Biology of three species of North American Triatominae (Hemiptera: Reduviidae: Triatominae) fed on rabbits

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Aspects related to hatching, lifetime, number of blood meals for molting, mortality, feeding time, and postfeeding defecation delay were evaluated and compared in each instar of three North American Triatominae: Triatoma gerstaeckeri, Triatoma lecticularia *and* Triatoma protracta, *all of them fed on rabbits. No significant differences ($p > 0.05$) were found among the three species regarding mean hatching rate, which was close to 20 days. Egg-to-adult development times were significantly shorter ($p < 0.05$) for* T. lecticularia. *Number of blood meals for molting to next instar ranged from one to five for* T. protracta, *and from one to six for* T. gerstaeckeri *and* T. lecticularia. *Mortality rates were higher in younger nymphs of* T. lecticularia *and* T. protracta, *while rates in* T. gerstaeckeri *were higher in fifth-instar nymphs. Mean feeding time was longest in* T. gerstaeckeri, *followed by* T. lecticularia. *More than twice the number of* T. gerstaeckeri *nymphs completed the development process, if compared to the nymphs from the other two species. Defecation delay was less than 10 min for* T. lecticularia, T. protracta *and the youngest nymphs of* T. gerstaeckeri. *Results point out that these three species may be important potential vectors of* Trypanosoma cruzi *for human populations, in areas of Mexico where these species are currently present.*

Key words: North America - Triatominae -biology - laboratory conditions

Chagas disease is considered an emerging illness in the United States. Although only a few chronic cases have been detected in that country, a significant number of presumed cases of American trypanosomiasis has been recorded, as well as at least twelve different species of reservoir hosts (Navin et al. 1985, Hanford et al. 2007) and a near number of triatomine species (Galvão et al. 2003). In Mexico, on the other hand, it is believed that Chagas disease represents an important problem (Cruz-Reyes & Pickeri-López 2006), with foci in some states on the USA border (e.g., Chihuahua, Sonora and Nuevo León) (Paredes et al. 2001, Licón-Trillo 2006, Molina-Garza et al. 2006), and also other probable foci in other border states of Baja California, Coahuila and Tamaulipas. *Triatoma gerstaeckeri* (Stål) is one of the major species of Triatominae in states on both sides of the USA-Mexico border, whereas *Triatoma lecticularia* (Stål) and *Triatoma protracta* (Uhler) are regionally important on that area. However, the three species stand out due to their distribution, association with human dwellings, and entomological indexes (Zárate & Zárate 1985, Galavíz-Silva et al. 1991a, Martínez-Ibarra et al. 1992, Beard et al. 2003, Galvão et al. 2003, Molina-Garza et al. 2006, 2007, Hanford et al. 2007). Studies on the behavior of triatomine species help to widen knowledge about their habits, what results in improving awareness with regard to decisions for vector control. Several studies have been devoted to specific aspects of behavior in *T. gerstaeckeri* and *T. lecticularia* (Pippin 1970, Jurberg & Costa 1989, Galavíz-Silva et al. 1991b, Torres-Estrada et al. 1993, 2002, García-Pérez et al. 1997, Seigler & Lampman 2000). However, life cycles and feeding and defecation behaviors of *T. gerstaeckeri* have been sparsely evaluated. In Pippin (1970), *T. gerstaeckeri* were fed on laboratory white mice or on adult white rats, and in Galavíz-Silva et al. (1991b), specimens were fed on white mice (1st-2nd instars) and on rabbits (3rd-5th instars and adults). Similarly, only few studies have been dedicated to investigate some of those biological behaviors in *T. lecticularia*, like one about fasting (Jurberg & Costa 1989), another study about life cycle, fed on rabbits (Silva et al. 1993), and that devoted to research about defecation patterns on *T. lecticularia,* fed fortnightly on rabbits (Nogueda-Torres et al. 2000). On the other hand, any study has been carried out on those biological parameters in *T. protracta.*

As part of a series of studies on the biology of Mexican Triatominae, the present study was conducted to examine life cycle, feeding and defecation behavior of one of the major species and two regionally important species in the transmission process of *Trypanosoma cruzi* to human populations from Mexico and, potentially, from the USA.

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Received 25 June 2007
Accepted 27 November 2007

MATERIALS AND METHODS

The laboratory colonies of *T. gerstaeckeri* and *T. lecticularia* used in this study were initiated in 2005 from specimens collected in Linares, Nuevo León. The colony of *T. protracta* was created in 2005 from specimens originally obtained in Caborca, Sonora. Colonies were maintained at 27 ± 1ºC, in a relative humidity (RH) of 30 ± 2%, and in a 12/12 h (light/darkness) regimen, conditions that are characteristic of the areas where these three species usually live. Triatomines were weekly fed on immobilized New Zealand rabbits.

Eggs of each species were grouped by oviposition date in order to initiate a cohort of 200 eggs each per species. After hatching, the first-instar nymphs were placed separately in individual plastic containers (5.5 cm diameter x 10.5 cm height) with a central upright absorbent cardboard support. Three days after hatching, the nymphs were individually fed on New Zealand rabbits for 1 h. Subsequent blood meals were provided weekly. Nymphs were observed from the beginning of the feeding process until 1 h postfeeding in order to record feeding and defecation behavior. The bugs were maintained in a dark incubator at a temperature of 27 ± 1ºC and 30 ± 2% RH, and they were daily checked for ecdysis or death. Among the insects that completed development to adult instar, ten couples from each cohort were placed in separated plastic containers (5.5 cm diameter x 10.5 cm height), and maintained as described above to determine oviposition patterns.

Variables showing a normal distribution were compared using Student's t-test or analysis of variance (ANOVA). In the case of ANOVA, *post hoc* comparisons were made using the Scheffé test. The Wilcoxon nonparametric test was used for variables with abnormal distribution. The chi-square test was used to compare frequencies. Differences were considered significant when $p < 0.05$.

TABLE I

Hatching rate and mean incubation period in *Triatoma gerstaeckeri*, *T. lecticularia* and *T. protracta* fed every seven days on rabbits

Species	Hatching rate (%)	Mean incubation period in days (range)
T. gerstaeckeri	75.0	22.4 ± 8.7 (15-28)
T. lecticularia	82.5	18.9 ± 7.4 (14-24)
T. protracta	76.0	20.7 ± 9.4 (19-25)

RESULTS

Egg eclosion rate was over 70% in all cohorts, with mean incubation periods of about 20 days in all three species. No significant ($p > 0.05$) differences were found among them (Table I). Average time for egg-to-adult development was seven months or more. Significant differ-

TABLE II

Egg-to-adult developmental cycle in *Triatoma gerstaeckeri, T. lecticularia* and *T. protracta* fed every seven days on rabbits

	Duration in days (range)					
	T. gerstaeckeri		*T. lecticularia*		*T. protracta*	
Instar	Number	Mean ± SD	Number	Mean ± SD	Number	Mean ± SD
Egg-NI	150	22.7 ± 0.7 (19-24)	165	18.9 ± 7.4 (16-27)	152	19.2 ± 8.4 (17-28)
NI-NII	138	22.6 ± 0.6 (20-23)	99	29.2 ± 8.8 (21-39)	91	34.6 ± 15.5 (19-85)
NII-NIII	127	21.8 ± 1.1 (19-34)	80	54.1 ± 20.6 (32-77)	75	49.6 ± 28.1 (20-62)
NIII-NIV	119	41.8 ± 0.7 (35-44)	58	58.6 ± 24.6 (31-86)	58	54.0 ± 34.0 (15-85)
NIV-NV	109	59.3 ± 1.3 (33-98)	49	44.2 ± 20.9 (23-79)	51	64.6 ± 38.6 (28-155)
NV-AD	90	97.9 ± 2.8 (75-119)	41	67.8 ± 19.5 (42-104)	48	70.5 ± 40.9 (32-161)
Total	90	278.6 ± 6.8[a] (255-313)	41	234.9 ± 20.6[a] (201-262)	48	269.6 ± 35.7[a] (196-331)

a: $p < 0.05$. NI-NV: 1st to 5th instar nymphs.

TABLE III

Mean number of blood meals for molting in *Triatoma gerstaeckeri, T. lecticularia* and *T. protracta* fed every seven days on rabbits, under laboratory conditions

	Number of blood meals (range)					
	T. gerstaeckeri		*T. lecticularia*		*T. protracta*	
Instar	Number	Mean ± SD	Number	Mean ± SD	Number	Mean ± SD
NI-NII	150	1.4 ± 0.1 (1-3)	165	2.4 ± 0.52 (2-5)	152	2.8 ± 1.0 (2-5)
NII-NIII	138	2.2 ± 0.1 (1-3)	99	3.4 ± 1.12 (2-5)	91	1.8 ± 0.7 (1-5)
NIII-NIV	127	4.1 ± 0.1 (1-5)	80	3.1 ± 2.71 (2-5)	75	2.1 ± 1.0 (1-4)
NIV-NV	119	3.6 ± 0.2 (2-6)	58	2.2 ± 0.69 (3-6)	58	2.7 ± 1.3 (2-5)
NV-AD	109	4.7 ± 1.3 (2-6)	49	3.2 ± 1.05 (3-6)	51	3.7 ± 1.5 (2-5)
Total	90	13.2 ± 0.2 (11-16)	41	14.9 ± 1.9 (14-20)	48	12.6 ± 2.9 (10-18)

NI-NV: 1st to 5th instar nymphs.

ences ($p < 0.05$) occurred between *T. gerstaeckeri* and *T. lecticularia*, and between *T. protracta* and *T. lecticularia*, but not between *T. gerstaeckeri* and *T. protracta* (Table II).

Mean number of blood meals for molting did not differ significantly ($p > 0.05$) among the three species (Table III). Mortality rates were considerably lower ($p > 0.05$) for *T. gerstaeckeri* than for the other two species, but no significant ($p > 0.05$) difference was observed when *T. lecticularia* and *T. protracta* were compared (Table IV). At the end of the egg-to-adult development cycle, there was a significantly different ($p < 0.05$) number of males and females for *T. gerstaeckeri*, while *T. lecticularia* and *T. protracta* had a similar number of specimens from each sex (Table V).

Mean feeding time (FT) was significantly longer ($p < 0.05$) than 10 min in most instars of *T. gerstaeckeri* and *T. lecticularia*, but remained close to 10 min in most instars of *T. protracta*. Older (4th and 5th instars) nymphs and adults of *T. gerstaeckeri* had significantly longer ($p < 0.05$) FTs than most of younger nymphs (1st and 3rd instars). On the other hand, FTs did not differ significantly ($p < 0.05$) among most instars of *T. lecticularia*, while longer FTs were observed in fifth-instar nymphs and females of *T. protracta,* although no significant differences ($p < 0.05$) were found (Table V).

Postfeeding defecation delay was less than 10 min only in younger nymphs of *T. gerstaeckeri*, and in all instars of *T. lecticularia* and *T. protracta* (Table VI).

TABLE IV

Instar mortality in *Triatoma gerstaeckeri, T. lecticularia* and *T. protracta* fed on rabbits, under laboratory conditions

	T. gerstaeckeri		*T. lecticularia*		*T. protracta*	
Instar	Number	% mortality	Number	% mortality	Number	% mortality
NI	150	8.0	169	41.4	152	40.1
NII	138	6.0	99	11.2	91	10.5
NIII	127	5.3	80	13.0	75	11.2
NIV	119	6.7	58	5.3	58	4.6
NV	109	12.7	49	4.7	51	2.0
Total	90	(38.7)[a]	41	(75.6)[a]	48	(68.4)[a]

a: $p < 0.05$. NI-NV: 1st to 5th instar nymphs.

TABLE V

Feeding times in minutes for *Triatoma gerstaeckeri, T. lecticularia* and *T. protracta* fed on rabbits, under laboratory conditions

	T. gerstaeckeri		*T. lecticularia*		*T. protracta*	
Instar	Number	Minutes (range)	Number	Minutes (range)	Number	Minutes (range)
NI	150	18.9 ± 1.1[a] (7-22)	99	19.7 ± 8.1 (4-26)	152	9.1 ± 5.4 (4-27)
NII	138	29.8 ± 0.9[a] (4-30)	80	19.1 ± 7.2 (3-26)	91	9.4 ± 3.9 (3-26)
NIII	127	21.8 ± 1.2[a] (7-24)	58	17.4 ± 7.7 (4-26)	75	11.3 ± 6.7 (4-27)
NIV	119	38.8 ± 2.1[a] (5-23)	49	20.3 ± 8.7 (3-25)	58	10.4 ± 6.3 (5-28)
NV	109	37.9 ± 1.5[a] (5-23)	41	24.1 ± 7.5 (5-26)	51	17.5 ± 8.9 (4-29)
Females	53	37.5 ± 1.7[a] (5-26)	22	21.2 ± 7.7 (4-29)	25	15.5 ± 5.7 (5-30)
Males	37	34.2 ± 1.6[a] (6-25)	19	20.7 ± 7.5 (3-29)	23	12.0 ± 4.24 (4-27)

a: $p < 0.05$. NI-NV: 1st to 5th instar nymphs.

TABLE VI

Defecation times in minutes for *Triatoma gerstaeckeri, T. lecticularia* and *T. protracta* fed on rabbits, under laboratory conditions

	T. gerstaeckeri		*T. lecticularia*		*T. protracta*	
Instar	Number	Minutes (range)	Number	Minutes (range)	Number	Minutes (range)
NI	150	7.5 ± 1.5 (1-22)	99	6.7 ± 4.7 (1-25)	152	6.8 ± 6.5 (1-20)
NII	138	8.1 ± 1.7 (1-19)	80	6.8 ± 6.2 (1-22)	91	6.9 ± 6.1 (1-21)
NIII	127	10.1 ± 3.3 (1-24)	58	8.8 ± 7.1 (1-25)	75	9.2 ± 6.3 (1-19)
NIV	119	13.8 ± 2.6 (1-31)	49	8.5 ± 6.7 (1-34)	58	7.7 ± 6.2 (1-33)
NV	109	13.6 ± 3.5 (1-44)	41	8.6 ± 7.2 (1-35)	51	8.4 ± 6.7 (1-42)
Female	53	14.5 ± 2.7 (1-50)	22	9.1 ± 7.6 (1-46)	25	1.3 ± 1.5 (1-46)
Male	37	12.7 ± 4.2 (1-53)	19	9.9 ± 8.7 (1-44)	23	6.6 ± 9.1 (1-32)

NI-NV: 1st to 5th instar nymphs.

DISCUSSION

As in most previously studied Mexican triatomine species (Galvão et al. 1995, Martínez-Ibarra et al. 2001, 2003a,b, 2004, 2005, 2006), in the present study hatching rates were above 70% for all three species, with mean incubation periods of about 20 days. This reflects the fact that maintenance conditions were favorable for a proper development of these species. Hatching rates were slightly lower than those reported for two of the most important vectors of Chagas disease, *Triatoma dimidiata* Latreille and *Triatoma infestans* (Klug) (Zeledón et al. 1970a, Rabinovich 1972). In the present study, the egg hatching rate (75%) for *T. gerstaeckeri* was similar to the rates reported for this species (71.2% and 66.9%) in two previous studies using specimens from Lackland Air Force Base, in Texas, and from General Terán, Nuevo León (Pippin 1970, Galavíz-Silva et al. 1991b). Both areas are near the locality where the parent specimens of our colony were collected. Egg hatching rate in *T. protracta* (76%) was similar to the rates in two related former subspecies of the *T. protracta* complex (now sinonimized to *T. protracta*): *T. p. navajoensis* Ryckman (74.2%) and *T. p. zacatecensis* Ryckman (81.9%), both fed on rabbits (Ryckman 1962).

Mean egg-to-adult development time in *T. gerstaeckeri* was longer than in most related species of the *Meccus phyllosomus* complex (Martínez-Ibarra et al. 2003a,b, 2004, 2005, 2006). It was also longer than development time in *T. gerstaeckeri* from Texas (Pippin 1970), but similar to the mean development time recorded using a Mexican population of the same species, from an area close to that of the former study (Galavíz-Silva et al. 1991b). Longer development times in Mexican rather than Texan populations of *T. gerstaeckeri* may be due to the use of rabbits as blood meal sources, as in the present study and in Galavíz-Silva et al. (1991b), whereas Texan *T. gerstaeckeri* was fed on *Neotoma micropus micropus* by Pippin (1970), a host more frequently associated with *T. gerstaeckeri* than rabbits.

Triatoma protracta had a mean egg-to-adult development time of about eight months in the present study, almost twice as long as the time (129 days in females and 136.8 in males) recorded for the former *T. p. navajoensis* (sinonimized to *T. protracta*), fed on rabbits (Ryckman 1962). On the other hand, *T. lecticularia* had the shortest development time of all three species in the present study, apparently because its specimens had a higher degree of adaptation to laboratory conditions. This is similar to the reported behavior in *Meccus mazzottii* (Usinger) and *M. phyllosomus* (Burmeister) concerning *M. bassolsae* (Alejandre-Aguilar et al.) on the cohorts fed on hens as well as in the cohorts fed on rabbits (Martínez-Ibarra et al. 2006). The mean development time of *T. lecticularia* in the present study was also shorter than the time reported for specimens of this species that had grown in Brazil at a temperature of 28 ± 0.1ºC and 70 ± 5% RH (318.1 and 317 days in males and females, respectively) (Silva et al. 1993). The mean egg-to-adult development time of the three studied species were similar to the time (240 days; range 180-336 days) reported for *T. dimidiata*, one of the most important vectors, which was fed fortnightly on rabbits and maintained at 26.5 ± 0.5ºC and 50 ± 5% RH (Zeledón et al. 1970b), and longer than the time (141 days) reported for specimens of *T. infestans,* another very important vector of Chagas disease, which was fed weekly on hens and maintained at 26 ± 1ºC and 60 ± 10% RH (Rabinovich 1972). Drier conditions (30% RH), which are closer to the natural conditions of the places where *T. lecticularia* is usually collected, probably favored their faster development in the current study.

On average, 70-80% of most instars of the three species studied here required three meals to molt to the next instar. Mean number of blood meals necessary for molting to the next instar was similar in all three species. It was also similar to some species values related to *T. gerstaeckeri*, such as *Meccus longipennis* (Usinger) in both cohorts (fed on hens or on white rats), *Meccus pallidipennis* (Stål) (fed on rabbits) and *Triatoma barberi* (Usinger) (fed on rabbits); however, it was smaller than the number of meals in *Triatoma nitida* (Usinger) (fed on pigeons); the two latter being related to *T. lecticularia* and *T. protracta* (Galvão et al. 1995, Martínez-Ibarra et al. 2004, 2005, Martínez-Ibarra & Novelo-López 2004).

Mortality rates were lower in *T. gerstaeckeri* than in the other two species studied, as in the case of certain related species, such as *T. dimidiata* (fed on rabbits) and *M. longipennis* (Martínez-Ibarra et al. 2001, 2004). On the other hand, mortality indexes for *T. lecticularia* and *T. protracta* were similar to that of larger Mexican species, such as *M. picturatus* (Usinger) (fed on rabbits or on hens) and *M. bassolsae* (fed on rabbits) (Martínez-Ibarra et al. 2003b, 2006). Whereas, the indexes were higher than those for *T. barberi* (25.5%) and *T. nitida* (57.6%) – two species related to *T. lecticularia* and *T. protracta* – and higher than those for *T. rubida* (Uhler) (34.6%; fed on rabbits), a species similar in size to *T. lecticularia,* which was collected in the same geographic area of *T. protracta* (Galvão et al. 1995, Martínez-Ibarra et al. 2005).

As for other species related to *T. gerstaeckeri* (those of the *M. phyllosomus* complex and *T. dimidiata*), to *T. lecticularia* and to *T. protracta* (*T. barberi* and *T. nitida*), the instar mortality rate for three species herein analyses showed an irregular pattern. The highest mortality rates in all three species were found in first or fifth instar nymphs, as recorded for numerous other species of Mexican Triatominae (Galvão et al. 1995, Martínez-Ibarra et al. 2001, 2003a,b, 2005, 2006). As in these latter species, in our study, youngest nymphs' mortality was apparently due to insects feeding incapacity, since usually no significant intestinal content was found in dead specimens (analyzed through direct observation). On the other hand, mortality in older nymphs seemed to occur in the molting period.

Mean FT was significantly longer ($p < 0.05$) than 10 min for most instars of *T. gerstaeckeri*. This is similar to the FT reported for this species, from Texas, and for Mexican specimens from an area near the locality where the parent specimens of our study were collected (Pippin 1970, Galavíz-Silva et al. 1991b). Mean FT for *T.*

lecticularia were similar to the times reported for *T. barberi*, a related species (Martínez-Ibarra et al. 2005). Like several other parameters in this study, mean FT in all three species is well within the range of published data for some other related Mexican species, such as *T. dimidiata*, the species of *M. phyllosomus* complex, as well as *T. barberi* and *T. rubida* (Martínez-Ibarra et al. 2001, 2003a,b, 2004, 2005, 2006), and the three most important vectors of Chagas disease, like *T. dimidiata*, *T. infestans* and *Rhodnius prolixus* Stål (all these three fed on mice) (Zeledón et al. 1977).

Postfeeding defecation delay was less than 10 min for younger nymphs of *T. gerstaeckeri*, all instars of *T. lecticularia*, as previously reported for the last species (Nogueda-Torres et al. 2000), and for all instars of *T. protracta.* The hypothesis presented by Dias (1956) and, later on, supported by Zeledón et al. (1977), points out that triatomines that defecate before 10 min postfeeding are potentially effective transmitters of *T. cruzi.* Therefore, all *T. lecticularia* and *T. protracta* instars may be potentially effective vectors of *T. cruzi*. From this point of view, these two *Triatoma* species may be considered as potentially effective in transmitting *T. cruzi* as *T. infestans* and *Rh. prolixus* (Zeledón et al. 1977).

It follows from Zeledón et al. (1977) that first and second-instar nymphs of *T. gerstaeckeri* may be important because of their capacity to transmit *T. cruzi*, as is also the case of specimens of this species from a nearby area in Mexico (Galavíz-Silva et al. 1991b). Unfortunately, comparison with Texan specimens is not possible, since the author of the latter study reported the numbers and percentages of triatomines defecating 2 min after feeding, but omitted data on the rest of the specimens of the study (Pippin 1970). *Triatoma gerstaeckeri* took longer to defecate than most related species (particularly those of *M. phyllosomus* complex), except for *M. bassolsae*, which presented similar times, and *T. dimidiata* and *T. nitida*, both with longer defecation delays (Galvão et al. 1995, Martínez-Ibarra et al. 2001, 2003a,b, 2004, 2006).

Most parameters used in this study lead us to conclude that all three species may be major potential vectors of *T. cruzi* for human populations in Mexican areas where these species are currently found, as previously suggested by several field studies (Martínez-Ibarra et al. 1992, Beard et al. 2003, Galvão et al. 2003, Molina-Garza et al. 2006, Hanford et al. 2007).

ACKNOWLEDGMENTS

To Verónica Ventura for helping in carrying out this study.

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