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Review Article

Tsetse flies: Their economic significance and current control methods

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Abstract

Tsetse flies, hematophagous insects of the genus *Glossina*, are significant vectors of trypanosomosis, a devastating disease in tropical regions, including Ethiopia. This parasitic disease impacts both humans and livestock, with economic losses in sub-Saharan Africa exceeding $1 billion annually. Ethiopia faces widespread infestation by four *Glossina* species: *G. pallidipes*, *G. morsitans submorsitans*, *G. fuscipes*, and *G. tachinoides*. These flies transmit pathogenic trypanosomes such as *Trypanosoma congolense*, *T. vivax*, and *T. brucei*, affecting approximately 200,000 km² of the country's land. Climate change exacerbates the challenge by altering vector distributions, threatening cattle, small ruminants, and equines. Control efforts should prioritize vector reduction, particularly targeting savannah tsetse species (*G. morsitans* and *G. pallidipes*), to minimize costs and operational time. Strategies like the sterile insect technique are cost-effective and efficient. Effective control requires collaborative efforts among communities, veterinary services, and governments to mitigate the impact of African trypanosomiasis and promote economic development.

Keywords: *Glossina*, Insecticide, Sterile insect techniques, Trypanosomiasis, Tsetse flies

Highlights

- Tsetse flies are significant vectors of trypanosomiasis, leading to over $1 billion in economic losses annually in sub-Saharan Africa, particularly in Ethiopia
- Ethiopia is home to four major species of tsetse flies: *G. pallidipes*, *G. morsitans submorsitans*, *G. fuscipes*, and *G. tachinoides*, which transmit various pathogenic trypanosomes
- Limited understanding of the ecology and behavior of tsetse flies hampers effective control, alongside resource allocation and infrastructure issues in affected regions

INTRODUCTION

Vector-borne diseases are predominantly spread by mosquitoes, ticks, mites, tsetse flies, rat fleas, and sandflies, with environmental factors playing a significant role in their distribution (Pal, 2007). Among these, tsetse-transmitted animal trypanosomosis poses a critical challenge to animal production and agricultural development in Ethiopia (Rebuma *et al.*, 2024). Tsetse flies are primarily restricted to tropical regions, including sub-Saharan Africa, where they infest approximately 10 million km² of fertile land across 37 countries (Bitew *et al.*, 2011). In Ethiopia, tsetse fly infestation covers an estimated area of 200,000 km², predominantly in the southern and western regions. These areas lie between longitudes 33°-38° East and latitudes 5°-12° North, encompassing lowlands and major river valleys such as the Blue Nile, Baro Akobo, Didessa, Ghibe, and Omo (Lemu *et al.*, 2019).

Glossina genus consists of 31 recognized species and subspecies, five of which are found in Ethiopia: *Glossina pallidipes*, *G. morsitans*, *G. fuscipes*, *G. tachinoides*, and *G. longipennis* (Bangu *et al.*, 2017). Among these, *Glossina fuscipes* subspecies are responsible for approximately 90% of human African trypanosomiasis (HAT) cases. Together with *Glossina palpalis* subspecies, they account for nearly 100% of cases of the Gambian form of the disease (*Trypanosoma brucei gambiense*), which represents approximately 97% of HAT cases globally (Simarro *et al.*, 2010). *Glossina morsitans* group primarily inhabits natural savannahs, while the *G. palpalis* group is associated with riverine forest vegetation. Both groups are epidemiologically significant as vectors of trypanosomiasis (Bouyer *et al.*, 2019). They transmit human African trypanosomiasis (HAT), commonly known as sleeping sickness, caused by *Trypanosoma brucei*, as well as animal African trypanosomiasis

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(AAT), also known as nagana, which affects cattle and poses a critical threat to livestock productivity (Cecchi *et al*., 2015).

Human African trypanosomiasis (HAT) is a neglected tropical disease transmitted by tsetse flies, posing serious health and economic burdens in sub-Saharan Africa (Brun *et al*., 2010; Pal, 2007). Animal African trypanosomiasis (AAT) severely impacts livestock production, causing the death of about three million cattle annually and leading to economic losses of up to US$1.2 billion due to reduced productivity and animal mortality (FAO, 2019; Samuel *et al*., 2018).

Understanding the ecology of tsetse flies, including their habitat preferences and interactions with the parasites they transmit, is critical for designing and implementing effective control strategies (Tewelde, 2001; Afewerk, 2008). Various governmental and non-governmental organizations have made efforts to control tsetse populations. Commonly employed control methods include habitat clearing, baited targets, sequential aerosol techniques (SAT), ground spraying, insecticide-treated cattle (ITC), and the sterile insect technique (SIT) (Shaw *et al*., 2017).

A comprehensive understanding of the tsetse population structure, behavior, host preferences, habitat, distribution, and temporo-spatial heterogeneity is vital for optimizing vector control strategies (La Greca and Magez, 2011). Innovations such as tiny targets small (50 x 25 cm) insecticide-impregnated cloth panels have emerged as a more cost-effective method for controlling tsetse populations compared to traditional approaches (Rayaisse *et al*., 2011). However, the effectiveness of control strategies remains hindered by limited information on the temporal and spatial dynamics of tsetse and trypanosomes. This knowledge gap, compounded by challenges in resource allocation, infrastructure, and political stability across sub-Saharan Africa, often reduces the success of control initiatives (Nnko *et al*., 2016).

The negative impact of tsetse flies extends beyond livestock health, affecting access to cultivable land, altering land use, and restricting opportunities for agricultural diversification and intensification. These challenges emphasize the need for a multidisciplinary approach to promoting sustainable agriculture and rural development (Mattioli *et al.,* 2013). Beyond understanding the ecology of tsetse flies, assessing the economic losses attributed to this vector and identifying the most effective control strategies are crucial for stakeholders, including farmers, researchers, and governments. The objective of this review is to delineate the economic impacts of tsetse flies as vectors of African trypanosomiasis and to explore integrated control strategies to mitigate their effects.

Tsetse fly

Tsetse Fly Morphology: Tsetse flies' range in size from 6 to 13.5 mm in length, with a slender body that can be yellow to dark brown. Their abdomens, visible from the dorsal side, vary from light to dark brown and are divided into six segments. Species identification of tsetse flies is based on morphological features such as size, tarsal claws, color, and proboscis (Kaba *et al*., 2017). The sex of male and female tsetse flies is determined by examining the posterior end of the ventral abdomen using a hand lens and finger palpation. Males can be identified by their enlarged hypopygium at the posterior ventral end of the abdomen (Duguma *et al*., 2015).

Tsetse flies can be easily distinguished from other large flies by two prominent features (Fig. 1). First, when resting, tsetse flies fold their wings completely so that one wing rests directly on top of the other, forming a scissor-like configuration over their abdomens. Wing venation includes a distinctive hatched-shaped cell in the middle of the wings. Second, tsetse flies possess a long proboscis that extends directly forward and is attached by a distinct bulb to the underside of their heads (Hordofa and Haile, 2017).

Epidemiological distribution: Tsetse flies are predominantly found in sub-Saharan Africa, specifically between latitudes 5°N and 20°S, where

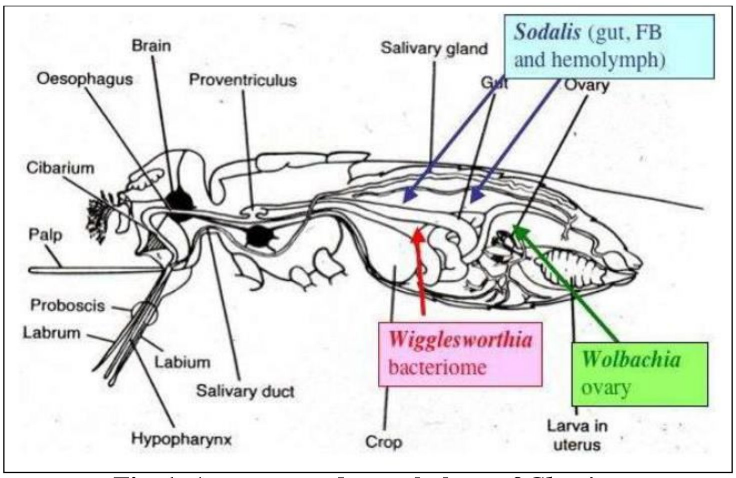

Fig. 1. Anatomy and morphology of *Glossina*
Source: (Itard, 2009)

the environmental conditions are ideal for their survival. They thrive in areas with an average yearly temperature ranging from 23°C to 25°C and require approximately 75% relative humidity (Geiger *et al.*, 2015). These flies are closely associated with vegetation that provides shelter from wind and sunlight. While they can also inhabit regions with slightly less rainfall, they are most commonly found in eco-climates with more than 1000 mm of annual precipitation, such as wooded areas (Meberate *et al.*, 2009).

Tsetse flies typically rest in shaded areas within forested environments, preferring the lower, woody sections of vegetation, and often hiding in gaps between roots or tree trunks. They spend only brief periods of the day searching for food, commonly resting near potential food sources (Taylor *et al.*, 2007). Water collection points, such as forest trails and riverbank vegetation, are common areas where both animals and humans may be exposed to tsetse bites, as they visit these sites to bathe, drink water, and wash clothes (Okoh *et al.*, 2012).

Climate significantly influences the distribution of tsetse flies by creating favorable microhabitats, which can differ from the surrounding environment in terms of temperature and humidity. These microhabitats, especially during harsh seasons or times of the day, provide the necessary conditions for tsetse fly survival and reproduction. Understanding these microhabitats is essential for effectively managing tsetse fly populations and designing targeted control measures, as they enable tsetse flies to thrive even when broader environmental conditions are less suitable. Such knowledge helps in refining control strategies and predicting tsetse fly distribution with greater accuracy (Vanden *et al.,* 2000).

Classification: Tsetse flies are classified into three groups based on the climate, vegetation, and fauna characteristics of their ecology: riverine, woodland, and savanna types (Krafsur, 2009). *Glossina morsitans*, commonly known as the savanna tsetse fly, is associated with watercourses and tends to congregate near water sources during the dry season. During the rainy season, they disperse across the woody savanna. This group primarily inhabits Sudanese savannas, with *G. submorsitans* found in West and Central Africa, and *G. morsitans* in East Africa. Large animals serve as the primary food source for this group of tsetse flies (Ford and Katonondo, 2001).

Riverine tsetse flies, particularly *G. palpalis*, are typically found closer to rivers where dense vegetation thrives, rather than at the margin of riverine forests. These flies inhabit riverine woodlands that extend into the savanna regions of West and Central Africa. Reptiles and ungulates are their primary food sources. On the other hand, *Glossina pallidipes* is a highland species found in East Africa. One variety of this species is confined to Kenya and Tanzania, while the other ranges from Ethiopia to Mozambique and can also be found in some coastal areas (Smyth, 2005).

The forest tsetse flies, classified under the Fusca group, thrive in regions where there is a transition between wooded areas and true forests. These flies prefer dense shade and thickets, often located near rivers. *Glossina longipennis*, a species within the Fusca group, is found only in specific regions, including Kenya, Ethiopia, southeastern Sudan, southern Somalia, northwestern Uganda, and northern Tanzania (Aksoy *et al.*, 2003).

Life cycle: Tsetse flies have a relatively long lifespan compared to many other insects, living for about 50 to 100 days, though they can survive up to 8 months in confinement. Female tsetse flies are viviparous, carrying 5 to 10 larvae in their uterus, which are nourished by the uterine milk. Every 10 days, the female lays its larvae on the ground, where they rapidly metamorphose into pupae and eventually emerge as adult flies, requiring no additional food resources during this transformation (Bouyer *et al.*, 2019).

Female tsetse flies generally mate only once and, after mating, remain fertile for life, capable of producing up to 12 larvae. These females are viviparous, meaning they produce one larva at a time, with a maximum of 8 to 12 larvae in their lifetime (Kahn, 2005). The fertilized egg takes about ten days to mature within the uterus, growing into a mobile larva that is 8-10 mm long. Over the course of those ten days, the larva develops inside the uterus before being deposited on damp soil or sand in shaded areas, often beneath fallen shrubs, logs, large stones, or buttress roots (Leak, 2009).

The larvae of tsetse flies complete their development in the mother's abdomen, and depending on the temperature, adult flies emerge between 22 and 60 days later (Smyth, 2005). Peak fly numbers typically occur at the end of the rainy season, with breeding continuing year-round (Smyth, 2005). Tsetse flies are obligate blood feeders and rely solely on the blood of vertebrates throughout their lives. During their blood meal, they inject saliva to prevent blood clotting and induce vasodilation, and if the saliva contains infective trypanosomes, these parasites are transmitted to the host (Franco *et al*., 2014). Female tsetse flies are generally believed to live longer than males, making them more likely to be exposed to trypanosome infection throughout their lifespan. In a study conducted in Southern Ethiopia, the infection rate in female flies was found to be 6.4%, compared to 0.49% in males (Rundassa *et al*., 2013).

Factors influencing the spread of Tsetse flies: Climate change has significant health impacts on both humans and animals, with direct effects including rising temperatures due to global warming, flooding, and heat waves, all driven by increased climate variability and extreme weather events. Indirect effects include the redistribution of vector species, prolonged seasonal transmission periods, and the geographical spread of vector-borne diseases. Additionally, some vector-borne diseases may disappear or shift in response to changing environmental conditions (Marselle *et al*., 2019).

The expected increase in average global temperatures is likely to disrupt the epidemiology of vector-borne diseases. Warmer conditions can accelerate the development rates and generation times of pathogens and vectors, leading to changes in the geographical spread of vectors and their hosts. This could affect transmission patterns and influence the susceptibility of hosts to infection. On the other hand, extremely high or low temperatures can be harmful to the activity of vectors and their capacity to transmit diseases, thereby altering the dynamics of these infections (Moore *et al*., 2012).

Several factors influence the susceptibility of tsetse flies to infection, including their age, genetics, symbionts, and immune system (Dyer *et al*., 2013). The vegetation in their habitat plays a significant role in their survival, as they prefer dense forests, bushy lands, and savanna grasslands, which protect them from sunlight and wind (Krafsur, 2009). These habitats enhance their chances of survival by offering shelter and favorable environmental conditions. Temperature and humidity are the two primary abiotic factors affecting tsetse dispersal, and trees provide shade for both pupae development and adult resting spots. The study of plant cover has been instrumental in understanding tsetse distribution and habitat preferences (Taylor *et al*., 2007).

Economic impacts of Tsetse flies: African trypanosomiasis affects the economic growth of tropical nations both directly and indirectly. Tsetse flies are generally significant vectors of trypanosome species, such as *T. vivax, T. brucei*, and *T. congolense*. The disease, nagana caused by *T. brucei* can be lethal if left untreated, among humans and animals (FAO, 2000). Those three trypanosome species are found in Ethiopia. The infection rates are determined by the parasite, the vector, the host, and the environment (Msang, 2009).

Tsetse-transmitted animal trypanosomosis is a significant and economically important disease, hindering efforts to achieve food self-sufficiency. The expenses related to treating livestock illnesses and controlling tsetse flies place an additional economic burden on affected nations. The threat of human infections, particularly sleeping sickness, which is caused by the same trypanosomes, further exacerbates the situation. Sleeping sickness, transmitted by tsetse flies, has profound social, economic, and agricultural impacts, particularly in rural communities, affecting both public health and livelihoods. Animal diseases, particularly trypanosomosis, are a major constraint on animal production in tropical Africa. Trypanosomosis leads to the death of approximately 3 million cattle annually, with around 35 million doses of trypanocidal drugs being administered to livestock in tsetse-infested areas to ensure their survival. The direct economic losses in cattle production alone range from US$1.0 to 1.2 billion. However, the broader indirect impact on the entire agricultural-livestock sector is estimated to amount to US$4.5 billion annually (Radostitis *et al*., 2007).

Control methods

Stationary attractive devices: Traps designed for tsetse control are typically made from a combination of blue and black fabrics with white netting on the top, creating a sharp corner. These traps exploit tsetse flies' attraction to contrasting visual stimuli, such as large moving objects, which they associate with potential resting places or blood meal sources. The traps are deployed in the morning and left in place for 72 hours to maximize fly capture. At 24-hour intervals, the trapped flies are removed and destroyed to reduce the population (Leak, 2009; Welburn *et al*., 2012).

Tsetse flies are particularly attracted to certain colors, especially blue. In tsetse traps, the blue screens are often combined with black screens, which encourage the flies to settle on the black surfaces. Once they are attracted to the trap, the flies move towards the upper parts of the trap, where they are guided by the light (Nagagi *et al*., 2017). Similarly, tsetse control targets consist of 1.15 m^2 sections of fabric that are sprayed with pesticide. These targets are strategically placed in tsetse fly habitats to attract and eliminate the flies (Hao *et al*., 2001).

Effective tsetse fly traps can attract flies from a distance of approximately 50 meters. Once the flies enter the trap, they may die due to exposure to insecticide impregnated in the trap material or from the sun's heat. The fundamental design of these traps is effective across all regions in Africa where tsetse flies are present, although local conditions may require adjustments to optimize their success. Different types of traps, such as monoconical, biconical, epsilon, and pyramidal traps, are commonly used in tsetse fly control programs (NTTICC, 2009). However, the effectiveness of impregnated targets can decrease when tsetse fly densities are very low (Dicko *et al*., 2014).

The effectiveness of tsetse fly traps and targets can be significantly improved by adding appropriate odour baits such as acetone, octenol, or bovine/buffalo urine (Rayaisse *et al*., 2010). This method of creating barriers is efficient, non-polluting, and economical, requiring less frequent maintenance when used alongside other control strategies. However, it does rely on pesticides, which can sometimes cause harm to humans, animals, and the environment, including the risk of bush fires (Vale *et al*., 2009). Traps and targets attract the flies, either killing them or guiding them into a non-return cage (Reichard, 2002).

Insecticides aerosols: Tsetse flies are highly sensitive to insecticides, and their control or elimination has been achieved in vast areas of Africa through extensive application, both from the ground and by air (Allsopp and Hursey, 2004). One of the techniques used is the Sequential Aerosol Technique (SAT), which involves aerial spraying of micro droplets containing pyrethroids at very low doses (0.33-0.35 grams of active ingredient per hectare). SAT is particularly effective against the Morsitans group in open environments but becomes more challenging to implement against the Palpalis group in dense vegetation or hilly areas (De Deken and Bouyer, 2018).

High levels of tsetse control can be achieved through sequential aerial spraying of ultralow doses of biodegradable products, including organochlorines like DDT and dieldrin, as well as synthetic pyrethroids, both of which have been widely used in tsetse fly control (Nagagi *et al*., 2017). Aerial spraying, however, is dependent on weather conditions, which can disrupt the timing of the application. It also requires trained personnel and specialized equipment. While this method effectively kills tsetse flies, it has a very short residual effect. Additionally, the area being sprayed must be evaluated for both its environmental impact and its economic potential (Hao *et al*., 2001).

The delivery methods of residual insecticides for tsetse control are primarily categorized into two approaches: ground spraying and the sequential aerosol technique (SAT). Ground spraying targets the resting and breeding sites of tsetse flies, or alternatively applies insecticides over the entire habitat from the air (Kgori *et al*., 2006). In contrast, the sequential aerosol technique (SAT) involves repeated spraying of non-residual insecticides over large areas using aircraft (Allsopp and Phillemon-Motsu, 2002). SAT's key advantage is its capacity to cover vast regions rapidly, making it highly effective in open environments and areas with little vegetation (Afewerk, 2008).

Fig. 2. Monoconical trap deployed for entomological study
Source: (Degneh *et al*., 2019)

However, SAT does have limitations. It is less effective against riverine species, such as *G. palpalis* in densely vegetated environments, as the insecticide reaches only small portions of the habitat. Additionally, gravid females are less susceptible to insecticides than males, which can reduce the overall success of the method (Kgori *et al*., 2006). Consequently, while aerial spraying is a potent tool for controlling tsetse populations, its effectiveness is influenced by environmental factors and the specific behavior of different tsetse species (Leak, 2009).

Ground spray: When a tsetse fly comes into prolonged contact with a treated surface, beyond its maximal pupal life, the residual treatment on the resting spot must be lethal to ensure control. In some cases, just one application of the insecticide may be enough to control and even eradicate tsetse flies in remote areas. The initial residual treatments were applied to riverine species such as *G. palpalis* and *G. fuscipes*, which are typically found along the edges of bodies of water. In certain situations, large gallery forests can be treated by opening channels that are frequently used by the flies, allowing the insecticide to spread more effectively. Dieldrin emulsions, which are effective for about a year or sometimes longer when applied at 4%, have largely replaced DDT-based products used in earlier trials. Residual pesticide control is most successful when fly habitats are limited or concentrated. However, this approach has not been tested extensively against high forest species, where tsetse flies inhabit more expansive and dense vegetation (Tewelde, 2001)

Live bait techniques: The live bait technique is a highly effective method for controlling tsetse flies, with the added advantage of simultaneously addressing other pests such as cattle ticks. This technique involves treating livestock with appropriate insecticide formulations, typically 1% deltamethrin, through various methods such as dips, or as pour-on, spot-on, or spray-on applications (Kuzoe *et al.*, 2014). These formulations are designed to make the animals more attractive as mobile targets for tsetse flies, drawing them in while also providing protection against other parasites (Leak *et al.*, 2009).

For example, when using the spray method, the entire body of the animal is treated with the insecticide solution. A typical preparation involves adding 50 mL of the concentrated deltamethrin to 10 L of water, which is then, applied using a knapsack sprayer. The treatment not only serves as an attractant for tsetse flies but also helps manage the cattle's exposure to other fly species and ticks (Aksoy *et al.*, 2001).

Control by sterile insect techniques (SIT): Sterile insect technique offers a promising approach for controlling tsetse fly populations, relying on the mass production of target *Glossina* species in specialized facilities, the sterilization of male flies through gamma irradiation, and their systematic release into target areas. Typically, sterile males are released at a ratio of 50 sterile males for every wild male, allowing them to out-compete the wild males for mating opportunities. This leads to the sterility of any offspring produced, as female tsetse flies typically mate only once in their lifetime, ensuring that mating with sterile males prevents reproduction and ultimately eliminates pupation (Kebede *et al.*, 2015).

As sterile males are continuously released into the environment, the absence of fertile mating results in the gradual elimination of the wild population. The technique is most effective when the target population density is low, as this enables more efficient suppression of the wild population (Parker and Mehta, 2007). Additionally, SIT does not harm non-target organisms and is particularly effective in the final stages of local tsetse eradication programs (Alderton *et al.*, 2018). Its efficiency improves as the ratio of sterile to wild males, with the technique becoming more effective as population density decreases (Vreysen and Robinson, 2011). Using other control methods to reduce the native population before applying SIT can further enhance its effectiveness (Bett, 2008).

However, several challenges exist with SIT, including the high costs associated with mass-rearing sterile flies, the low competitiveness of released males (Whitten and Mahon, 2005), and the difficulty in maintaining effective release and monitoring strategies. Additionally, odor-based attractants are increasingly being integrated with SIT and other vector control strategies to improve trapping efficiency and reduce tsetse populations more sustainably (Mireji *et al.*, 2022).

Challenges to control tsetse flies: During colonial administrations, efforts to control tsetse flies and the parasites they transmit were initially successful. However, the continuity of these successes was hindered by infrastructural breakdowns, political instability, conflicts, and neglect (Yusuf *et al.*, 2015). Despite these efforts, the parasite has evolved strategies to evade the host's immune system, and in the absence of a suitable vaccine, control methods such as surveillance, diagnosis, and treatment with existing drugs are often insufficient. Consequently, vector control remains a crucial aspect in reducing the incidence of animal African trypanosomosis (Zongo *et al.*, 2016).

Currently, vaccines for trypanosomosis are not available, and their development is unlikely due to the antigenic variation exhibited by the trypanosomes in their mammalian hosts. The drug treatment options for both human and animal trypanosomosis are increasingly problematic, relying on outdated and sometimes hazardous drugs. Moreover, resistance to these treatments is a growing concern (Holmes, 2013). In addition to these challenges, the quality of insect populations used in vector control programs can be compromised by factors such as overcrowding, suboptimal rearing conditions, diet, pathogen load, genetic drift, and laboratory adaptation, as well as issues arising during handling, irradiation, packaging, and release procedures (Simmons *et al.,* 2010).

Conclusion

To effectively manage tsetse flies and the trypanosomosis they transmit in Ethiopia, a combination of integrated control methods such as insecticide-treated traps, the sterile insect technique, and habitat management should be employed, tailored to local environmental conditions. Strengthening surveillance, public awareness, and community engagement is crucial for early detection and intervention. Additionally, investing in research for new control strategies and fostering collaboration between governments, NGOs, and international organizations can improve the effectiveness and sustainability of control efforts. This multifaceted approach is key to reducing the impact of tsetse flies on agriculture, livestock, and public health. Given the importance of addressing tsetse fly-borne diseases, the following recommendations can help enhance control efforts:

All affected communities, veterinary authorities, and the government ought to be involved in efforts to manage these African trypanosomes vectors. It is even more important to educate animal owners about the dangers associated with trypanosome infection and how to control it. Veterinarians should raise community understanding about tsetse vectors so that people can protect themselves and their cattle astsetse not only affects livestock health but also public health. To prevent economic effects from nagana, where tsetse flies are highly concentrated, strategic management of tsetse flies is essential. Tsetse-transmitted trypanosomosis can be prevented by controlling tsetse flies, but doing so will have an influence on the ecosystem and the cost-benefit analysis of the management methods.

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Author's contribution: AB: Writing original draft**;** AB, TR: Conceptualization, resources, & validation; MP, TR: Writing review and editing, data curation**,** formal analysis, investigation, project administration, supervision & visualization; MP, AB, TR: Methodology & software.

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