The biology of three Mexican-American species of Triatominae (Hemiptera: Reduviidae): *Triatoma recurva*, *Triatoma protracta* and *Triatoma rubida*

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The values of biological parameters related to hatching, lifespan, the number of blood meals between moults, mortality, time lapse before the beginning of feeding, feeding time and defecation delay for each instar of three Mexican-American species of Triatominae, Triatoma recurva, Triatoma protracta *(former subspecies* protracta*) and* Triatoma rubida *(former subspecies* uhleri*), were evaluated and compared. No significant (p > 0.05) differences were recorded among the three species with respect to the average time required to hatch. This time was approximately 19 days. The average egg-to-adult development time was significantly (p < 0.05) shorter for* T. rubida. *The number of blood meals at each nymphal instar varied from one-five for each species. The mortality rates were higher for the first-instar nymphs of the three species studied. The mean time lapse before the beginning of feeding was between 0.3-3 min for most nymphs of all instars of each species studied. The mean feeding time was the longest for* T. recurva, *followed by* T. protracta. *The defecation delay was less than 10 min for* T. recurva *and* T. rubida. *Given these results, only* T. rubida *should be considered an important potential vector of* Trypanosoma cruzi *transmission to humans in areas of Mexico where these species exist, whereas* T. recurva *and* T. protracta *would be of secondary importance.*

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

Biological information is widely available for the 13 most common domestic triatomines (Hemiptera: Reduviidae: Triatominae) among the 30 species described in Mexico (Martínez-Ibarra et al. 2007, Salazar-Schettino et al. 2010). Information about the remaining species is scarce, primarily because these species have rarely been collected and are difficult to raise under laboratory conditions. Three of these rare species are *Triatoma recurva* (Stal), *Triatoma protracta* (Uhler) and *Triatoma rubida* (Uhler). Although these three species are considered to be of low epidemiological importance, specimens of at least two of these species (*T. recurva* and *T. rubida*) collected from inside human dwellings were found to be infected with *Trypanosoma cruzi* (Paredes-González et al. 2001, Licón-Trillo 2006, Breniere et al. 2010, Licón-Trillo et al. 2010). Studies on the behaviour of triatomine species provide a greater understanding of the habits of these insects and therefore facilitate improved decision-making regarding the priorities for vector control. To our knowledge, there has been no study of the biological parameters (life cycle and feeding and defecation behaviours) of *T. recurva*; in contrast, two recent studies were devoted to the examination of certain behaviours of *T. protracta* (Martínez-Ibarra et al. 2007, Klotz et al. 2009) and three studies focused on *T. rubida* (Martínez-Ibarra et al. 2005,

Klotz et al. 2009, Reisenman et al. 2011). Even though the biological parameters of the two latter species have been studied previously, it is necessary to determine the particular behaviours of geographically distinct populations of the same species because it is likely that differing environmental conditions result in different behaviours for distinct populations of the same triatomine species (Licón-Trillo et al. 2010).

As part of a series of studies on the biology of Mexican Triatominae, a study of the feeding and defecation behaviours and the life cycles of three Triatominae species of secondary importance in the transmission of *T. cruzi* to human populations in Mexico was conducted.

MATERIALS AND METHODS

A laboratory colony of *T. recurva* established in 2009 from specimens collected in Jesús María, Nayarit, Mexico, was used. A colony of *T. protracta* (morphologically similar to the synonymised subspecies *protracta*) was established in 2008 with specimens originally obtained from Caborca, Sonora, Mexico. In addition, a colony of *T. rubida* (morphologically similar to the synonymised subspecies *uhleri*) from Saucillo, Chihuahua, was included. The colonies were maintained at 25ºC ± 1ºC and 50% relative humidity (RH) ± 5% RH to match the typical habitat conditions of the three species. The colonies were fed on immobilised and anaesthetised New Zealand rabbits on a weekly basis. These rabbits were anaesthetised following the Norma Official Mexicana regulations with 0.25 mL/kg of ketamine delivered intramuscularly (SAGARPA 1999).

Eggs from 20-25 mating pairs of each studied species were grouped based on the date of oviposition for a period of one week to initiate a cohort of each species of 200 eggs each. After eclosion, groups of first-instar nymphs from each species were separated individually into plastic containers (5.5 cm diameter × 10.5 cm height) with a centre support of absorbent cardboard. Three days after eclosion, each cohort of nymphs was individually fed on immobilised and anaesthetised (as previously described) New Zealand rabbits for a 1-h period; the nymphs were fed weekly thereafter. The nymphs were observed from the beginning of feeding until 1 h postfeeding to record the feeding and defecation behaviours. To estimate the potential of three triatomine species studied to serve as transmission vectors, only the data on the postfeeding defecation times were considered in the calculation of the defecation delay, as in Zeledón et al. (1977) The insects were maintained in a dark incubator at 25ºC ± 1ºC and 50% RH ± 5% RH with a 12/12 h (light/dark) photoperiod and were checked daily for ecdysis or death.

From among the insects that completed development into adults, 10 adult pairs from each cohort were placed in individual containers (5.5 cm diameter × 10.5 cm height) and maintained as previously described to determine the oviposition patterns.

Variables having a normal distribution were compared using Student's *t*-test or analysis of variance (ANOVA). For the ANOVA, *post hoc* comparisons were performed with the Scheffé test. A Wilcoxon nonparametric test was used to analyse the variables that did not follow a normal distribution. The chi-squared test was used to compare frequencies. Differences were considered significant when p < 0.05.

RESULTS

The egg eclosion rate was greater than 66% in all cohorts and reached 72.5% for *T. protracta*. The average incubation periods were approximately 19 days for the three species studied and did not differ significantly among the species.

The average egg-to-adult development time varied from four months for *T. rubida* to 6.7 months for *T. protracta* and was greater than 8.5 months in *T. recurva*. The differences in the development times between species were significant (Table I).

The average number of blood meals between moults did not differ significantly among the three species (Table I). *T. rubida* had a significantly lower mortality rate than the other two species; no significant difference in the mortality rate was found between *T. recurva* and *T. protracta* (Table II). The mean time lapse between the presentation of the blood meal source and the beginning of feeding was between 0.3-3 min for the nymphs of all instars of each species with the exception of the fifth-instar nymphs of *T. protracta*. No significant differences in this parameter were found among the instars of *T. recurva*, but the fifth-instar nymphs and adults differed significantly from the remaining four instars of *T. protracta*. Similarly, the adults of *T. rubida* had significantly longer mean time lapses than the nymphal instars (Table II).

The mean feeding times were longer than 10 min for all instars of *T. recurva* and for most instars of *T. protracta*, whereas the feeding times for most instars of *T. rubida* were shorter than 10 min. For *T. recurva*, the adults of both sexes had significantly longer feeding times than the nymphs. However, the feeding times for most instars of *T. protracta* and *T. rubida* were not significantly different (Table III).

The mean defecation delay was less than 10 min for all nymphal instars and adults of *T. recurva* and *T. rubida* (with the exception of the males) and for three nymphal instars (NII, NII and NIV) of *T. protracta* (Table III).

DISCUSSION

As for various previously studied triatomine species, such as *Triatoma brasiliensis* Neiva, *Triatoma dimidiata* (Latreille) and *Triatoma ryckmani* Zeledón and Ponce (Daflon-Texeira et al. 2009, Reyes & Angulo 2009, Zeledón et al. 2010, Reyes-Novelo et al. 2011), the egg eclosion rate was greater than 70% for two of the three species studied, the exception being *T. recurva*. All of the species studied had average incubation periods of approximately 19 days, reflecting the favourability of the maintenance conditions for the development of these species. The egg hatching rate for *T. protracta* (72.5%) was similar to the rates observed for three related former subspecies of *T. protracta* (currently synonymised to *T. protracta*): *Triatoma protracta navajoensis* Ryckman (74.2%), *Triatoma protracta nahuatlae* Ryckman (76%) and *Triatoma protracta zacatecensis* Ryckman (81.9%), all of which were fed on rabbits (Ryckman 1962, Martínez-Ibarra et al. 2007). The egg eclosion rate of *T. rubida* in the current study (72%) was similar to the eclosion rate (70.5%) of the former subspecies *Triatoma rubida sonoriana* (currently synonymised to *T. rubida*) found in a previous study of specimens from Caborca, a municipality that is distant from the area from which the founder specimens of our *T. rubida* colony were collected (Martínez-Ibarra et al. 2005). These eclosion rates reflect the potential risk posed by *T. protracta* and *T. rubida* in the locations where they are currently distributed (Paredes-González et al. 2001, Licón-Trillo 2006).

The average egg-to-adult development time for *T. recurva* was similar to the corresponding times for *Triatoma gerstaeckeri* (Stål) and *T. dimidiata* (Martínez-Ibarra et al. 2007, Reyes & Angulo 2009), whereas the development times for *T. protracta* and *T. rubida* were shorter. *T. gerstaeckeri* (Stål) and *T. dimidiata* are considered among the most important vectors of *T. cruzi* in Mexico and in Latin America, respectively (Salazar-Schettino et al. 2010).

Approximately 70-80% of the instars of *T. recurva* required an average of 3.5 meals prior to moulting to the next instar, whereas *T. protracta* and *T. rubida* needed 2.5 meals prior to moulting. The average numbers of blood meals required for moulting to the next instar for *T. protracta* and *T. rubida* were similar to the values found for *Rhodnius colombiensis* (Mejia, Galvão, Jurberg), *Rhodnius prolixus* (Stål) and *Rhodnius ecuadoriensis* (Lent and León), whereas the average number of blood meals for *T. recurva* was higher than the average numbers for these three latter species (Arévalo et al. 2007a,

TABLE I

Egg to adult development cycle and number of blood meals to moult on
Triatoma recurva, Triatoma protracta and *Triatoma rubida* under laboratory conditions

| | *T. recurva* | | | *T. protracta* | | | *T. rubida* | | |
Instar	Nymphs (n)	Duration in days (mean ± SD)	Number of blood meals (mean ± SD)	Nymphs (n)	Duration in days (mean ± SD)	Number of blood meals (mean ± SD)	Nymphs (n)	Duration in days (mean ± SD)	Number of blood meals (mean ± SD)
Egg-NI	133	20.7 ± 2.9	-	145	21.1 ± 7.7	-	137	17.4 ± 4.9	-
NI-NII	78	14.7 ± 4.7	2.1 ± 1.6	103	35.4 ± 14.5	1.6 ± 0.8	115	13.3 ± 0.3	1. 2 ± 0.2
NII-NIII	74	31.1 ± 14.6	4.3 ± 2.0	97	37.2 ± 18.3	1.8 ± 0.7	102	15.6 ± 0.3	1.9 ± 0.2
NIII-NIV	65	40.2 ± 15.6	3.9 ± 1.8	64	47.1 ± 26.4	2.3 ± 1.3	95	18.7 ± 0.4	2.7 ± 0.3
NIV-NV	47	67.1 ± 23.3	4.4 ± 1.7	61	43.4 ± 22.8	2.7 ± 1.6	89	25.6 ± 0.3	2.9 ± 0.3
NV-AD	29	91.1 ± 22.4	3.1 ± 1.5	44	57.1 ± 35.8	3.3 ± 2.1	67	36.2 ± 2.7	4.6 ± 0.3
Total	29	259.9 ± 33.6[a]	17.6 ± 4.7[a]	44	201.2 ± 41.5[b]	10.5 ± 2.5[a]	67	125.9 ± 3.3[c]	13.3 ± 0.6[a]

similar letters indicate no significant (p > 0.05) differences; SD: standard deviation.

TABLE II

Instar mortality and mean time-lapse for beginning feeding for
Triatoma recurva, Triatoma protacta and *Triatoma rubida* under laboratory conditions

| | *T. recurva* | | | *T. protracta* | | | *T. rubida* | | |
Instar	Nymphs (n)	Mortality (%)	Time (min) for starting a blood meal (mean ± SD)	Nymphs (n)	Mortality (%)	Time (min) for starting a blood meal (mean ± SD)	Nymphs (n)	Mortality (%)	Time (min) for starting a blood meal (mean ± SD)
NI	133	41.4	1.3 ± 0.7[a]	145	29	1.5 ± 0.9[a]	137	16.1	1.3 ± 0.9[a]
NII	78	3	1.1 ± 0.3[a]	103	4.1	1.9 ± 1.8[a]	115	9.5	1.8 ± 1.4[a]
NIII	74	6.8	0.5 ± 0.3[a]	97	22.7	2.9 ± 2.1[a]	102	5.1	3.1 ± 1.1[a]
NIV	65	13.5	1.5 ± 1.4[a]	64	2.1	1.2 ± 1.1[a]	95	4.4	1.7 ± 1.4[a]
NV	47	13.5	0.6 ± 0.4[a]	61	11.7	11.1 ± 5.5[b]	89	16.1	1.8 ± 1.5[a]
Female	16	-	2.3 ± 1.1[a]	21	-	12.6 ± 4.9[b]	34	-	9.6 ± 4.4[b]
Male	13	-	2.4 ± 1.4[a]	23	-	12.3 ± 5.2[b]	33	-	10.3 ± 5.8[b]
Total	-	78.2[a]	-	-	69.6[a]	-	-	51.2[b]	-

similar letters indicate no significant (p > 0.05) differences; SD: standard deviation.

TABLE III

Feeding and defecation times for *Triatoma recurva, Triatoma protacta* and *Triatoma rubida* under laboratory

| | *T. recurva* | | | *T. protracta* | | | *T. rubida* | | |
Instar	Nymphs (n)	Feeding times (min) (mean ± SD)	Defecation time (mean ± SD)	Nymphs (n)	Feeding times (min) (mean ± SD)	Defecation time (mean ± SD)	Nymphs (n)	Feeding times (min) (mean ± SD)	Defecation time (mean ± SD)
NI	133	11.4 ± 5.4[a]	± 0.3[a]	145	9.2 ± 4.6[a]	12.4 ± 8.0[a]	137	7.9 ± 0.8[a]	1.3 ± 0.4[a]
NII	78	14.9 ± 7.5[a]	1.2 ± 0.2[a]	103	9.9 ± 3.8[a]	8.4 ± 7.7[a,b]	115	10.1 ± 1.1[a]	4.7 ± 0.8[a]
NIII	74	15.8 ± 2.7[a]	0.8 ± 0.1[a]	97	11.4 ± 5.7[a]	6.9 ± 9.5[b]	102	8.7 ± 1.2[a]	3.6 ± 0.9[a]
NIV	65	13.9 ± 6.4[a]	0.6 ± 0.3[a]	64	13.0 ± 5.2[a]	5.6 ± 6.3[b]	95	7.1 ± 1.2[a]	3.5 ± 0.9[a]
NV	47	12.9 ± 8.9[a]	0.7 ± 0.1[a]	61	11.9 ± 6.7[a]	15.9 ± 7.2[a]	89	8.1 ± 1.3[a]	5.2 ± 0.7[a]
Female	16	25.8 ± 10.9[b]	± 1.1[a]	21	14.9 ± 4.9[a,b]	17.4 ± 8.4[a,c]	34	12.1 ± 1.8[a,b]	7.7 ± 3.1[a]
Male	13	28.9 ± 12.7[b]	2.3 ± 1.4[a]	23	16.7 ± 6.8[b]	19.7 ± 11.5[c]	33	13.4 ± 1.9[b]	25.7 ± 4.1[b]

similar letters indicate no significant (p > 0.05) differences; SD: standard deviation.

Villacís et al. 2008). Because an increase in the number of vector-host interactions (for blood feeding) increases the probability of transmission of *T. cruzi* to hosts (Rocha et al. 2001), the three currently studied species could be considered potentially epidemiologically important with respect to *T. cruzi* transmission to human populations.

The mortality rates of *T. rubida* were low (the lowest of the 3 species studied). This finding may be one reason that *T. rubida* is by far the most common of the three species in virtually its entire area of distribution (Licón-Trillo 2006, Reisenman et al. 2010). In contrast, the mortality rates of *T. recurva* were high (the highest of the three species studied). This finding could partially explain the low abundance of this species in its area of distribution (Breniere et al. 2010, Licón-Trillo et al. 2010, Bern et al. 2011). Similar mortality rates have been recorded for *Rhodnius neglectus* Lent and *Rhodnius robustus* Larrouse, the two principal wild triatomine species (corresponding to *T. recurva*) in Brazil (Barreto-Santana et al. 2011).

As observed for some other triatomine species, the instar-specific mortality rates of the species studied had an irregular pattern. The highest percentages of mortality for two (*T. recurva* and *T. rubida*) of the three species were observed in the first or fifth nymphal instar, as reported for other triatomine species (Martínez-Ibarra et al. 2008, Barreto-Santana et al. 2011). As reported for the species previously cited, mortality in the youngest nymphs appeared to be caused by the inability of the insects to feed because dead triatomines were generally found without significant intestinal content. In contrast, the mortality of older nymphs appeared to occur during moulting.

The mean time lapse before the beginning of feeding was less than 2 min for most instars of the three species studied. Similar behaviour was recorded for cohorts of *Mepraia spinolai* (Porter), *T. rubida* (from southwestern USA), *R. colombiensis, R. prolixus, R. neglectus* and *R. robustus*, which are considered potentially important vectors for the transmission of *T. cruzi* (Alzamora et al. 2007, Arévalo et al. 2007b, Klotz et al. 2009, Barreto-Santana et al. 2011, Reisenman et al. 2011). The short mean time lapse before the beginning of feeding implies efficient feeding behaviour. Such efficient feeding increases the probability of survivorship of the species (Guarneri et al. 2000).

The mean feeding times were longer than 10 min for all instars of *T. recurva*, for most instars of *T. protracta* and for the adults of *T. rubida*. These mean feeding times were similar to those for *M. spinolai, T. rubida* and *T. protracta* (both *Triatoma* species from southwestern USA) and for *R. neglectus* and *R. robustus* (Alzamora et al. 2007, Klotz et al. 2009, Barreto-Santana et al. 2011, Reisenman et al. 2011). According to Zeledón et al. (1977), species that feed longer than 10 min could be considered potentially important vectors of *T. cruzi* because prolonged vector-host contact could increase the probability of the interruption of feeding, thereby increasing the risk of contact with the faeces of these insects.

The data on defecation patterns showed that for a fraction (less than 10%) of defecation events, the specimens of the three studied species in all instars tended to defecate before finishing a blood meal. The defecation delay was less than 10 min for all studied instars of *T. recurva* and *T. rubida* (with the exception of the males in the latter species) and for the second, third and fourth-instar nymphs of *T. protracta*. Zeledón et al. (1977) hypothesised that the triatomines that defecate before 10 min postfeeding could be considered potentially effective transmitters of *T. cruzi* because these triatomines are usually in contact with their host for at least 10 min. In the light of this hypothesis, the following instars of the three species studied could be considered effective vectors of *T. cruzi*: all instars of *T. recurva*, almost all instars of *T. rubida* and the second, third and fourth-instar nymphs of *T. protracta*.

The parameters studied support the conclusion that the three species considered herein may have different potentials to transmit *T. cruzi* to humans in those areas of Mexico where these species currently exist. *T. rubida* could be considered an efficient vector, whereas *T. recurva* and *T. protracta* would be of secondary importance, as previously suggested in other field studies (Kjos et al. 2009, Breniere et al. 2010, Licón-Trillo et al. 2010, Reisenman et al. 2010).

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