Life history of two abundant populations of *Dipetalogaster maximus* (Uhler, 1894) (Hemiptera: Reduviidae: Triatominae) in northwestern Mexico

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ABSTRACT: We focused on the analysis of biological parameters of two different abundant populations of *Dipetalogaster maximus* (Uhler) (Hemiptera: Reduviidae: Triatominae) from northwestern Mexico. The biological parameters were related to hatching of eggs, life cycle, and meal needed for molting by each instar of two populations from environmentally similar areas (El Fandango and San Dionisio) with a similar number of available hosts as blood meal sources. The *D. maximus* populations from the two locations were evaluated and compared. No significant differences (P>0.05) were recorded for the average hatching time of the two cohorts. The median egg-to-adult development time and the number of blood meals at each nymphal group were significantly shorter (P<0.05) for the El Fandango cohort. The number of obtained females at the end of the cycles, number of eggs laid, and rate of egg hatching were significantly higher (P<0.05) for the El Fandango cohort. These results contribute to the estimation of abundances of the studied populations of *D. maximus* in areas where many tourists go for camping and have an increased risk of being bitten and infected by this species. ***Journal of Vector Ecology* 43 (1): 104-109. 2018.**

Keyword Index: Triatomines, *Dipetalogaster maximus*, laboratory conditions, *Trypanosoma cruzi* transmission, Chagas disease, Mexico.

INTRODUCTION

Chagas disease is one of the most important vector-borne diseases in Latin America, and because of the current extent of globalization, it is now present in some European countries (namely Spain and Italy), Japan, Australia, Canada, and the United States. As no vaccine is currently available, the main strategy for controlling Chagas disease is based on vector transmission prevention (Crompton 2013). Triatomine species have been divided into three big groups: domestic, synanthropic, and sylvatic species. Domestic species can be controlled by chemical and physical measures, but controlling synantropic and sylvatic species are rigorous, as their habitats are commonly inaccessible to control measures. The synantropic and sylvatic triatomine species, which are frequently considered as "secondary vectors," are significant as they maintain the sylvatic cycle of *T. cruzi* by infecting or reinfecting wild reservoirs, which leads to a permanent risk of *T. cruzi* transmission to humans as they contact human populations (Silveira 2014). One of the secondary vectors is *Dipetalogaster maximus* (Uhler). This species infected by *T. cruzi* has been collected inside domestic areas, as well as in piles of granitic rocks in the cape region of Baja California Sur State, Mexico (Jiménez and Palacios 1999, Jiménez et al. 2003, Astorga et al. 2015). The World Health Organization (2012), as well as the United States Army (Webber et al. 2017) considered that travellers are at risk of exposure to blood-sucking bugs when trekking, camping, or using poor-quality accommodation. *Dipetalogaster maximus* is an aggressive triatomine and commonly leaves its shelter when hungry, even in daylight, to get a blood meal that includes human blood. This species has been reported from many collection points in the Cape region which have included camping areas close to some small localities devoted to "adventure tourism," where open air sleeping is commonly practiced (Jiménez and Palacios 1999, Jiménez et al. 2003, Astorga et al. 2015). However, even when searched habitats have been similar, such as crevices on granitic rocks, the abundance of the triatomines have been remarkably different (Jiménez et al. 2003, Astorga et al. 2015). A possible explanation for this phenomenon is that the abundance of populations of the same triatomine species is different due to varying environmental conditions among the localities although they are geographically close (Martínez-Ibarra et al. 2014). An alternative explanation could be the strong influence of host availability for feeding in that referred abundance (Jiménez et al. 2003). The third possible explanation could be as populations are intrinsically different, their "performance" on the biological parameters, as a consequence, is remarkably different. A similar phenomenon has been previously reported for other triatomines (Martínez-Ibarra et al. 2003, Herrera-Aguilar et al. 2009).

As part of a series of studies on the biology of Mexican triatomine species, we conducted a study of two geographically close populations of *D. maximus* that were collected from environmentally similar habitats to determine their "perfomance" on different biological parameters and their potential risk as vectors of *T. cruzi.*

MATERIALS AND METHODS

Study sites

Some specimens of *D. maximus* were collected for colonization purposes in June and July, 2016 from two small tourist communities, El Fandango and San Dionisio, in the cape region of Baja California Sur State, Mexico. Although the same methodology has been carried out in search of specimens, a remarkably different number of *D. maximus* has been previously collected in those areas (Jiménez et al. 2003, Astorga et al. 2015). The two localities have similar environmental characteristics, are geographically close (approximately 30 km) and have no geographic barrier between them (Figure 1). El Fandango (109º 51' W, 23º 49' N,) is located 350 m above sea level, whereas San Dionisio (109º 51' W, 23º 36' N,) is situated 380 m above sea level. Both areas have a dry desert climate, with a mean annual temperature of 26° C and are characterized by the presence of sweet mango (*Mangifera indica* L), lemon (*Citrus limon* L), squash (*Cucurbita maxima* Duchesne), guava (*Psidium guajava* (L) Kunze), papaya (*Carica papaya* L), and cacaloxuchitl (*Plumeria rubra* L) (INAFED 2015). A previous study on available animals as blood meal sources for *D. maximus* showed that the abundance of blood meal sources was comparable (Astorga et al. 2015).

Survey protocol

The *D. maximus* specimens were collected during two three-day travels to selected localities in the summer of 2016. We searched intradomiciliary and peridomiciliary areas of selected localities where *D. maximus* specimens have been previously collected, as well as the surrounding natural ecotopes (Jiménez et al. 2003, Astorga et al. 2015). The sampling included all natural ecotopes of triatomines such as holes in the ground, rock piles, heaps of stones, and crevices on stones. The presence or absence of triatomines in each residence was assessed by performing a 20 min intradomicile and 20 min peridomicile timed manual collection for adult or nymphal triatomines. Daytime searches were conducted by spraying an irritant insecticide and by using a flashlight to search into cracks and crevices throughout the interior of buildings, cupboards, behind portraits on walls, and under furniture and bedding. A team of three trained personnel conducted the searches on every single house in each village. The intradomiciliary area included the interiors of houses and attached buildings, and all rooms circumscribed by the main walls of the dwelling in which inhabitants normally sleep. The peridomiciliary area was defined as the area surrounding the homestead, which was usually enclosed by a fence and in which rocks, mounds of construction materials, animal shelters, and agricultural products can often be seen. Consequently, human dwellings or intradomiciliary and peridomiciliary areas included areas that are 20 to 30 m away from the main dwellings. Areas beyond the said parameter were considered as sylvatic habitats (Grant-Guillén et al. 2017). In addition, we used 30 wire-netting bait-traps based on Noireau traps, where each contained a Wistar rat (Noireau et al. 2002). The traps were placed every night in ten sylvatic and ten peridomestic sites, including natural bug ecotopes as described above. Triatominae were collected by hand during the day with the aid of flashlights and using tweezers, they were placed inside plastic containers labeled with collection data, such as place of capture and sex.

Specimens were collected live and transported to Laboratorio



Figure 1. Places where founders of studied populations of *Dipetalogaster maximus* were initially collected.

de Entomologia Medica at the Centro Universitario del Sur of the Universidad de Guadalajara, where they were identified according to the taxonomic key of Lent and Wygodzinsky (1979).

Colonies of *Dipetalogaster maximus*

After the collection of a minimum of 30 specimens for each of the two studied populations of *D. maximus*, a colony of each group was established. Biological parameters of the second generation colonies were obtained and compared. Although laboratory rearing imposes a certain degree of selection pressure on aspects of triatomine biology, the studied colonies were exposed to standardized environmental conditions that were favorable to triatomine survival. Hence, it was assumed that the biological parameter estimates derived from data collected from colonized wild populations represent a maximum expression of their biological parameters and are likely to reflect true differences between populations. Similar assumptions were made by Martínez-Ibarra et al. (2015, 2016) in comparing the life-table strategies of geographically distinct strains of *Meccus phyllosomus picturatus* (=*M. picturatus*) (Usinger) and interbreeding populations of *M. p. mazzottii* (=*M. mazzottii*) (Usinger) and *M. p. pallidipennis* (Stål) after colonization in standard laboratory conditions.

Biological parameters

The studied populations were maintained under conditions similar to those in the study by Costa et al. (1987) with *D. maximus*. The laboratory conditions were 27 ± 1º C and 60 ± 5% relative humidity (RH) under a 12:12 (light:dark) photoperiod. The eggs from each population were grouped by date of oviposition to result in populations with 100 eggs each. After eclosion, the groups of each population of 1st instar nymphs were separated into groups of five individuals. Each triatomine was then distinguished by markings on its conexivum and placed into a plastic container (5.5 cm diameter x 10.5 cm height) with a central vertical support of absorbent cardboard. Each container was labeled with a distinguishing number and the date when the 1st instar nymphs inside were born. Three days after eclosion of the nymphs in each plastic container, they were allowed to feed by container on immobilized and anesthetized New Zealand rabbits for 1 h; their subsequent blood meals were given on a fortnightly basis, by taking into account the eclosion date of each group. Rabbits were selected as the blood source, since as has been previously reported, *D. maximus* show better results in biological parameter after feeding on mammals (e.g., mouse) than on birds (e.g., dove and hen) (Costa et al. 1987). Rabbits were anesthetized as per Norma Oficial Mexicana (NOM-062-ZOO-1999) regulations and were inoculated with 0.25 ml/kg of ketamine intramuscularly (SAGARPA 1999). The studied triatomines were individually observed from the onset until the end of feeding under medium light conditions. The nymphs were checked daily for ecdysis or death. Among the insects that completed their development into adults, the ten first obtained adult pairs were taken from each cohort, placed in individual containers (5.5 cm diameter x 10.5 cm height) and were maintained, as previously described, to determine the oviposition patterns. The eggs were daily collected for 30 days and were placed in individual containers until hatching.

Statistical analysis

A nonparametric *Mann-Whitney U-test* was used to compare the developmental cycle periods, number of blood meals needed to molt, and the number of eggs laid by females of both studied cohorts; moreover, the Shapiro Wilk's test results for all comparisons was $P < 0$ when the comparison among cohorts considered each of the studied parameters. A Student's *t*-test ($P < 0.05$) was used to compare the number of eggs laid by each female. The Chi-square test was used to compare the frequencies of both cohorts. Sigma Stat 3.1 software (version 3.1 for Windows, Systat Software Inc., San Jose, CA) was used for statistical analysis.

RESULTS

The median egg-to-adult developmental period of the two cohorts significantly varied (U = 191.5, df = 1, P<0.001); the El Fandango and the San Dionisio cohorts had 190 days and 205 days of development, respectively. The two studied populations also showed significant differences (U = from 428.5 to 1,567.5, df = 1, P = from 0.03 to <0.001) when their median nymphal developmental times were compared (Table 1).

The number of blood meals needed for molting to the next instar of the two cohorts differed significantly (U = from 177 to 1,817, df = 1, P>0.001) when paired comparisons were carried out. Similarly, a significant lower total number of meals (U = 0, df = 1, P<0.001) needed to molt through each nymphal instar until the adult stage was recorded for El Fandango cohort (seven meals) as compared to the San Dionisio cohort (12 meals) (Table 1).

No significant (X^2 = from 0.19 to 2.62, df = 1, P=from 0.1 to 0.68) differences were recorded in the mortality rates of the studied cohorts when paired comparisons (including total percentages) were carried out (Table 2). At the end of the cycles, the percentages of the obtained females were found to be significantly different (X^2=37.51, df = 1, P<0.001) among the two studied cohorts and comparable results were obtained when the percentages of obtained males were compared (Table 2).

The mean number of eggs laid per day per female for a month was significantly higher (t = 6.2, df = 1, P<0.02) in the El Fandango cohort (1.96 eggs) than in the San Dionisio cohort (0.49) (Table 2).

The egg eclosion rates of the El Fandango cohort (96.43%) were significantly higher (X^2 = 4.03, df = 1, P<0.044) than those of the San Dionisio cohort (89.80%), with a similar median incubation period of approximately 19 days and with no recorded significant differences (P>0.05).

DISCUSSION

The median egg-to-adult development time of the El Fandango cohort was shorter than that of the San Dionisio cohort. However, as compared to a previous published study on *D. maximus*, carried out under uncontrolled temperature and HR conditions, the development times of both currently studied cohorts were shorter than those 368.5 and 361.5 days for females and males, respectively (Jiménez and Palacios 2002). The developmental time of El Fandango cohort (190 days) was slightly longer than that of *Triatoma lecticularia* Stål (168.5 days), which is an important vector in the United States of America and comparable to that of *M. p. longipennis* (Usinger) (198 days), which is considered as one

Table 1. Time of development (median and interquartile range) from egg to adult and blood meals to molt (median and interquartile range) of two populations of *D. maximus* fed every 15 days on rabbits under laboratory conditions.

Instar	El Fandango			San Dionisio		
	n	Time of development (days)	Blood meals	n	Time of development (days)	Blood meals
Egg-N1	97	20[a] (18-21)	--	90	19[a] (18-21)	--
N1-N2	85	19[a] (17-21)	1[a] (1-1)	85	23[b] (20-26)	1[b] (1-2)
N2-N3	78	24[a] (21-29)	1[a] (1-1)	70	27[b] (23-32)	2[b] (1-2)
N3-N4	67	31[a] (28-34)	1[a] (1-2)	56	38[b] (31-44)	2[b] (1-3)
N4-N5	47	41.5[a] (36.2-51)	2[a] (1-2)	47	49[b] (41.5-54)	3[b] (2-3)
N5-AD	39	70[a] (55.7-83)	2[a] (1-3)	33	70[a] (58-87)	4[b] (2-4)
Total	39	190[a] (170.2-198.5)	7[a] (6-8)	33	205[b] (195-228)	12[b] (11-12)

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

Table 2. Percentage of accumulative mortality, percentage of obtained females, number of laid eggs (mean ± SD), and percentage of egg eclosion of two populations of *Dipetalogaster maximus* fed every 15 days on rabbits under laboratory conditions.

Population	Accumulative mortality %	Females %	Males %	Average eggs laid	Egg eclosion rate %
El Fandango	59.79[a] (n = 97)	69.23[a]	30.77[a] (n = 39)	2.1 ± 0.3[a]	96.43[a] (n = 589)
San Dionisio	63.33[b] (n = 90)	48.48[b]	51.52[b] (n = 33)	0.46± 0.1[b]	89.8[b] (n = 147)

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

of the most important vectors of *T. cruzi* to humans in Mexico (Salazar-Schettino et al. 2010, Bern et al. 2011; Grant-Guillén et al. 2017, Martínez-Ibarra et al. 2017b). Moreover, the egg-to-adult development time of El Fandango cohort was similar to that of *T. carcavalloi* Jurberg, Rocha and Lent and *T. boliviana* Martínez, Chávez, Sossa, Aranda Vargas, and Vidaurre, sylvatic species important for the transmission of *T. cruzi* to hosts in Brazil and Bolivia, respectively (Cardozo de Almeida et al. 2014, Durán et al. 2014).

The median number of blood meals for molting through each nymphal instar until the adult stage was lower for the El Fandango cohort as compared to the San Dionisio cohort. The median blood meals of both cohorts were lower than that of *T. sherlocki* Papa, Jurberg, Carcavallo, Cerqueira, and Barata, (16 blood meals), *T. boliviana* (15), and *T. carcavalloi* (13.4) (Cardozo de Almeida et al. 2014, Durán et al. 2014, Lima-Neiva et al. 2017). Furthermore, the median blood meals of both cohorts were similar to that of *M. p. mazzottii* and *M. p. pallidipennis,* which were 11.97 and 11.73 blood meals, respectively (Martínez-Ibarra et al. 2017a). These species are considered as two of the most important Mexican species for the transmission of *T. cruzi* to humans (Salazar-Schettino et al. 2010). A recorded low median number of blood meals for molting shows that the El Fandango cohort would have greater survival opportunities than the San Dionisio cohort, because triatomines are at risk each time they leave shelter to find a host (Costa et al. 2009).

The mortality rate of both studied cohorts was around 60%, which was higher than those of *M. p. mazzottii* and *M. p. pallidipennis*, which were 25.3% and 21.3%, respectively (Martínez-Ibarra et al. 2017a). The mortality rates of both currently studied cohorts were similar to *T. carcavalloi* (57.2%) but lower than that of *Panstrongylus chinai* (Del Ponte) (84.9%) and *T. boliviana* (76%) (Cardozo-De Almeida et al. 2014, Durán et al. 2014, Mosquera et al. 2016). This parameter contributes to explaining the low number of *D. maximus* collected in its distribution area (Jiménez and Palacios 1999, Jiménez et al. 2003, Astorga et al. 2015).

The percentage of females at the end of the cycles was higher in the El Fandango cohort than in the San Dionisio cohort. In line with this, we conclude, through female proportion, that the El Fandango cohort has more potential to increase in number under favorable conditions as compared to the San Dionisio cohort; thus, this could result in an increased risk of *T. cruzi* transmission to vertebrate hosts, including humans in the studied tourist areas.

The mean number of eggs laid per day for one month was

higher in the El Fandango cohort than in the San Dionisio cohort. A higher number of eggs laid represents a potential higher number of individuals and, as a consequence, a greater risk of the presence of more infective triatomines. This biological parameter explains why greater number of specimens have been collected in El Fandango than in San Dionisio (Jiménez et al. 2003, Astorga et al. 2015).

The egg eclosion rates were both elevated and were similar to those of *P. chinai* (95.9%), *T. lecticularia* (93%), and *M. p. pallidipennis* (86.5%) (Mosquera et al. 2016, Grant-Guillén et al. 2017, Martínez-Ibarra et al. 2017a). The high number of eggs laid, along with high eclosion rates, explains the remarkable differences recorded between studied cohorts, which could be extrapolated at some extent to explain the differences in the abundance of natural populations of *D. maximus*.

The median incubation period of the two studied cohorts was approximately 19 days, which is shorter as compared to that of *T. sherlocki* (41 days), *D. maximus* in a previous study (33), *P. chinai* (25.6), and *T. carcavalloi* (22.7), thus indicating how favorable the laboratory conditions were for the development of *D. maximus* (Cardozo-De Almeida et al. 2014, Silva-Monte et al. 2014, Mosquera et al. 2016).

Most of the studied parameters, except accumulative mortality and median incubation period of eggs, showed significant differences between the two studied populations. The notable differences among the four studied biological parameters of the studied cohorts reflect the previously recorded remarkable differences in the abundances of natural populations of *D. maximus* from El Fandango and San Dionisio, as environmental conditions and availability of hosts as blood meal sources were similar between both areas (Jiménez et al. 2003, Astorga et al. 2015).

Studies of current biological parameters of different natural populations of *D. maximus* can help in estimating how abundant each population will be, thus increasing its importance in areas where tourists go for camping activities in the open air and be in risk of being bitten by *D. maximus* and being infected by *T. cruzi* through its feces (Jiménez et al. 2003). This assumption is also applicable to the widely distributed, and most epidemiologically important Mexican triatomine species, *M. p. mazzottii* and *M. p. pallidipennis*, that were previously collected from tourist camping areas in Guerrero state, for *M. p. longipennis* that were collected from tourist camping areas in Chihuahua state, and for *T. dimidiata* (Latreille), collected surrounding Zoh-Laguna, embedded in the Calakmul biosphere reserve in Campeche State (Licón-Trillo et al. 2010, Rodríguez-Bataz et al. 2011, Valdez-Tah et al. 2015). Similar collections have been done in Hawaii, where *T. rubrofasciata* (De Geer) have been reported (Bern et al. 2011).

Currently reported biological parameters could also contribute to the selection of more appropriate populations for colonization research purposes to have more abundant specimens in shorter periods of time (Azevedo-Franco et al. 2002, Thomsen and Voigt 2006).

Our study confirms the importance of studying the biological parameters of local populations to determine their specific dynamics as previously reported for other triatomine species (Martínez-Ibarra et al. 2015, 2017b).

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