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RESEARCH

Biological Characteristics of Geographically Isolated Populations of *Meccus mazzottii* (Hemiptera: Reduviidae) in Southern Mexico

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ABSTRACT. Chagas disease, caused by *Trypanosoma cruzi* Chagas, is one of the most epidemiologically important vector-borne zoonoses in Mexico. Among the 32 reported triatomine species from Mexico, *Meccus mazzottii* (Usinger) (Hemiptera: Reduviidae) is one of the most important vectors of *T. cruzi* in the southern part of the country. Variability among populations of triatomines has been recorded for several species (*Meccus longipennis* (Usinger) and *Meccus pallidipennis* (Stal)) that are closely related to *M. mazzottii*, showing an apparent influence of local environmental conditions on the biology of each population, which could modify the impact of vector control measurements. Therefore, this study sought to compare the biological features of populations of *M. mazzottii* from two geographically far apart areas that have similar environmental characteristics and to compare populations from close geographical areas that have different environmental characteristics. The mean longevity, percentages of mortality of nymphs, the total mean number of bloodmeals to molt (considered instar by instar), the mean number of eggs laid by females, and the percentage of hatched eggs were similar between the two localities that are geographically far apart but have similar environmental characteristics. On the other hand, important differences were noticed when a comparison was carried out on the two localities with similar environmental conditions with respect to that locality with different conditions, independent of geographic distance. Most of the studied parameters led us to conclude that the three studied populations are very highly influenced by local environmental conditions. The results of this study indicate the importance of studying the biological characteristics of local populations of triatomines to carry out specific control measurements, instead of using standard ones that could fail if they are not adapted to the target population.

Key Words: *Meccus mazzottii,* population, biological variation, life statistics, laboratory condition

Triatomines are hemipteran bugs acting as vectors of the protozoan parasite *Trypanosoma cruzi* Chagas. This parasite causes Chagas disease, one of the most neglected tropical diseases, named after Carlos Chagas, who first described it >100 yr ago. That is one of the major parasitic diseases in the Americas, where *T. cruzi* infection affects 9–11 million people, mostly in Latin America. In the past decades, mainly because of increased population movements, the number of diagnosed cases has increased also in nonendemic countries in Northern America (Canada and the United States), in the countries of west and central Europe and in the Western Pacific regions (Australia and Japan) (World Health Organization (WHO) 2010, Gourbière et al. 2012). Mexico has also a serious health problem by Chagas disease, where >30 species of triatomines have been reported. Among these species, the seven species of the Phyllosoma complex are considered to be responsible for 74% of vectorial transmissions of *T. cruzi* to humans in Mexico (Ibarra-Cerdeña et al. 2009). One of them, *Meccus mazzottii* (Usinger) (Hemiptera: Reduviidae) has been historically reported in six Mexican states (Salazar-Schettino et al. 2010), although a recent publication (Benítez-Alva et al. 2012) have reported it in only two southern Mexican states, Guerrero and Oaxaca. In the state of Guerrero, over 45,000 seropositive cases of people infected by *T. cruzi* were reported, whereas >84,000 were reported in the state of Oaxaca (Ramsey et al. 2003). In these states, *M. mazzottii* is considered an important vector of *T. cruzi* to human populations (Benítez-Alva et al. 2012).

Different biological parameters have been studied in different vector species, and it has been concluded that differences on biological features are important criteria to determine the relationship between populations of the same species (Grech et al. 2010). Triatomines occurring in distinct locations normally adapt to local conditions (Schofield 1985). Over time, ecological isolation and adaptation to local conditions may lead to the development of geographically isolated populations that differ in various biological features, such as in fecundity and survivorship, which gives rise to variation in a range of population parameters (Martínez-Ibarra et al. 2012, 2013a,b). These biological parameters, such as reproductive and survival parameters, are important factors that contribute to determining the vectorial capacity of such important disease vectors. Distinctive biological attributes have been found in populations of species closely related to *M. mazzottii* (*Meccus pallidipennis* (Stal) and *Meccus longipennis* (Usinger)) from different geographic and ecological areas of Mexico (Martínez-Ibarra et al. 2012, 2013a,b). Moreover, important differences were recorded when populations of *M. longipennis* from far apart geographic localities with different environmental characteristics were compared (Martínez-Ibarra et al. 2013a,b).

Taking into account this previous knowledge, it was hypothesized that 1) studied populations of *M. mazzottii* from areas that are geographically far apart but that have similar environmental characteristics will not differ in their biological parameters and 2) studied populations from geographically close areas but with different environmental characteristics will differ in their biological parameters, because they appear to adapt to their respective local environments. To test these hypotheses, biological attributes under standardized laboratory environments were assessed in three cohorts of populations of *M. mazzottii* from a range of distinct isolated habitats in Mexico.

Materials and Methods

Although laboratory rearing imposes a certain degree of selection pressure on aspects of triatomine biology, all colonies were exposed to standardized environmental conditions that were favorable to triatomine survival. Hence, it was assumed that estimates of biological parameters derived from data collected from the colonized wild populations represent a maximum expression of their biological parameters and are likely to reflect true differences between geographically isolated populations. Similar assumptions were made by Suman et al. (2011) to compare the life-table strategies of geographically distinct strains of *Culex quinquefasciatus* after colonization in standard laboratory conditions for many generations.

Triatomines. To carry out this study, three laboratory colonies of *M. mazzottii* established in 2011 from at least 30 specimens were used. These triatomines were collected in two localities (Santiago Textitlán, 16° 41' N, 97° 15' W and Santo Reyes Nopala, 16° 06' N, 97° 09' W) that are close to each other (≈70 km) in the Oaxaca state but which have different environmental characteristics. A third colony was initiated with specimens from El Parotal (17° 35′ N, 100° 59′ W) in the state of Guerrero, a locality about 480–500 km west of the two localities in the state of Oaxaca (Fig. 1), with environmental characteristics (Secretaría de Gobernación (SEGOB) 2010) similar to those of Santo Reyes Nopala (Table 1). The specimens were identified according to the taxonomic key of Lent and Wygodzinsky (1979), taking into account the revalidation of the genus *Meccus* (Carcavallo et al. 2000).

Biology. Colonies were maintained under conditions similar to those in a previously published study on the biology of *M. mazzottii* (Martínez-Ibarra et al. 2006), at 27 ± 1°C and 75 ± 5% relative humidity (RH) and a photoperiod of 12:12 (L/D) h. Individuals were fed on immobilized and anesthetized New Zealand rabbits (*Oryctolagus cuniculus*) on a fortnightly basis. The rabbits were anesthetized according to the Norma Oficial Mexicana regulations using 0.25 ml/kg of ketamine, which was applied intramuscularly according to established guidelines (Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA) 1999). Eggs from a minimum of 10 females of each colony were grouped by date of oviposition to initiate a cohort by population of 100 eggs each. After eclosion, the groups of each species of first-instar nymphs were separated individually into

Table 1. Environmental characteristics of the localities where founders of the three studied populations of *M. mazzottii* were initially collected

Environmental characteristics	Santiago Textitlán	El Parotal	Santos Reyes Nopala
Altitude (m.a.s.l.)	1,710	260	460
Climate	Cw	Aw	Aw
Vegetation	*Pinus hartwegii* *Quercus* spp. *Abies religiosa*	*P. teocote* *Enterolobium cyclocarpum* *Quercus alba* *Cedrela odorata*	*P. teocote* *E. cyclocarpum* *Q. alba* *C. odorata* *Brahea armata* *Elaeis guineensis*
Mean annual temperature	20°C	27°C	26°C
Pluvial precipitance (mm)	2,750	900	1,100

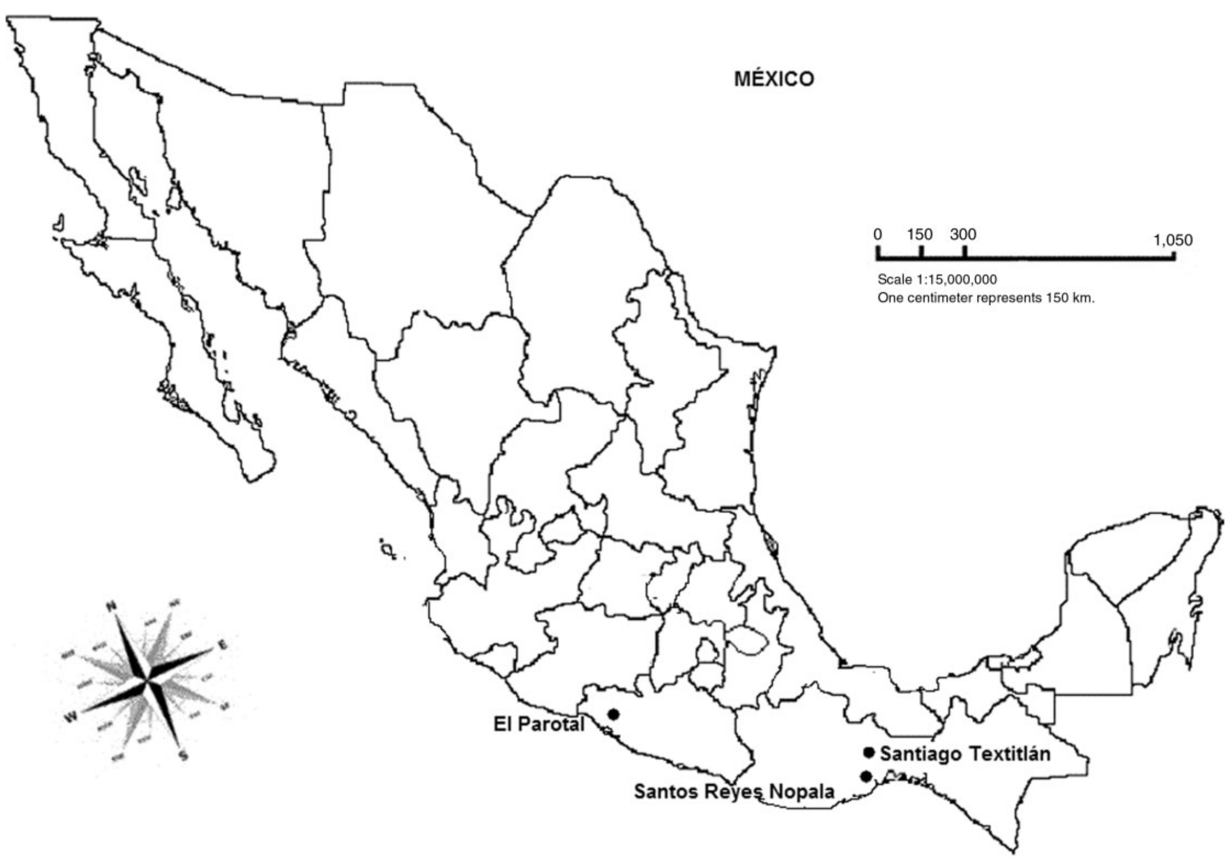

Fig. 1. Locations where the populations were initially collected.

plastic containers (5.5 cm in diameter by 10.5 cm in height), with an upcenter support of absorbent cardboard. Three days after eclosion, each cohort of nymphs was individually fed on New Zealand rabbits for a 1 h period; for the subsequent bloodmeals, they were fed weekly. Nymphs were observed at the end of feeding for recording of blood ingestion. The bugs were maintained in a dark incubator at 27 ± 1°C and 75 ± 5% RH and were checked daily for ecdysis or death. At the end of the cycle, the sex ratio of each studied cohort was recorded. From the insects that completed development to adult instar, 10 adult couples of each cohort were placed in individual containers (5.5 cm in diameter by 10.5 cm in height) and maintained as previously described to determine oviposition patterns. Eggs were collected every day along 30 d and placed in individual containers until hatching.

Statistical Analysis. Variables showing normal distribution were compared using a one-way analysis of variance (ANOVA). After that, the Holm–Sidak (HS) test was used to compare the amount of eggs laid per female, the developmental cycle periods, and the number of bloodmeals before molt in the three cohorts studied. The chi-square test was used to compare frequencies. Differences were considered significant at $P < 0.05$.

Results

Nonsignificant differences (ANOVA, $F = 0.6$, df = 2, $P > 0.05$) were found when the longevity (d) of the eggs of the three studied populations was compared. On the other hand, significant differences (ANOVA, $F = 6.32$, df = 2, $P < 0.01$) were found when the longevity (d) of the first-instar nymphs of the three studied populations was compared. However, nonsignificant differences (HS, $t = 0.74$, df = 1, $P = 0.46$) were recorded when the populations from El Parotal and Santos Reyes Nopala were compared. Similar results were recorded when an instar-by-instar comparison of the three studied populations was carried out. Similarly, significant differences (ANOVA, $F = 38.1$, df = 2, $P < 0.001$) were recorded when the longevity (d) from first-instar nymph to adult of the thee studied populations was also compared (Table 2). Nonsignificant differences (HS, $t = 0.15$, df = 1, $P = 0.88$) were recorded when the populations from El Parotal and Santos Reyes Nopala were compared.

Percentages of mortality were higher in first- and second-instar nymphs. Percentages of mortality from first-instar nymph to adult were significantly different ($\chi^2 = 11.55$, df = 2, $P = 0.03$) when the three studied populations were compared. The differences, however, were not significant ($\chi^2 = 1.1$, df = 2, $P = 0.29$) when the populations from El Parotal and Santos Reyes Nopala were compared (Table 2).

The comparison on the total mean number of bloodmeals to molt growth stage by stage showed significant differences ($P < 0.001$) in the population from Santiago Textitlán from the two other studied populations, except on third-instar nymphs when the three populations were not significantly different (ANOVA, $F = 0.8$, df = 2, $P = 0.45$) and on second-instar nymphs when the three studied populations were different (ANOVA, $F = 23.86$, df = 2, $P = 0.001$), one to each other (Table 3). The total mean of bloodmeals to molt from first-instar nymphs to adult was not significantly different (ANOVA, $F = 1.41$, df = 2, $P = 0.32$) among the three studied populations (Table 3).

The mean numbers of eggs laid by the females of the three studied populations were significantly different (ANOVA, $F = 9.65$, df = 2, $P < 0.001$) when the three studied populations were compared. However, the differences were not significant (HS, $t = 1.63$, df = 2, $P = 0.11$) between the populations from Santiago Textitlán and El Parotal (Table 4). The mean numbers of hatched eggs laid by studied females were also significantly different (ANOVA, $F = 8.67$, df = 2, $P < 0.001$) when the three studied populations were compared. The percentages of hatched eggs were significantly different ($\chi^2 = 361.14$, df = 2, $P = 0.001$) among the three studied populations. Similar to some other studied biological parameters, the differences were not significant ($\chi^2 = 0.59$, df = 2, $P = 0.44$) when the populations of the El Parotal and Santos Reyes Nopala were compared (Table 4).

Discussion

The mean longevity for the three studied cohorts was short (slightly longer than five months). They were similar to the longevity for three

Table 2. The longevity (d) and mortality (%) of different growth stages of three populations of *M. mazzottii* under laboratory conditions

Growth stage	Mean ± SD (d)			Mortality (%)		
	Santiago Textitlán	El Parotal	Santos Reyes Nopala	Santiago Textitlán	El Parotal	Santos Reyes Nopala
Egg	19.6 ± 2.8^a	19.2 ± 2.1^a	20.06 ± 4.8^a	—	—	—
First nymph	24.1 ± 6.7^a	20.1 ± 4.80^b	21.2 ± 5.10^b	7.87	0	21.18
Second nymph	24.64 ± 7.5^a	19.41 ± 3.71^b	22.14 ± 3.57^b	40.11	10.2	4.71
Third nymph	28.67 ± 8.3^a	20.45 ± 4.80^b	21.37 ± 4.68^b	6.74	4.08	2.35
Fourth nymph	43.46 ± 9.12^a	37.7 ± 9.20^b	35.6 ± 10.10^b	10.11	4.08	2.35
Fifth nymph	59.78 ± 14.02^a	51.48 ± 9.36^b	49.37 ± 9.44^c	19.1	8.16	4.71
First nymph to adult	182.11 ± 14.67^a	151.91 ± 11.21^b	151.31 ± 13.19^b	53.93^A	26.52^B	35.30^B

Different small letters among columns of longevity indicate significant differences ($P < 0.05$). Different capital letters among columns of mortality indicate significant differences ($P < 0.05$).

Table 3. Number of bloodmeals to molt for three populations of *M. mazzottii* under laboratory conditions

Growth stage	Number of bloodmeals								
	Santiago Textitlán			El Parotal			Santos Reyes Nopala		
	Min	Max	Total (mean ± SD)	Min	Max	Total (mean ± SD)	Min	Max	Total (mean ± SD)
First nymph	1	3	1.64 ± 0.28^a	1	2	1.14 ± 0.35^b	1	2	1.22 ± 0.42^b
Second nymph	1	4	2.02 ± 0.38^a	1	3	1.61 ± 0.58^b	1	2	1.15 ± 0.36^c
Third nymph	1	7	2.32 ± 0.41^a	1	3	2.12 ± 0.71^a	1	3	2.45 ± 0.56^a
Fourth nymph	1	6	2.45 ± 0.99^a	1	4	3.03 ± 0.92^b	1	5	3.17 ± 0.87^b
Fifth nymph	1	7	3.22 ± 1.04^a	2	4	3.86 ± 1.01^b	1	6	3.46 ± 0.97^b
First nymph to adult	6	16	11.46 ± 3.67^a	9	16	11.38 ± 4.01^a	9	15	11.27 ± 3.31^a

Different letters among columns indicate significant differences ($P < 0.05$).

Table 4. Percentage of hatched eggs laid by three populations of *M. mazzottii* under laboratory conditions

Population	Eggs laid	Hatched eggs	Percentage of hatched eggs ± SD
Santiago Textitlán	731[a]	347	47.47 ± 7.45[a]
El Parotal	874[a]	749	85.70 ± 8.74[b]
Santos Reyes Nopala	492[b]	429	87.20 ± 9.56[b]
DF	2	2	2
F value	9.65	8.67	—
χ^2 value	—	—	361.14
P	0.0001	0.0001	0.0001

Different letters among lines of the same column indicate significant differences ($P < 0.05$).

populations of *M. pallidipennis* (143.73-162.37 d) and four of *M. longipennis* (173.9-181.8 d) (Martínez-Ibarra et al. 2012, 2013a,b), two closely related species, and members of the Phyllosoma complex, similar to *M. mazzottii*. Data for *M. mazzottii* (181.9 d) in a previous study (using specimens from the city of Oaxaca, in the state of Oaxaca) (Martínez-Ibarra et al. 2006) showed a longer mean longevity than the mean longevities for two of the three studied populations of *M. mazzottii* in this study; in contrast, those data for the specimens from the city of Oaxaca were similar to those for the population from Santiago Textitlán, from this study. A possible explanation to that phenomenon is that the city of Oaxaca and Santiago Textitlán share some environmental characteristics, such as altitude, mean annual temperature, and climate (Cw) (Secretaría de Educación Pública (SEP) 2010).

Percentages of mortality were higher on the youngest nymphs of the three studied populations. The total mean of bloodmeals to molt from first-instar nymphs to adult was similar among the three studied populations. On the other hand, longevity, mortality, and the mean number of bloodmeals to molt, considering growth stage by stage, were similar in both localities (El Parotal and Santos Reyes Nopala) with similar environmental conditions (altitude, climate [Aw], vegetation, mean annual temperature, and pluvial precipitation), independent of the long geographical distance between them (≈500 km). In contrast, the comparison of the two close geographical (not farther apart by >70 km) populations sited in the state of Oaxaca (Santiago Textitlán and Santos Reyes Nopala), but with very different environmental conditions (as described above), showed important differences.

The mean number of eggs laid by females of the populations of Santiago Textitlán and El Parotal were between 50% and 75% higher than that mean number for females of the population from Santos Reyes Nopala. However, the percentage of hatched eggs was the highest (over 87%) in that last population. The percentages of hatched eggs (over 85%) in the populations from El Parotal and Santos Reyes Nopala contribute to explain the high abundance of *M. mazzottii* in these geographic areas and the scarcity of this species in Santiago Textitlán (Ramsey et al. 2000; Benítez-Alva et al. 2012).

As previously established (Dujardin et al. 2002), triatomines are "K" strategist, which frequently fix those most adapted phenotypes to each specific environment on their habitats, and they also regulate themselves according the capacity of supporting them by the environment. It has been also established that the most important climatic factors related to development of triatomines are the RH and the temperature. On that way, temperatures lower than 20°C affects triatomines metabolism producing an extension of the life cycles and sometimes, impacts in the reproductive cycle (Curto de Casas et al. 1999). Those established facts fit with those results for Santiago Textitlán on the current studied parameters, which apparently reflect the influence of nonfavorable environmental conditions on that town.

The results of this study lead to conclude that is important studying the biological characteristics of local populations of triatomines to carry out specific control measurements, instead of using standard ones that could have a not expected impact on the target population. That conclusion is complimentary to those from previous studies (Barbu et al. 2009, 2010, 2011) on *Triatoma dimidiata* dispersal characteristics and on nonconventional control of nondomiciliated triatomines, which suggest that spatially targeted interventions by pyrethroid spraying in the periphery of the village (with higher abundances of insects), use of insect screens, and peridomicile cleaning may allow to optimize the cost efficacy of vector control activities within villages.

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