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LIFE TABLES OF *BACTERICERA COCKERELLI* (HEMIPTERA: TRIOZIDAE) ON TOMATO UNDER LABORATORY AND FIELD CONDITIONS IN SOUTHERN TEXAS

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ABSTRACT

The potato psyllid or tomato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), has become severely detrimental to the fresh tomato market by transmitting the plant pathogen '*Candidatus* Liberibacter psyllaurous' (syn. solanacearum). Because suppression of insect transmitted plant diseases relies on sensible insect vector management, the life table parameters of *B. cockerelli* reared on tomato under both laboratory and field conditions in southern Texas were determined and the population dynamics were estimated according to the life table results. Generally, *B. cockerelli* reared on tomato in the laboratory had greater survival, fecundity, and longevity than those reared on tomato in the field, and the intrinsic mortality was the primary factor contributing to population decrease. In contrast, up to 74.2% of *B. cockerelli* were missing in the field. *B. cockerelli* reared under field conditions had a longer developmental time, shorter preoviposition and oviposition periods, shorter adult longevity, lower fecundity and higher mortality than those reared under laboratory conditions. Therefore, the intrinsic rate of increase (r_m), finite rate of increase (λ), and net reproductive rate (R_0) of field-reared *B. cockerelli* in south Texas were lower than the laboratory reared. These results could help in the understanding of *B. cockerelli* population dynamics under natural conditions in tomato fields, as well as suggest possible biotic and abiotic mortality factors that may contribute to sound insect vector management, and a better understanding of the epidemiology of *B. cockerelli* related diseases of tomato in south Texas and elsewhere.

Key Words: potato psyllid, tomato psyllid, population dynamics, life table, psyllid yellows

RESUMEN

El psílido de la papa, tambien conocido coo el psílido del tomate, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), se ha convertido gravemente perjudicial para el mercado del tomate fresco mediante la transmisión de los patógenos de plantas '*Candidatus* Liberibacter psyllaurous' (sinónimo solanacearum) Debido a la supresión de las enfermedades de las plantas de transmisión de insectos depende sobre el manejo sensato del vector, los parámetros de la tabla de vida de *B. cockerelli* alimentados con tomate, tanto en condiciones de laboratorio y de campo en el sur de Texas se determinaron y la dinámica poblacional se estimó de acuerdo a los resultados de la tabla de vida. Generalmente, *B. cockerelli* alimentados con tomate en el laboratorio tuvo una mayor supervivencia, fecundidad, y la longevidad que los alimentados con tomate en el campo, y la mortalidad intrínseca fue el factor primario que contribuye a la disminución de la población. en contraste, hasta el 74,2% de *B. cockerelli* faltaban en el campo. *B. cockerelli* criados en condiciones de campo tenía más tiempo de desarrollo, preoviposición cortos y períodos de oviposición, menor longevidad de adultos, menor fecundidad y una mortalidad más alta que los criados en condiciones de laboratorio. Por lo tanto, la tasa intrínseca de crecimiento (r_m), tasa finita de crecimiento (λ), y la tasa neta de reproducción (R_0) de campo criado *B. cockerelli* en el sur de Texas, fueron inferiores a los criados en laboratorio. Estos resultados podrían ayudar en la comprensión de la dinámica de la población *B. cockerelli* en condiciones naturales en los campos de tomate, así como sugerir posibles factores de mortalidad bióticos y abióticos que pueden contribuir a la buena gestión insecto

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vector, y una mejor comprensión de la epidemiología de las enfermedades relacionadas con *B. cockerelli* de tomate en el sur de Texas y en otras partes.

Palabras Clave: psílido de la papa, psílido del tomate, dinámica de la población, tabla de vida, amarillamiento de psilidos

The potato/tomato psyllid, *Bactericerca cockerelli* (Šulc) (Hemiptera: Triozidae), is a phytophagous phloem-feeding insect pest, with an extensive host range of > 20 plant families, principally in the family Solanaceae (Knowlton & Thomas 1934). *B. cockerelli* is economically detrimental to several cultivated solanaceous crops in the United States, Mexico, Central America and New Zealand (Pletsch 1947; Liu & Trumble 2006; Munyaneza et al. 2007a, b; Liefting et al. 2008, 2009a, b; Munyaneza 2012). Feeding by *B. cockerelli* on tomato (*Solanum lycopersicum* L.) results in a physiological disorder that reduces fruit quality (Hansen et al. 2008; Liefting et al. 2008, 2009a, b; Munyaneza 2009), with symptoms including leaf yellowing (psyllid yellow disease), up curling, distortion, and plant stunting (Richards & Blood 1932; Al-Jabr 1999). Furthermore, *B. cockerelli* vectors a bacterium *Candidatus* Liberibacter psyllaurous (syn. solanacearum) that had also caused extensive damage to potato (*Solanum tuberosum* L.) production (US EPA 2005; Hansen et al. 2008; Liefting et al. 2008, 2009a, b), due to the destructive disease named potato 'Zebra Chip' (Munyaneza et al. 2007a, b, 2008, 2009).

Infestations of *B. cockerelli* on tomato have caused significant fresh tomato market losses in North America, with notable yield reductions up to 50% in California and 80% in Baja California, Mexico (Liu & Trumble 2004, 2005, 2006). In California, USA and Baja California, Mexico, a genetically unique invasive biotype of *B. cockerelli* has been identified (Liu & Trumble 2007), suggesting the regional cropping system of certain tomato cultivars provides specific food sources to enhance opportunities for genetic differentiation. Therefore, failure to control *B. cockerelli* could enhance not only the economic threat to global tomato production regions, but also frequency of pest outbreaks (CNAS 2006).

Southern Texas, especially the Lower Rio Grande Valley (LRGV), has been reported as one of the areas where *B. cockerelli* overwinters and breeds (Janes 1937; Pletsch 1947; Wallis 1954; Cranshaw 1994, 2001; Gao et al. 2009). The subtropical climate of south Texas provides *B. cockerelli* with optimal breeding conditions during the temperate winter season, which potentially raises the likelihood of outbreaks (Goolsby et al. 2012). Thus, it is important to elucidate the population dynamics of *B. cockerelli* under the unique climatic conditions of south Texas. Although tomato is not a major crop in south Texas at present (NASS-USDA 2013), the tomato is nevertheless an important alternative host for *B. cockerelli*. Monitoring *B. cockerelli* in tomato fields not only reveals their population dynamics, but also those life table traits that specifically result in the highest field mortalities, which could help decrease incidence of *B. cockerelli* related diseases as well as possible migration to other crops, including potato.

Life table studies are an important tool for understanding population dynamics, having been widely using in IPM programs of numerous insect pests (Birch 1948; Goodman 1982; Horowitz et al. 1984; Chi 1988; Chi & Yang 2003, 2006; Naranjo & Ellsworth 2005). Although life table parameters such as the intrinsic rate of natural increase (r_m) of *B. cockerelli* have not been investigated on tomato under laboratory and field conditions, our study of the life table of *B. cockerelli* on potato revealed that certain life table parameters noticeably differed under similar environmental conditions found in the laboratory and field (Yang et al. 2010). Therefore, a study of age-specific life table studies of *B. cockerelli* will elucidate drivers of population dynamics along with possible mortality factors that may contribute to population decrease. This information will aid in determining best timing to control *B. cockerelli*, as well as providing best management practices to suppress psyllid yellows disease, in tomato.

In the present study, the objectives were to determine the age specific life table, including the gross reproduction ($\sum m_x$), the intrinsic rate of natural increase (r_m), the finite rate of increase (λ), the net reproductive rate (R_0), the mean generation time (T) and doubling time (DT), and life history parameters, including immature developmental times, adult longevity, fecundity, female adult preoviposition and oviposition period, sex ratio, of *B. cockerelli* reared on tomato plants under both laboratory and field conditions in southern Texas in 2009, and to provide information on the population dynamics of the *B. cockerelli*, discuss potential key factors of mortality, and suggest ways of better managing this pest on tomato.

Materials and Methods

Host Plants

Tomato (var. 'Florida Lanai'), was seeded first in seedling transplant trays with cone-shaped cells (3 × 3 × 4 cm) in a naturally-lit greenhouse at 28-32 °C. One week after germination, the tomato seedlings were individually transplanted into 1

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L plastic pots. Seedlings were fertilized weekly with 0.6 g L^{-1} Water Soluble Plant Food (N:P:K = 15:30:15) (Chemisco, Division of United Industries Corp. St. Louis, Missouri, USA) and watered as needed. Four weeks after emergence, tomato plants with 6-8 fully expanded leaves were used in all laboratory life table experiments. The top 2-3 fully expanded leaves were excised while being immersed in water. Leaves were individually inserted into plastic transparent vials (1.8 cm in diameter and 7.5 cm in depth) that were filled with reverse osmosis water. The vials containing the leaves were individually placed in cages made from 0.9-L clear, plastic cups (Liu & Stansly 1995). The 9-cm top of each cup was covered with 52-mesh polyethylene screen. An access hole on the side (1.2 cm in diameter) permitted introduction of *B. cockerelli*, after which this access hole was plugged with a cork.

Field life table study was conducted in the field in March 2009 because tomato is generally planted at this time of the year. Tomato plants were first propagated in a greenhouse at 28-32 °C under naturally illuminated conditions. Four weeks after germination, 60 pots of tomato seedlings were transplanted into a ≈0.08 ha (≈0.02 acre) field plot (4 rows × 30 m in length). The field plots were drip irrigated regularly as needed.

Liberibacter-free colony

Bactericera cockerelli adults were originally collected from a potato field at the Texas A&M AgriLife Research experiment station at Weslaco, Texas, USA in May 2006. They were then separately reared on tomato plants inside screened cages. Voucher specimens of *B. cockerelli* were deposited in the Voucher Collection at the Subtropical Pest Management Research Laboratory, Texas A&M AgriLife Research and Extension Center at Weslaco, Texas, USA.

Laboratory Study

Life History and Life Table Studies

The life table studies of *B. cockerelli* were similar to previous research performed with this insect by Yang & Liu (2009) on potato. The experiment was conducted in an air-conditioned insectary at 26.7 ± 2 °C, 75 ± 5% RH and 14:10 h L:D. Light intensities inside cages were measured as photosynthetically active radiation (39-44 µ mol/m^2/s) (Steady State Porometer, model LI-1600; LI-COR, Lincoln, Nebraska, USA).

Egg Collection

Life history and life table parameters studies were started from newly oviposited eggs. Ten pairs (n = 20) of *B. cockerelli* adults were aspirated from a colony of tomato-reared insects. Each pair of aspirated insects was introduced into a cup containing a fresh tomato leaf. Adults were allowed to mate and lay eggs for 24 h, and then removed with an aspirator. Excess eggs were removed to ensure there were no more than 10 eggs per leaf. Therefore approximately 90-95 eggs, 1-10 eggs per leaf using a total of 11 tomato leaves that were each enclosed in the cup, were used for the laboratory experiment.

Development and Survivorship of Immatures

Bactericera cockerelli eggs were individually marked near the stalk of the egg using a non-toxic colored marker pen. Because *B. cockerelli* is mostly sessile during the nymphal stages, the hatched nymphs were also individually marked on the leaf surface in close proximity to the individual using a non-toxic colored pen, and they were observed daily for development, molting, and mortality until they either emerged as adults or died during an immature stage. Any missing nymphs were excluded from the data analysis. A total of 73 individual nymphs were observed.

Adult Longevity and Fecundity

From each host plant, newly emerged (<2 h old) *B. cockerelli* adults were collected and sexed. They were then paired and individual pairs were then each introduced into a cup cage containing a fresh leaf. Leaves were replaced daily and all eggs on each leaf were counted under a binocular stereomicroscope (SZ30, Olympus Optical Co., Ltd, Tokyo, Japan). A total of 10 male-female pairs were monitored daily until all insects had died.

Field Study

The field life table study used a similar methodology to the laboratory study. The field study was conducted from 20 Mar to 23 May 2009 on the Research Farm of the Texas A&M AgriLife Research & Extension Center at Weslaco, located in the LRGV, south Texas, USA (N 26° 09' 27" W 95° 57' 47"). To initiate the study, approximately 20 male-female pairs of *B. cockerelli* adults were introduced into clip-on leaf-cages (7.5 cm in diameter and 5 cm in height), with 1 pair per cage, on each of 30 tagged tomato leaves in the field on 20 Mar 2009. The cages and the *B. cockerelli* were removed after 24 h. A total of 908 eggs were deposited on all tomato leaves for this study. Eggs were observed daily using an OptiVisor binocular magnifier (Donegan 2X, Lenexa, Kansas) and afterwards immature development and survival recorded. Missing and non-viable eggs of *B. cockerelli* were also documented during the study.

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To ensure that at least 1 female and 1 male emerged for the adult longevity and female adult fecundity studies, leaves that had more than 5 fifth instar nymphs of *B. cockerelli* were tagged from 13 tomato plants, and each leaf was confined within a polyester mesh-leaf-sleeve (12 cm long × 10 cm wide × 2 cm high). Adults were sexed after emergence, and only 1 pair of male and female *B. cockerelli* was left within the mesh-leaf-sleeves for further observation. Therefore, a total of 13 pairs of *B. cockerelli* were observed. Eggs were counted daily and adults were transferred to a new leaf every day by using an aspirator until both adults died.

Temperature and relative humidity data from 20 Mar (day 79 of 2009) to 23 May (day 143 of 2009) were obtained from a weather station at the Texas A&M AgriLife Research and Extension Center at Weslaco, Texas, approximately 150 m from the tomato field where this study was conducted.

Life Table and Life History Analysis

Developmental time, survival, oviposition and duration of preoviposition, longevity, and fecundity of *B. cockerelli* were calculated and analyzed based on life table theory and the life history traits (Birch 1948; Chi 1988), and means associated with each independent variable were separately analyzed using the least significant difference (LSD) test at $P = 0.05$ when significant F values were obtained (SAS Institute 2000).

Life table parameters of *B. cockerelli* populations were calculated based on repeated measures in the life history experiment (PROC MIXED; SAS Institute 2000). The gross reproduction (Σm_x), intrinsic rate of natural increase (r_m), net reproductive rate (R_0), mean generation time (T), doubling time (DT), and finite capacity of increase (λ) were computed using a SAS program, written by Maia et al. (2000), incorporating survival rates and development times, and the life table parameter confidence limits were calculated using the Jackknife procedure (Birch 1948; Hulting et al. 1990).

Results

Development of Immatures

Laboratory and field temperature and relative humidity are shown in Fig. 1. The average temperature in the field during the experimental period

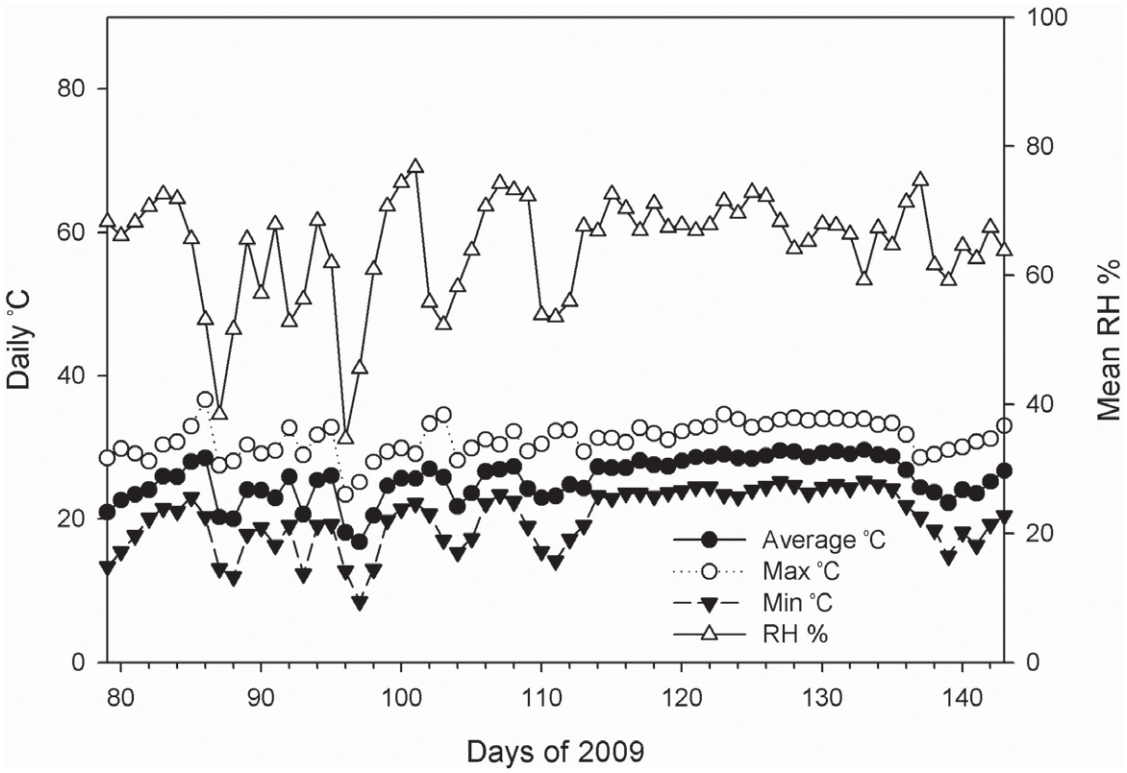


Fig. 1. Temperature (°C) and relative humidity (%) during the field study in Weslaco, Texas (N 26° 09¢ 27² W 95° 57¢ 47²; Mar to May 2009).

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was 25.6 °C, which was slightly lower than temperatures under laboratory conditions. Furthermore, field temperatures fluctuated from 8.5 to 36.6 °C, as opposed to a constant laboratory temperature of 26.7 ± 2 °C. Statistical comparisons in the present study indicated that the development time of immature *B. cockerelli* on tomato was generally faster under laboratory conditions (Table 1). Immature *B. cockerelli* developed in an average of 18.7 days (range: 17-27 days) under laboratory conditions, and 25.3 days (range: 24-29 days) under field conditions, and the development time from first to fifth instars averaged 3.3 days shorter in the laboratory than in the field. Fifth instar *B. cockerelli* developed on average 1.5 days faster under laboratory conditions than under field conditions.

Adult Longevity

Longevity of both male and female *B. cockerelli* was shorter under field conditions than under laboratory conditions (Table 2). On average, females (60.5 ± 8.4 days; range: 15-82 days) lived significantly longer than males (38.0 ± 3.2 days; range: 6-82 days) (F = 6.23; df = 1,19; P = 0.0225) under laboratory conditions. However, under field conditions, female longevity (16.2 ± 0.9 day; range: 9-18 days) was not significantly different from male longevity (17.6 ± 0.7 day; range: 14-20 days) (F = 1.55; df = 1,18; P = 0.2295).

Preoviposition, Oviposition Periods, and Age-Specific Fecundity

The adult sex ratios (% females) of *B. cockerelli* were found to be similar under both laboratory and field conditions (Table 3). However, preoviposition and oviposition periods averaged 8.8 and 45.0 days under laboratory conditions respectively, but these were 2- and 4-fold longer, respectively, under field conditions. The mean lifetime fecundity was found to be 3.2-fold higher in the laboratory than in the field (Table 3).

Nymphal Survivorship and Life Table Parameters

The survival trends of *B. cockerelli* nymphal stages under laboratory and field conditions are plotted in Fig. 2. The survival trend sharply declined under field conditions and there was 50% lower survival of fifth instar nymphs under field conditions than under laboratory conditions. The survival rates of eggs and small nymphs (first to third instars) were also much lower in the field. However, most large nymphs (third to fifth instar) survived equally well under both field and laboratory conditions. Under field conditions, an average of 74.2% of *B. cockerelli* eggs were missing whereas only 0.8% of eggs were found missing in the laboratory. Non-viable eggs averaged 21.7% in the field, while those in the laboratory averaged 16.1%.

The life table parameters of *B. cockerelli* indicated slower development of field populations than those in the laboratory (Table 4). The gross reproduction ($\sum m_x$) of *B. cockerelli* was 239.3 offspring per female in the laboratory, compared with 59.8 offspring in the field. The intrinsic rate of natural increase (r_m) value of *B. cockerelli* was much greater under laboratory conditions (0.1856) than under field conditions (0.0703). The finite rate of increase (λ) showed a similar tendency, with a λ of 1.2039 in the laboratory and 1.0729 in the field. The net reproductive rate (R_0) values were also much greater in the laboratory than in the field. The mean generation time (T) and doubling time (DT) were markedly shorter in the laboratory than in the field.

Discussion

Understanding the population dynamics of *B. cockerelli* will provide important information useful for effective management of the psyllid-induced plant disease 'psyllid yellows', as well as 'Zebra Chip' disease. Knowledge of insect pest life tables in field situations is conducive for making

Table 1. Developmental times of *Bactericera cockerelli* immature stages reared on tomato under field and laboratory conditions.

Stage	Developmental time (days ± SE)		$F_{1,95}$	P
	Field	Laboratory		
Eggs	7.7 ± 0.2 a	4.4 ± 0.1 b	744.72	< 0.0001
Nymphs	17.6 ± 0.3 a	14.3 ± 0.4 b	38.79	< 0.0001
First instar	3.4 ± 0.2 a	3.0 ± 0.1 b	6.55	0.0121
Second instar	3.6 ± 0.2 a	2.0 ± 0.1 b	95.3	< 0.0001
Third instar	3.8 ± 0.2 a	2.0 ± 0.1 b	109.42	< 0.0001
Fourth instar	3.9 ± 0.2 a	2.7 ± 0.1 b	41.49	< 0.0001
Fifth instar	3.1 ± 0.2 b	4.6 ± 0.1 a	28.34	< 0.0001
Eggs to adults	25.3 ± 0.4 a	18.7 ± 0.5 b	137.99	< 0.0001

Means in the same row followed by the same letters are not significantly different at P = 0.05 (LSD test; SAS Institute 2000).

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TABLE 2. ADULT LONGEVITY OF *BACTERICERA COCKERELLI* REARED ON TOMATO UNDER FIELD AND LABORATORY CONDITIONS.

	Adult longevity (days ± SE)			
Sex	Field	Laboratory	$F_{1,19}$	P
Females	16.2 ± 0.9 bA	60.5 ± 8.4 aA	27.33	< 0.0001
Males	17.6 ± 0.7 bA	38.0 ± 3.2 aB	38.92	< 0.0001
$F_{1,18}$	1.55	6.23		
P	0.2295	0.0225		

Means in the same row (lowercase letters) and column (uppercase letters) followed by the same letters do not differ significantly at $P = 0.05$ (LSD test; SAS Institute 2000).

sound management decisions for economically important crops. The differences seen between the field and laboratory studies reported here, along with the life table analysis is important to prevent the inappropriate extrapolation of laboratory results to field applications, and also the more precise information will serve as a database platform to make informed cropping management decisions. Based on our life table results, enhancement of *B. cockerelli* nymphal mortality in the field should be a focus of IPM programs, as it suggests an optimum timing for suppressing the *B. cockerelli* population, especially in the egg and small nymphal stages.

In the study reported here, our results clearly showed that *B. cockerelli* required a longer time to develop under field conditions relative to constant temperature laboratory conditions. The age-specific development of *B. cockerelli* immatures on host plants is an important measure of the suitability of the host plant to nymphs. Our study found that *B. cockerelli* immature development times were longer under field conditions than the laboratory condition, except for the fifth instars. List (1939) reported that fluctuating climatic conditions could largely affect *B. cockerelli* immature development and cause them die unexpectedly in the field. A previous study (Pletsch 1947) reported that *B. cockerelli* immature development times in the laboratory ranged from 16 to 34 days, and this was consistent with our results under laboratory conditions. Compared with our previous *B. cockerelli* life table studies on eggplant (*Solanum melongena* L.) and bell pepper (*Capsicum annuum* L.; Solanales: Solanaceae) (Yang & Liu 2009), and potato (Yang et al. 2010), our data clearly showed that *B. cockerelli* immature development on tomato was similar to that of those reared on potato and, except for the fifth instar, development was significantly faster on tomato than on eggplant and bell pepper, indicating that tomato was a better host plant for *B. cockerelli* immatures than eggplant and bell pepper. Compared with our previous study of *B. cockerelli* on potato (Yang et al. 2010), immature development time from egg to adult, as well as those of the third and fourth instars, were significantly longer when reared on tomato than on potato, but the differences were generally within 1 day.

Longevities of males and females in our study were consistent with previous studies of *B. cockerelli* on potato and tomato in controlled environments under laboratory conditions (Knowlton & Janes 1931; Abdullah 2008; Yang et al. 2010). Moreover, both *B. cockerelli* male and female longevities were shorter under field conditions than under laboratory conditions, and these results further confirmed our previous results on potato (Yang et al. 2010). However, in contrast to our previous studies on potato (Yang et al. 2010) or eggplant (Yang & Liu 2009), male and female longevities on tomato was not significantly (male: $P = 0.7720$; female: $P = 0.9494$) different under laboratory conditions, but male longevity was significantly shorter than when reared on bell pepper ($P = 0.05$).

Our data showed that *B. cockerelli* female lifetime fecundities were lower on tomato under field conditions than under laboratory conditions. Compared to our previous study (Yang & Liu 2009), fecundity of female *B. cockerelli* reared on

TABLE 3. REPRODUCTIVE PARAMETERS OF *BACTERICERA COCKERELLI* FEMALES REARED ON TOMATO UNDER BOTH FIELD AND LABORATORY CONDITIONS.

Parameter	Field	Laboratory	$F_{1,19}$	P
Preoviposition period (d)	3.9 ± 0.3 b	8.8 ± 1.5 a	10.89	< 0.0001
Oviposition period (d)	10.5 ± 0.6 b	45.0 ± 8.7 a	15.91	< 0.0001
Fecundity	122.8 ± 5.8 b	392.2 ± 96.4 a	7.78	0.0121
Sex ratio (% ♀)	44.2 ± 4.3 a	43.7 ± 7.6 a	0	0.9596

Means in the same row followed by the same letters do not differ significantly at $P = 0.05$ (LSD test; SAS Institute 2000)

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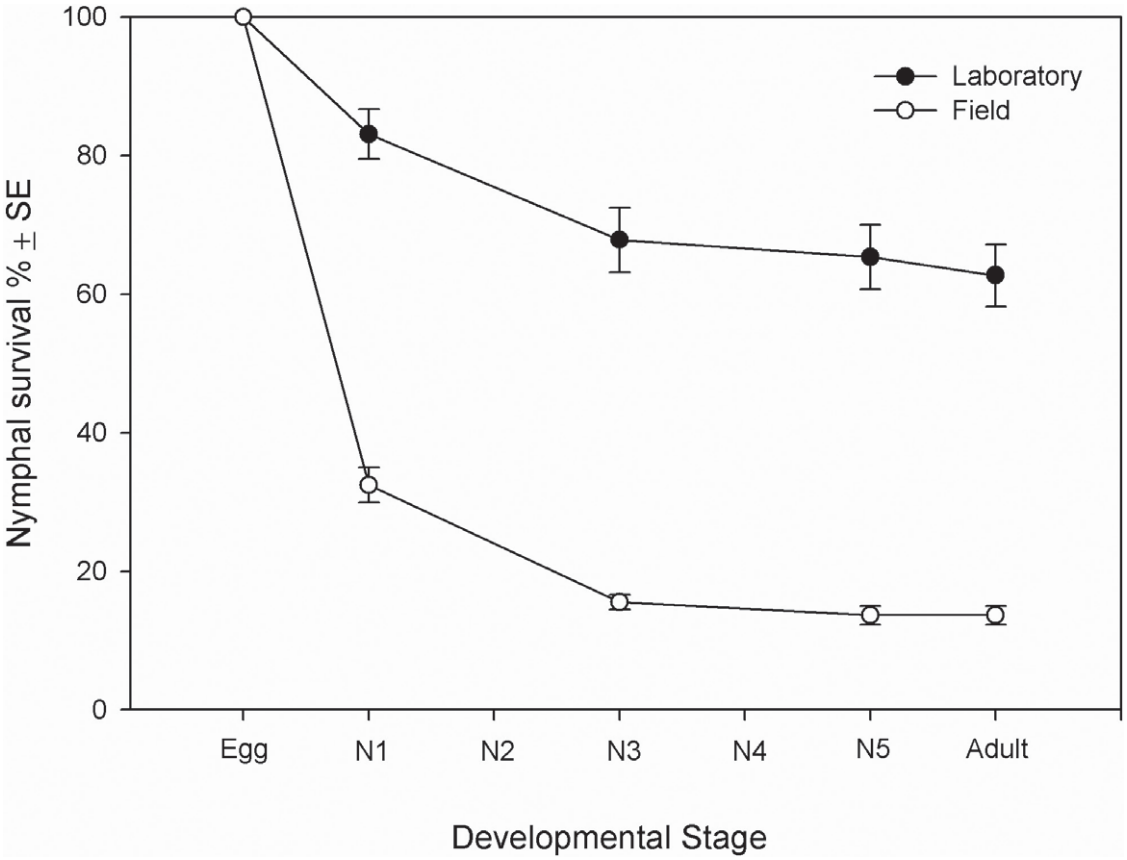


Fig. 2. Nymphal survivorship of *Bactericera cockerelli* reared on tomato under both laboratory and field conditions.

tomato in the laboratory was greater than when reared on eggplant or bell pepper, but was similar to that observed on potato. Compared with our previous field study on potato (Yang et al. 2010), our results showed that female *B. cockerelli* laid much fewer eggs in the field, but was still within the range reported on tomato in by Lehman (1930) and Davis (1937). The oviposition and preovposition periods were similar to our previous studies under laboratory conditions on eggplant and bell pepper (Yang & Liu 2009) and on potato (Yang et al. 2010), but they were largely shortened under field conditions. Although the exact reasons were not known, the preoviposition period of newly

TABLE 4. LIFE TABLE PARAMETERS OF *BACTERICERA COCKERELLI* REAR ED ON TOMATO UNDER BOTH FIELD AND LABORATORY CONDITIONS.

	Field		Laboratory	
Parameters*	True calculation	Jackknife estimate (95% CLs)	True calculation	Jackknife estimate (95% CLs)
$\sum m_x$	59.8	—	239.3	—
r_m	0.0703	0.0704(0.0669~0.0739)b	0.1856	0.1853(0.1688~0.2018)a
R_0	7.7	7.7(6.9~8.6)b	116.602	116.60(51.74~181.46)a
T (d)	29.1	29.1(28.5~29.6)a	25.6	25.8(23.3~28.4)b
DT (d)	9.8	9.8(9.3~10.3)a	3.7	3.7(3.4~4.1)b
λ	1.0729	1.0729(1.0692~1.0767)b	1.2039	1.2034(1.1837~1.2234)a

*All life table parameters were calculated using an SAS program written by Maia et al. (2000). The parameters of the two Jackknife estimates in the same row followed by the same letters on the two host plants are not significantly different at $P = 0.05$ if their 95% CLs overlap.

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emerged adults reported here were still within the range reported by Lehman (1930) and Hariri (1966), who also reported that preoviposition period was negatively correlated with the nutritional quality of the host plant. Our data showed that 74.2% of the total number of eggs laid under field conditions went missing. Although exact reasons for the missing eggs are unknown, factors that such as climate, management activities, and natural enemies could all have contributed to the disappearance of eggs.

Age-specific survivorship of *B. cockerelli* played an important role in determining the population dynamics in our life table research. In our study, immature survivorship of *B. cockerelli* on tomato was significantly greater under laboratory conditions than under field conditions (Fig. 2). The lower and fluctuating temperatures under field conditions compared with the higher and constant temperatures under laboratory conditions during the study could cause some of the decline of field populations (Chi & Yang 2006). The overall survival rate of *B. cockerelli* on tomato in the laboratory (from egg to adult) indicated that 37.3% nymphal mortality intrinsically affected *B. cockerelli* population growth. A similar result was found when *B. cockerelli* was reared on eggplant, but was significant lower when reared on bell pepper (Yang & Liu 2009). The first 3 instars suffered higher mortality than the fourth and fifth instars when reared on tomato, with only 68.0% of total nymphs molting to the fourth instar. This result is consistent with previous studies of *B. cockerelli* reared on potato, eggplant, and bell pepper (Knowlton 1933; Davis 1937; Yang & Liu 2009; Yang et al. 2010). Under field conditions, numerically greater mortality of *B. cockerelli* young nymphs was observed, with mortality up to 84.5% of *B. cockerelli* occurring during the first 3 instars, and this result further confirmed previous studies (Liu & Trumble 2007; Pletsch 1947; Davis 1937; Yang & Liu 2009; Yang et al. 2010), also suggesting younger nymphal stages suffer higher mortality.

Several studies have shown that weather factors, including wind, rain, temperature, and relative humidity are important in governing the population dynamics and survival of hemipteran pest insects such as *Bemisia tabaci* (Gameel 1970; Sharaf 1982; Naranjo et al. 2003). Certainly, *B. cockerelli* encounters numerous biotic and abiotic factors in the field, such as extreme weather conditions, many species of potential predators, such as lacewings, lady beetles, minute pirate bug, and spiders, and a parasitoid (*Tamarixia triozae*), that would not otherwise be experienced in the laboratory; and any of these factors may affect the physiological state of nymphal *B. cockerelli*. For example, *B. cockerelli* body temperature is influenced by ambient temperatures, and afterwards processes including development, feeding behavior, oviposition, survival, and movement may be affected (Wellington et al. 1998). List (1939) reported that high temperature (> 35 °C) affects *B. cockerelli* immature development and causes high mortality. Life history traits calculated under field conditions were much different than those calculated under laboratory conditions, primarily because the developmental time was substantially lengthened by field conditions. We observed that most *B. cockerelli* nymphs on the abaxial surfaces of the leaf rarely moved once they found a stable food source, and few nymphs were lost during immature studies in the field. Thus, we believe that reductions in egg populations contributed the most to population decreases in the field; possibly egg populations were decimated by various biotic and abiotic factors. Therefore, further study on the interactions of *B. cockerelli* with its complex environment will be required.

In the present study, the major life table parameters (r_m, R_0, $\sum m_x$, T, and DT) indicated that *B. cockerelli* development was much faster under laboratory conditions than under field conditions. Differences in these parameters from previous studies by Yang & Liu (2009) and Yang et al. (2010) indicate that tomato is a significantly better quality host for *B. cockerelli*, and certain parameters, including immature development time, immature survival and adult longevity were all to some extent primary factors contributing to population decreases. 'Psyllid yellows' is a systemic disorder disease that is destructive to tomato plants (Carter 1939), and the first new biotype of *B. cockerelli* in California was first detected on tomato plants (Liu & Trumble 2007). These reasons suggest that the biochemical profile of tomato may be unique in comparison to other solanaceous host plants.

Although our data showed *B. cockerelli* suffer substantial mortality in a tomato field in south Texas, those *B. cockerelli* that survived could still threaten tomato production. Thus, it is important to monitor and manage *B. cockerelli* in tomato using IPM practices that include applications of biorational insecticides and eradication of alternate breeding hosts (i.e., the silverleaf nightshade, *Solanum elaeagnifolium* Cav.; Solanales: Solanaceae) to enhance the mortality of *B. cockerelli* in south Texas. Future research regarding the evaluation of important mortality factors will be helpful in elucidating the *B. cockerelli* population increase mechanisms on tomato plants under field conditions, and studies on the effects of varying temperatures under laboratory conditions will also be needed.

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