatic warming can affect abundance (Kroschel et al. 2013, Huang and Hao 2020), geographic distribution (Bale et al. 2002, Hardy et al. 2014), phenology (Stefanescu et al. 2003, Hodgson et al. 2011) and migration (Sparks et al. 2005, 2007) of Lepidoptera. In the present study, we evaluated the influence of five constant temperatures (15, 20, 25, 30, and 35°C) on the developmental duration, survival rate, female fecundity, and life table parameters of *C. chalcites* when it is fed on a semi-synthetic diet under laboratory conditions. This information is essential to predict its population dynamics and to develop management strategies under crop conditions. Several authors (Gaumont and Moreau 1961, Vilardebo and Guérout 1964, Rashid et al. 1971, Harakly and Farag 1975, Goodey 1991, Alami et al. 2014) have previously shown the strong influence of different host plants and temperatures on the demographic parameters of *C. chalcites*. However, studies related to its demography on semi-synthetic diets are very limited (Amate et al. 1998). Our results exhibited that the developmental time of the four stages (egg, larvae, pupa, and adult) of *C. chalcites* was influenced by the temperature, decreasing the duration of each stage when it was increased from 15 to 30°C. According to our studies, no development occurred at 35°C and egg hatching failed, indicating that this tested temperature

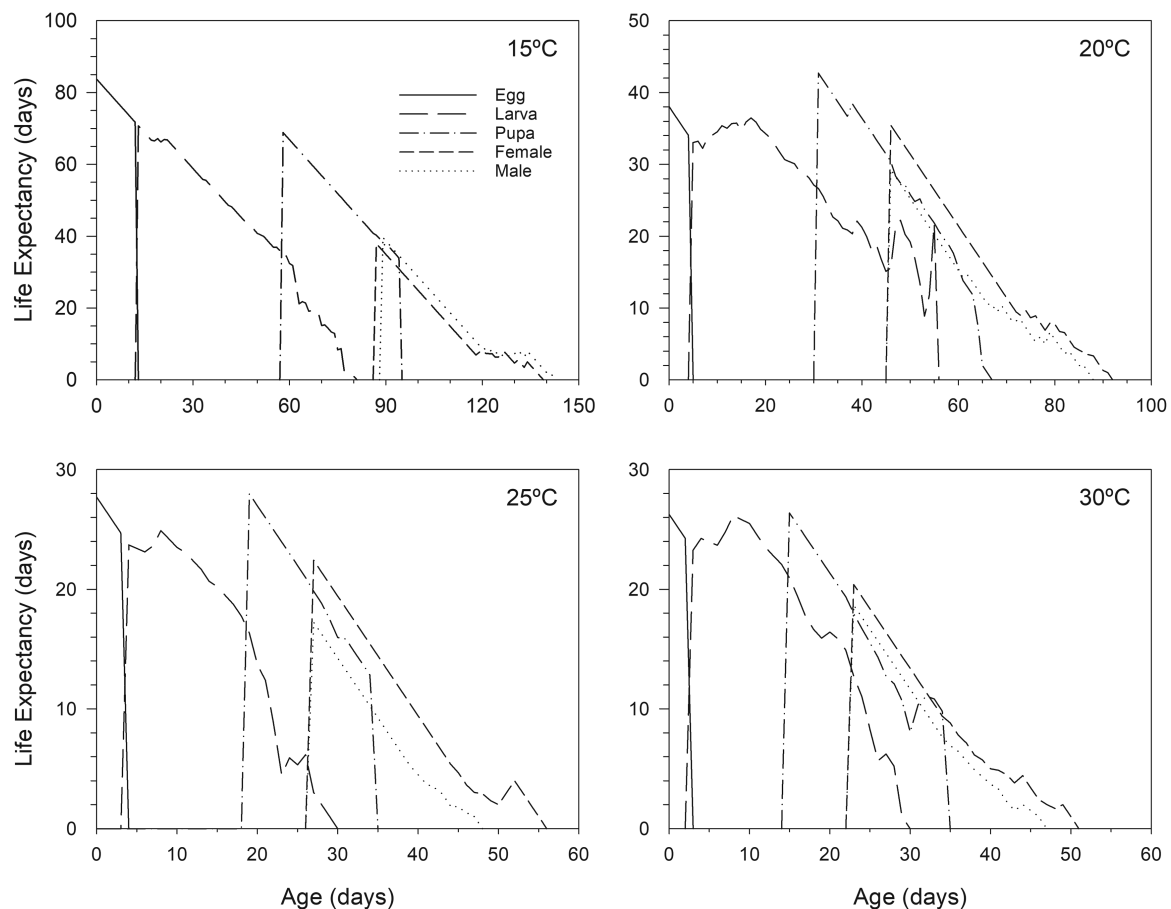


Fig. 3. Age-stage-specific life expectancy ( $e_x$ ) of *Chrysodeixis chalcites* reared at 15, 20, 25, and 30°C, using the age-stage, two-sex life table.

exceeded the upper threshold. Similar upper-temperature threshold value has been previously recorded for other Plusiinae (Noctuidae) species as *Trichoplusia ni* Hübner (Cabello 1988). Several authors recorded that the egg incubation period of *C. chalcites* at 25°C was 3 d on different host plants (Vilardebo and Guérout 1964, Rashid et al. 1971, Gasim and Younis 1989, Alami et al. 2014, Nouri-Ganbalani et al. 2015), which is lower than 4 d registered in Amate et al. (1998) and in our study, when *C. chalcites* is reared on semi-synthetic diet. However, the egg incubation period at 20°C was similar to that reported by Gaumont and Moreau (1961), but lower than published by others (Vilardebo and Guérout 1964, Goodey 1991). Other studies conducted under laboratory conditions recorded that the most frequent egg incubation period at 25°C for other Plussinae species varied from 3 to 4 d (Cayrol 1972, Cabello 1988, Chi and Tang 1993).

The larval development period varied from 16.80 to 51.59 d in accordance with the temperature and it was similar than the values published by Vilardebo and Guérout (1964) at 20 and 25°C on banana, but lower than published by others authors at 20°C on tomato (Gaumont and Moreau 1961, Rashid et al. 1971). Larvae developed on high temperatures (25 and 30°C) had a smaller duration of immature stages compared to the larvae reared on low temperatures (15 and 20°C). According to Cabello (1988), the developmental time in larval stage can commonly differ depending on the rearing conditions (temperature, humidity, etc.), host diet, or host phenology. Although some studies of *C. chalcites* did not specify the environmental conditions considered (Gaumont and Moreau 1961, Vilardebo and Guérout 1964), others were carried

out under comparable temperatures, but the RH varied from 40 to 80% (Rashid et al. 1971, Harakly and Farag 1975). In line with Amate et al. (1998), our results showed that *C. chalcites* pass through six larval instars when reared at 25°C on semi-synthetic diet. However, five instars are described by Alami et al. (2014) and Nouri-Ganbalani et al. (2015) when *C. chalcites* was fed with different cultivars of bean and tomato, respectively. Finally, Vilardebo and Guérout (1964) described that this species may have six to seven larvae instars on banana. According to Naseri et al. (2009), this variation in the number of instars of *C. chalcites* could be associated with changes in rearing conditions and the nutritional properties of the used host plant. In our experiments, five larval instars were recorded at 30°C and supernumerary larval stages were achieved at 15 and 20°C. The presence of supernumerary larval stages for *C. chalcites* depending on temperature and diet used have been previously reported by different authors (Gaumont and Moreau 1961, Vilardebo and Guérout 1964, Cayrol 1972), which can be a disadvantage in colonies reared in the laboratory for experimental purposes (Barrionuevo et al. 2012). Similar behavior has been described for other noctuid pests such as *T. ni* (Toba et al. 1973, Cabello 1988) and *Spodoptera exigua* Hübner (Belda 1994).

There are no references about the existence of diapause in *C. chalcites* populations. Results obtained here indicate that the increase of larval developmental time and the presence of supernumerary larval stages at low temperatures can influence the ability of this species to survive in the winter months as middle-instar larvae in the state of facultative diapause (Saulich et al. 2017). The pupal development time varied from 7.25 to 27.22 d according to the

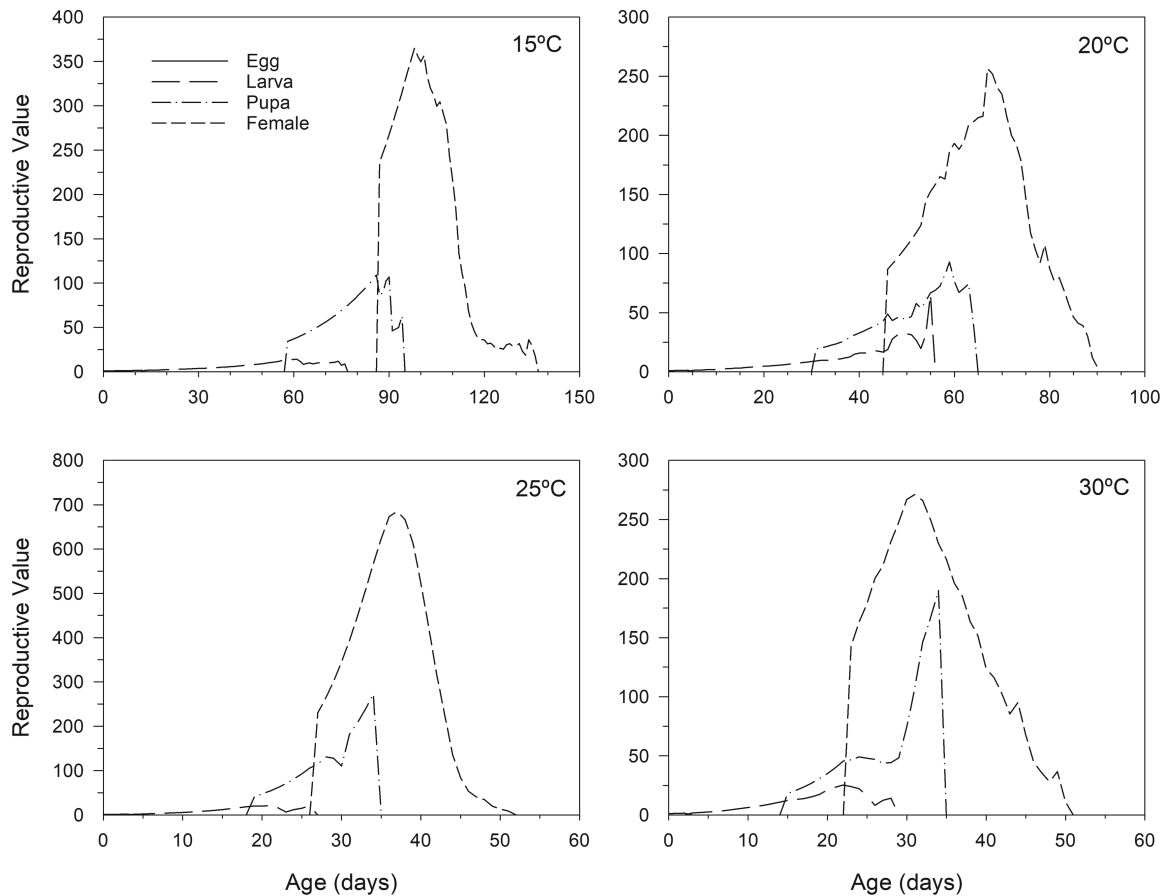


Fig. 4. Age-stage reproductive value ( $v_{xj}$ ) of *Chrysodeixis chalcites* reared at 15, 20, 25, and 30°C, using the age-stage, two-sex life table.

tested temperatures, with 7.86 d at 25°C, a substantially lower value than the 10.34 d recorded by Amate et al. (1998) using the same semi-synthetic diet that used in our study. Finally, the egg to adult development of *C. chalcites* at 25°C was completed in 29.31 d, very close to those published by other authors on different host plants (Harakly and Farag 1975, Alami et al. 2014, Nouri-Ganbalani et al. 2015), and the 31.81 d find by Amate et al. (1998) on semi-synthetic diet at the same temperature. Differences between our results and those could be ascribed to the different origin of *C. chalcites* populations (Vargas and Carey 1989), as well as to the different experimental conditions (rearing techniques, food, humidity, and photoperiod) (Jarošík et al. 2002, Lee and Roh 2010). However, the rearing techniques and semi-artificial diet used in our study have been successfully used to rear *C. chalcites* (Amate et al. 1998) and other polyphagous noctuids like *S. exigua* and *Helicoverpa armigera* Hübner (Cabello et al. 1984, Belda 1994, Amate et al. 2000) under laboratory conditions.

In this study, the developmental rates of each immature life stage of *C. chalcites* fit the linear model suggested by Ikemoto and Takai (2000) at the temperature interval of 15–30°C. Our results show that the developmental threshold temperature ( $t$ ) and the effective accumulated temperature ( $k$ ) values for eggs to adult preoviposition of *C. chalcites* were 9.42°C and 562.39 °d, respectively. This information could help to predict the number of generations per year, the phenology and geographical distribution of this important pest in the Canary Islands (del Pino et al. 2015, Fuentes et al. 2018). Based on the  $k$  and  $t$  values obtained for the TPOP and on the daily temperature data of 2017, 2018, and 2019 recorded in Las Galletas (Arona,

Tenerife), one of the main banana production regions of the Canary Islands, the effective accumulated temperatures for *C. chalcites* were 4317.00, 4015.95, and 4185.55 °d, occurring 7.67, 7.14, and 7.44 generations annually, respectively. Therefore, we predicted *C. chalcites* could occur between seven and eight generations annually, in line with the number of generations per year previously observed for natural populations in North Africa (Rashid et al. 1971, Harakly and Farag 1975) and the Canary Islands (del Pino 2011). Some authors have linked the existence of a long preoviposition period to the migratory nature of many species of the subfamily Plusiinae (Holloway et al. 1987, Saulich et al. 2017). However, although the ecology of *C. chalcites* is not much studied, considering previous phenology studies using pheromone traps (del Pino 2011) and the results obtained in this study, we could conclude that this species is clearly resident in the Canary Islands (Waring and Townsend 2003).

Our results suggest that environmental temperature has drastic implications on the adult longevity of *C. chalcites*. Female longevity was analogous those recorded by Alami et al. (2014) and Nouri-Ganbalani et al. (2015) at 25°C under laboratory conditions but differed from those reported by others (Rashid et al. 1971, Goodey 1991, Amate et al. 1998). However, few data on adult longevity are published for this moth under field conditions (Vilardebo and Guérout 1964). Thus, the results also prove that *C. chalcites* can reproduce through the studied temperature range of 15–30°C. According to Amate et al. (1998), the total fecundity was 1,224.74 eggs per female at 25°C. In this sense, the consulted references show an important variation in the number of eggs oviposited by the females of *C. chalcites* according to the diet provided. For example,



Vilardebo and Guérout (1964) reported females laying from 340 to 769 eggs on banana. On the other hand, fecundity was 640.33 eggs per female when *C. chalcites* was developed on tomato (Gasim and Younis 1989). In contrast, Alami et al. (2014) reported the mean number of eggs can range from 136.7 to 674.4 eggs per female according to the bean cultivar tested. We consider that those differences with our longevity and fecundity values could be due to the laboratory conditions (temperature or humidity) where such studies were carried out. Likewise, it is known that the adult longevity and reproductive skills may change in accordance with the nutritional value of the diet taken by the larvae during their development (Verkerk and Wright 1996) and food in the adult stage (Shorey 1963, Simmons and Lynch 1990).

The life expectancy curves ( $e_x$ ) indicated the critical ages of mortality. In the case of *C. chalcites* individuals developed on semi-synthetic diet, we have found that the mortality was higher at early stages (egg and first instar larvae) but was lower than described by Alami et al. (2014) at the same stages on different bean cultivars. The age-specific survival rate curves ( $l_x$ ) of *C. chalcites* on all temperatures studied followed a similar shape than those previously reported (Alami et al. 2014, Nouri-Ganbalani et al. 2015), with the highest mortality in egg period, first, second, and third instars larvae, and then gently decreasing until the last adult died.

Two-sex life tables are a powerful instrument to describe the probable development of a species (Chi and Liu 1985). Results obtained in this work indicate that *C. chalcites* was able to quickly increase its populations in the temperature range of 15 to 30°C. Previous studies for other lepidopteran pests have demonstrated that life table parameters are often influenced by temperature (Chi 1988, Murúa and Virla 2004, Sandhu et al. 2010). In this study, the net reproductive rate ( $R_0$ ) was lowest at 15°C and highest at 25°C, which was close to the maximum value reported by Alami et al. (2014) when *C. chalcites* is reared on a common bean cultivar. The intrinsic rate of increase ( $r$ ) is an effective parameter that includes development, survival, and reproduction (Farhadi et al. 2011). Results show that intrinsic rate of increase ( $r$ ), finite rate of increase ( $\lambda$ ), and net reproductive rate ( $R_0$ ) values increased significantly until temperature reached 25°C, while the mean generation time ( $T$ ) was lowest at 30°C (Table 3).

Analyzing the results obtained in this work, we can appreciate the high biotic potential of *C. chalcites* as a pest, mainly due to the high proportion of larvae that reach the adult stage, its high fecundity and its short population double time at optimal temperature of 25°C. These biological characteristics would explain the overlapping of the different stages of *C. chalcites* in the banana groves of the Canary Islands, together with its extensive oviposition period, which would determine the adequate prediction of the seasonal occurrence of life stages as well as the development of appropriate sampling methods and control techniques for this pests (del Pino et al. 2015, Fuentes et al. 2018, Cakmak et al. 2019). The Canary Islands experience a Mediterranean-type climate characterized by hot and dry summers and mild, wet winters, which is suitable for *C. chalcites* (Fernández-Palacios and Nicholas 1995). The results obtained in this study and the age-stage two-sex life-table analysis could also describe why the *C. chalcites* populations and associated crop damages of this pest are more abundant in banana groves during late April and in mid-November (del Pino 2011), when the average monthly temperature is about 25°C and the crop is in a susceptible growth stage (Cakmak et al., 2019).

The observed performance at different temperatures could also help to understand the current distribution and potential expansion of this pest to other areas globally. For example, an increase

in temperature associated with climatic change would increase *C. chalcites* survival due to low winter larval mortality, increased population built-up, early infestations, and resultant crop damage. Increased temperatures may also result in faster development and consequently the increase the number of *C. chalcites* generations produced annually, thereby enabling the insect to become multivoltine in the northern latitudes of Europe and North America where it is currently reported to be univoltine (Murillo et al. 2013, CABI 2019). This would imply an increase in the number of reproductive events per year, leading to an increase in population and increased levels of infestation (Caffarra et al. 2012). In addition, future global warming can affect the length of the flight period of *C. chalcites* adults and the time elapsed between generations (Roy and Sparks 2000, Stefanescu et al. 2003, Kocsis and Hufnagel 2011). This will encourage temperate *C. chalcites* populations colonize new areas with higher altitude and latitude where this pest species can optimally reproduce (Hickling et al. 2006) and it would not be limited by host availability because of its high polyphagia (CABI 2019). These infestations will occur only under specific environmental conditions and only if the host plant is in a susceptible growth stage (Chakraborty et al. 2000). Finally, further climate warming will change the migration routes and increase the numbers of migratory *C. chalcites* populations reaching northern Europe (Sparks et al. 2007), as it has been recorded in eastern England during the last decades (Waring and Townsend 2003).

However, it should be noted that *C. chalcites* population projections were determined at constant temperatures under laboratory conditions using a semi-synthetic diet as food, and many other factors such as food availability, light, and humidity can also affect pest population dynamics (Bale et al. 2002). Therefore, the current study should be supplemented with other studies of environmental effects on *C. chalcites*.

In conclusion, the age-stage, two-sex life-table analysis obtained from this research has provided fundamental information on the effects of temperature on the developmental time, survivorship, reproduction, and longevity of *C. chalcites*. The current results also give valuable insights into the optimal environmental conditions which allow rapid reproduction and spread of *C. chalcites* in a scenario of climatic change. These results have implications for predicting population dynamics, distribution, and dispersal of this insect pest and for developing sustainable and integrated strategies for its management.

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## References Cited

- Alami, S., B. Naseri, A. Golizadeh, and J. Razmjou. 2014. Age-stage, two-sex life table of the tomato looper, *Chrysodeixis chalcites* (Lepidoptera: Noctuidae), on different bean cultivars. *Arthropod-Plant Inte.* 8: 475–484.
- Amate, J., P. Barranco, and T. Cabello. 1998. Life cycle of *Chrysodeixis chalcites* (E.) (Lepidoptera: Noctuidae) under controlled conditions. *Bol. Sanid. Veg., Plagas* 24: 425–428. (in Spanish)
- Amate, J., P. Barranco, and T. Cabello. 2000. Biology of noctuids pest under controlled conditions (Lep.: Noctuidae). *Bol. Sanid. Veg., Plagas* 26: 193–201. (in Spanish)

- Bailey, R., N. T. Chang, P. Y. Lai, and T. C. Hsu. 2010. Life table of cycad scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae), reared on *Cycas* in Taiwan. *J. Asia Pac. Entomol.* 13: 183–187.
- Bale, J., G. J. Masters, I. D. Hodkins, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.* 8: 1–16.
- Barrionuevo, M. J., M. G. Murúa, L. Goane, R. Meagher, and F. Navarro. 2012. Life table studies of *Rachiplusia nu* (Guenée) and *Chrysodeixis* (= *Pseudoplusia*) *includes* (Walker) (Lepidoptera: Noctuidae) on artificial diet. *Fla. Entomol.* 95: 944–951.
- Begon, M., J. L. Harper, and C. R. Townsend. 2006. *Ecology: from individuals to ecosystem*, 4th ed. Blackwell Publishing, Oxford, United Kingdom.
- Belda, J. E. 1994. Biología, ecología y control de *Spodoptera exigua* (Hübner, 1808) (Lep.: Noctuidae) en cultivo de pimiento en invernadero. M.S. thesis, University of Granada, Granada, Spain.
- Bernal, A., T. Williams, E. Hernández-Suárez, A. Carnero, P. Caballero, and O. Simón. 2013. A native variant of *Chrysodeixis chalcites* nucleopolyhedrovirus: the basis for a promising bioinsecticide for control of *C. chalcites* on Canary Islands' banana crops. *Biol. Contr.* 67: 101–110.
- Bernal, A., O. Simón, T. Williams, D. Muñoz, and P. Caballero. 2018. Remarkably efficient production of a highly insecticidal *Chrysodeixis chalcites* nucleopolyhedrovirus (ChchNPV) isolate in its homologous host. *Pest Manag. Sci.* 74: 1586–1592.
- Broza, M., and B. Sneh. 1994. *Bacillus thuringiensis* spp. *kurstaki* as an effective control agent of lepidopteran pests in tomato fields in Israel. *J. Econ. Entomol.* 87: 923–928.
- Cabello, T. 1988. Influence of temperature and photoperiod on the biology of *Trichoplusia orichalcea* F. (Lepidoptera: Noctuidae). *Bol. San. Veg., Plagas* 14: 241–247. (in Spanish)
- Cabello, T., H. Rodríguez, and P. Vargas. 1984. Development, longevity and fecundity of *Sopodoptera littoralis* (Boisd.) (Lep.: Noctuidae) reared on eight artificial diets. *J. Appl. Entomol.* 97: 494–499.
- Cabello, T., M. P. González, L. Justicia, and J. E. Belda. 1996. Plagas de noctuidos (Lep.; Noctuidae) y su fenología en cultivos en invernaderos. *Informaciones Técnicas 39/96*. Dirección General de Investigación y Formación Agraria. Consejería de Agricultura y Pesca. Junta de Andalucía, Sevilla.
- (CABI) Centre for Agriculture and Biosciences International. 2019. *Chrysodeixis chalcites*. In *Invasive Species Compendium*. CAB International, Wallingford, United Kingdom. [www.cabi.org/isc](http://www.cabi.org/isc)
- Caffarra, A., M. Rinaldi, E. Eccel, V. Rossi, and I. Pertot. 2012. Modelling the impact of climate change on the interaction between grapevine and its pests and pathogens: European grapevine moth and powdery mildew. *Agric. Ecosyst. Environ.* 148: 89–101.
- Cakmak, T., A. Piedra-Buena, E. Hernández-Suarez, and C. Álvarez. 2019. *Chrysodeixis chalcites* (Esper) (Lepidoptera: Noctuidae) oviposition preferences on different growing stages of banana (*Musa acuminata* Colla, Musaceae) plants. *Phytoparasitica* 47: 485–498.
- Carey, J. R. 1993. *Applied demography for biologists with special emphasis on insects*. Oxford University Press, New York, NY.
- Cayrol, R. A. 1972. Famille des Noctuidae, pp. 1255–1520. In A. S. Balachowsky (ed.) *Entomologie appliquée à l'agriculture*. Lépidoptères. Tome II, vol 2. Masson et Cie, Paris, France.
- Chakraborty, S., A. V. Tiedemann, and P. S. Teng. 2000. Climate change: potential impact on plant diseases. *Environ. Pollut.* 108: 317–326.
- Chi, H. 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. *Environ. Entomol.* 17: 26–34.
- Chi, H. 2013. TWSEX-MSChart: computer program for age stage, two-sex life table analysis. <http://140.120.197.173/ecology/>.
- Chi, H., and W. M. Getz. 1988. Mass rearing and harvesting based on an age-stage, two-sex life table: a potato tuber worm (Lepidoptera: Gelechiidae) case study. *Environ. Entomol.* 17: 18–25.
- Chi, H., and H. Liu. 1985. Two new methods for the study of insect population ecology. *Bull. Inst. Zool. Acad. Sin.* 24: 225–240.
- Chi, H., and H. Y. Su. 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environ. Entomol.* 35: 10–21.
- Chi, H., and D. S. Tang. 1993. Age stage, two sex, life table of the cabbage looper. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie* 8: 627–632.
- Chi, H., and T. C. Yang. 2003. Two-sex life table and predation rate of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Environ. Entomol.* 32: 327–333.
- Collins, L., A. Korycinska, and R. Baker. 2014. Rapid Pest Risk Analysis for *Crysodeixis chalcites*. Food and Environment Research Agency, United Kingdom. <http://www.fera.defra.gov.uk/plants/plantHealth/pestsDiseases/documents/chrysodeixisChalcites.pdf>
- (CPHST) Center for Plant Health Science and Technology. 2013. Pest Datasheet for the Cooperative Agriculture Pest Survey (CAPS): *Chrysodeixis chalcites*. USDA-APHIS Plant Protection and Quarantine, Center for Plant Health Science and Technology, Raleigh, NC. [http://caps.ceris.purdue.edu/webfm\\_send/2046](http://caps.ceris.purdue.edu/webfm_send/2046)
- del Pino, M. 2011. Biología, ecología y control de *Chrysodeixis chalcites* (Esper, 1789) (Lepidoptera: Noctuidae) en cultivos de platanera de Canarias. M.S. thesis, University of La Laguna, Santa Cruz de Tenerife, Spain.
- del Pino, M., A. Carnero, T. Cabello, and E. Hernández. 2011. La lagarta o bicho camello, *Chrysodeixis chalcites* (Esper, 1789), una plaga emergente en los cultivos de platanera de Canarias. *Phytoma* 225: 21–24.
- del Pino, M., P. Rugman-Jones, E. Hernández-Suárez, A. Polaszek, and R. Stouthamer. 2013. Rapid molecular identification of five species of *Trichogramma* occurring in the Canary Islands with notes on their distribution in banana groves. *BioControl* 58: 515–524.
- del Pino, M., A. Carnero, E. Hernández-Suárez, and T. Cabello. 2015. Bases para la gestión integrada de *Chrysodeixis chalcites* (Lep.: Noctuidae) en cultivos de platanera de Canarias. *Phytoma* 271: 40–46.
- Efron, B., and R. J. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman & Hall, New York, NY.
- Farhadi, R., H. Allahyari, and H. Chi. 2011. Life table and predation capacity of *Hippodamia variegata* (Coleoptera: Coccinellidae) feeding on *Aphis fabae* (Hemiptera: Aphididae). *Biol. Control* 59: 83–89.
- Fernández-Palacios, J. M., and J. P. Nicholas. 1995. Altitudinal pattern of vegetation variation on Tenerife. *J. Veg. Sci.* 6: 183–190.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, United Kingdom.
- Fuentes, E. G., E. Hernández-Suárez, O. Simón, T. Williams, and P. Caballero. 2017. *Chrysodeixis chalcites* nucleopolyhedrovirus (ChchNPV): natural occurrence and efficacy as a biological insecticide on young banana plants in greenhouse and open-field conditions on the Canary Islands. *PLoS One* 12: e0181384.
- Fuentes, E. G., Hernández-Suárez, E., Simón, O., Williams, T., and P. Caballero. 2018. *Chrysodeixis chalcites*, a pest of banana crops on the Canary Islands: incidence, economic losses and current control measures. *Crop Prot.* 108: 137–145.
- Gabre, R. M., F. K. Adhan, and H. Chi. 2005. Life table of *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae). *Acta Oecol.* 27: 179–183.
- Galán-Sauco, V., and J. Cabrera. 2006. El cultivo del plátano (Banano, *Musa acuminata* Colla AAA, subgrupo Cavendish) en las Islas Canarias. pp. 289–301. *Memorias de la XVII Reunión Internacional de ACORBAT* Joinville, Brasil.
- Gasim, G. Y., and H. T. Younis. 1989. Biological studies on tomato leaf-worm *Plusia chalyces* L. (Noctuidae: Lepidoptera) under effect of constant temperatures. *Mesopotamia Journal of Agriculture* 21: 325–334 (In Arabic)
- Gaumont, R., and R. Moreau. 1961. Observations on the bionomics of *Plusia chalcites* Esp. (Lepidoptera, Noctuidae). *Revue de Zoologie Agric.* 60: 31–36 (In French)
- Goodey, B. 1991. *Chrysodeixis chalcites* (Esper, 1789) (Lep.: Noctuidae) - observations on the life cycle in captivity. *Entomologists Record* 103: 111–118.

- Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. *Am. Nat.* 119: 803–823.
- Gutiérrez, A. P., and L. Ponti L. 2014. Analysis of invasive insects: links to climate change, pp. 45–61. *In* L. H. Ziska and J. S. Dukes (eds.), *Invasive species and global climate change*. CABI Publishing, Wallingford, United Kingdom.
- Harakly, F. A., and S. S. Farag. 1975. Biological studies on the tomato looper *Chrysodeixis chalcites* (Esper) in Egypt. *Bull. Soc. Ent. Egypte*. 59: 295–299.
- Hardy, P. B., T. H. Sparks, and R. L. H. Dennis. 2014. The impact of climatic change on butterfly geography: does climatic change produce coincident trends in populations, distributions and ranges? *Biodivers. Conserv.* 23: 855–876.
- Hernández-Borges, J., J. Cabrera, M. A. Rodríguez-Delgado, E. M. Hernández-Suárez, and V. Galán. 2009. Analysis of pesticide residues in bananas harvested in the Canary Islands (Spain). *Food Chem.* 113: 313–319.
- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biol.* 12: 450–455.
- Hodgson, J. A., C. D. Thomas, T. H. Oliver, B. J. Anderson, T. M. Brereton, and E. E. Crone. 2011. Predicting insect phenology across space and time. *Global Change Biol.* 17: 1289–1300.
- Holloway, J. D., J. D. Bradley, and D. J. Carter. 1987. CIE guides to insects of importance to man, 1. Lepidoptera. C.A.B.-British Museum, Natural History, Wallingford, United Kingdom.
- Horowitz, A. R., P. G. Weintraub, and I. Ishaaya. 1998. Status of pesticide resistance in arthropod pests in Israel. *Phytoparasitica* 26: 231–240.
- Huang, Y. B., and H. Chi. 2012. Age–stage, two–sex life tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) with a discussion on the problem of applying female age–specific life tables to insect populations. *Insect Sci.* 19: 263–273.
- Huang, J., and H. Hao. 2020. Effects of climate change and crop planting structure on the abundance of cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). *Ecol. Evol.* 10: 1324–1338.
- IBM Corp. 2013. IBM SPSS Statistics for Windows, Version 22.0. IBM Corp, Armonk, NY.
- Ikemoto, T., and K. Takai. 2000. A new linearized formula for the law of total effective temperature and the evaluation of line-fitting methods with both variables subject to error. *Environ. Entomol.* 29: 671–682.
- Jarosik, V., A. Honek, and A. F. Dixon. 2002. Developmental rate isomorphy in insects and mites. *Am. Nat.* 160: 497–510.
- Kavousi, A., H. Chi, K. Talebi, A. Bandani, A. Ashouri, and V. H. Naveh. 2009. Demographic traits of *Tetranychus urticae* (Acari: Tetranychidae) on leaf discs and whole leaves. *J. Econ. Entomol.* 102: 595–601.
- Kocsis, M., and L. Hufnagel. 2011. Impacts of climate change on Lepidoptera species and communities. *Appl. Ecol. Environ. Res.* 9: 43–72.
- Kroschel, J., M. Sporleder, H. E. Z. Tonnang, H. Juárez, P. Carhuapoma, J. C. Gonzales, and R. Simon. 2013. Predicting climate-change-caused changes in global temperature on potato tuber moth *Phthorimaea operculella* (Zeller) distribution and abundance using phenology modeling and GIS mapping. *Agr. Forest Meteorol.* 170: 228–241.
- Lee, K. P., and C. Roh. 2010. Temperature by nutrient interactions affecting growth rate in an insect ectotherm. *Entomol. Exp. Appl.* 136: 151–163.
- Lehmann, P., T. Ammunét, M. Barton, A. Battisti, S. D. Eigenbrode, J. U. Jepsen, G. Kalinkat, S. Neuvonen, P. Niemelä, J. S. Terblanche, et al. 2020. Complex responses of global insect pests to climate warming. *Front. Ecol. Environ.* 18: 141–150.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika.* 33: 183–212.
- Lewis, E. G. 1942. On the generation and growth of a population. *Sankhya* 6: 93–96.
- Li, W., Y. Yang, W. Xie, Q. Wu, B. Xu, S. Wang, X. Zhu, S. Wang, and Y. Zhang. 2015. Effects of temperature on the age-stage, two-sex life table of *Bradysia odoriphaga* (Diptera: Sciaridae). *J. Econ. Entomol.* 108: 126–134.
- López-Cepero, J. 2015. Análisis de residuos y gestión integrada de plagas en platanera. *Phytoma* 271: 48–52.
- Murillo, H., D. W. A. Hunt, and S. L. Van Laerhoven. 2013. First records of *Chrysodeixis chalcites* (Lepidoptera: Noctuidae: Plusiinae) for east-central Canada. *Can. Entomol.* 145: 1–5.
- Murúa, M. G., and E. Virla. 2004. Population parameters of *Spodoptera frugiperda* (Smith) (Lep.: Noctuidae) fed on corn and two predominant grasses in Tucumán (Argentina). A laboratory study. *Acta Zool. Mexicana, Nueva Serie* 1: 199–210.
- Naseri, B., Y. Fathipour, S. Moharrampour, and V. Hosseinaveh. 2009. Comparative life history and fecundity of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on different soybean varieties. *Entomol. Sci.* 12: 147–154.
- Nouri-Ganbalani, G., M. Mardani-Talaei, and M. R. Haji-Ramezani. 2015. Age-stage, two-sex life history of the golden twin spot moth, *Chrysodeixis chalcites* (Lepidoptera: Noctuidae), on six commercial tomato cultivars under laboratory conditions. *Can. Entomol.* 00: 1–10.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. S.* 37: 637–669.
- Perera, S., and M. J. Molina. 2007. Plagas y enfermedades en el cultivo ecológico de la platanera, pp. 77–118. *In* C. Nogueroles and J. Líbano (eds.), *El cultivo ecológico de la platanera en Canarias*. Gabinete de Proyectos Agroecológicos SL, Tenerife, Spain.
- Polaszek, A., P. F. Rugman-Jones, R. Stouthamer, E. Hernández-Suárez, T. Cabello, and M. del Pino-Pérez. 2012. Molecular and morphological diagnoses of five species of *Trichogramma*: biological control agents of *Chrysodeixis chalcites* (Lepidoptera: Noctuidae) and *Tuta absoluta* (Lepidoptera: Gelechiidae) in the Canary Islands. *BioControl* 57: 21–35.
- Rashid, F. E., S. M. Hammad, and S. M. Hassan. 1971. The biology of *Autographa chalcites* L. in Alexandria region (Lepidoptera: Noctuidae). *Bull. Soc. Ent. Egypte* 55: 419–426.
- Régnière, J., J. Powell, B. Bentz, and V. Nealis. 2012. Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *J. Insect Physiol.* 58: 634–647.
- Roy, D. B., and T. H. Sparks. 2000. Phenology of British butterflies and climate change. *Global Change Biol.* 6: 407–416.
- Sandhu, H. S., G. S. Nuessly, S. E. Webb, R. H. Cherry, and R. A. Gilbert. 2010. Life table studies of *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on sugarcane. *Environ. Entomol.* 39: 2025–2032.
- Saulich, A. K., I. V. Sokolova, and D. L. Musolin. 2017. Seasonal cycles of noctuid moths of the subfamily Plusiinae (Lepidoptera, Noctuidae) of the Palaearctic: diversity and environmental control. *Entomol. Rev.* 97: 143–157.
- Sharma, H. C. 2014. Climate change effects on insects: implications for crop protection and food security. *J. Crop Improv.* 28: 229–259.
- Shorey, H. H. 1963. The biology of *Trichoplusia ni* (Lepidoptera: Noctuidae). II. Factors affecting adult fecundity and longevity. *Ann. Entomol. Soc. Am.* 56: 476–480.
- Simmons, A. M., and R. E. Lynch. 1990. Egg production and adult longevity of *Spodoptera frugiperda*, *Helicoverpa zea* (Lepidoptera: Noctuidae), and *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae) on selected adult diets. *Fla. Entomol.* 73: 665–671.
- Simón, O., A. Bernal, T. Williams, A. Carnero, E. Hernández-Suárez, D. Muñoz, and P. Caballero. 2015. Efficacy of an alphabaculovirus–based biological insecticide for control of *Chrysodeixis chalcites* (Lepidoptera: Noctuidae) on tomato and banana crops. *Pest. Manag. Sci.* 71: 1623–1630.
- Sparks, T. H., D. B. Roy, and R. L. H. Dennis. 2005. The influence of temperature on migration of Lepidoptera into Britain. *Global Change Biol.* 11: 507–514.
- Sparks, T. H., R. L. H. Dennis, P. J. Croxton, and M. Cade. 2007. Increased migration of Lepidoptera linked to climate change. *Eur. J. Entomol.* 104: 139–143.
- Stefanescu, C., J. Peñuelas, and I. Filella. 2003. Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biol.* 9: 1494–1506.
- Toba, H. H., A. N. Kishaba, R. Pangaldan, and P. V. Vail. 1973. Temperature and the development of the cabbage looper. *Ann. Entomol. Soc. Am.* 66: 965–974.
- Vargas, R. I., and J. R. Carey. 1989. Comparison of demographic parameters for wild and laboratory adapted Mediterranean fruit fly (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 82: 55–59.

- Verkerk, R. H. J., and D. J. Wright. 1996. Multitrophic interactions and management of the diamondback moth: a review. *Bull. Entomol. Res.* 86: 205–216.
- Vilardebo, A., and R. Guérout. 1964. *Plusia chalcites* Esp. (Lépidoptère Noctuidae) nuisible au bananier dans les Régions cotées de l'ouest africain. *Fruits* 19: 195–208. (in French)
- Waring, P., and M. Townsend. 2003. Field guide to the moths of Great Britain and Ireland. British Wildlife Publishing, Rotherwick, Hampshire, United Kingdom.
- Yang, T. C., and H. Chi. 2006. Life tables and development of *Bemisia argentifolii* (Homoptera: Aleyrodidae) at different temperatures. *J. Econ. Entomol.* 99: 691–698.
- Yin, J., Y. Sun, G. Wu, M. N. Parajulee, and F. Ge. 2009. No effects of elevated CO<sub>2</sub> on the population relationship between cotton bollworm, *Helicoverpa armigera* Hubner (Lepidoptera: Noctuidae), and its parasitoid, *Microplitis mediator* Haliday (Hymenoptera: Braconidae). *Agric. Ecosyst. Environ.* 132: 267–275.
- Yin, J., Y. Sun, G. Wu, and F. Ge. 2010. Effects of elevated CO<sub>2</sub> associated with maize on multiple generations of the cotton bollworm, *Helicoverpa armigera*. *Entomol. Exp. Appl.* 136: 12–20.
- Yu, J. Z., H. Chi, and B. H. Chen. 2005. Life table and predation of *Lemnia biplagiata* (Coleoptera: Coccinellidae) fed on *Aphis gossypii* (Homoptera: Aphididae) with a proof on relationship among gross reproduction rate, net reproduction rate, and preadult survivorship. *Ann. Entomol. Soci. Am.* 98: 475–482.
- Yu, J. Z., H. Chi, and B. H. Chen. 2013. Comparison of the life tables and predation rates of *Harmonia dimidiata* (F.) (Coleoptera: Coccinellidae) fed on *Aphis gossypii* Glover (Homoptera: Aphididae) at different temperatures. *Biol. Control* 64: 1–9.