

Review

A scoping review of triatomine control for Chagas disease prevention: current and developing tools in Latin America and the United States

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Subject Editor: Juan Carlos Navarro

Received on 28 November 2023; revised on 11 February 2024; accepted on 15 March 2024

Chagas disease is an infectious disease of human and animal health concern, with 6–8 million chronic human infections and over 50,000 deaths throughout the Americas annually. Hematophagous insects of the subfamily Triatominae, also called kissing bugs, vector the protozoan parasite, *Trypanosoma cruzi* Chagas (Trypanosomatida: Trypanosomatidae), that causes Chagas disease. Despite the large human health burden, Chagas disease is a neglected tropical disease with inadequate funding for research and preventive practices. Given the resource-poor environment of most agencies trying to protect public health, it is critical to consider all control options for reducing vector populations and the risk of human exposure to *T. cruzi* to identify the most appropriate tools for each context. While numerous triatomine control methods exist, the literature lacks a compilation of the strategies used, a critical examination of their efficiency, and a particular focus on triatomine control in the United States compared to elsewhere in the Americas. Here, we present a review of the literature to assess historical intervention strategies of existing and developing triatomine control methods. For each method, we discuss progress in the field, future research to further advance the method, and limitations. While we found that pyrethroid insecticide is still the most commonly used method of triatomine and Chagas disease control, we suggest that complementing these techniques with alternative control methods in development will help to achieve Chagas disease reduction goals.

Key words: pyrethroid, xenointoxication, environmental control, biological control

Introduction

Vector-borne disease is increasing in human incidence in both the United States and the rest of the world. Due to factors such as climate change, globalization, and persistent poverty, vectors are shifting their geographic distribution and now occupy habitats that were once unsuitable (Gonzalez-Salazar et al. 2022). A vector-borne and neglected tropical disease resulting in one of the largest human disease burdens is American trypanosomiasis, or Chagas disease, which is spread by insect vectors of the subfamily Triatominae (Hemiptera: Reduviidae). These vectors, also known as “kissing bugs,” “conenose bugs,” or other names used locally such as barbeiro or bicudo in Brazil, bush chinche in Belize, or chipo in Venezuela, harbor the flagellate protozoan parasite, *T. cruzi*, which causes Chagas disease in many mammalian hosts, such as humans and canines.

Chagas disease is a debilitating infection endemic to Latin America that affects 6–10 million people worldwide, with an estimate of

65–100 million people residing in regions at infection risk (Manne-Goehler et al. 2016, Lidani et al. 2019). Of these infections, approximately 50,000 per year result in mortality, and others often leave those infected with lifelong health complications. Chagas disease is reported as a neglected tropical disease by WHO, and it primarily affects low-income populations with limited healthcare (Lidani et al. 2019). This leads to significant underreporting of Chagas disease cases, as well as a significant number of chronic infections, which can occur when the acute infection is untreated. Most mortality, morbidity, and economic burden are caused by chronic Chagas disease infections, which are responsible for an estimated \$627.5 million per year in healthcare costs globally (Lidani et al. 2019). Notably, the WHO has outlined a goal of eliminating Chagas disease in 15 countries (34% of the current distribution) by 2030 (World Health Organization 2021).

Transmission of *T. cruzi* is mostly facilitated by triatomine vectors in a fecal-oral route of transmission (Monteiro et al. 2018).

Triatomines shed the parasite in feces, which may then enter the body through ingestion, mucous membranes, or an open wound (Lidani et al. 2019). Some animals may also ingest infected triatomines or fruit contaminated with infected triatomine or their feces, which is an efficient route of transmission (Shikanai-Yasuda and Carvalho 2012). Other routes of transmission include congenital transmission, blood transfusions, and consumption of contaminated food (Pereira et al. 2009).

Vector transmission of *T. cruzi* is limited to the Americas, predominantly in rural areas of Latin America, where housing conditions promote the colonization of homes by domestic triatomine species (Sommerfeld and Kroeger 2015). While over 150 triatomine species have been documented and are potential vectors of *T. cruzi* (Lent and Wygodzinsky 1979, Galvão 2021), only a subset are considered intrusive with higher levels of domiciliation and thus responsible for the majority of human risk of exposure to *T. cruzi* (Waleckx et al. 2015a). These domestic triatomines thrive in and around homes, which increases contact between humans and domestic animals with infected vectors. Domestic triatomine populations are the major contributor to human infection of *T. cruzi* (Cahan et al. 2019). However, the epidemiology of Chagas disease is changing as urban sprawl encroaches on sylvatic habitat and is predicted to change further in response to projected climate change (Medone et al. 2015). Spillover of triatomines and *T. cruzi* from sylvatic cycles in natural habitats that enter the domestic or peridomestic habitat may also occur (Waleckx et al. 2015a), although the extent to which these sylvatic vectors contribute to human infection is not well established (Stevens et al. 2013).

There is a long history of intervention strategies aimed at controlling triatomine vectors, yet Chagas disease remains a significant burden in the Americas in both endemic and nonendemic regions. Here, we compile triatomine control methods currently in use and in development to discuss the advantages and disadvantages of each

(Fig. 1). We further highlight unique aspects of triatomine control in the United States as it relates to Latin America (Table 1). The goal of this review is to comprehensively cover the diverse approaches that have been evaluated in lab and small-scale trials, as well as others that have reached area-wide interventions coordinated by local ministries of health. Each control method covered by this review may not be feasible or appropriate for all contexts and all triatomine species, given the diverse ecological and social contexts across the Americas. Therefore, this review does not serve as guidelines or provide specific suggestions for triatomine control to professionals and public health officials. Instead, this comprehensive review provides a broad compilation of control approaches that have been considered for triatomines.

Vector-Targeted Intervention

Environmental Insecticides

In the past 40 years, the control of Chagas disease has primarily relied on vector control using insecticides, with the most common class being pyrethroids (Gürtler and Cecere 2021). Insecticides sprayed in indoor and outdoor environments have made great progress in controlling domestic triatomines as well as other domestic insect pests (Dias and Schofield 1999). Different pyrethroids, such as deltamethrin, lambda-cyhalothrin, beta-cyfluthrin, and alpha-cypermethrin, have been used as wettable powder and suspension concentrate and applied by indoor and outdoor residual spray (Rozendaal 1997, Hashimoto et al. 2006, Gurevitz et al. 2013, Goncalves et al. 2021a). Other formulations, such as microencapsulated pyrethroids and ultra-low volume spraying, have been tried but were not as effective and cost-efficient as traditional indoor spraying (Dias and Schofield 1999). However, newer developed insecticide delivery methods, such as insecticide-impregnated paints and curtains, provide additional options for triatomine

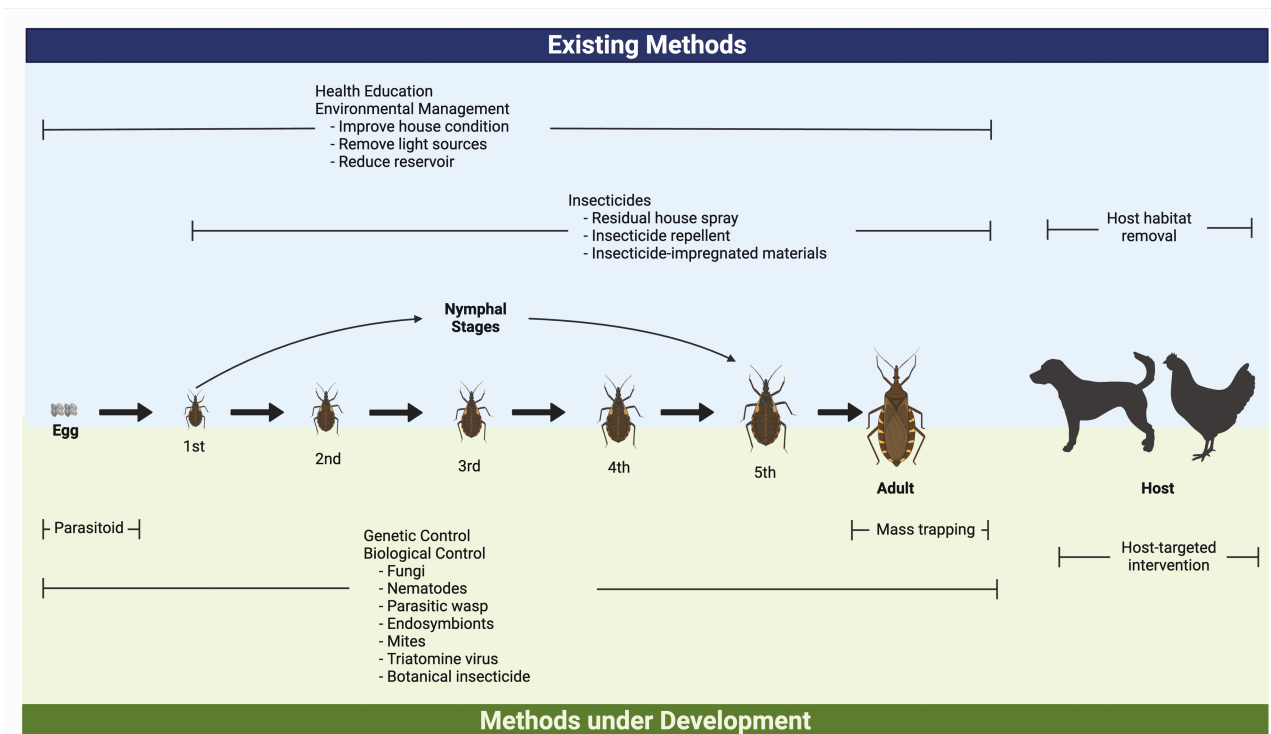


Fig. 1. Existing and developing methods of triatomine control for Chagas disease prevention. Figure design adapted from Achee et al. (2015).

Table 1. Control methods against triatomines that currently exist (E) with area-wide application or are under development (D) in the United States and Latin America. Control methods not receiving active research to our knowledge or are performed sporadically are classified as under development

Category	Subcategory	United States	Latin America
Environmental insecticide ^a	House spraying (Spraying insecticides, mainly pyrethroids, on house walls)	D	E
	Insecticide-impregnated materials (Insecticide-treated curtains, paints, and other materials that are used in the household)	D	E
	Repellent (Chemicals that can be used to repel triatomines to prevent infestation and contact with humans)	D	D
Biological control	Entomopathogenic fungi (Fungi that can infect and kill triatomines)	D	D
	Nematodes (Nematodes that can infect and kill triatomines)	D	D
	Parasitic wasps (Wasps that live on, obtain resources from, and eventually kill triatomines)	D	D
	Mites (Mites parasitize triatomines and reduce their fitness)	D	D
	Triatoma virus (Virus that can infect triatomines and increase their mortality)	D	D
	Botanical insecticides (Products extracted from plants that exhibit insecticidal properties)	D	D
	Paratransgenesis (Engineered symbionts delivered to triatomines to make refractory to <i>T. cruzi</i>)	D	D
Mass trapping	Traps (Deployment of a large number of traps to suppress triatomine populations)	D	D
Host-targeted intervention	Xenointoxication (Treatment of triatomine hosts with systematic insecticide to produce toxic bloodmeals for triatomines)	D	D
Environmental management	Household improvement (Improve household conditions, such as house wall material, house hygiene, the removal of firewood piles, host habitat, and lights to reduce triatomine habitat suitability)	E	E
	Reduction of artificial lights (Reduce light attraction to dispersing triatomines to reduce infestation)	E	E
	Reservoir control (Reduce <i>Trypanosoma cruzi</i> prevalence in triatomines or triatomine populations by reducing populations of important hosts such as rats or chickens)	E	E
	Health education (Increase the public awareness of triatomines and Chagas disease and their control tools)	E	E

^aCurrently, no insecticide is labeled to control triatomines.

control using insecticide, although these methods are currently limited in use.

Despite the efficiency and wide usage of insecticides, adverse effects of pyrethroid insecticide exposure in aquatic wildlife are well documented (Antwi and Reddy 2015), and adverse effects in humans are still under investigation, with some studies suggesting high human exposure is linked to behavioral problems in children (Oulhote and Bouchard 2013, Burns and Pastoor 2018). This is especially problematic as domestic species of triatomine are commonly found in and around homes, with pesticides sprayed indoors, creating a high likelihood of human insecticide exposure. However, exposure to insecticides is relative to the dosage of the product and frequency of application. Where some endemic areas may undergo periodic treatments, which may risk increased human exposure, other areas may rarely undergo insecticide treatments. Ultimately, the hazards of insecticide use are dependent on the appropriate application of products, as outlined by vector control professionals. In addition to the exposure risk, some areas may struggle with the

increasing resistance to pyrethroid insecticides with widely used and high application frequency of pyrethroids (Mougabure-Cueto and Picollo 2015).

House spraying. House spraying with pyrethroids has been used widely in controlling triatomines in rural and urban areas due to its high efficiency (Dias 2007). Successful reductions of triatomines after pyrethroids house spray have been reported in many countries and areas. In Guatemala, the triatomine *Rhodnius prolixus* (Stål) (Hemiptera: Reduviidae) and *Triatoma dimidiata* Latreille (Hemiptera: Reduviidae) infestation index (number of houses infested by triatomines/number of houses examined × 100) reduced from 14% (2000) to 0.8% (2001) including cases of complete elimination in Zacapa (Nakagawa et al. 2003) and from 20.8% (July 2000–April 2001) to 1.4% (April 2002–August 2003) in Jutiapa (Hashimoto et al. 2006) after a single house spraying with deltamethrin, beta-cyfluthrin, lambda-cyhalothrin, or beta-cyfluthrin. Higher infestation index reductions of 46%–96.7% (6–12 months post spray) were achieved against *T. pallidipennis*

(Stål) (Hemiptera: Reduviidae) and *T. barberi* (Usinger) (Hemiptera: Reduviidae) in a village in Mexico that was sprayed with bifenthrin, cyfluthrin, or deltamethrin (Ramsey et al. 2003). Similar high effectiveness was also observed in other countries such as Paraguay (de Arias et al. 2004), Nicaragua (Yoshioka et al. 2015), Bolivia (Guillen et al. 1997), and Argentina (Bezerra et al. 2014, Gaspe et al. 2015). However, reinfestation often occurs after pyrethroid house spraying (Gürtler et al. 1994, Dumonteil et al. 2013, Bezerra et al. 2014), which may be related to households not participating in the control campaign (Barbu et al. 2014) or from recolonization from sylvatic habitat (Bezerra et al. 2020).

The efficacy of pyrethroid house spraying is affected by multiple factors, including house structure and material, the peridomestic (outdoor) structures used by domestic or synanthropic animals, the accuracy of pyrethroid dilutions, the level of education, and rodent control (Ramsey et al. 2003, Pojo De Rego et al. 2006, Walter et al. 2007, De Urioste-Stone et al. 2015, Goncalves et al. 2021b). de Arias et al. (2004) reported high variability of pyrethroid deposition in roof treatment samples, where some areas remained untouched. In addition, the highest reduction of pyrethroid toxicity occurred on the porous surface due to its strong absorption (de Arias et al. 2004). Therefore, household improvement can enhance the efficiency of house spraying (Goncalves et al. 2021b). Although following the same insecticide preparation formulas, variable alpha-cypermethrin concentrations were reported between houses and independent spray tanks by Goncalves et al. (2021a). In addition, De Urioste-Stone et al. (2015) demonstrated the transmission risk can be reduced by insecticide application accompanied by education and rodent control. Besides the technical difficulties, the intense labor requirement of house spraying will not only increase the cost but also decrease the feasibility of house spraying in certain areas. However, motorized vehicle-mounted sprayer provides a potential solution to reduce the labor cost as it had similar performance to manual compression sprayers, which reduced house infestation from 100% to 21%, 0%, and 8% at 0, 1, 4, and 12 months postintervention without significant difference between the 2 methods (Carbajal-de-la-Fuente et al. 2017).

Insecticide-impregnated materials and paints. In addition to house spraying, newer insecticide delivery methods have shown high control efficiency. Insecticide paint was proposed in the 1980s (Dias and Jemmio 2008) and has now been commercialized to control multiple vectors such as mosquitoes, flies, cockroaches, bedbugs, and ticks. Commercial paints with pyriproxyfen, pyrethroids (Inesfly 5A IGR NG), and organophosphates (Inesfly 5A IGR) were evaluated against *T. infestans* Klug (Hemiptera: Reduviidae) nymphs at multiple days postpainting (DPP) under laboratory conditions (Amelotti et al. 2009). High mortalities of 100% and 99% of *T. infestans* nymphs were observed at 1 and 365 DPP with the organophosphates paint; respectively, 100% and 83% were observed with the pyrethroid paint. At 80 DPP, the mortality of *T. infestans* exposed to the pyrethroid paint dropped to 73%–80%, which may be due to the reduced nymphal motility from the low temperature (around 0 °C). In addition, Maloney et al. (2013) compared the organophosphate paint to standard deltamethrin against *T. infestans* nymphs and revealed that the paint caused higher mortalities (>90%), but had more host-seeking nymphs cross the paint than standard deltamethrin up to 9 months. The commercial product with organophosphates was evaluated in Camiri, Bolivia, and similarly demonstrated high control efficiency for up to 72 months with highlights of good house appearance and high acceptance by the local population and authorities (Dias and Jemmio 2008). In 1999, insecticidal paint containing malathion and polyvinyl acetate was evaluated for its effectiveness and

community acceptance (Ávila Montes et al. 1999). The acceptance by the community and field operators was low (28.8%) due to its low effectiveness compared to traditional insecticide spray, transport and application difficulty, and unpleasant smell. However, with the improvement of the paint formulation and active ingredients, insecticidal paints now have excellent acceptance given the high efficiency, easy handling, and good appearance of homes in the community in Bolivian Chaco (Dias and Jemmio 2008).

Insecticide-treated bed nets are another common addition to households in areas with endemic vector-borne diseases such as malaria (Robert 2020) and leishmaniasis (Kroeger et al. 1999, Chowdhury et al. 2019). Similarly, insecticide-treated bed nets have been evaluated as randomized controlled trials in Columbia (Kroeger et al. 2003) and as protection of sentinel peridomestic animals in Peru (Levy et al. 2008), reporting evidence of killing triatomines and protecting humans from vector bites. Bed nets are most commonly treated with pyrethroids, including deltamethrin (Kroeger et al. 1999) and lambda-cyhalothrin (Kroeger et al. 2003). In addition to inducing mortality in vectors, studies show insecticide-treated bed nets protect humans from triatomine bites and subsequent infection with *T. cruzi* (Schwarz et al. 2011). While traditionally reserved for areas of high *T. cruzi* endemicity, treated bed nets may also provide a protective effect in the United States, where populations may experience allergic reactions to triatomine bites (Klotz et al. 2014). Despite the potential utility of bed nets for triatomine use in Chagas endemic regions, one factor that limits the use is reduced air circulation and excessive heat, which are common in many tropical areas (Pulford et al. 2011, Poosesod et al. 2021).

Repellent. In addition to reducing triatomine vector populations using insecticide, repellents can also reduce contact between triatomine and humans and other animal hosts. Some repellent ingredients in commercial products labeled against mosquitoes and ticks and other chemicals have been studied to repel triatomines, such as DEET, IR3535, and picaridin (Alzogaray et al. 2000, Terriquez et al. 2013, Reynoso et al. 2017). N-ethylmaleimide, a sulfhydryl reagent, was demonstrated to have a feeding deterrent effect on *T. infestans* nymphs (Picollo et al. 1993). Alzogaray et al. (2000) documented a significantly higher repellency effect of DEET for *T. infestans* nymphs than the control treatment within 60 min. The repellency index (area occupied by nymphs in acetone treated arena/area occupied by nymphs in DEET treated arena) ranged approximately from 1.25 to 190 depending on the experiment design and DEET dose. Reynoso et al. (2017) reported minimum effective concentrations of 1.15 ug/cm² for both DEET and IR3535 to produce repellency against *T. infestans* nymphs, while Terriquez et al. (2013) documented the lowest concentrations of 10% and 7% for DEET and picaridin, respectively, to significantly reducing *T. rubida* (Uhler) (Hemiptera: Reduviidae) feeding. Besides the synthetic insecticides, plant essential oils and their compounds have been studied widely as repellents against triatomines due to their volatile properties (see *Botanical insecticides* section). Spatial repellents have been successful in disrupting mosquito–human contact (Achee et al. 2012, Revay et al. 2013, Dame et al. 2014, Mannino et al. 2019, Morrison et al. 2022). However, we were unable to find studies evaluating spatial repellents for triatomines. The closest such example is irritants, such as pyrethroids, used in the standard flush-out method for surveillance by spraying in crevices in homes to encourage triatomines to escape the crevices, which aids in the detection and collection (Gürtler et al. 1993, 2001, Reynoso et al. 2017). Exploring spatial repellents for reducing triatomine colonization of households is warranted.

Although repellents may have great effects on interrupting contacts between triatomine and host, it is highly dose-dependent to achieve, especially for long-lasting effects. For example, 15% DEET shows repellency of mosquitoes for 6 h (Colucci and Müller 2018), which indicates the need for reapplication. The need to reapply repellents in Chagas endemic contexts could be a barrier to use and the commercializing of products labeled specifically for triatomines. Exploring more insecticides and formulations that are safe and long-lasting would be beneficial. We also highlight that repellents could be effective when the risk of exposure to triatomines is ephemeral, such as deployed warfighters.

Pyrethroid resistance. Although few studies have reported low resistance to fipronil in triatomine populations (Tolozza et al. 2008, Germano et al. 2010, 2012), resistance to pyrethroids is a major problem in triatomine control resulting in failures in different regions with persistent or rapid recovery of infestations (Gurevitz et al. 2012, 2013, Bezerra et al. 2014, Mougabure-Cueto and Picollo 2015, 2021). The major mechanisms of pyrethroid resistance are target site insensitivity, metabolic detoxification, and reduced penetration, which have been summarized and explained in Mougabure-Cueto and Picollo (2015, 2021). Pyrethroid resistance was reported in triatomines collected in Brazil and Venezuela, where *T. infestans* from Brazil demonstrated resistance to deltamethrin, beta-cyfluthrin, and cypermethrin, while *R. prolixus* from Venezuela were resistant to lambda-cyhalothrin and cypermethrin (Vassena et al. 2000). However, the resistance was not considered as a contributing factor to the control failures in 1998 where fast recovery of high-level infestation was observed after pyrethroid sprays (Picollo et al. 2005, Zaidenberg 2012, Gürtler and Cecere 2021). However, subsequent research revealed high resistance to deltamethrin (resistance ratio = 50.5–133.1) was reported in 2005 in Salta, Argentina, along with resistance to beta-cypermethrin, beta-cyfluthrin, and lambda-cyhalothrin, resulting in ineffective control in the field (Picollo et al. 2005). In addition, Gurevitz et al. (2012) reported persistent infestations in 28.4% of the deltamethrin-treated houses in the Gran Chaco region of Argentina due to resistance with a resistance ratio range of 4.47–11.50. Likewise, pyrethroid resistance has been recorded in Mexico (Davila-Barboza et al. 2019), Bolivia (Lardeux et al. 2010, Depickere et al. 2012), and Colombia (Torres et al. 2013). Therefore, alternative control strategies to complement insecticides are needed for effectively controlling vectors of Chagas disease in the affected areas (Fig. 1).

Biological Control

Biological control involves the introduction of a natural enemy or predator to control a pest (Waage and Greathead 1988). In the past, this method has demonstrated success in controlling vector populations such as mosquitos, where predatory larvae and mosquitofish have been used to reduce populations (Benelli et al. 2016). Similarly, we will discuss below several types of biological control that have been evaluated as potential candidates for triatomine vector control. Biological control can target vectors with reduced nontarget effects and environmental impact and, in some cases, may target populations that demonstrate resistance to traditional insecticides. Further, biological control often involves a delayed action, allowing the reproduction of part of the adult population before they are killed, thereby preventing the evolution of resistance (Benelli et al. 2016).

While biological control has many successes and benefits, there are multiple barriers to applying it to large-scale interventions. As agents of biological control are live organisms, the acceptance of applying them in a domestic environment where humans

and other animals reside may be low due to multiple factors, including differences in culture, value, and regions, and knowledge of pest management and biological control (Barratt et al. 2021). In addition, pesticides, including biological control agents, have been heavily regulated with lengthy and expensive testing and documentation (Messing and Brodeur 2018). Nontarget effects are one of the concerns of using biological controls, which extends the regulatory process and necessitates agency approval in each country or region (Messing and Brodeur 2018). These challenges can significantly impede the transition from laboratory evaluation to large-scale application of innovative biological control methods.

Fungi. The effects of entomopathogenic fungi on triatomines were evaluated as early as 1987, and high mortality was demonstrated in *R. prolixus* that was sprayed with *Beauveria bassiana* (Bals.-Criv.) Vuill. (Hypocreales: Cordycipitaceae) (Romana et al. 1987). Thereafter, more studies have been conducted to explore its mechanisms (Forlani et al. 2015, Lobo et al. 2015), effects on triatomine oviposition (Forlani et al. 2015), immune response (Lobo et al. 2015, Mannino et al. 2019), fungal formulations (Luz et al. 1999, Luz and Batagin 2005, Forlani et al. 2011), and strains (Lecuona et al. 2001). *Beauveria bassiana* has shown a significant effect in *T. infestans* mortality up to 100% under both field and laboratory conditions (Forlani et al. 2011, 2015). Field studies have distributed the fungus through boxes baited with carbon dioxide (Pedrini et al. 2009) or triatomine pheromones (Forlani et al. 2015). The fungus is then transmitted horizontally to exposed insects, similar to autodissemination traps used to treat tsetse flies with entomopathogenic fungus (Maniania et al. 2006). *Beauveria bassiana* has been shown not only to increase vector mortality but also to significantly affect *T. infestans* oviposition, where the infected females produce significantly fewer eggs than uninfected females (Forlani et al. 2015). However, there was no significant difference in fertility. Triatomines also showed a measurable attractiveness to the fungi, compared to repulsion from some chemical insecticides (Forlani et al. 2015). The use of *B. bassiana* provides a potential effective control for pyrethroid-resistant triatomines given that *B. bassiana* degrades the thickened cuticle (Napolitano and Juarez 1997, Pedrini et al. 2009), which is a pyrethroid resistance mechanism (Pedrini et al. 2009). Pedrini et al. (2009) reported 52.4% mortality in pyrethroid-resistant insects exposed to entomopathogenic fungi in experimental houses and rural human dwellings. However, the use of entomopathogenic fungi, especially in the indoor environment, will require regulatory approval, public acceptance, and minimal nontarget impacts.

Nematodes. Entomopathogenic nematodes are widely used as biological control to target agricultural pests and can be applied using traditional spraying equipment. Entomopathogenic nematodes form symbiotic relationships with enteric bacteria, which create virulent bacteria-nematode complexes that can kill insects (Stock and Blair 2008). The third juvenile stage is the infective stage of the parasite, which leaves the insect, traveling in the soil to seek a new host. Entomopathogenic nematodes are mainly found in 2 families, Steinernematidae and Heterorhabditidae, which have been developed as biological control agents and used to control agricultural pests (Campos-Herrera 2015). In addition, it has been evaluated extensively against the aquatic mosquito larval stage with high mortality (Cagnolo and Almirón 2010, Peschiutta et al. 2014, Dilipkumar et al. 2019) as well as against ticks (Kocan et al. 1998, Samish and Glazer 2001, Goolsby and Shapiro-Ilan 2020, Filgueiras et al. 2023).

While entomopathogenic nematodes have been studied against other vectors, the research on their effects against triatomines is limited. Two genera of nematodes, *Heterorhabditis* and *Steinernema*, have

demonstrated the ability to kill *T. infestans* and *R. prolixus* under laboratory conditions (Eliceche et al. 2022). Laboratory experiments found that *T. infestans* parasitized by the nematodes had mortalities of up to 90% in as little as 3 days postexposure, and the experiment was equally successful in both insecticide-resistant and nonresistant triatomines (Eliceche et al. 2022). In addition, Martins et al. (2020) reported the parasitism of mermithid nematodes (Mermithidae) on *T. sordida* (Stål) (Hemiptera: Reduviidae) collected from Brazil, which provided another candidate for triatomine biological control. While field studies of the mermithids have not been evaluated for triatomine control, boxes containing pheromones used in experiments to attract triatomines to traps containing entomopathogenic fungi (Forlani et al. 2015) may also be used to attract the insects to be treated with entomopathogenic nematodes. Although entomopathogenic nematodes seem to be promising candidates for triatomine control, there are still challenges to overcome before implementation in the field and communities. For example, field evaluations need to confirm the interaction between nematodes and triatomines as well as the efficacy of control. The mass production of nematodes could also be a prohibiting factor to consider, as well as the formulation and application technology (Askary and Abd-Elgawad 2021) and transport challenges to remote Chagas endemic locations. In addition, contact between nematodes and human and companion animals may be a concern.

Parasitic wasps. Parasitoids are organisms that live on and obtain resources from their hosts, which often eventually cause death in hosts. Most parasitoids are insects in the orders of Hymenoptera and Diptera that lay eggs in other insects, where they develop and emerge as an adult. Parasitoids have been an important biological control tool in integrated pest management and have been used to control multiple economically and medically important pests, such as filth flies (Machtinger et al. 2015, Smith et al. 2022) and fruit flies (Garcia et al. 2020). Multiple parasitoid species of triatomines have been reported, such as *Telenomus fariai* Costa Lima (Hymenoptera: Scelionidae), *T. costalimai*, *Megaselia scalaris*, and *Aprostocetus asthenogmus*, which parasitize different triatomine species (Felicciangeli and Rabinovich 1985, Costa et al. 2007, dos Santos et al. 2014, Ramirez-Ahuja et al. 2021).

Telenomus fariai was proposed as a biological control of triatomines as early as 1957 (Zeledón 1957) and was widely studied (Rabinovich 1970). Gorla and Schofield (1985) documented that *Te. fariai* appeared at the end of summer and attacked up to 37% of *T. infestans* eggs, which then decreased to zero in winter due to the low triatomine egg production. Fernandes et al. (1990) found 70.9% parasitism in eggs of *Panstrongylus megistus* (Burmeister) and *T. vitticeps* (Stål) and observed an average of 10 parasitoids per *T. infestans* egg in the laboratory. However, the triatomine egg age influences the parasitism of *Te. fariai*, which was reduced as the egg matured (Rabinovich 1970). However, egg parasitism resulted in high mortality, high egg production in a limited period, and the low effectiveness of *Te. fariai* under natural conditions limit the potential for using parasitoids as biological control field settings (Gorla and Schofield 1985, Noya et al. 2019, Gorla 2020).

The parasitoid *M. scalaris*, was documented infesting a *T. brasiliensis* colony in the laboratory in Brazil. Costa et al. (2007) reported that *M. scalaris* larvae were discovered feeding inside *T. brasiliensis* nymphs and adults and the fly pupa was found in the colony container. dos Santos et al. (2014) observed *A. asthenogmus* near the *T. infestans* and *T. vitticeps* colonies and subsequently demonstrated the wasp's ability to parasitize *T. infestans* and *T. vitticeps* eggs with rates of 56.8% and 45.5%, respectively. With more parasitoid species of triatomines being discovered, using parasitoids remains a viable biological control option for triatomines.

Endosymbionts. Endosymbionts have been playing an important role in vector and vector-borne diseases, especially in mosquitoes. *Wolbachia* is one of them that has been widely studied in mosquito management as it can not only suppress pathogen replication, such as Dengue virus, yellow fever virus, and Zika virus, but also negatively affect mosquito reproduction, resulting in population reduction (Yen and Failloux 2020). It is favored and considered a more acceptable tool as it can be vertically transmitted and does not involve gene editing. *Wolbachia* infection in insects is high, with an estimated 66% of insect species being infected (Hilgenboecker et al. 2008), including triatomines (Espino et al. 2009, Kieran et al. 2019, Waltmann et al. 2019). However, it is unclear how *Wolbachia* affects triatomines as there are no observed beneficial or negative effects (Kieran et al. 2019, Salcedo-Porras et al. 2020). Unlike *Wolbachia*, *Serratia marcescens* is a common bacteria found in some triatomine species and regulates the population of *T. cruzi* in triatomine by producing prodigiosin that hinders *T. cruzi* establishment. From the in vitro experiments, 2 strains of *S. marcescens* reduced *T. cruzi* population in triatomine at 30 °C and killed flagellates at 0 °C (Azambuja et al. 2004). More studies further explored the effects of *S. marcescens* on the humoral immunity of *R. prolixus* (Batista et al. 2021) and as a potential antagonist of *T. cruzi* (da Mota et al. 2018). While *S. marcescens* has the ability to regulate *T. cruzi* population in triatomines, it remains unknown whether *S. marcescens* can be used as a biological tool to control *T. cruzi* transmission. Additional endosymbiont bacteria are being isolated and evaluated for advancing the utility of using symbiotic bacteria to create populations of triatomines refractory to *T. cruzi* (Cambronero-Heinrichs et al. 2024).

Mites. Mites have been found parasitizing on triatomine head, thorax, abdomen, and legs (Anderson 1968, Dye-Braumuller et al. 2021) with different preferences of triatomine species. Marti et al. (2017a) summarized the literature and their laboratory data and reported 8 mite species in the genus *Pimeliaphilus* parasitizing 12 *Triatoma* species in North and South America. In addition to those species, mites in the genus *Leptus* were found on *Mepraia spinolai*, an endemic triatomine vector for *T. cruzi* in Chile (Gonzalez-Moraga et al. 2015). *Archeogozetes magnus* was also reported to parasitize *T. dimidiata* in Mexico (Waleckx et al. 2018). Dye-Braumuller et al. (2020) reported a 25% mite prevalence in *T. rubida* collected from Texas.

Besides the high prevalence in some triatomine colonies, mite infection can reduce triatomine fecundity and nymphal molting rate, as well as increase triatomine mortality (Anderson 1968, Martinez-Sanchez et al. 2007). Anderson (1968) reported that in the laboratory, triatomine molting success reduced as the number of attached female mites increased. The high parasitism produced in the laboratory study also caused death in early triatomine instars. Martinez-Sanchez et al. (2007) also demonstrated the effects of mite parasitism on triatomine biology by exposing different stages of *Meccus pallidipennis* to 40 *P. plumifer*. The survival times of the triatomines infested with mites were significantly shorter than those without mite infestation. In addition, mite infestation also had effects on reproductive capacity by significantly reducing eggs and hatching rates, similar to another study (Zumaquero et al. 2004). These findings indicated the potential of using mites as biological control of triatomines by interrupting molting, reducing survival and reproduction, which may subsequently reduce triatomine populations and Chagas disease risk. However, there are barriers that hinder the use of mites to control populations of field triatomines. The effects of mites on triatomines were observed with high intensity under confined conditions, which may not be the same in the field. Mite prevalence in field-collected triatomines varied greatly. For example,

Anderson (1968) collected 507 triatomines from the field with an average mite: triatomine ratio of 1:3.1 (0.32 mite/triatomine), while in the 408 triatomines collected from Arizona and New Mexico, 13.2% of them had mites attached with an average of 1.56 and 1.71 mites per *T. rubida* and *T. protracta* Uhler (Hemiptera: Reduviidae), respectively (Dye-Braummuller et al. 2021). In addition, mites as a biological control tool may be less accepted for use in the indoor environment given nontarget impacts such as human allergies. There have been many successful cases of using mites to control other pests, such as whiteflies, and many of them have been commercialized and play a leading role in biological control (Knapp et al. 2018). Therefore, more research, especially field evaluations and application strategies, are needed to explore and develop the use of mites as a biological control for triatomines.

Triatoma virus. Triatoma virus (TrV) is a nonenveloped virus in the family Dicistroviridae (Czibener et al. 2000, Squires et al. 2013). It was first isolated from *T. infestans* and has been found in 15 species of triatomine (Muscio et al. 1988, Ceccarelli et al. 2015), such as *T. patagonica* (Rozas-Dennis et al. 2002), *T. delpontei*, *Psammolestes coreodes* (Susevich et al. 2012), and *T. sordida* (Marti et al. 2009). It is the only documented pathogenic virus of triatomines (Querido et al. 2015) and has only been found infecting triatomines (Marti et al. 2020). The primary transmission route of TrV is the fecal-oral route in triatomines, while other routes, such as feeding on infected chickens and transovarial infection, may also occur (Muscio et al. 2000). TrV replicates in the triatomine's intestinal epithelium cells after infection. Beyond TrV, Brito et al. (2021) described 7 single-strand RNA viruses isolated from *R. prolixus* and named RpV1-7. However, current evidence suggests these viruses are not pathogenic to triatomines.

Muscio et al. (1997) found 10% of wild *T. infestans* in Argentina harbor TrV, while the virus has also found its way into triatomine laboratory colonies in Argentina and Brazil, causing significant problems within insectaries (Marti et al. 2013, 2015). Marti et al. (2017b) explored the interaction between TrV and *T. cruzi* and concluded that TrV infection could assist *T. cruzi* in invading triatomines' intestinal cells but not vice versa. On the other hand, TrV infection affects the development and mortality of triatomines. The survival time of *T. infestans* nymphs displayed a negative relationship with the amount of virus ingested (Marti et al. 2015). Muscio et al. (1997) reported a 97.6% mortality of nymphal *T. infestans* and inhibitions of nymphal molting with TrV infection, while Rozas-Dennis and Cazzaniga (2000) reported a shorter longevity and lower fecundity of infected females compared to those of uninfected *T. infestans*. These results indicated that TrV is a strong candidate for biological control of triatomines, especially for *T. infestans*, the major vector of *T. cruzi* in South America, in addition to its high host specificity (Marti et al. 2020).

Insect-specific viruses have previously been proposed to be used as a biological control for vectors and vector-borne diseases (Bolling et al. 2015, Carvalho and Long 2021), inspired by the success of *Wolbachia* controlling mosquitoes, which can reduce vector competence of mosquitoes by shortening mosquito lifespan and blocking pathogen replication (Xue et al. 2018). Similar concepts can be applied using insect-specific viruses. Multiple mosquito-borne viruses, such as West Nile virus, Zika virus, dengue virus, and chikungunya virus, have been documented to be suppressed by insect-specific viruses (Bolling et al. 2012, Romo et al. 2018, Baidaliuk et al. 2019). Although no evidence suggests TrV suppresses *T. cruzi* in triatomines, it can induce high mortality in *T. infestans* and subsequently reduce populations, which is promising to be used as a biological control for triatomines and Chagas disease. In addition to being a biological

control tool, virus-like particles from TrV also have the potential to be used as an adjuvant to develop vaccines against Chagas disease (Queiroz et al. 2021). Similar ideas have been proposed and further explored in other vector-borne diseases, such as diseases caused by the Zika virus and West Nile virus (Porier et al. 2021, Zhang et al. 2023).

Botanical insecticide. Due to the development of pyrethroid resistance, alternative insecticides are needed to replace or facilitate the traditional pyrethroids. Botanical products have a long history of being used as insecticides, which was recorded 3,000 years ago (Pavela 2016). The botanical insecticide has attracted a lot of attention to be used as an alternative to synthetic insecticides, such as pyrethroids, for more efficient control of vectors and low toxicity to mammals. Some essential oils are currently used in commercial products (Luiz de Oliveira et al. 2018, Isman 2020). Multiple insecticidal properties of botanical insecticides against pests have been reported, including repellents, antifeedants, toxicants, growth regulators, and attractants (Ahmed et al. 2021). In 1997, essential oils extracted from 63 Bolivian plants were tested against *T. infestans*, and most of them exhibited insecticidal activities (Laurent et al. 1997). Moretti et al. (2013) evaluated 10 botanical monoterpenes from plants against *T. infestans* and *R. prolixus*, revealing significant effects on the locomotion of both species as well as repellency that was comparative to DEET (positive control). The monoterpenes also exhibited knock-down effects but were not as strong as dichlorvos (positive control). For *T. rubida*, *T. protracta*, and *T. recurva* collected in Arizona, citronella oil (Terriquez et al. 2013) and its major components, geraniol and citronellol (Zamora et al. 2015), demonstrated significant inhibition of feeding. Besides the direct effects on triatomines, botanical monoterpenes also act as synergists to synthetic insecticides. For example, the toxicity of azamethiphos was significantly increased against *T. infestans* when applied with eugenol, menthol, or menthyl acetate (Reynoso et al. 2020), with similar effects on bed bugs (*Cimex lectularius*) (Gaire et al. 2020). With multiple modes of action (Jankowska et al. 2017), using essential oils as insecticides will potentially slow down the resistance development as essential oils are a mix of many compounds.

Due to the volatile property of essential oil, they may have poor environmental stability, which leads to a short effective control period and subsequently increases the cost of triatomine control. However, the development of nanotechnology may contribute to essential oil formulation as pesticides and provide a long-lasting efficacy and cost-friendly delivery method (Luiz de Oliveira et al. 2018). One limitation of commercializing botanical products as pesticides is the plant availability and standard extraction techniques to ensure consistent product quality. In addition, the regulatory process may hinder the application and commercialization of essential oils as pesticides in different regions (Luiz de Oliveira et al. 2018).

Genetic Control

The modification of symbionts in the arthropod is another way to achieve vector population control or make populations refractory to the transmission of disease-causing agents (Coutinho-Abreu et al. 2010). Symbiotic bacteria can be engineered and delivered to populations of insects, which may harbor the symbiont throughout their life (Hurwitz et al. 2011). Triatomine vectors, including *R. prolixus* and *T. infestans*, have been the subject of successful paratransgenesis experiments (Beard et al. 1992, Durvasula et al. 1999, 2008, Hurwitz et al. 2011). *Rhodococcus rhodnii* is a soil-associated actinomycete that lives in *R. prolixus* gut lumen and can be transferred from adult to offspring through coprophagy (Hurwitz et al. 2011). This bacterium plays a vital role in *R. prolixus*

development and sexual maturation (Durvasula et al. 2003). Early studies of paratransgenesis in triatomines found that introducing genetically modified bacteria *Rh. rhodnii* into *R. prolixus* can produce a trypanolytic antimicrobial peptide (AMP) called cecropin A, which targets *T. cruzi* in *R. prolixus* (Durvasula et al. 1997, 1999). Durvasula et al. (1997) reported that out of 7 *R. prolixus* from the genetically transformed *R. prolixus*-carrying group, 5 had no detectable metacyclic trypomastigotes (Durvasula et al. 1997). Several subsequent studies have examined ways to improve the lethality of *T. cruzi*, finding that combined AMPs can achieve up to 100% lethal concentration levels (Fieck et al. 2010). Additional AMPs that are effective against *T. cruzi* include apidaecin, Magainin II, and melittin (Fieck et al. 2010). *Rhodococcus rhodnii* has been the subject of other experiments assessing antitrypanosomal molecules, such as β -1,3-glucanase (Hurwitz et al. 2012, Jose et al. 2013). Besides *Rh. rhodnii*, *Corynebacterium* sp. is necessary for triatomine development and has been engineered to secrete an immunologically active antibody fragment against *T. cruzi* (Durvasula et al. 2008).

Despite the success of laboratory studies, there are barriers to the successful implementation of paratransgenesis strategies, including their ability to be transferred to wild triatomine populations. CRUZIGARD, a product containing modified *Rh. rhodnii* designed to simulate triatomine feces, was developed as a delivery medium (Beard et al. 2001). Durvasula et al. (1999) conducted a laboratory and field-simulation study of *R. prolixus*, allowing eggs from wild-caught triatomines to emerge inside cages impregnated with CRUZIGARD. The results indicated that 100% and 56% of the triatomines carried the bacteria under laboratory and simulated field conditions (Durvasula et al. 1999), indicating that CRUZIGARD is effective in delivering genetically transformed *Rh. rhodnii* into the field *R. prolixus* populations, which could be part of the integrated pest management and supplement of insecticide applications (Beard et al. 2001).

Still, the field release of engineered bacteria is risky. An additional barrier to the implementation of this intervention is the possibility of unintended environmental impacts. Paratransgenesis may threaten microbiome diversity and influence horizontal gene transfer (Hurwitz et al. 2011). Mathematical models and simulations may provide more insight into the possible ramifications and safety of such an intervention (Hurwitz et al. 2011, Matthews et al. 2011). In addition, human health and safety concerns may rise as paratransgenesis develops. However, the engineered bacteria that target *T. cruzi* are not pathogenic to mammals (Beard et al. 2001).

Mass Trapping

While traps for arthropod vectors are primarily utilized for surveillance, the deployment of large numbers can kill sufficient numbers that can result in vector population suppression (Day and Sjogren 1994). Several success stories exist with mass trapping and population control of mosquitoes (Johnson et al. 2017). In Caguas City, Puerto Rico, applications of 78,126 autocidal gravid ovitraps in 60%–80% of buildings successfully reduced *Aedes aegypti* populations by about 75%, as well as the infection with dengue, chikungunya, and Zika viruses (Barrera et al. 2019). Significant reduction or elimination of *Culex quinquefasciatus* and *Aedes albopictus* were observed in Maldivian islands with the deployment of baited mosquito traps and oviposition traps, as well as larval source management (Jahir et al. 2022).

Similar mass trapping concepts can be applied to triatomine control, and several traps have been developed to capture a large number of triatomines. In 1964, 3 light traps around a rural residence in Arizona captured 398 *T. protracta* (Sjogren and Ryckman

1966). This trap was a fluorescent black light placed next to a white wall surrounded by an insecticide (Malathion)-treated gutter that trapped and killed all triatomines that arrived at the light. Three of these light traps around a rural residence captured and killed 398 *T. protracta*, with the homeowners noticing fewer triatomines around the home compared to typical years (Sjogren and Ryckman 1966). This observation suggested the potential for mass trapping to control populations of triatomines and reduce the risk of human and animal exposure to *T. cruzi*. In Argentina, 3 light traps consisting of a cross panel with diode lights captured 39 triatomines containing 4 species during 270 trap nights (Abraham et al. 2011). More recently, Updyke and Allan (2018) deployed cross-vane traps baited with UV lights, which autonomously captured 24 adult *R. pallidus* during 85 trap nights in Panama. A different light trap design was also used, which contained a vertical white cloth with fluorescent light and required manual collection. Although it requires more labor, a total of 101 triatomines were collected within 14 days of trapping from 1982 to 1984 (Wisnivesky-Colli et al. 1993). Similar traps were used in Mexico, and a total of 544 adult *T. dimidiata* were caught within 8 sampling nights (Rebollar-Tellez et al. 2009). While these light traps are efficient for flying triatomines that are attracted by light sources, other traps, such as baited traps and sticky traps, can target both flying and walking triatomines. In artificial chicken coops, yeast-baited traps captured significantly more *T. infestans* than nonbaited traps, with a peak capture of 39 in one trap overnight (Lorenzo et al. 1998). Abraham et al. (2011) used sticky traps as dispersal barriers around chicken coops and goat corrals and caught 32 triatomines over 270 trap nights in Argentina. Mouse-baited sticky traps (Noireau traps) have been a gold standard trap for triatomines in nidicolous and domiciliary environments (Noireau et al. 1999, 2002).

With the high capture rate, the deployment of a large number of mixed traps that target different triatomine behaviors can potentially reduce triatomine numbers as well as slow down the infestation and reinfestation in residences by capturing dispersing adults. However, to achieve high capture rates, it is important to understand the seasonal phenology of triatomine dispersal, as well as the effects of the environment on triatomine behaviors. Given the large number of traps needed, labor requirements may be intense for deployment and maintenance. Therefore, the development of traps that require minimal maintenance and autonomously capture triatomines would be beneficial for developing mass trapping as a control tool.

Host-Targeted Intervention

Triatomines are obligatory hematophagous insects, and many species require multiple bloodmeals to advance from one nymphal life stage to another (Guarneri et al. 2000). This biology necessitates frequent contact with vertebrates to obtain blood. Systemic insecticides or insecticide-treated collars given to the vertebrate hosts can result in toxic bloodmeals able to kill triatomines, a control strategy known as xenointoxication (Rocha E Silva et al. 1969). This strategy is more efficient when the vertebrate species responsible for the majority of triatomine bloodmeals are targeted, for example, domestic dogs in the peridomestic environment, which have been shown to account for a large number of triatomine bloodmeals (Gürtler and Cardinal 2015).

Xenointoxication for the control of triatomines builds on companion animal products targeting protection from ectoparasites such as ticks and fleas but also has broad spectrum control of other arthropods (Rokhsar et al. 2023). Deltamethrin dog collars have been shown to reduce triatomine feeding success in dogs, although

it did not affect bug mortality (Reithinger et al. 2005). Similarly, the evaluation of insecticides with topical application of fipronil on dogs showed no significant effect on *T. infestans* mortality (Gürtler et al. 2009). However, a later study found a topical application of the combination of fipronil and permethrin resulted in 100% mortality of *R. prolixus* within 24 h after feeding on dogs that were 0–5 wk posttreatment (Ucan-Mezquita et al. 2019). Topical formulations of cypermethrin have also shown effectiveness against *T. infestans* when applied to chickens, and a topical formulation of imidacloprid was effective against pyrethroid-resistant *T. infestans* populations when applied to pigeons (Amelotti et al. 2010, Carvajal et al. 2014). Although the topical formulations tested on chicken and pigeons were designed as contact insecticides instead of systemic insecticides used on dogs, it is also possible that some of the active ingredients reached the blood and became systemic. Topical formulations can exhibit variability in the ability to disperse through the skin or enter blood becoming systemic and in some cases, insufficient active ingredient reaches feeding arthropods (Amelotti et al. 2010).

Insecticides given as oral formulations improve the systemic treatment of the animal, creating toxic bloodmeals for feeding arthropods. Several active ingredients have been tested and are labeled for use in animals to target internal parasites (e.g., endoparasiticides) or ectoparasites (e.g., ectoparasiticides). Ivermectin is a commonly used endectocide, a drug with endoparasitocidal and ectoparasitocidal activity on endoparasites and ectoparasites in humans and other animals (Chaccour et al. 2013, Sharun et al. 2019). Ivermectin-treated blood from in vitro blood feeding or direct feeding on vertebrates had high efficiency in killing or controlling multiple pests and vectors such as *C. lectularius* (Sheele and Ridge 2016), *Anopheles* mosquitoes (Chaccour et al. 2013), *Culex* mosquitoes (Holcomb et al. 2022), and *Rhipicephalus microplus* (Davey et al. 2010). In addition, consuming ivermectin-treated blood can also reduce fecundity, feeding success, and development in those surviving individuals (Sheele and Ridge 2016). Dogs treated with ivermectin injections caused high mortality of *T. infestans* after blood feeding with a peak occurring at 24 h posttreatment (Dias et al. 2005). Dadé et al. (2014) evaluated the xenointoxication effects of ivermectin in chickens against *T. infestans* by feeding the 5th instar nymphs directly on the chickens treated with a spot-on formulation. Mortality of the nymphs was observed when feeding occurred 24–336 h posttreatment, with a peak (47.5%) observed at 120 h posttreatment. The mortality generally matched the ivermectin concentration in plasma, where the peak concentration was observed at 48 h posttreatment. However, Durden et al. (2023) did not observe any mortality from *T. gerstaeckeri* nymphs that fed on chickens treated with ivermectin orally, which may be because the first feeding occurred at the 3 days posttreatment and missed the ivermectin concentration peak. Similar results were documented by Busselman et al. (2023), who found no mortality in triatomines that fed on blood from dogs treated with ivermectin; the first evaluation of toxic bloodmeals posttreatment was 7 days. However, cypermethrin-treated chickens also produced higher mortality in *T. infestans* nymphs (Amelotti et al. 2014), which was not the case with fipronil-treated dogs (Gürtler et al. 2009).

In addition to ivermectin, other active ingredients have been tested as systemic insecticides to manage triatomines. Fluralaner is a member of the isoxazoline drug class. It is commercially available in the United States as Bravecto to treat ticks and fleas on dogs and cats. Although triatomines are not labeled as the targeted parasites, fluralaner has been reported to be effective against triatomines that feed on dogs orally treated with Bravecto, with up to 100% mortality of *R. prolixus*, *T. brasillensis*, and *T. infestans* (Laino et al. 2019, 2022, Queiroga et al. 2021, Ortega-Pacheco et al. 2022).

Field studies of fluralaner-treated dogs reported a significant reduction in human-triatomine contact, *T. cruzi* infections, and overall *T. infestans* populations (Gürtler et al. 2022). Fluralaner has also been reported to be effective in chickens to kill other pests, such as bed bugs and mites, without safety issues in chicken health and egg production (Huyghe et al. 2017, Thomas et al. 2017, Gonzalez-Morales et al. 2023). Durden et al. (2023) confirmed the treatment of poultry with fluralaner killed *T. gerstaeckeri* for up to 14 days posttreatment. Therefore, fluralaner may be promising in terms of treating multiple key host species in the Chagas disease system.

Although xenointoxication had promising effects in killing triatomines, there are other aspects to be considered when applying this method community-wide. As *T. cruzi* can be transmitted not only by triatomine feces but also by consuming infected triatomines. While xenointoxication could potentially reduce triatomine populations by killing the feeding triatomines, the dead triatomines could increase the chance of being consumed by dogs and subsequently facilitating *T. cruzi* transmission in dogs (Fiatsonu et al. 2023, Rokhsar et al. 2023). Rokhsar et al. (2023) developed a simulation model to evaluate the impact of xenointoxication in dogs for *T. cruzi* transmission. The simulation indicated that in the low prevalence area, *T. cruzi* prevalence in dogs increased after one fluralaner treatment, while it generally stayed stable in the endemic area. Therefore, xenointoxication must be carefully evaluated before being applied in communities.

Environmental Management

Besides using chemical and biological control agents, environmental control has been playing a critical role in pest management, especially for triatomines, as reinfestation often occurs after chemical control (Monroy et al. 2009). To prevent reinfestation and achieve long-term effectiveness, environmental modifications, such as household improvements, light reduction, and reservoir control, have been used. In addition, community participation, which is promoted by health education, is a key factor in successful triatomine management (Curtis-Robles et al. 2015, Lardeux et al. 2015).

Triatomine reinfestation could occur due to the residual populations in a refuge that are not treated with pesticides and the dispersal of triatomines from other infested areas (Monroy et al. 2009). Household conditions, such as house wall material, house hygiene, the presence of firewood piles, host habitat, and lights, are related to triatomine habitat suitability (Dumonteil et al. 2013, Zamora et al. 2015). Household improvements such as removing or reducing objects or materials that serve as a refuge for triatomines or hosts and outdoor lights that attract dispersing adult triatomines reduce the risk of Chagas disease (Cecere et al. 2003). Multiple control programs that include household improvements, such as Healthy Living Initiative (Bates et al. 2023), Ecohealth intervention (Monroy et al. 2012, Lucero et al. 2013), and ecosystem approach to health (Waleckx et al. 2015b), have been implemented with successful results. Zeledon and Rojas (2006) reported that in Costa Rica, removing objects or materials and modifying artificial ecotopes that serve as hiding and breeding sites in houses can greatly reduce or eliminate *T. dimidiata* populations. Those houses remained triatomine-free for at least 4–5 years except for 2 houses that had a chicken coop and inappropriate use of storage space (Zeledón et al. 2008). This result indicates that household improvement has a sustainable effect of successfully reducing and even eliminating triatomine populations, while artificial ecotypes like chicken coops may provide habitat and blood sources for triatomine and result in reinfestation. A different result was observed in Jutiapa, Guatemala,

where ecosystemic interventions, including health education, wall plastering, insecticide application, backyard reforestation, and traditional interventions (health education and insecticide application) were implemented in villages (Monroy et al. 2009). Both interventions resulted in lower *T. dimidiata* infestations (number of infested houses) and colonization (number of houses with nymphs) and higher crowding (average of collected bugs from infested houses). However, a spatial shift of triatomine distribution from domestic to the peridomestic environment was observed in all villages, which likely reduced disease transmission by reducing human-vector contacts (Monroy et al. 2012). Similar studies using ecohealth interventions were also conducted in Bolivia (Lardeux et al. 2015). However, Horstick and Runge-Ranzinger (2018) concluded after a systematic review that although waste management and cleanup campaigns can reduce vector populations, the results were not consistent, and house structure modification had no effects on Chagas disease. Therefore, more research and evidence are needed to clarify the effects of household improvement and environmental modification for reducing Chagas disease to ensure these are economically feasible solutions for large-scale implementation.

Besides household conditions, artificial lights can facilitate triatomine reinfestation and spread. Minoli and Lazzari (2006) revealed that both *T. infestans* and *R. prolixus* tended to fly toward white light compared to UV light, although the light presence did not increase the take-off rate at night. Similar results were also observed in *T. dimidiata* (Pacheco-Tucuch et al. 2012). Therefore, artificial lights can serve as an attractant for dispersing adults and subsequently allow sylvatic triatomines to arrive in the domestic and peridomestic environment (Minoli and Lazzari 2006, Castro et al. 2010). Di Iorio and Gürtler (2017) reported the capture of 288 triatomines over 425 daily collections using 29 mercury-vapor lamps as an attractant, with most of them caught nearly sunset with temperature >20 °C and sex ratio varied by species. Pacheco-Tucuch et al. (2012) evaluated the relationships between houses infested with *T. dimidiata* and artificial light distributions in the Yucatan peninsula, Mexico. The results indicate that the infested houses had significantly shorter distances to street light sources than the noninfested houses. However, the domestic light sources did not have significant effects on the infestations, which may be due to the lights normally being turned on for a short period after dusk. Therefore, increasing the distance between houses and lights or reducing lights at night around homes may help prevent triatomines infestations and reinfestations. In addition, triatomines are more attractive to the spectrum of 397–555 nm (Reisenman and Lazzari 2006), which provided another potential solution to reduce the light attractiveness by using long wavelengths (Pacheco-Tucuch et al. 2012).

Another important element in environment modification is reducing *T. cruzi* reservoirs and triatomine blood sources, such as chicken and rats, to interrupt the transmission cycle. Studies have reported that triatomine spatial distribution was affected by local host abundance and density of semisylvatic habitats (Vazquez-Prokopec et al. 2008, Rossi et al. 2015). Chickens serve as a great blood source for triatomines but are not a reservoir of *T. cruzi*. Bustamante et al. (2014) reported 64% *T. dimidiata* fed on chickens. In Brazil, *T. sordida* mainly occurs in peridomestic environments with chicken coops (Rossi et al. 2015). A study has reported that chicken coops can lead to reinfestations, while houses without chicken coops remained triatomine-free for at least a couple of years (Zeledón et al. 2008). Unlike chickens, rodents serve as both a blood source and a *T. cruzi* reservoir, which makes them important in maintaining the *T. cruzi* transmission cycle (Cortez et al. 2006). In addition, wild animals, such as raccoons, canine species, and opossums, are reservoirs

for *T. cruzi* (Gunter et al. 2017). Integrated vector management, including insecticide application, education, and rodent and chicken control, can result in lower triatomine nymph and rat infestations compared to the communities without interventions (De Urioste-Stone et al. 2015). Therefore, reservoir control, such as removing wild animal nests and trash and avoiding living in rural areas, is an important element in Chagas disease control in areas with persistent triatomine infestation.

Triatomine Control in the United States

Although human Chagas disease is not considered endemic in the United States (World Health Organization 2021, 2023a, 2023b), 11 triatomine species have been reported in the United States, primarily distributed in the southern United States, and the detections of triatomine have been reported in 28 states from 1939 to 2010 (Bern et al. 2011). All 11 species have also been documented to occur in Mexico except *T. sanguisuga* (LeConte) and *T. rubrofasciata* (De Geer) (Hemiptera: Reduviidae) (Bern et al. 2011). The *T. cruzi* infection rates in triatomines collected in the United States varied, where infection rates of 56% ($n = 18$), 41.5% ($n = 164$), 21.1% ($n = 161$), and 78% ($n = 153$) were reported in Louisiana (Dorn et al. 2007), Arizona (Reisenman et al. 2010), California (Hwang et al. 2010), and Texas (Kjos et al. 2013). With 1,510 triatomines acquired from 17 states in the United States, Curtis-Robles et al. (2018) reported an average *T. cruzi* infection prevalence of 54.4%, which varied among species. Although it is rare for triatomines to colonize in houses in the United States, the urbanization of habitat with sylvatic cycles of triatomines and *T. cruzi* is increasing the risk of human exposure (Bern et al. 2011). In addition, migration from endemic areas increases the US burden of Chagas disease. In 2005, more than 300,000 cases of *T. cruzi* infection were estimated in the United States by applying the seroprevalence figures to immigrant populations by country (Bern and Montgomery 2009). In 2012, this estimate was reduced to 238,091, with over 10,000 cases in California, Texas, Florida, and New York (Manne-Goehler et al. 2016).

Chagas disease also occurs in other animals and presents a notable burden to domestic animals, especially canines (Busselman and Hamer 2022). Besides vector transmission, oral transmission by consuming infected triatomine, their feces, or infected animals through predation is likely to be the major transmission route for veterinary Chagas disease (Hamer and Saunders 2022). Canine Chagas disease has been reported in at least 8 states with varied prevalence despite the lack of standardized surveillance (Hamer and Saunders 2022). Dogs can serve as reservoirs for *T. cruzi* and facilitate the transmission cycle, which makes canine kennels with triatomines a high-risk environment (Curtis-Robles et al. 2017). Busselman et al. (2021) reported that 29.4% of the *T. cruzi*-negative dogs converted to positive over a 1-year observation period with *T. cruzi*-positive dogs in the same kennel. A thorough review of veterinary Chagas disease can be found in Hamer and Saunders (2022).

The control of triatomines and Chagas disease in the United States presents a unique context compared to many regions in Latin America where Chagas is endemic, and only a subset of control approaches are suitable in the United States (Table 1; Klotz et al. 2014). While triatomine and Chagas control in many Latin American contexts are managed by local ministries of health agencies, this is not the case in the United States. Only mosquito control has historically received area-wide control by local public health agencies in at least some regions. Triatomine control is similar to tick control in the United States, where the reduction of exposure to tick-borne diseases falls on the individual responsibility, although initiatives are

encouraging a shift towards a professionally staffed integrated tick management (Eisen 2020).

Triatomine colonization of homes in the United States is rare, partly because of higher housing quality. As a result, indoor residual spraying, which is common in Latin America, is not justified in most scenarios in the United States. Much of the risk in the United States of human and animal contact with triatomines involves dispersing adults from sylvatic to peridomestic habitat. In addition, triatomines are able to colonize the peridomestic environment, which often involves dogs, chickens, or other animals as bloodmeal hosts. Residual insecticides used around dog kennels, chicken coops, and household perimeters are a common practice, although we are not aware of studies confirming efficacy. There are no insecticides specifically labeled for use against triatomines in the United States, although several active ingredients have been shown to be effective based on work in the lab or in Latin America (Beatty et al. 2023; Table 1). Active ingredients of products found in the United States used for structural pest control that are known to kill triatomines include deltamethrin and cypermethrin.

The most common form of triatomine control in the United States that is alternative to insecticides is environmental control. The same methods performed in Latin America can apply to the United States. For example, reducing household permeability to triatomines with the use of screens and other mechanical methods can mitigate triatomines entering the home. Reducing triatomine habitat suitability around the home and peridomestic environment is recommended, such as minimizing natural or artificial harborage or refuse that can create habitat for triatomines or hosts. This is similar to the control of ticks and Lyme disease in the northeastern United States through yard management, such as the removal of wood piles of trash and separating the lawn from adjacent forest (Fischhoff et al. 2019). This is especially important with urban sprawl and as homes are built in sylvatic habitats that increase the opportunity for contact with infected vectors. Outdoor safety lights are common in the United States, but these can attract kissing bugs, so removing these lights or using longer wavelengths in the yellow-red spectrum (>550 nm) that are less attractive to insects is recommended. Reducing wild or domestic vertebrate hosts that provide bloodmeals to triatomines around the peridomestic environment can help reduce environmental suitability for triatomines. Rats, opossums, and other wild animals that nest near homes can be removed by trapping to block their ability to nest in structures. Domestic animals that are desired, such as dogs and chickens, can receive the systemic insecticides discussed above to create toxic bloodmeals for triatomines.

In combination with environmental control, the mass capture of dispersing adult triatomines from the sylvatic habitat arriving at the peridomestic habitat was first acknowledged as a control option in the United States in 1966 (Sjogren and Ryckman 1966). Advancements in technology will facilitate newer trap designs that autonomously capture triatomines with minimal maintenance, which will provide future options for triatomine control in the United States. Options for biological control in the United States have received minimal attention compared to areas in Latin America.

Conclusions

In the past 40 years, pyrethroid insecticides targeting the triatomine vector have been the primary control tool for triatomine vectors of *T. cruzi* (Gürtler and Cecere 2021). However, insecticide resistance, global climate change, lack of sustained control effort, and globalization have all contributed to the emergence or reemergence of

triatomines and the persistent Chagas disease burden (Medone et al. 2015). Despite long-term interventions and changes in health policy in endemic countries, *T. cruzi* continues to cause new infections, and new interventions are needed now more than ever (Hotez et al. 2020).

Alternative insecticides, such as botanicals, should also be further investigated as a potential for insecticide-resistant triatomine populations (Moretti et al. 2013). Treating dogs, chickens, cats, wildlife, or other hosts with commercially available systemic insecticides may be especially effective at targeting triatomines in peridomestic habitats, and many products can be easily given to animals by their owners (Gürtler et al. 2022, 2009). Similarly, biological control in the form of mites, fungi, wasps, and other predators may be especially effective in endemic areas with extremely high triatomine burdens or areas with insecticide-resistant triatomines (Forlani et al. 2015). However, biological control has limitations, such as the potential for nontarget effects and an extensive regulatory process, which could be a barrier to area-wide use. Mass trapping may also be a useful addition to triatomine control to intercept dispersing adults flying from sylvatic to domestic habitats (Sjogren and Ryckman 1966). The goal of reducing human and animal infection with *T. cruzi* can be achieved by having fewer infected triatomines and breaking transmission cycles. Therefore, control of *T. cruzi* reservoirs, such as rodents, can aid in the reduction of *T. cruzi* circulating in triatomine and host populations. All the control tools covered in this review require community engagement and partnerships (Juarez et al. 2022). Education and engagement are vital for successful triatomine interventions (Curtis-Robles et al. 2015, De Urioste-Stone et al. 2015, Lardeux et al. 2015, Rivera et al. 2023), and it is possible that strategies can be implemented at the household level to prevent colonization and reinfestation of triatomine vectors (Cecere et al. 2003).

To effectively control triatomine vectors, it is vital that we update our understanding of both current and developing control interventions. Rigorous investigations into new control tools and their epidemiological and entomological outcomes are needed in order to advance the scale-up of intervention evaluations. This review captures the diverse control tools that have been evaluated over the last century for triatomines and offers options to consider for local public health agencies. Ultimately, it will take the collaboration between researchers, public health officials, and community members to translate control tools into sustainable initiatives that can protect human and animal health.

Author Contributions

Yuxun Tian (Conceptualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Cassandra Durden (Conceptualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), and Gabriel Hamer (Conceptualization [equal], Writing—review & editing [equal])

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