Trypanosoma Cruzi Affects The Sensory Biology of Triatoma Dimidiata (Hemiptera: Reduviidae).

Irving J. May-Concha (irving.may@correo.uady.mx)
Regional Centre of Research Dr Hideyo Noguchi: Centro de Investigaciones Regionales Dr Hideyo Noguchi

Maryrose J. Escalante Talavera
Regional Centre of Research Dr Hideyo Noguchi: Centro de Investigaciones Regionales Dr Hideyo Noguchi

Jean-Pierre Dujardin
Institut de recherche pour le développement: Institut de recherche pour le developpement

Etienne Waleckx
Regional Centre of Research Dr Hideyo Noguchi: Centro de Investigaciones Regionales Dr Hideyo Noguchi

Research

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Abstract

Background: *Triatoma dimidiata* is a vector of the protozoan parasite *Trypanosoma cruzi*, the etiologic agent of Chagas disease. Phenotypic plasticity allows an organism to adjust its phenotype in response to stimuli or environmental conditions. Understanding the effect of *T. cruzi* on the phenotypic plasticity of its vectors, known as triatomines, has attracted great interest because of the implications of the parasite-triatomine interactions in the eco-epidemiology and transmission of the parasite. We investigated whether the infection of the vector with *T. cruzi* can change the antennal phenotype of sylvatic, domestic, and laboratory-reared populations of *T. dimidiata*.

Methods: The abundance of each type of sensillum (bristles, basiconic, thick- and thin-walled trichoid) on the antennae of *T. cruzi*-infected and non-infected *T. dimidiata* reared in the laboratory or collected in sylvatic and domestic ecotopes were measured under light microscopy and compared using Kruskal–Wallis non-parametric tests and Permutational Multivariate Analysis of Variance.

Results: We found significant differences between sensilla patterns of infected and non-infected insects within sylvatic and domestic populations. Conversely, we found no significant differences between sensilla patterns of infected and non-infected insects within the laboratory-reared population. Besides, our results show that the infection with *T. cruzi* affects the sexual dimorphism linked to antennal phenotype in sylvatic and domestic populations.

Conclusion: These differences could be linked, for infected insects, to higher efficiency in the perception of odor molecules related to the search of distant mates and hosts and for flight dispersal in search of new habitats, and the possibility of a positive effect on population dynamics and on the vectorial transmission of *T. cruzi*.

1. Background

Phenotypic plasticity is of great interest in ecology and evolution because it allows an organism to actively adjust its phenotype in response to stimuli or environmental conditions [1–8]. The response may or may not be adaptive, and it may involve changes in morphology, physiological state, behavior, or some combination of these [9]. Besides, phenotypic plasticity is also widely recognized as an important factor for the evolution, population biology, and ecological interactions of many species [10–13]; thus, it is a major mechanism of ecological adaptation [14]. Most information on phenotypic plasticity comes mainly from social insects [14–16], triatomines [17–20], grasshoppers [21, 22] and butterflies [13, 23].

In insects, the olfactory system plays an important role in many behavioral contexts, such as food, refuges and mate finding, alarm and aggregation behaviors, as well as avoidance of natural enemies [24]. In triatomines, the antennal phenotype (AP) comprises the type and number of sensilla (classified as mechanoreceptors and chemoreceptors) distributed on the antennae. Sensilla act as an interface between the external and internal environments of insects (inter and intraspecific communication), capturing different stimuli from the external environment and directing them to the central nervous

system [24–26]. This then triggers specific behavioral responses, such as the selection of a host for feeding, oviposition behavior, mate finding, as well as alarm and aggregation behaviors [27–33].

AP has been widely used to analyze genetic diversity, as well as environmental influences on populations [33–35]. In certain species or complexes, AP analysis complements other phenotypic and genetic characteristics [34, 36–39] or provides evidence for species´ differentiation [40, 41]. On the other side, previous studies have established that the types of sensilla on an insect's antennae may show a degree of morphological plasticity between populations that seems associated with adaptations to sensorial requirements of different habitats [17, 37]. Besides, the number of sensilla may also vary because of selection pressure, sex, infection by a microorganism, and feeding habits [37, 39, 42–46]. Such changes show the degree of phenotypic plasticity exhibited by the species [17].

As vectors of *Trypanosoma cruzi*, the causal agent of Chagas disease, the insects of the subfamily Triatominae (Hemiptera: Reduviidae), have special relevance in Latin America [47]. The parasite is transmitted to humans and other animals when feces or urine of infected insects come into contact with mucous membranes or damaged areas of mammal skin [48]. The co-evolution between triatomines and *T. cruzi* has promoted the development of powerful and sophisticated strategies, which can modify a wide range of physiological processes of the insects, including those related to the input, development, and discharge of the parasite [49]. The existence of these modifications as a characteristic of an association between *T. cruzi* and triatomines could be the consequence of different adaptive or nonadaptive scenarios (e.g., adaptive host manipulation) [50–51]. While several works have analyzed the mechanisms associated with *T. cruzi*-vector dynamics (e.g., biotic and abiotic factors) to understand the *T. cruzi*-triatomine interactions, under a co-evolutionary scenario [52], literature about how the parasites may influence the insects is more limited, and the studies have only been focused on the parasite's effects on four patterns of the vector's behavior: life-history traits, feeding, defecation, and dispersion/locomotion [53]. Different studies have found negative effects of *T. cruzi* infection on vector's survival [54–57], fecundity [57, 58], post-embryonic development [57, 59, 60], behavior [53, 61–65], and physiological processes [54, 58, 66–68], while other studies have not identified these effects on patterns of alimentation/defecation [54, 69], development and reproduction [70–72]. Overall, most of these studies determined that the effects of *T. cruzi* are species-dependent, age-dependent, sex-dependent, and even environment/physiology-dependent.

Although the AP, infection with *T. cruzi*, and phenotypic plasticity of the triatomines have been extensively studied [17, 34, 52], the phenotypic plasticity linked to the infection with *T. cruzi* in triatomines has not been investigated so far. In this study, we performed a series of analyses to test whether the infection with *T. cruzi* modifies the AP of *T. dimidiata* from Yucatan, Mexico. More specifically, we investigated whether the infection with *T. cruzi* modifies the AP and sexual dimorphism of sylvatic, domestic and laboratory-reared *T. dimidiata* populations.

2. Methods

2.1. Insects

Laboratory-reared *T. dimidiata* came from a colony maintained for the past 10 years at the Parasitology Laboratory of the Regional Research Center Dr. Hideyo Noguchi, Autonomous University of Yucatan. New insects have been periodically added to this colony to avoid inbreeding depression. The colony is reared and maintained at 27 ± 1°C, 70 ± 5% RH, a photoperiod of 12: 12 (L: D) h, and insects are fed on immobilized pigeons (*Columba livia*). The domestic and sylvatic populations were composed of insects collected during entomological surveillance inside and outside human dwellings of the rural village of Teya (21.05º N, 89.07º W), Yucatan, Mexico, and in the sylvatic habitat surrounding this village, respectively [73–74]. The study was approved by the Institutional Bioethics Committee of the Autonomous University of Yucatan.

2.2. Trypanosoma cruzi

For infection of triatomines, the “V strain”, a TcI strain of *T. cruzi* maintained in the laboratory by cyclical passages in BALB/c adult mice was used.

2.3. Infection of the laboratory-reared triatomines

After a two-week starvation period, the initial infection of the laboratory-reared triatomines was carried out with nymphs that had just molted to their 5th instar. Nymphs were fed ad libitum on BALB/c mice 15 days after these were infected with 1×10^6 parasites ml^{-1} of blood (i.e., during the parasite's exponential stage of growth; [63]). Approximately 30 days after infection, we corroborated infection status through examination of a fecal drop observed under a light microscope at 40× magnification. Control group insects were fed under the same conditions on non-infected mice. The nymphs of both groups were maintained under rearing conditions and were fed fortnightly on infected/non-infected mice until they molt to the adult stage. For *T. dimidiata* collected in natural conditions (i.e. domestic and sylvatic populations), *T. cruzi* infection status was assessed by amplifying parasite DNA from each bug midgut by PCR using TCZ primers, as previously described [75].

2.4. Antennal preparation

We examined a total of 130 antennae of *T. cruzi*-infected and non-infected females and males from the sylvatic, domestic and laboratory-reared populations of *T. dimidiata* (Table 1). One antenna per specimen was removed using fine forceps and scissors. Antennae were processed with sodium hydroxide 4% for 6 hr at 60°C and then neutralized with glacial acetic acid 5% for 2 min. This procedure allowed cuticle diaphanization and allowed the identification and counting of the sensilla using a stereo microscope Zeiss Primostar® at 400×. The number and type of sensilla on antennal segments was counted manually using a procedure reported previously [33]. The ventral side of the three distal segments of the antennae (P: pedicel, F1: flagellum 1, and F2: flagellum 2) was evaluated, by identifying and counting the following sensilla: bristles (BR), thin-walled trichoid (TH), thick-walled trichoid (TK), and basiconic (BA) (nomenclature according to Catalá and Schofiel [36]), thus giving a total of 12 morphological variables.

Table 1
Number of *T. dimidiata* specimens used in this study. Population, sex and infection status of the specimens are indicated.

Populations	Infected		Non-infected		Overall
	♀	♂	♀	♂	
Laboratory-reared	10	10	10	11	41
Domestic	10	10	10	10	40
Sylvatic	10	10	13	16	49
Overall	30	30	33	37	**130**

2.5. Data analysis

Differences on the AP between *T. cruzi*-infected (I) and non-infected (NI) insects were explored overall populations, within each sex, within each population, and within each sex within each population using univariate and multivariate analyzes. Means and standard deviations of abundance were calculated for each type of sensilla (chemoreceptors: BR, TH, TK, and mechanoreceptors: BA) and antennal segment (pedicel, flagellum 1 and flagellum 2). As original data and their transformations were not normally distributed using Shapiro-Wilk tests [76]. Kruskal – Wallis non-parametric tests were thus used for univariate analyses. Data were analyzed with the MINITAB Statistical Software, version 17 (Minitab Inc., PA, U.S.A.). In all cases, $P < 0.05$ was considered statistically significant. Moreover, the sources of variation of the AP were assessed using two-way Permutational Multivariate Analysis of Variance (PERMANOVA) on Bray-Curtis similarity matrices of square-root with 9999 permutations. These analyses were conducted in PAST version 3.05.

3. Results

3.1 Overall data

Abundances of the sensilla found for all the *T. dimidiata* specimens included in this study are shown in Table A1, Supplementary data. All the insect's antennae presented three types of chemoreceptors (TH, TK, and BA) and one mechanoreceptor (BR) on the three segments. The average number of sensilla per insect was of 669.52 ± 176.45. Overall, the TH sensillum of the pedicel (P-TH) was the more abundant (183.42 ± 92.70) while the BR sensillum of the flagellum 2 (F2-BR) was the less abundant (17.45 ± 12.51). The pedicel was the segment with the highest number of sensilla (322.42 ± 115.54) while the flagellum 2 was the segment with the lowest number of sensilla (149.63 ± 54.43).

3.2. Effect of the infection with T. cruzi *on the AP of* T. dimidiata

Differences of each sensillum on the three antennal segments between infected and non-infected insects' overall populations, within each sex, within each population, and within each sex within each population, are summarized in Table 2.

Table 2

Comparisons of the abundances of each sensillum between infected and non-infected insects overall populations, within each sex, within each population, and within each sex within each population of *Triatoma dimidiata*. BR: bristles; BA: basiconic; TH: thin-walled trichoid; TK: thick-walled trichoid. F: female and M: male. I: infected; NI: non-infected. D: domestic, S: Sylvatic, and L: Laboratory reared. Asterisks represent a significant difference between infected and non-infected insects (P < 0.05*; P < 0.01**; P < 0.001***; – no difference).

Factor	Pedicel				Flagellum 1				Flagellum 2			
	BR	BA	TH	TK	BR	BA	TH	TK	BR	BA	TH	TK
Overall populations (I *vs* NI)	–	**	–	–	–	–	–	*	–	–	–	–
Whitin females (I females *vs* NI females)	–	–	*	–	–	–	–	–	–	–	–	–
Whitin males (I males *vs* NI males)	–	–	–	–	–	–	–	**	–	–	–	–
Whitin domestic insects (I D *vs* NI D)	*	–	*	*	***	*	–	*	*	***	*	–
Whitin sylvatic insects (I S *vs* NI S)	–	***	–	–	***	**	–	***	**	**	*	**
Whitin laboratory-reared insects (I L *vs* NI L)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin females of the domestic population (F D I *vs* F D NI)	–	–	*	–	–	–	–	–	–	*	*	–
Whitin females of the sylvatic population (F S I *vs* F S NI)	–	***	–	–	**	**	–	–	*	*	–	*
Whitin females of the laboratory-reared population (F L I *vs* F L NI)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin males of the domestic population (M D I *vs* M D NI)	*	–	–	–	***	–	–	–	*	***	–	–

Factor	Pedicel				Flagellum 1				Flagellum 2			
Whitin males of the sylvatic population (M S I *vs* M S NI)	–	*	–	–	**	–	–	***	*	–	*	–
Whitin males of the laboratory-reared population (M L I *vs* M L NI)	–	–	–	–	–	–	–	–	–	–	–	–

Table 3
Two-way PERMANOVA based on Bray-Curtis distance matrix assessing the sources of variation of the AP of *T. dimidiata* populations. P-values are based on 9999 permutations.

A) Domestic population				
Source of variation	Sum of squares	Mean square	*F*	*P*
Infection	0.188	0.188	7.151	0.0001
Sex	0.039	0.0.39	1.5179	0.1776
Interaction	0.031	0.031	1.1887	0.2993
B) Sylvatic population				
Infection	0.209	0.209	7.418	0.0001
Sex	0.121	0.121	4.288	0.0021
Interaction	0.103	0.013	0.368	0.125
C) Laboratory-reared				
Infection	0.031	0.031	0.708	0.569
Sex	0.083	0.083	1.869	0.104
Interaction	0.052	0.052	0.126	0.473

1. **3.2.1. Overall populations.** When infected and non-infected insects were compared, significant increases in the numbers of BA sensilla on pedicel (P-BA) and TK sensilla on flagellum 1 (F1-TK) were observed in infected insects (Kruskal–Wallis test, $P = 0.007$ and $P = 0.01$, respectively).
2. **3.2.2. Within each sex.** When infected and non-infected insects were compared for each sex (I females *vs* NI females; I males *vs* NI males), a significant decrease in the number of TH sensilla on pedicel (P-TH) was observed in infected females compared to non-infected females (Kruskal–Wallis test, $P = 0.04$). Conversely, a significant increase in the number of TK sensilla on flagellum 1 (F1-TK) was observed in infected males compared to non-infected males (Kruskal–Wallis test, $P = 0.008$).

3. **3.2.3. Within each population.** In the domestic population, when infected and non-infected insects were compared, a significant increase in the number of BR sensilla on pedicel (P-BR) was observed in infected insects (Kruskal–Wallis test, $P = 0.01$). On the other side, significant decreases in the number of TH and TK sensilla on pedicel; BR, BA, TK sensilla on flagellum 1, and BR, BA, TH sensilla on flagellum 2 were observed in infected insects compared to non-infected insects (Kruskal–Wallis test, $P < 0.05$ in all cases). Additionally, the two-way PERMANOVA test revealed that the infection with *T. cruzi* affected the AP of the domestic population (F = 7.15; $P = 0.0001$), while the sex and the interaction infection*sex did not have significant effects (F = 1.51; $P = 0.177$ and F = 1.188; $P = 0.299$, respectively; Table 3A).

In the sylvatic population, when infected and non-infected insects were compared, significant increases in the number of BA sensilla on pedicel; BR, BA, and TK sensilla on flagellum 1; BR, BA, TH and TK sensilla on flagellum 2 were observed in infected insects (Kruskal–Wallis test, $P < 0.05$ in all cases). The two-way PERMANOVA test revealed that the infection with *T. cruzi* and the sex affected the AP of the sylvatic population (F = 7.41; $P = 0.0001$ and F = 4.28; $P = 0.002$, respectively), while the interaction infection*sex did not have significant effect (F = 0.368; $P = 0.125$; Table 3B).

Finally, in the laboratory-reared population, when infected and non-infected insects were compared, no difference in the number of sensilla were observed (Kruskal–Wallis test, $P > 0.05$ in all cases). In the same way, the two-way PERMANOVA test did not reveal significant effects of the infection with *T. cruzi*, of the sex and of the interaction infection*sex on the AP of laboratory-reared insects ($P > 0.05$; Table 3C).

3.2.4. Within each sex within each population. Differences in the abundances of each sensillum on the three antennal segments between infected and non-infected insects within each sex within each population are shown in Table A1 (Supplementary data) and are summarized in Table 2.

Domestic population. The antennae of infected females of the domestic population showed a significant decrease in the number of TH sensilla on pedicel and flagellum 2, and in the BA sensilla on flagellum 2, compared to non-infected females (Kruskal–Wallis, $P < 0.05$ in all cases). On the other side, infected males of the domestic population showed an increase in the number of BR sensilla on pedicel (P-BR), compared to non-infected males (Kruskal–Wallis test, $P = 0.01$). Moreover, infected males of the domestic population showed a decrease in the BR sensilla on flagellum 1 and flagellum 2, and in the BA sensilla on flagellum 2, compared to non-infected males (Kruskal–Wallis, $P < 0.05$ in all cases).

Sylvatic population. The antennae of infected females of the sylvatic population showed a significant increase in the number of BA sensilla on the three segments of the antennae, in the BR sensilla on flagellum 1 and flagellum 2, and in the TK sensilla on flagellum 2, compared to non-infected females (Kruskal–Wallis test, $P < 0.05$ in all cases). On the other side, infected males of the sylvatic population showed an increase in the BA sensilla on pedicel, in the BR and TK sensilla on flagellum 1, and in the BR and TH sensilla on flagellum 2, compared to non-infected males (Kruskal–Wallis test, $P < 0.05$ in all cases).

Laboratory-reared population. In the laboratory-reared population, there were no differences in the number of sensilla between infected and non-infected females and males (Kruskal–Wallis test, $P > 0.05$).

3.3. *Effect of the infection with* T. cruzi *on the sexual dimorphism of* T. dimidiata.

Differences in the abundances of each sensillum between non-infected females and males, and between infected females and males overall populations, and within each population, are summarized in Table 4.

Table 4
Comparisons of the abundances of each sensillum between infected females and males and between non-infected females and males overall populations, and within each population of *Triatoma dimidiata*. BR: bristles; BA: basiconic; TH: thin-walled trichoid; TK: thick-walled trichoid. F: female and M: male. I: infected; NI: non-infected. D: domestic, S: Sylvatic, and L: Laboratory reared. Asterisks represent a significant difference between infected and non-infected insects (P < 0.05*; P < 0.01**; P < 0.001***; – no difference).

Factor	Pedicel				Flagellum 1				Flagellum 2			
	BR	BA	TH	TK	BR	BA	TH	TK	BR	BA	TH	TK
Overall non-infected insects (NI females *vs* NI males)	–	–	–	–	–	–	–	–	–	–	–	–
Overall infected insects (I females *vs* I males)	–	–	**	–	–	–	–	–	–	–	–	–
Whitin non-infected domestic insects (F D NI *vs* M D NI)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin infected domestic insects (F D I *vs* M D I)	–	–	–	–	–	–	*	–	–	–	–	–
Whitin non-infected sylvatic insects (F S NI *vs* M S NI)	–	–	*	–	–	–	**	–	–	–	–	–
Whitin infected sylvatic insects (F S I *vs* M S I)	–	**	*	–	–	*	–	–	–	–	–	–
Whitin non-infected laboratory-reared insects (F L NI *vs* M L NI)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin infected laboratory-reared insects (F L I *vs* M L I)	–	–	–	–	–	–	–	–	–	–	–	–

1. **3.3.1. Overall populations.** When non-infected females and males were compared, no significant difference in the number of sensilla was observed (Kruskal–Wallis test, $P > 0.05$). However, when infected females and males were compared, a significant difference in the number of TH sensilla on pedicel (P-TH) was observed (Kruskal–Wallis test, $P = 0.002$).

2. **3.3.2. Domestic population.** When non-infected females and males were compared, no significant difference in the number of sensilla was observed (Kruskal–Wallis test, $P > 0.05$). However, when infected females and males were compared, a significant difference in the number of TH sensilla on flagellum 1 (F1-TH) was observed (Kruskal–Wallis test, $P = 0.01$).
3. **3.3.3. Sylvatic population.** When non-infected females and males were compared, significant differences in the number of TH sensilla on pedicel (P-TH) and flagellum 1 (F1-TH) were observed (Kruskal–Wallis test, $P = 0.02$ and $P = 0.003$, respectively).

When infected females and males were compared, the significant difference in the numbers of TH sensilla on pedicel (P-TH) was still observed (Kruskal–Wallis test, $P = 0.04$), while the difference in the number of TH sensilla on flagellum 1 (F1-TH) was not observed anymore. However, significant differences in the numbers of BA sensilla on pedicel (P-BA) and flagellum 1 (F1-BA) were observed (Kruskal–Wallis test, $P = 0.003$ and $P = 0.04$, respectively).

3.3.4. Laboratory-reared population. In the laboratory-reared population, there was no sexual dimorphism in infected and non-infected insects (Kruskal–Wallis test, $P > 0.05$).

4. Discussion

Phenotypic plasticity has been analyzed in different triatomine species in response to ecological factors [17, 35, 78], or to assess the effect of ecotope [18], food source [19], environment [35, 43, 79, 80], and sex [78]. The present study is the first to analyze phenotypic plasticity related to the infection with *T. cruzi* in domestic, sylvatic, and laboratory-reared populations of *T. dimidiata*.

Our results demonstrate that the infection with *T. cruzi* modifies the AP of *T. dimidiata*. We observed that infected and non-infected insects from the domestic and sylvatic populations showed significant differences in the number of some sensilla types. Besides, our results show that the sexual dimorphism tended to increase in *T. cruzi*-infected populations. Importantly, these differences and the effect of *T. cruzi* infection in the sexual dimorphism was not observed in the laboratory-reared population. Because in this study, the laboratory-reared insects were infected during their 5th development stage, this suggests that we should have established the infection in the earliest development stages to see the effect of *T. cruzi* on the AP. Indeed, insects infected in early development stages are more likely to be manipulated as suggested by Poulin et al. [81]. However, this would need to be further investigated in the current case.

Infected insects of the domestic and sylvatic populations showed, in general, a significant increase in the numbers of BR sensilla compared to non-infected insects. These mechanoreceptors allow insects to perceive contact stimuli, vibratory signals (through stridulation) during mating, and variations in the air current [82–84]. Besides, these play an important role in orientation towards odor-laden currents [85]. Various studies have determined that the infection by *T. cruzi*, can impair the fecundity, fertility, and mating performance of triatomines (e.g., Fellet et al. [58]). Hence, the increase in these mechanoreceptors in infected insects may help limiting this phenomenon, which is disadvantageous for the parasite. However, this deserves to be further investigated.

Concerning the chemoreceptors (BA, TH and TK), it has previously been reported that BA sensilla have an olfactory and/or gustative function for detection of habitats, shelters, hosts, and couple [86, 87]. Besides, these sensilla seem involved in the detection of presumed pheromones in conspecific feces [88, 89]. TH sensilla have an olfactory function for the detection of new habitats, sexual pairs, and hosts [34, 36, 90, 91]. On the other side, although TK sensilla have been shown to predominate in triatomines [34], their chemosensory function has not been confirmed [86, 92]. However, it may be related to the detection of a pheromone by contact, thus acting as olfactory sensilla [93], as has been shown in the insect *Cimex lectularius* L. [94]. In our study, variations in the olfactory sensitivity because of *T. cruzi* infection in the domestic and sylvatic populations is suggested. Indeed, in these populations, infected and non-infected insects showed significant differences in the number of some specific chemoreceptors. Surprisingly, infected insects of the domestic populations showed a decrease in some chemoreceptors. Conversely, in the sylvatic population, the infection with *T. cruzi* increased in all cases the number of chemoreceptors. If these differences between populations are not easy to explain, in general, the infection with *T. cruzi* significantly increased the number of chemoreceptors, which may be linked to an improved capacity for dispersal and invasion of different habitats [79, 90], and better efficiency in the perception of odor molecules in the search of distant mates and hosts and for flight dispersal in search of new habitats, as it has been suggested by other authors [80, 95–98], thus conferring an advantage to *T. cruzi*.

Although several studies show the effect of *T. cruzi* on behavioral changes [53, 61–65], so far, no study has analyzed whether there are differences in the olfactory physiology between infected and non-infected and a possible correlation of behavioral changes with their AP. In this context, it is possible to ask if the behavioral changes may be due to the AP modification in infected insects. Although the present work did not aim to answer this question, considering the recently reviewed information and the results of this study, we could suggest a possible correlation of behavioral changes with the AP as it has been suggested by May-Concha et al. [34]. Therefore, it could be interesting to evaluate the olfactory system of infected insects and non-infected towards chemical cues to find components of attractive blends that could contribute to the list of volatile compounds that modulate the behavior between infected and non-infected insects, to design better strategies for behavioral manipulation of this triatomines.

Several studies have provided information about the sexual dimorphism in non-infected triatomines from different species, populations, rearing, and ecotopes [38, 78, 99]. However, our study reports for the first time the sexual dimorphism in the AP of infected insects of *T. dimidiata*. In general, the sexual dimorphism observed in infected insects of *T. dimidiata* was based on an increase in the number of TH sensilla in infected males and/or an increase of BA sensilla in infected females. These chemoreceptors have an olfactory function for the detection of sexual pairs, habitats, hosts as mentioned above. Evidence of this study and previous works [79, 100, 101] suggest that the sexual dimorphism in the AP may be linked to the perception of molecules related to sexual behavior and to differences in sensing sexual pheromones, as it has been suggested by other authors (e.g., May-Concha et al. [34]; Souza et al. [80]). May-Concha [102] provides information on a chemical signal produced during *T. dimidiata* mating since fewer mating attempts were observed when the opening of female glands was occluded. Besides, that study describes a chemical signal which promotes the attraction of males to volatiles emitted by females

and to mating couples [30]. On the other side, based on previous works on olfactory receptors [24–26], we propose that the increased number of TH chemo-sensilla in infected males could suggest a greater efficiency in the perception of odor molecules involved in sexual communication compared with infected females. In contrast, the increased number of BA chemo-sensilla in infected females could suggest a greater efficiency in the perception of host odors compared with infected males. Therefore, the increase in the odor perception in infected insects probably elicits a positive effect on population dynamics and could affect the vectorial transmission of *T. cruzi*. However, to achieve depth in the knowledge on this subject, studies on the effects of the infection with *T. cruzi* on the behavior of aggregation, alarm, sexual pair, feeding, excretion/defecation, and host foraging in *T. dimidiata* should be carried out.

5. Conclusion

This is the first report of the effect of the infection with *T. cruzi* on the antennal phenotype of *T. dimidiata*. Our study shows that the infection with this parasite modifies the antennal phenotype of this vector and reveals a significant difference between infected and non-infected insects within natural populations of *T. dimidiata*. Overall, the increased number of some sensilla in infected insects suggests a greater contact/vibratory stimuli perception and olfactory perception compared to non-infected insects. Besides, the increase in these perceptions in infected insects probably elicits a positive effect on population dynamics which could favorize the vectorial transmission of *T. cruzi*.

Abbreviations

AP: antennal phenotype; P: pedicel; F1: flagellum 1; F2: flagellum 2; BR: bristles; TH: thin-walled trichoid; TK: thick-walled trichoid; BA: basiconic; I: *T. cruzi*-infected; NI: *T. cruzi* non-infected.

Declarations

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Authors' contributions

IJMC and EW contributed to the design of the Project. IJMC and MJET contributed to sample collection and laboratory analysis. IJMC, EW, MJET and JPD analyzed

the data. IJMC, EW and JPD wrote the manuscript. All authors read and

approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the present study available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Tables

Table 1. Number of *T. dimidiata* specimens used in this study. Population, sex and infection status of the specimens are indicated.

Populations	Infected		Non-infected		Overall
	♀	♂	♀	♂	
Laboratory-reared	10	10	10	11	41
Domestic	10	10	10	10	40
Sylvatic	10	10	13	16	49
Overall	30	30	33	37	**130**

Table 2. Comparisons of the abundances of each sensillum between infected and non-infected insects overall populations, within each sex, within each population, and within each sex within each population of *Triatoma dimidiata*. BR: bristles; BA: basiconic; TH: thin-walled trichoid; TK: thick-walled trichoid. F: female and M: male. I: infected; NI: non-infected. D: domestic, S: Sylvatic, and L: Laboratory reared. Asterisks represent a significant difference between infected and non-infected insects ($P < 0.05$*; $P < 0.01$**; $P < 0.001$***; – no difference).

Factor	Pedicel				Flagellum 1				Flagellum 2			
	BR	BA	TH	TK	BR	BA	TH	TK	BR	BA	TH	TK
Overall populations (I *vs* NI)	–	**	–	–	–	–	–	*	–	–	–	–
Whitin females (I females *vs* NI females)	–	–	*	–	–	–	–	–	–	–	–	–
Whitin males (I males *vs* NI males)	–	–	–	–	–	–	–	**	–	–	–	–
Whitin domestic insects (I D *vs* NI D)	*	–	*	*	***	*	–	*	*	***	*	–
Whitin sylvatic insects (I S *vs* NI S)	–	***	–	–	***	**	–	***	**	**	*	**
Whitin laboratory-reared insects (I L *vs* NI L)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin females of the domestic population (F D I *vs* F D NI)	–	–	*	–	–	–	–	–	–	*	*	–
Whitin females of the sylvatic population (F S I *vs* F S NI)	–	***	–	–	**	**	–	–	*	*	–	*
Whitin females of the laboratory-reared population (F L I *vs* F L NI)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin males of the domestic population (M D I *vs* M D NI)	*	–	–	–	***	–	–	–	*	***	–	–
Whitin males of the sylvatic population (M S I *vs* M S NI)	–	*	–	–	**	–	–	***	*	–	*	–
Whitin males of the laboratory-reared population (M L I *vs* M L NI)	–	–	–	–	–	–	–	–	–	–	–	–

Table 3. Two-way PERMANOVA based on Bray-Curtis distance matrix assessing the sources of variation of the AP of *T. dimidiata* populations. P-values are based on 9999 permutations.

A) Domestic population				
Source of variation	Sum of squares	Mean square	*F*	*P*
Infection	0.188	0.188	7.151	0.0001
Sex	0.039	0.0.39	1.5179	0.1776
Interaction	0.031	0.031	1.1887	0.2993
B) Sylvatic population				
Infection	0.209	0.209	7.418	0.0001
Sex	0.121	0.121	4.288	0.0021
Interaction	0.103	0.013	0.368	0.125
C) Laboratory-reared				
Infection	0.031	0.031	0.708	0.569
Sex	0.083	0.083	1.869	0.104
Interaction	0.052	0.052	0.126	0.473

Table 4. Comparisons of the abundances of each sensillum between infected females and males and between non-infected females and males overall populations, and within each population of *Triatoma dimidiata*. BR: bristles; BA: basiconic; TH: thin-walled trichoid; TK: thick-walled trichoid. F: female and M: male. I: infected; NI: non-infected. D: domestic, S: Sylvatic, and L: Laboratory reared. Asterisks represent a significant difference between infected and non-infected insects (P < 0.05*; P < 0.01**; P < 0.001***; – no difference).

Factor	Pedicel				Flagellum 1				Flagellum 2			
	BR	BA	TH	TK	BR	BA	TH	TK	BR	BA	TH	TK
Overall non-infected insects (NI females *vs* NI males)	–	–	–	–	–	–	–	–	–	–	–	–
Overall infected insects (I females *vs* I males)	–	–	**	–	–	–	–	–	–	–	–	–
Whitin non-infected domestic insects (F D NI *vs* M D NI)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin infected domestic insects (F D I *vs* M D I)	–	–	–	–	–	–	*	–	–	–	–	–
Whitin non-infected sylvatic insects (F S NI *vs* M S NI)	–	–	*	–	–	–	**	–	–	–	–	–
Whitin infected sylvatic insects (F S I *vs* M S I)	–	**	*	–	–	*	–	–	–	–	–	–
Whitin non-infected laboratory-reared insects (F L NI *vs* M L NI)	–	–	–	–	–	–	–	–	–	–	–	–
Whitin infected laboratory-reared insects (F L I *vs* M L I)	–	–	–	–	–	–	–	–	–	–	–	–

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