Received: 3 May 2023 | Accepted: 31 October 2023

DOI: 10.1111/mve.12702

ORIGINAL ARTICLE

Medical and Veterinary Entomology

How to repel a killer; chemical identification and effective repellent activity of commercial essential oils against kissing bugs

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Funding information
CONSEJO NACIONAL DE CIENCIA Y TECNOLOGIA, MEXICO

Associate Editor: Lisa J Reimer

Abstract

Triatomines are haematophagous insects, some species are vectors of *Trypanosoma cruzi*, the aetiological agent of Chagas disease. The main strategy for interrupting *T. cruzi* transmission is to avoid contact of the vector populations with humans. Volatiles from commercial essential oils are excellent candidates to serve as repellents of kissing bugs. We used an exposure device to assess the repellence effect of eight commercial essential oils on *Triatoma pallidipennis*. The most effective oils were blended and evaluated against *T. infestans*, *T. pallidipennis* and *Rhodnius prolixus*. The blend was also evaluated on parasitised *T. pallidipennis*. Data were compared with the commercial repellent NN-diethyl-3-methylbenzamide. We recorded the time the insects spent in the proximity of the host and determined if any of the evaluated oils served as kissing bug repellent. We found commercial essential oils and a blend that significantly reduced the time spent in the proximity of the host. The blend was effective for use by human males and females, repelling infected and non-infected insects. The study of essential oils as repellents of blood-sucking disease-vector insects could shed light on the development of new control strategies.

KEYWORDS
Chagas disease, chemical ecology, ethology, vectors

INTRODUCTION

Triatomines (Hemiptera: Heteroptera: Reduviidae) commonly known as kissing bugs, are insects of medical importance because of severe allergies induced by their bites as well as their potential for transmission of the parasite *Trypanosoma cruzi* (Kinetoplastida: Trypasomatidae), the aetiological agent of Chagas disease in mammals (including humans) (Zamora et al., 2015). Approximately 100 million people live in areas where there is the risk of infection (Tietbohl et al., 2019), and as occurs with other zoonotic diseases, Chagas disease has remained far from being controlled.

Some kissing bug species are of particular importance given their close contact with humans (Córdoba-Aguilar, 2020; Cruz-López et al., 2001; Lazzari et al., 2013; Ramírez-González et al., 2019).

Triatoma infestans and *Rhodnius prolixus* are the two main vector species; both are widely distributed geographically and successfully transmit the parasite to humans (Pita et al., 2018) (*Triatoma pallidipennis* is responsible for more than 70% of vectorial transmission in Mexico (Flores-Villegas et al., 2016). It is crucial to stop transmission of the parasite by avoiding contact of the bugs with humans. In this regard, the use of insect repellents has become a priority (Tietbohl et al., 2019). For decades, NN-diethyl-3-methylbenzamide (DEET) has been the most common repellent used against biting arthropods worldwide (Ramírez et al., 2020; Terriquez et al., 2013). (However, many societies have alternatively relied on plants and associated essential oils to repel or kill biting arthropods (Terriquez et al., 2013). Plant secondary metabolites represent a huge source of products with significant biological activity. Among these products, essential oils have shown high efficacy, low toxicity on non-target vertebrates, and multiple modes of action (Benelli & Pavela, 2018). Because of their high toxicity for insects and their minimal environmental effects, essential oils are a potential tool for the development of insect repellents (Sfara et al., 2009). Essential oils are considered the least toxic chemicals that can be applied to skin and sprayed into the environment (Kaur et al., 2021). In addition, in terms of insect vector management context, repellents based on essential oils are a good alternative to biological control because of the slow action of the former (Vargas-Abasolo et al., 2023). Developing safe repellents based on essential oils against triatomines is a relevant perspective for their use as active substances to develop repellent products for personal protection against these insects (Benelli & Pavela, 2018; Vargas-Abasolo et al., 2023). The repellent and insecticidal activities of essential oils against triatomines have been actively investigated (Guerreiro et al., 2018; Kaur et al., 2021; Terriquez et al., 2013; Vilaseca et al., 2004; Zamora et al., 2015). In this regard, anise (*Pimpinella anisum*) and bergamot (*Citrus bergamia*) have been studied as insecticides against triatomines, but not as repellents (Benelli & Pavela, 2018; Sainz et al., 2012). Citronella (*Cymbopogon nardus*), lavender (*Lavandula* spp.), and mint (*Mentha arvensis*) have been shown to be good repellents of some triatomines species (Benelli & Pavela, 2018; Kaur et al., 2021; Sainz et al., 2012; Sfara et al., 2009; Terriquez et al., 2013; Zamora et al., 2015). However, juniper berry (*Juniperus* spp.), peanut (*Arachis hypogaea*) and rosemary (*Rosmarinus officinalis* L.) have been scarcely investigated as repellents of triatomines. The use of essential oils as repellents is highly important for public health, offering a new perspective in the control of arthropod vectors (e.g., triatomines, which are directly linked to the spread Chagas disease) (Benelli & Pavela, 2018). Since the repellent effect of essential oils be caused by synergistic effects of its metabolites, we could expect a higher synergistic repellence in blends of essential oils of multiple plant species resulting in greater repellence than that in individual essential oils (Alavez-Rosas et al., 2022; Benelli & Pavela, 2018).

Most of the studies performed with essential oils as triatomines repellents have been conducted using bioassays with non-human hosts. In addition, little is known of aspects such as the effect of repellent activity on insect development (Abramson et al., 2006), parasite infection (Córdoba-Aguilar, 2020), or bug preference for male or female human hosts. The aims of this work were (a) to identify the volatile compounds of eight commercial essential oils and (b) to evaluate the repellent activity of single commercial essential oils and a blend of three commercial essential oils on three species of triatomines, considering human host sex, insect development and *T. cruzi* infection. To reach these goals, we extracted volatiles from the oils and evaluated the repellent activity of different commercial essential oils on *T. pallidipennis*. Then, we blended the three most active commercial essential oils and evaluated the blend against *T. pallidipennis*, *T. infestans* and *R. prolixus*. In addition, the blend was evaluated against *T. cruzi*-infected *T. pallidipennis* adults and nymphs.

MATERIALS AND METHODS

Insects

We used adults and fifth-stage *T. pallidipennis* nymphs, and fifth-stage *T. infestans* and *R. prolixus* nymphs, which were kept under controlled temperature, humidity and photoperiod (28 ± 2°C, 60 ± 5 RH and 12:12 D:L). Bugs were obtained from colonies reared at the Instituto Nacional de Salud Pública (INSP) located in Cuernavaca City, Mexico. The colonies of different triatomines were established approximately 5 years ago, constantly adding the first generation of adults, from wild kissing bugs free of *T. cruzi*.

Parasite *Trypanosoma cruzi*

T. cruzi parasites were kept in specific facilities of INSP. We used the *T. cruzi* strain ITRI/MX/12/MOR (Morelos), named in accordance with WHO nomenclature. Parasites were maintained at 28°C in liver infusion tryptose (LIT) culture media. LIT axenic medium was prepared according to previous reports with modifications (Camargo, 1964). LIT medium was supplemented with 5% fetal bovine serum and Hemin (Sigma-Aldrich) in a 1:200 (LIT-SH) proportion. Starting from a culture at 28°C and in exponential growth in LIT-SH medium, an aliquot containing 5×10^6 parasites was placed in 5 mL of fresh LIT-SH medium and kept in an incubator at 28°C. The parasites were counted every 24 h to determine the start of exponential growth. We used epimastigote parasite 7–10 days after starting its growth to be able to reach its exponential growth phase. A Neubauer chamber was used to determine the number of parasites per mL. To determine the number of parasites used, it was necessary to multiply the number of parasites counted by 10^4 because of the dilution factor. For feeding/infection of the fifth instar *T. pallidipennis* nymphs, we used 4×10^6 parasites per mL. Each fifth instar nymph eats around 400–800 μL (Camargo, 1964).

T. pallidipennis infection by *T. cruzi*

Fifth instar nymphs of *T. pallidipennis* (unfed for 25–30 days after moulting) were infected with *T. cruzi* using artificial feeders.

The artificial feeder is a jacketed glass with conical bottom that maintains the blood warm with circulating water. These feeders have a capacity of 1500 μL, with a surface of 4.5 cm. We covered them with Parafilm-M on which the triatomines make contact (Rutledge et al., 1964). To carry out triatomine infection, parasites were resuspended in used blood. Before resuspending the parasites, it was necessary to separate the plasma by centrifugation (2500 rpm, 5 min) from the haematocrit (Guarneri et al., 2000). Plasma was collected from the surface, and it was inactivated (i.e., immune response cells that could attack *T. cruzi* are inactivated) at 55°C for 30 min (Vieira et al., 2014). Haematocrit was washed once with saline solution and centrifuged at 2500 rpm for 10 min. Once the plasma was inactivated, the washed haematocrit was added. Finally, parasites were removed from the culture medium by centrifugation (2500 rpm, 5 min) and added to plasma inactivated with washed haematocrit. Using 4×10^6 parasites per mL, we confirmed kissing bug infection using a faecal sample obtained from each bug. A drop of isotonic saline solution was placed on a microscope slide; then, the expulsion of faeces or urine was provoked by rectal stimulation and gentle abdominal compression of the insect. The sample was observed under a microscope at ×40 magnification. The entire sample was searched for the presence of parasites, considering insects positive for *T. cruzi* when they presented at least one parasite in the sample. The parasites were found in the form of blood trypomastigotes, epimastigotes and transitional (spheromastigotes).

Commercial essential oils and chemicals

Commercial essential oils from citronella (*C. nardus*), lavender (*Lavandula* spp.) and mint (*M. arvensis*) were obtained from Pharmakos Rambal (Tuxtla Gutiérrez, Chiapas, Mexico). Commercial essential oils from peanut (*A. hypogaea*), bergamot (*C. bergamia*), anise (*P. anisum*) and juniper berry (*Juniperus* spp.) were obtained from Sigma-Aldrich (Toluca, Mexico). All the oils were reported as >99% pure and were thus used without further purification. N,N-Diethyl-m-toluamide (DEET, analytical standard) and ethanol (HPLC grade) were obtained from Sigma Aldrich (Toluca, México).

Chemical analysis of commercial essential oils

A 100 ng/μL solution of each commercial essential oil was prepared in ethanol (the mass in the concentration corresponds to the mass of the oil). One μL of each solution was analysed separately using a gas chromatograph (Shimadzu GC-2010 plus) coupled to a triple-quadrupole mass spectrometer (Shimadzu TQ8040) using electron-impact ionisation at 70 eV, 250°C. A DB-5 fused silica capillary column (30 m × 0.25 mm internal diameter) was temperature programmed from 50°C (held for 2 min) increasing 15°C min^{-1} to 280°C and held at 280°C for 10 min. The temperature of the injector was held at 250°C. Helium was used as the carrier gas at a constant flow of 1 mL min^{-1}. Compounds were identified comparing retention indices (Kovats and arithmetic) and mass spectral profiles using the National Institute of Standards and Technology (NIST) library. Mass spectral identifications were confirmed by comparison of retention times and mass spectra using synthetic standards. Synthetic compounds (95% pure) were obtained from Sigma-Aldrich-Fluka (Toluca, Mexico). The relative amount (percentage) of a given component was calculated relative to the sum of all areas under the peaks.

Repellence bioassay

Evaluation of single commercial essential oils was tested against *T. pallidipennis* nymphs, whereas a blend of citronella, lavender and mint was tested against *T. infestans*, *T. pallidipennis* and *R. prolixus*. We used a procedure similar to the one previously reported (Ramírez et al., 2020) with slight modifications. A glass tube (10 cm long × 2 cm diameter) was divided into three zones: host, intermediate and refuge zones (2.5, 5 and 2.5 cm, respectively). Initially, one bug was placed in the refuge zone, and after 5 min of acclimation, the experiment started when the insect was allowed to freely move from the refuge to the other two zones. Insects attracted by the stimuli from the forearm of a volunteer (we used male and female, separately) walked to the host zone, whereas mesh prevented them from biting the volunteer. Experiments lasted 3 min. We recorded the time that the bug spent near the host in the presence or absence of the treatment tested. Volunteers were co-authors of the present paper: ARR and JEFJ. To avoid different profiles of volatile organic compounds (VOCs) from the hosts, we always tested the same forearm of the two volunteers. During the time that the experiments were carried out, volunteers avoided the use of any soap when taking a shower, and did not drink alcohol, eat any spicy food or use any perfumed cosmetics or skin products. Volunteers do not smoke and had no chronic illnesses, nor did they use any medication on a regular basis. Both lived in the same house. Ten different insects per treatment were used; these were randomly assigned to each treatment. Treatments consisted of host odour, host odour + solvent (ethanol), different concentrations (0.001, 0.01, 0.1, 1, 10, 25, 50 and 100% V/V) of the commercial essential oils, and one blend of commercial essential oils or DEET. In this study, we used DEET as positive control because the effectiveness of DEET against all groups of biting arthropods has granted it the title of the gold standard among repellents. In addition, it was recently demonstrated effective repellent effect against *R. prolixus* (Ramírez et al., 2020). The blend used was 1:1:1 citronella, lavender and mint commercial essential oils. The test odour stimulus consisted of 10 μL of the solution (or solvent) loaded onto a filter paper strip (1.0 × 3.0 cm). The paper strip with the test solution or solvent control was carefully placed in the space between the host's forearm and the mesh in the tube. Neither the host's skin nor the insects were in direct contact with the compounds tested. We performed the bioassays between 18:00 and 22:00 h in a room at 28–30°C and 50%–60% RH. Illumination was provided by a red LED light bulb (Phillips, 8 W, 4 lux), placed at 100 cm directly above the test tube.

We evaluated the blend of commercial essential oils against *T. pallidipennis* nymphs and adults non-infected and infected with

TABLE 1 Percentage ± SE of compounds found in the headspace of different commercial essential oils and in the blend of three of these oils.

No.	KRI	ARI	LRI	Compound	Anise (percentage ± SE)	Bergamot (percentage ± SE)	Citronella (percentage ± SE)	Juniper berry (percentage ± SE)	Lavender (percentage ± SE)	Mint (percentage ± SE)	Peanut (percentage ± SE)	The blend (percentage ± SE)
1	733	733	730	Isopentyl alcohol[a,b]	21.89 ± 14.20							
2	922	921	928	α-Pinene[a,b]		4.32 ± 0.60		60.03 ± 4.09		1.47 ± 0.14		0.62 ± 0.23
3	976	974	977	ß-Pinene[a,b]				6.43 ± 0.16				
4	982	981	985	Myrcene[a,b]				4.95 ± 0.26				
5	972	970	1025	Limonene[a,b]		22.70 ± 1.78	3.72 ± 0.05			5.96 ± 0.55		3.83 ± 0.82
6	998	997	1037	ß-Ocimene[a]		2.51 ± 0.17		6.71 ± 0.73				
7	1055	1055	1052	Eucalyptol[a]					1.26 ± 0.11			0.30 ± 0.08
8	1058	1057	1058	6,10-Dihydromyrcenol[a]		2.18 ± 0.35			3.94 ± 0.12		29.12 ± 1.43	1.01 ± 0.35
9	1059	1058	1085	Linalool[a,b]		5.79 ± 0.51	0.87 ± 0.08		12.24 ± 1.07			3.56 ± 1.33
10	1096	1095	1134	Citronellal[a,b]		12.87 ± 0.42	44.19 ± 3.31		18.61 ± 1.01		7.08 ± 0.23	19.28 ± 2.45
11	1170	1169	1170	Isomenthone[a]						20.18 ± 0.38		8.38 ± 2.56
12	1179	1178	1172	Menthone[a]						10.15 ± 0.38		4.24 ± 1.31
13	1182	1181	1182	Isomenthol[a]						4.14 ± 0.62		1.56 ± 0.23
14	1190	1190	1187	Menthol[a,b]						46.67 ± 1.10		18.92 ± 5.03
15	1195	1195	1190	1,7,7-Trimethylbicyclo[2.2.1]heptan-2-ol[a]					0.84 ± 0.20			0.18 ± 0.03
16	1238	1236	1225	Citronellol[a,b]			17.98 ± 0.69		1.07 ± 0.13			6.35 ± 0.93
17	1242	1241	1245	Linalyl acetate[a]		39.20 ± 0.23			40.47 ± 0.48		22.17 ± 0.15	10.12 ± 3.18
18	1250	1249	1250	Geranial[a,b]		10.41 ± 1.27			15.21 ± 0.78		31.85 ± 1.09	3.95 ± 1.41
19	1259	1258	1259	(E)-Geraniol[a]			19.44 ± 2.86					6.68 ± 1.53
20	1296	1296	1294	Menthyl acetate[a]						11.47 ± 0.48		4.80 ± 1.50
21	1320	1319	1300	(*E*)-Anethole[a]	78.11 ± 14.20							
22	1353	1352	1354	β-Citronellyl acetate[a]			5.41 ± 0.08					1.82 ± 0.22
23	1382	1382	1381	Geranyl acetate[a]			4.65 ± 0.18					1.57 ± 0.23
24	1403	1403	–	{204 (M+); 107 (50%); 93 (90%); 69 (100%); 41 (80%)}			3.74 ± 0.08					1.27 ± 0.19
25	1438	1437	–	{204 (M+); 105 (55%); 91 (100%); 69 (75%); 41 (70%)}				9.46 ± 1.66	0.77 ± 0.08		9.78 ± 0.26	0.18 ± 0.04

TABLE 1 (Continued)

No.	KRI	ARI	LRI	Compound	Anise (percentage ± SE)	Bergamot (percentage ± SE)	Citronella (percentage ± SE)	Juniper berry (percentage ± SE)	Lavender (percentage ± SE)	Mint (percentage ± SE)	Peanut (percentage ± SE)	The blend (percentage ± SE)
26	1474	1473	–	{204 (M+); 105 (20%); 93 (100%); 80 (30%); 45 (35%)}				3.67 ± 0.53				
27	1498	1498	1486	Germacrene D[a]				4.29 ± 1.00				
28	1529	1528	–	{204 (M+); 161 (15%); 105 (100%); 119 (60); 91 (55%)}				4.42 ± 0.97	5.58 ± 0.22			1.37 ± 0.40

Note: For the non-identified compounds, their mass spectra information is presented (mass fragment [relative abundance]).
Abbreviations: ARI, Arithmetic Retention Index; KRI, Kovats Retention Index; LRI, Library Retention Index (NIST database: https://webbook.nist.gov/chemistry/).
[a]Identification based on the comparison of chromatographic and mass-spectra data with NIST library.
[b]Identification based on comparison with standard.

T. cruzi. We followed the same experimental conditions mentioned above. The volunteer for this part was DAR following the same skin and diet care conditions to avoid different VOC profiles, and we always tested the same forearm of the volunteer. Ten different insects per treatment were used. Treatments consisted of host odour, host odour + solvent (ethanol), and different concentrations (0.001, 0.01, 0.1, 1, 10, 25, 50 and 100% V/V) of the mixture of commercial essential oils or DEET. These bioassays were performed at the INSP.

Statistical analysis

The time that bugs stayed in the host zone was analysed using a factorial analysis of variance. For the experiments with individual commercial essential oils, the independent variables were volunteers, treatments (commercial essential oils or DEET) and concentrations. For the experiments using the blend of essential oils against different species of triatomines, the independent variables were volunteers, species and concentrations. For the experiment using *T. pallidipennis* infected insects, we used development stage (fifth instar nymphs or adults), status of infection (infected or non-infected), treatments (commercial essential oils, solvent or DEET) and concentrations as independent variables. Original data did not follow the assumptions of a normal distribution and homoscedasticity; individual commercial essential oils against *T. pallidipennis* (Shapiro–Wilk test [$W = 0.88$, $p < 0.001$], Levene test [$F_{159,1440} = 2.15$, $p < 0.001$]), blend of commercial essential oils against *T. pallidipennis*, *T. infestans* and *R. prolixus* (Shapiro–Wilk test [$W = 0.89$, $p < 0.001$], Levene test [$F_{59,740} = 2.89$, $p < 0.001$]) and blend of commercial essential oils against infected and non-infected *T. pallidipennis* (Shapiro–Wilk test [$W = 0.93$, $p < 0.001$], Levene test [$F_{79,720} = 2.27$, $p < 0.001$]). Thus, data were transformed using Box–Cox transformation (with $\lambda = 0.505051$, 0.464647 and 0.585859, respectively) to ensure normality and homoscedasticity. All analyses were performed using the statistical software R version 4.2.1 (R Development Core Team, 2022).

RESULTS AND DISCUSSION

Chemical identification

The chemical composition of the head space of the commercial essential oils is presented in Table 1. Twenty-eight compounds were identified, mostly terpenoids. For anise commercial essential oil, two compounds were found, isopentyl alcohol (22%) and (E)-anethole (78%). This latter compound is the principal compound reported for this oil (Gende et al., 2009). For bergamot commercial essential oil, the most abundant compound was linalyl acetate (39%), followed by limonene (22%) and citronellal (13%). Although these species possess highly variable volatile compounds, we found a similar profile to those reported by other studies (Dugo et al., 2012). For citronella commercial essential oil, citronellal (45%), citronellol (18%) and geraniol (19%) were found in higher percentages, to those described for this oil (Kaur et al., 2021; Verma et al., 2020). For juniper berry commercial essential oil, α-pinene was found in major

proportion (60%) with other terpenoids and three unidentified compounds (Meriem et al., 2022; Moghaddam et al., 2018). For lavender commercial essential oil, the most abundant compound was linalyl acetate (41%), followed by citronellal (19%) and geranial (15%), as was described for various species of *Lavandula* (Tomi et al., 2018). For mint commercial essential oil, menthol (47%), isomenthone (20%), menthyl acetate (11%) and menthone (10%) were the most abundant compounds, as previously reported (Chagas et al., 2020). For peanut commercial essential oil, geranial (32%), citronellal (29%) and linalyl acetate (22%) were found in higher percentages. The most abundant volatiles from the blend were citronellal (19%), menthol (18%) and linalyl acetate (10%). Some concerns have arisen about the biological activity of commercial essential oils because their chemical composition is different from that of non-commercial essential oils (Dohi et al., 2009; Ibrahim & Abd El-Salam, 2015; Luís et al., 2017). In this context, because the chemical composition of the commercial essential oils used in this study was mostly the same as that found in other studies performed with steam-distilled essential oils, we were able to correlate the repellent activity of the oils with their chemical composition (Chagas et al., 2020; Dugo et al., 2012; Gende et al., 2009; Meriem et al., 2022: Moghaddam et al., 2018; Tomi et al., 2018; Verma et al., 2020).

Evaluation of single commercial essential oils against *T. pallidipennis* nymphs

Mint and lavender commercial essential oils were the most effectives oils, exhibiting a stronger repellent effect than DEET (Figure 1). Higher repellent effect of commercial essential oils compared with DEET has been also observed for repellents derived from coconut oil against bloodsucking insects (Zhu et al., 2018). This could be explained by the chemical composition of these oils, since their most abundant compounds produce higher repellent activity against insects (Terriquez et al., 2013; Tietbohl et al., 2019). However, other minor compounds could be contributing to the biological activity (Miladinović et al., 2021). The factorial analysis showed that the repellence of commercial essential oils against *T. pallidipennis* was affected by the volunteers, treatments (commercial essential oils and DEET) and concentrations. Furthermore, all

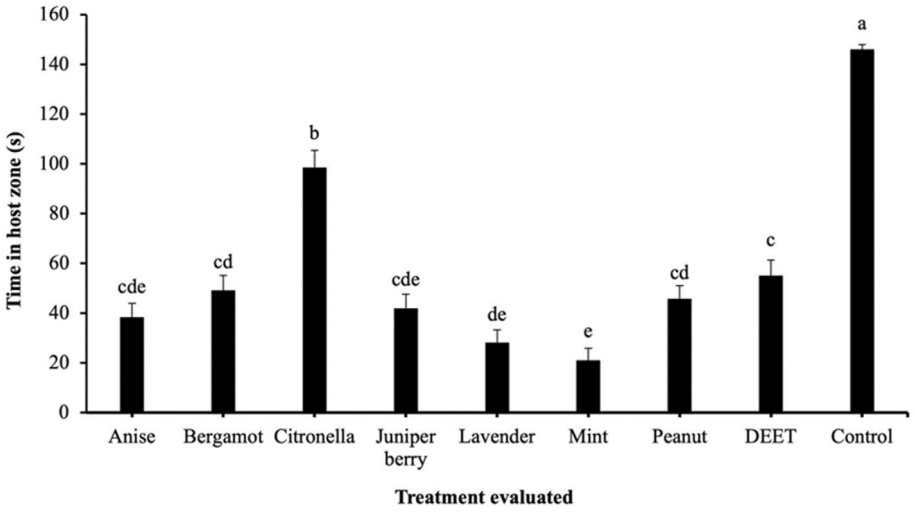

FIGURE 1 Mean number of responses (time in host zone ± SE) of *T. pallidipennis* nymphs against evaluated treatments (commercial essential oils, DEET and solvent as control). Different letters mean statistical differences according to the Tukey test ($\alpha = 0.05$).

TABLE 2 Factorial analysis results of the effect of the volunteers, treatments (commercial essential oils and DEET) and concentrations on the repellence of commercial essential oils against *T. pallidipennis* nymphs.

	Sum Sq	df	*F* value	Pr (>*F*)
Volunteer	254	1	24.173	9.82×10^{-7}***
Treatments	1166.9	7	15.8673	$<2.2 \times 10^{-16}$***
Concentrations	11877.9	9	125.621	$<2.2 \times 10^{-16}$***
Volunteer:Treatments	1174.7	7	15.9732	$<2.2 \times 10^{-16}$***
Volunteer:Concentrations	259.7	9	2.7466	3.49×10^{-3}**
Treatments:Concentrations	1802.2	63	2.7228	3.87×10^{-11}***
Volunteer:Treatments:Concentrations	1452	63	2.1938	3.94×10^{-7}***
Residuals	15128.4	1440		

**$p < 0.01$; ***$p < 0.0001$.

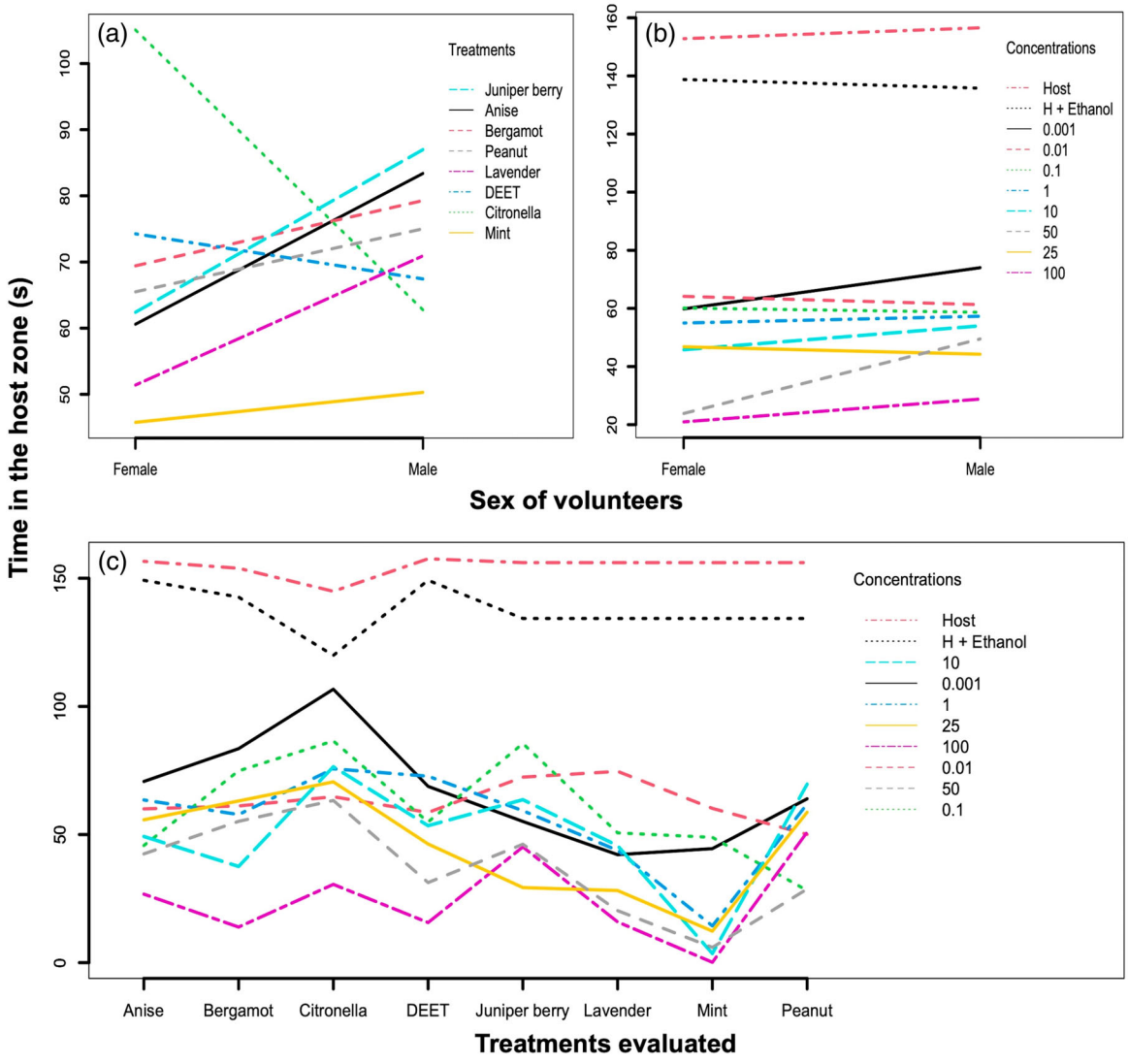

FIGURE 2 Interaction graphs of the evaluation of single commercial essential oils against *T. pallidipennis* nymphs. (a) Time in the host zone (in seconds) against sex of volunteers, analysing the commercial essential oils tested and DEET. (b) Time in the host zone (in seconds) against sex of volunteers analysing the overall concentrations tested. (c) Time in the host zone (in seconds) against treatments evaluated (commercial essential oils and DEET), analysing the concentrations of each commercial essential oil.

TABLE 3 Factorial analysis results of the effect of the volunteers, species, and concentrations on the repellence of a blend of citronella, lavender, and mint commercial essential oils, against *T. pallidipennis*, *T. infestans* and *R. prolixus* nymphs.

	Sum Sq	df	*F* value	Pr (>*F*)
Volunteer	0.7	1	0.0635	0.8011
Species	457.3	2	19.5086	5.54×10^{-9}***
Concentration	6049.8	9	57.3548	$<2.2 \times 10^{-16}$ ***
Volunteer:Species	35.4	2	1.5091	0.2218
Volunteer:Concentration	597.6	9	5.6652	1.32×10^{-7}***
Species:Concentration	252.8	18	1.1985	0.2552
Volunteer:Species:Concentration	180.7	18	0.8564	0.6329
Residuals	8672.8	740		

**$p < 0.01$; ***$p < 0.0001$.

interactions were significant (Table 2). Commercial essential oils were more effective in the human female (bugs spent less time in the host's zone, Figure 2a). Citronella was an exception as it was more effective in the human male, and it was more effective than DEET. The ability to differentiate between females and males through the examination of human volatiles has been demonstrated (Curran et al., 2005; Ramírez et al., 2020). It is interesting to note that bugs spent less time in the host zone when DEET was used by the human male than when used by the female. In other words, DEET was more effective for the human male than for the female. However, we did not evaluate the human skin odour of the volunteers, which could have influenced bugs' preference for the human female (de Obaldia et al., 2022). In this context, more studies are needed to determine the influence of volatiles from humans in the repellent effect of essential oils against triatomines. Higher concentrations had stronger repellent effect as observed in other blood-sucking insects (Abbas et al., 2023). All tested concentrations repelled the bugs. Lower concentrations were more effective for the human female, whereas higher concentrations were more effective for human male (Figure 2b). Mint commercial essential oil was the most effective at any concentration tested, even more effective than DEET (Figure 2c), possibly because of the components of the oil. Geraniol and menthyl acetate have been described as good repellents of kissing bugs (Sfara et al., 2009). To our knowledge, this is the first study in triatomines to assess the repellent effect of commercial essential oils using an exposure device (Ramírez et al., 2020) that provide a realistic and rapid way to test the repellence of essential oils on these insects.

Evaluation of a blend of citronella, lavender and mint against *T. infestans*, *T. pallidipennis* and *R. prolixus* nymphs

As mint, lavender and citronella commercial essential oils were the strongest repellents (citronella only for the human male), we blended these three commercial essential oils and evaluated them against kissing bugs. The repellence of the blend over *T. pallidipennis*, *T. infestans* and *R. prolixus* nymphs was affected by species and concentration, but not by volunteer (Table 3). None of the interactions were significant, except for volunteer: concentration. *T. pallidipennis* was more repelled by the blend, whereas *T. infestans* was less repelled, and no influence of the volunteer was observed (Figure 3a). In this scenario, using the

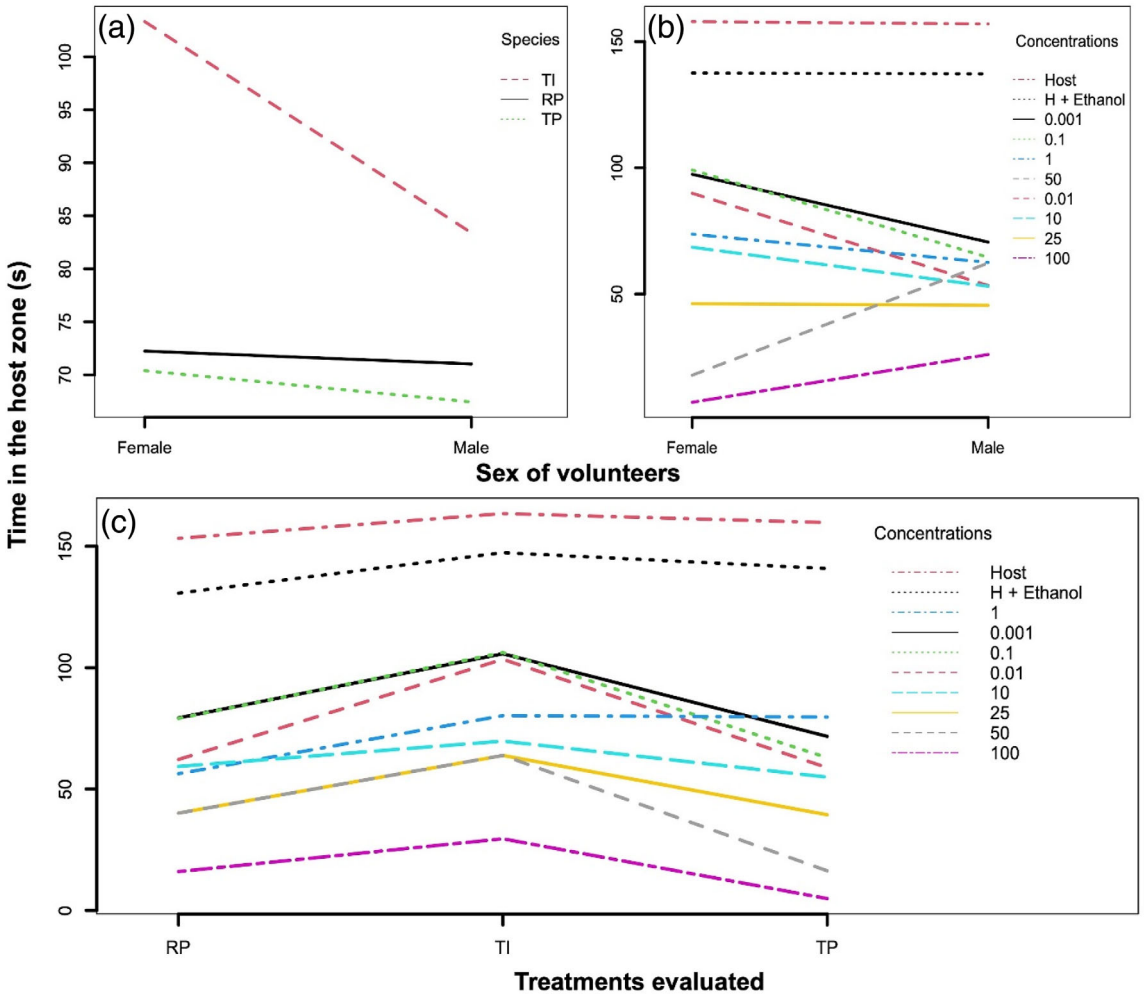

FIGURE 3 Interaction graphs of the evaluation of a blend of citronella, lavender and mint commercial essential oils against nymphs of *T. infestans*, *T. pallidipennis* and *R. prolixus*. (a) Time in the host zone (in seconds) against sex of volunteers, analysing the three insect species. (b) Time in the host zone (in seconds) against sex of volunteers analysing the concentrations of the blend. (c) Time in the host zone (in seconds) against triatomine species, analysing the concentrations of the blend.

blend of commercial essential oils could protect both human females and males in the same manner. We tried to avoid environmental biases in the volatile emanation of volunteers and found that lower concentrations were more effective for the human male to repel bugs, yet higher concentrations were more effective for the human female (Figure 3b). This could be explained in two possible ways. First, volatiles produced by human females may be more attractive to triatomines than those of males. Second, if females and males produce the same volatiles, the quantity of compounds is higher in females. However, more studies are needed to explain these results because human volatiles differ according to age, persons and genders, and also the volatiles produced by the same person differ throughout the day (Curran et al., 2005; Ramírez et al., 2020). Higher concentrations produced higher repellence against the three species. However, *T. infestans* was less repelled at any concentration of the blend (Figure 3c). Blending the essential oils increases the chemical diversity of compounds and could increase the repellence effect (Alavez-Rosas et al., 2022). However, in this study, the blend was not more effective than individual commercial essential oils, probably because the blend has lower concentration of active compounds (Zhu et al., 2018), and as shown in the results, higher concentrations of the oils were more effective at repelling kissing bugs.

Evaluation of the commercial essential oils blend against both *T. cruzi*-infected and non-infected *T. pallidipennis* nymphs and adults

Repellence of the blend of commercial essential oils was affected by the insect stage (5th instar nymphs or adults), treatments and concentrations, but it was not affected by the infection status. The following interactions were significant: stage:treatment, stage:concentration, treatment:concentration and stage:treatment:concentration (Table 4). Adults spent less time in the host zone, meaning that both DEET and the blend repelled adults more effectively than nymphs (Figure 4a). However, at higher concentrations, nymphs and adults were equally repelled by both treatments (Figure 4b). DEET was more effective than the blend at lower concentrations, but the blend was more effective against bugs at higher concentrations (Figure 4c). *T. cruzi* infection likely modifies the host's behaviour (Marliére et al., 2015), the sensilla patterns of the kissing bugs (May-Concha et al., 2022) and thus the sensory ecology of the bug (Latorre-Estivalis et al., 2017). However, we found that commercial essential oil-based repellents are effective against both infected and non-infected kissing bugs, which is the ultimate objective of the ethological control, manipulating insect behaviour to avoid interaction between infected bugs and humans (Rosecrans et al., 2014). More studies are needed to determine how long the repellent effect of oils and the blend lasts (Luker et al., 2023; Zhu et al., 2018), the influence of the age of the insect when it was infected and its nutritional status (Estay-Olea et al., 2020).

It is recognised that essential oils possess valuable biological activity because of their chemical composition. However, some components may have toxic effects, even at low concentrations (Fuentes et al., 2021; Wojtunik-Kulesza, 2022). Their negative influence upon the human organism has to be underlined in the case of their usage as repellents, and a detailed toxicological assessment is highly recommended for each essential oil (Lanzerstorfer et al., 2021). In our study, we did not extract the essential oils from natural sources and we used commercial essential oils. However, the chemical richness of the oils is maintained and their biological activity as repellents is comparable

TABLE 4 Factorial analysis results of the effect of stage, infection status, treatment (the blend or DEET) and concentrations on the repellence of the commercial essential oils blend against *T. pallidipennis* nymphs.

	Sum Sq	df	*F* value	Pr (>*F*)
Stage	20,190	1	23.1249	1.85×10^{-6}***
Status	495	1	0.5664	0.451928
Treatment	26,232	1	30.0444	5.85×10^{-8}***
Concentration	1,781,506	9	226.713	$<2.2 \times 10^{-16}$***
Stage:Status	89	1	0.1021	0.7494613
Stage:Treatment	9200	1	10.5376	0.0012238**
Status:Treatment	54	1	0.0613	0.8044522
Stage:Concentration	54,810	9	6.9751	1.08×10^{-9}***
Status:Concentration	429	9	0.0546	0.9999711
Treatment:Concentration	66,846	9	8.5067	3.73×10^{-12}***
Stage:status:Treatment	96	1	0.1099	0.7404107
Stage:status:Concentration	600	9	0.0764	0.9998796
Stage:Treatment:Concentration	25,445	9	3.2381	0.0007261***
Status:Treatment:Concentration	794	9	0.1011	0.9996118
Stage:Status:Treatment:concentration	569	9	0.0724	0.9999038
Residuals	628,636	720		

**$p < 0.01$; ***$p < 0.0001$.

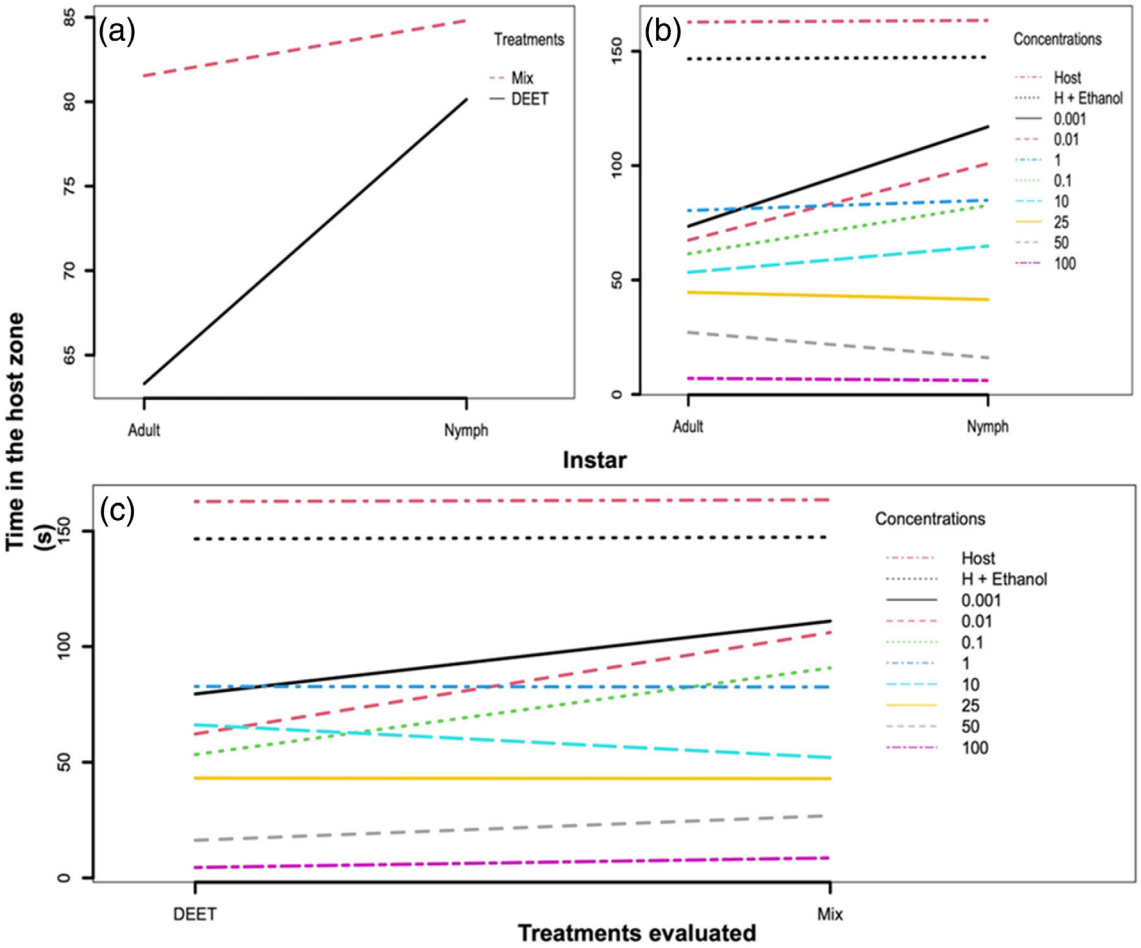

FIGURE 4 Interaction graphs of the evaluation of the commercial essential oils blend against *T. pallidipennis* nymphs and adults in both conditions, non-infected and infected with *T. cruzi*. (a) Time in the host zone (in seconds) against insect instar, analysing the blend (mix) and DEET. (b) Time in the host zone (in seconds) against insect instar, analysing the concentrations tested. (c) Time in the host zone (in seconds) against treatments evaluated (blend (mix) and DEET), analysing the concentrations tested.

with those extracted in situ from natural sources. Taking the above into account and using our results, the study of commercial essential oils remains a promising strategy for control of triatomines and, thus, Chagas disease.

CONCLUSION

Commercial essential oils of citronella, mint and lavender were as effective as DEET in repelling Chagasic bugs. Human host's sex influences the repellence effect of the oils but does not influence the effect of the blend. The blend of the most effective commercial essential oils was effective against *T. pallidipennis*, *T. infestans* and *R. prolixus*. Adults were repelled by the blend more than nymphs, and the *T. cruzi*-infected and non-infected insects were equally repelled with the blend.

AUTHOR CONTRIBUTIONS

Azhary Rito-Rueda: Methodology. **Juan Eduardo Flores-Jiménez:** Methodology. **Ana Erika Gutiérrez-Cabrera:** Writing – review and editing; investigation. **Samuel Cruz-Esteban:** Methodology; data analysis; writing – review and editing. **Alex Córdoba-Aguilar:** Investigation; writing – review and editing; funding acquisition. **Leopoldo Cruz-Lopez:** Conceptualization; writing – review and editing; investigation; funding acquisition. **David Alavez-Rosas:** Writing – original draft; conceptualization; writing – review and editing; investigation; methodology; data analysis.

FUNDING INFORMATION

Part of this work was funded by The National Council of Science and Technology (CONAHCyT), with the project 'Ciencia de Frontera 2019, clave 376136, número 292'.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

Approval was obtained from the ethics committee from Centro de Investigación Sobre Enfermedades Infecciosas, Instituto Nacional

de Salud Pública (CISEI-INSP). Approval number CI: 1730 CB: 1720. Being part of the project 'Influence of *Trypanosoma cruzi* infection in the intraspecific chemical communication of Chagasic bugs: a first step towards Chagas disease prevention' Number/ID: 292/376136.

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How to cite this article: Rito-Rueda, A., Flores-Jiménez, J.E., Gutiérrez-Cabrera, A.E., Cruz-Esteban, S., Córdoba-Aguilar, A., Cruz-López, L. et al. (2023) How to repel a killer; chemical identification and effective repellent activity of commercial essential oils against kissing bugs. *Medical and Veterinary Entomology*, 1–12. Available from: https://doi.org/10.1111/mve.12702