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Minireview

Tsetse flies: Their biology and control using area-wide integrated pest management approaches

Marc J.B. Vreysen [a,*], Momar Talla Seck [b], Baba Sall [c], Jérémy Bouyer [b,d]

[a] Insect Pest Control Laboratory, Joint FAO/IAEA Division of Nuclear Techniques in Food and Agriculture, International Atomic Energy Agency, Vienna, Austria
[b] ISRA-LNERV, Service de Parasitologie, BP 2057 Dakar-Hann, Senegal
[c] Direction des Services Vétérinaires, Ministry of Livestock, Senegal
[d] Cirad, UMR CIRAD-INRA Contrôle des Maladies Animales, Campus International de Baillarguet, F34398 Montpellier, France

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ABSTRACT

Tsetse flies are the cyclical vectors of trypanosomes, the causative agents of 'sleeping sickness' or human African trypanosomosis (HAT) in humans and 'nagana' or African animal trypanosomosis (AAT) in livestock in Sub-saharan Africa. Many consider HAT as one of the major neglected tropical diseases and AAT as the single greatest health constraint to increased livestock production. This review provides some background information on the taxonomy of tsetse flies, their unique way of reproduction (adenotrophic viviparity) making the adult stage the only one easily accessable for control, and how their ecological affinities, their distribution and population dynamics influence and dictate control efforts. The paper likewise reviews four control tactics (sequential aerosol technique, stationary attractive devices, live bait technique and the sterile insect technique) that are currently accepted as friendly to the environment, and describes their limitations and advantages and how they can best be put to practise in an IPM context. The paper discusses the different strategies for tsetse control i.e. localised versus area-wide and focusses thereafter on the principles of area-wide integrated pest management (AW-IPM) and the phased-conditional approach with the tsetse project in Senegal as a recent example. We argue that sustainable tsetse-free zones can be created on Africa mainland provided certain managerial and technical prerequisites are in place.

Contents

* Corresponding author. Address: International Atomic Energy Agency, Wagramerstraße 5, A-1400 Vienna, Austria. Fax: +43 1 2600 28222.
E-mail address: M.Vreysen@iaea.org (M.J.B. Vreysen).

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1. Introduction

Tsetse flies, appropriately referred to by (Nash, 1969) as 'Africa's bane', are solely responsible for the cyclical transmission of trypanosomes, the causative agents of 'sleeping sickness' or human African trypanosomosis (HAT) in humans and 'nagana' or African animal trypanosomosis (AAT) in livestock. Both male and female tsetse flies are obligatory blood suckers and during feeding on an infected animal, the trypanosomes are ingested by the fly together with the mammalian host's blood, and they undergo a cycle of development within the insect. The duration of the cycle depends on the trypanosome species and the temperature. There are 31 living tsetse fly species and subspecies known to science (Moloo, 1993), all placed in the genus *Glossina* of the family Glossinidae (Buxton, 1955), and this list could possibly be expanded in view of recent genetic studies (Dyer et al., 2011; Solano et al., 2010a). Only 8–10 species of tsetse fly are considered of economic (agricultural–veterinary) or human sanitary importance.

Tsetse flies occur in 38 African countries infesting a total area of 10 million km^2 in sub-Saharan Africa. Sixty million people are continuously exposed to the risk of infection but only 3–4 million of these people are covered by surveillance (Cattand et al., 2001; WHO, 1998). Although the World Health Organisation estimates the disease prevalence at 300,000–500,000, this probably represents only 10–15% of the actual number infected (Cattand et al., 2001) as screening is poor due to a decline in health service and surveillance coverage. Due to increased surveillance and availability of drugs, a higher number of technicians trained and a bigger commitment of the international community in the last 10 years (2000–2010), the prevalence of HAT has declined and the situation seems to be more encouraging (Simarro et al., 2011).

Many agricultural and veterinary experts consider AAT as the single greatest health constraint to increased livestock production in sub-Sahara Africa. Direct annual production losses in cattle are estimated at USD 600–1200 million (Hursey and Slingenbergh, 1995). Estimates of the overall annual lost potential in livestock and crop production have been as high as USD 4750 million (Budd, 1999). Moreover, tsetse prevents the integration of crop farming and livestock keeping, which is crucial to the development of sustainable agricultural systems (Feldmann and Hendrichs, 1995). In sub-Saharan Africa, the availability of productive livestock would be required to significantly improve agriculture and is considered a prerequisite to alleviate hunger, food insecurity and poverty. The presence of tsetse and trypanosomosis can therefore rightfully be considered one of the *major root causes of hunger and poverty* in sub-Sahara Africa. This is exemplified by the remarkable correlation and overlap between the 38 tsetse-infested countries and the 34 heavily indebted poor countries in Africa (Feldmann et al., 2005).

2. Taxonomy and distribution

The genus *Glossina* is divided into three distinct taxonomic groups using morphological characters such as the external genitalia of the male flies (Newstead, 1911), their habitat requirements (Glasgow, 1970) and preferred hosts (Weitz, 1970). The genus is restricted to the African continent but *Glossina tachinoides* (Scott, 1939), *Glossina morsitans submorsitans*, and *Glosssina fuscipes fuscipes* have been recorded on the Arabian Peninsula (Elsen et al., 1990). The northern limit of their distribution corresponds with the southern edges of the Sahara and Somali deserts and in the south, no tsetse flies are found south of the Kalahari and the Namibian desert and in the eastern part below 29° S.

The species belonging to the *fusca* group (subgenus Austenina) of tsetse flies are of little or no economic importance as their habitat is confined to the lowland rain forests or the border areas of the forest and isolated relic forests (Haeselbarth et al., 1966). All species are difficult to trap, are not attracted by and rarely feed on man (Jordan, 1986). However, in East Africa, *Glossina brevipalpis* is of localised importance and inhabits forest islands often associated with water courses whereas *Glossina longipennis* inhabits the more arid regions (Ford, 1970; Jordan, 1986).

The distribution of the *palpalis* group (subgenus Nemorhina) species is likewise associated with lowland rain forest but their habitat is extended along river systems in the humid savannah (Jordan, 1986). Their distribution extends from the wet mangrove and rain forests of the coastal regions of West Africa northward into drier savannah areas. They can tolerate a wide range of climatic conditions such as occur in the savannah belt due to their association with specific vegetation like riparian forests that line the hydrographical network or plantations of certain crops like mangoes that buffer the prevailing macro-climatic conditions of the savannah. The species belonging to this group are important vectors of AAT in West Africa (*G. tachinoides*, *Glossina palpalis palpalis* and *Glossina palpalis gambiensis*) and HAT in Central Africa (*G. f. fuscipes* and *Glossina fuscipes quanzensis*), since they are opportunistic feeders and tolerate a high degree of disturbance of the landscape (Van den Bossche et al., 2010). They can even be found in large cities like Abidjan (Ivory Coast) or Dakar (Senegal) (Bouyer et al., 2010b).

All species belonging to the *morsitans* group (subgenus *Glossina sensu stricto*) are restricted to savannah woodlands (Jordan, 1986) and their distribution and abundance often correspond with that of wild animals. *Glossina morsitans* spp. and *Glossina pallidipes* are the most important species of this group and are major vectors of AAT and HAT in Eastern and Southern Africa. These species are more sensitive than riverine flies to human encroachment and their abundance decreases when the human population exceeds 5 people/km^2 (Van den Bossche et al., 2010).

3. Life cycle and reproduction

Tsetse flies reproduce by adenotrophic viviparity i.e. the egg contains sufficient yolk to sustain the entire embryonic development and the larva in the uterus is nourished by special maternal organs (Hagan, 1951). All nutrients required for the development of the egg up to the adult stage are maternally derived (Tobe and Langley, 1978). The female fly mates on the first or second day after emergence, possibly when she takes her first blood meal (Saunders, 1970a). It is assumed that in nature, female flies most likely only mate once, but polyandry has been recorded in small laboratory cages (Jordan, 1986; Vreysen and Van der Vloedt, 1990) and more recently in wild populations of *G. f. fuscipes* (Bonomi et al., 2011).

The female tsetse fly has two ovaries, each containing two polytrophic ovarioles, which are always at different stages of development (Saunders, 1960, 1970b). Eggs develop sequentially in the female fly and only one oocyte undergoes vitellogenesis and matures per pregnancy cycle (Tobe and Langley, 1978). Ovulation occurs every 9–10 days depending on the temperature, and as a result, tsetse flies have a very low rate of reproduction. They are typical *k* strategists i.e. displaying traits associated with living at densities close to carrying capacity, and being strong competitors in crowded niches that invest in few offspring, each of which has a relatively high probability of surviving to adulthood, in contrast to most other insects that produce large numbers of eggs, have a high growth rate, and exploit less-crowded ecological niches that are classed as *r* strategists (Leak, 1998). The maternal care given by the female tsetse to each larva enables a high degree of survival of each offspring. Under laboratory conditions, a female tsetse can produce 10 offspring in its reproductive life, but it is assumed that this is less in nature.

The cyclical development and maturation of the four follicles in relation to the content of the uterus allows accurate determination of the physiological age of a female fly population (Challier, 1965); an important tool to assess mortality rates of tsetse populations (Challier and Turner, 1985; Dransfield et al., 1990) and progress in control programmes that use the release of sterile males (Vreysen et al., 2000; Vreysen, 2005).

The mechanical stimulus of mating but not insemination is a prerequisite for normal ovulation of the first oocyte (Chaudhury and Dhadialla, 1976), although chemical endocrine components are also suspected of playing a role (Saunders and Dodd, 1972). After a successful mating, viable sperm is stored in the spermathecae for the rest of the female's adult life (Langley, 1977). Each oocyte is fertilised when it descends and enters the uterus. The entire embryonic development occurs *in utero* and is completed in 50–60 h with the hatching of a first instar larva (L1) (Saunders and Phelps, 1970). The intra-uterine development of the larvae proceeds with the formation of a second instar larva (L2) and is completed with the development of a third instar larva (L3). All larval stages are nourished by lipids and proteinaceous secretions produced by the milk gland which is a highly modified female accessory gland (Tobe et al., 1973). The development of two polypneustic lobes is characteristic for the second instar larva and these blacken 1–2 days before larviposition. The female fly becomes very active a few hours before parturition and different diurnal parturition rhythms have been observed in the laboratory for different species (Leak, 1998). After the larviposition of the L3, the negatively phototactic larva (Parker, 1955) burrows itself rapidly in the soil at a depth of 1–5 cm depending on the species, the season and the soil type (Lewis, 1934). Aggregation pheromones allow the other females to locate suitable larviposition sites (Solano et al., 2010b). Pupal development period varies according to temperature but takes around 30 days at 24 °C. After emergence, the freshly emerged fly will dig its way up in the soil by means of the rhythmic contractions of the ptilinum (a special organ in the head) and flight muscles begin their development after the first blood meal (Bursell, 1961).

The entire process of spermatogenesis occurs in the male pupa between day 6 (onset of meiosis) and day 21–23 (formation of mature spermatozoa) (Itard, 1970). Consequently, male flies emerge from the pupae with their entire complement of sperm and they can successfully inseminate a female fly every 2–3 days, up to 6–10 times under laboratory conditions (Pollock, 1974; Jordan, 1972).

4. Population ecology and dynamics

C.F.M. Swynnerton, Director of Tsetse Research Department in Tanzania in the 1920s, was the first to be convinced that the most promising approach to managing trypanosomosis "lay in an attack on the insect vector based on a sound knowledge of its ecology" and this marked the onset of many studies on the ecology of the fly as a basis for its control (Jordan, 1986).

Fly movement, their mobility, dispersal and spatial occupation of the habitat are all elements of the ecology of tsetse flies critical for their control. These aspects of tsetse ecology can only be studied when adequate sampling techniques are available. In the early days of ecological studies, man or oxen fly rounds were used that typically consisted of a mobile bait (person or oxen) accompanied by fly boys with hand nets who walked a certain transect and stopped at predetermined sites to catch the flies that were attracted to the bait. Fly rounds were not very suitable for tsetse species that were repellent to humans, and often the samples were very biased in favour of male and very hungry flies. Consequently, other methods were required and, over the years, a vast array of stationary sampling tools, mainly traps that attract flies into a non-return cage have been developed (FAO, 1992a; Leak et al., 2008).

Despite the availability of traps, it is notoriously difficult to acquire accurate data on mobility of flies in nature, as the sample composition and size depend very much on the effectiveness of traps, and this in turn influenced by the availability of flies which is very much determined by their activity patterns, mobility and dispersal. All trapping devices are biased and it is very important for the correct interpretation of trap catches to understand the biases of the used traps (Vreysen, 2005).

Tsetse flies are capable of fast flight (a vehicle needs to drive faster than 25 km/h to prevent savannah type flies from entering) but are inactive for most of the time. Activity always occurs in short bursts and female *G. m. morsitans* probably do not spent more than a few minutes a day in flight, young males about 15 min and older males between 30 and 50 min (Bursell and Taylor, 1980).

Movement of tsetse within a uniform habitat has been assumed to be random and to consist of fairly constant step lengths (Rogers, 1977; Bouyer and Guerrini, 2007d; Hargrove, 2000). Much of the movement of tsetse flies is related to the need for a blood meal and hence, its host seeking behaviour. Hosts are located using a combination of olfactory and visual cues and the host seeking behaviour is modulated both by exogenous (temperature, vapour pressure deficit, visual and olfactory stimuli) and endogenous (circadian rhythm of activity, level of starvation, age, sex and pregnancy status) factors (Colvin and Gibson, 1992).

Daily displacements of tsetse flies seem to be closely associated with landscape structure and characteristics and tsetse species. Savannah species such as *G. pallidipes*, *Glossina swynnertoni* and *G. morsitans* spp. were recorded to disperse daily between 145 and 540 m/day in Eastern Africa (Davies and Blasdale, 1960; Hargrove, 2003; Jackson, 1933; Ford, 1960; Brightwell et al., 1992;) with a maximum dispersal of 2250 m from the point of release for *G. pallidipes* in Zimbabwe (Hargrove and Vale, 1979). Riverine species inhabiting gallery forests in West Africa seem to have greater dispersal capacity than savannah species, which is probably due to their association with riverine forests as one-dimensional dispersal networks. Maximum dispersal distances of 12 and 25 km were observed for *G. palpalis* in the 1970s in the Congo and *G. p. gambiensis* in the 1980s in Burkina Faso, respectively (Cuisance et al., 1985; Carnevale and Adam, 1971).

Both direct (mark-release–recapture) and indirect (genetic isolation by distance) methods to assess tsetse fly dispersal have indicated that habitat fragmentation significantly reduced dispersal of the riverine species *G. p. gambiensis* in Burkina Faso. Dispersal coefficients were 10 times lower (0.046–0.057 $km^2\ day^{-1}$) as compared to those obtained in the 1980s (0.29–0.46 $km^2\ day^{-1}$) when the riverine forests were still homogeneous, un-fragmented and pristine (Bouyer et al., 2007b, 2009a; Cuisance et al., 1985). Dispersal of *G. tachinoides*, another riverine species inhabiting West African gallery forests, was far greater in fragmented riparian habitats (0.3 $km^2\ day^{-1}$) than that of *G. p. gambiensis* (0.05 $km^2\ day^{-1}$) resulting in complete panmixia and average displacements of 2.5–3 km during its lifespan (Bouyer et al., 2006; Koné et al., 2011). It therefore seems that the dispersal of *G. tachinoides* was less influenced by landscape fragmentation because it is more xerophylous (Koné et al., 2010).

As density dependent mortality is considered an important factor for the regulation of tsetse populations (Rogers and Randolph, 1984, 1985) and feeding success is negatively correlated with their relative densities (Torr and Mangwiro, 2000), it is probable that tsetse dispersal is likewise density dependent (i.e. increases with density), which might explain the reduced efficiency of fixed trapping devices at lower population densities (see below).

5. Control of tsetse populations

Several methods have been used to manage the disease trypanosomosis, and these include in the case of HAT, the screening and curative treatment of humans and in the case of AAT, the prophylactic and curative treatment of animals with trypanocidal drugs, the promotion of trypanotolerant cattle and suppression or eradication of the vector, the tsetse fly.

The curative and prophylactic use of trypanocidal drugs, generally administered by the farmers themselves remains the most important method of controlling AAT in Africa today (Leak, 1998); an estimated number of 35 million doses of diminazene, isometamidium, and homidium are administered every year to livestock to contain the disease (Geerts and Holmes, 1998; Holmes and Torr, 1988). These drugs are very often used indiscriminately and unsupervised which has resulted in increased levels of drug resistance of the parasite (Codjia et al., 1993; Geerts and Holmes, 1998; Delespaux et al., 2008).

In areas of low to medium trypanosomosis challenge, maintaining trypanotolerant cattle that show a certain degree of resistance to AAT has given some promising results. They are however, not very popular with livestock owners in view of their small size, low milk and meat productivity and lack of strength to provide adequate draught power (Holmes, 1997; Hursey and Slingenbergh, 1995). In addition, their distribution is mostly restricted to West Africa.

Controlling the vector of the disease remains theoretically the most desirable way of containing the disease (Jordan, 1986; Leak, 1998; Bouyer et al., 2010b). The absence of eggs and a free larval stage in nature and the fact that the pupal development occurs in the soil makes the adult fly the only phase easily accessible for control purposes. A broad gamut of vector control tools is available, which all have certain advantages and limitations. Early methods to control the tsetse fly such as the removal of preferred vegetation or the destruction of host game animals were very effective but have become unacceptable on environmental grounds (Dransfield et al., 1991; Ford and Blaser, 1971). The spraying of residual insecticides (e.g. DDT, dieldrin, endosulfan) of tsetse sites from the ground (targeting mainly day resting sites) or with helicopters (targeting mainly night resting sites) in the dry season was likewise a very effective control tactic, despite being very labour intensive, requiring close supervision and detailed planning. The use of helicopters, as opposed to fixed wing aircraft was required to ensure that the persistent insecticides were not randomly dispersed but confined to these habitat types know to harbour the tsetse (Jordan, 1986). In West Africa, a two helicopter unit could reclaim 3000–4000 km^2 in 4–5 months during the dry season at a rate of 40–50 ha per flying hour and aiming for 15% discrimination (Spielberger et al., 1977).

The most successful example of the widespread use of persistent insecticides resulted in the elimination of *G. m. submoristans*, *G. p. palpalis* and *G. tachinoides* from 200,000 km^2 of savannah area in northern Nigeria. Conducted between 1955 and 1978, the campaign mainly used ground spraying and to a lesser degree helicopter spraying. Five operational spraying teams (each team consisting of 350 staff) cleared tsetse from on average 8000 km^2 each dry season. The entire campaign consumed 745 metric tons of DDT and dieldrin to achieve this goal. This campaign was extremely well organised and can probably be considered as the most successful ever undertaken (Jordan, 1986).

The abundant use of persistent insecticides over large areas in often, fragile eco-systems had several negative effects: (1) the potential of insects developing resistance to the insecticide, (2) the killing of beneficial non-target insects, (3) outbreaks of other pests due to the elimination of predators, (4) the general pollution of the environment due to the accumulation of the insecticide in the food chain, and (5) the health hazard posed to the staff of the spray-teams. In the 1970s and 1980s, the application of persistent insecticides was gradually replaced by the aerial spraying of non-residual ultra-low volume insecticides with fixed wing aircraft or helicopters i.e. the sequential aerosol technique (SAT) followed by an upsurge of trapping methods.

There are currently four methods to manage populations of tsetse flies that are commonly accepted as friendly to the environment: some are based on the use of insecticides (the SAT), others on bait technologies (traps and targets, live bait technique), and others on genetics (sterile insect technique) (SIT).

5.1. Sequential aerosol technique (SAT)

Fixed wing aircraft or helicopters (in more difficult terrain) are used to spray a mist of ultra-low volume of non-residual insecticides 10–15 m above the tree canopy in 5–6 subsequent spraying cycles separated by 16–18 days depending on the temperature (Allsopp and Hursey, 2004). Selection of the appropriate droplet size is of prime importance for the method to be successful i.e. the droplets should be small enough to remain suspended sufficiently long in the air and large enough to prevent upward drift. Electrically or air driven rotary atomizers are used at a speed of 16,000 rpm to produce an aerosol of droplets of 30–40 μm (Lee et al., 1978). This control tactic aims at killing all adult flies in each spraying cycle through direct contact with the insecticide mist and then to kill all emerging flies in the subsequent cycles before they can start reproducing. The insecticides have to be applied during periods of temperature inversion (i.e. night time) and there can be no delays or interruption in the timing of the cycles. Use of modern GPS-guided navigation and spray systems (e.g. SATLOCK) makes this tool very effective for area-wide tsetse suppression in dense humid forest ecosystems (Van der Vloedt et al., 1980) or eradication in open savannah-type ecosystems (Kgori et al., 2006).

The SAT, in some cases in combination with other control tactics, was used successfully in South Africa, Kenya, Zambia, Uganda, Botswana and in Zimbabwe (du Toit, 1954; Jordan, 1986; Shereni, 1990). In 2001 and 2002, 7180 km^2 and 8722 km^2 of the Okavango delta in Botswana, respectively were treated with deltamethrin applied at a dose rate of 0.26 g/ha (Allsopp and Phillemon-Motsu, 2002). An environmental study that accompanied the spraying campaign indicated that both aquatic and terrestrial invertebrates recovered well after the spraying with populations of species of most families returning to pre-spraying abundances after 1 year (Perkins and Ramberg, 2004). The total cost of the spraying campaign was less than USD 270/km^2 and although entomological monitoring has been quite limited, tsetse seemed to have disappeared from the sprayed areas (Kgori et al., 2006). The 2001–2002 operation showed that (i) the SAT is a rapid, efficient and cost effective method for tsetse elimination in the open savannah areas of East and Southern Africa and (ii) the SAT does not have any serious lasting negative environmental impact. More recently, the SAT was used to suppress a *G. tachinoides* and *G. p. gambiensis* population with more than 99% in a savannah area of 6745 km^2 in the Upper West Region of Ghana (Bouyer, pers. com.).

5.2. Stationary attractive devices

With this technique female tsetse flies are attracted to a device e.g. cloth traps or targets that either kill the flies through tarsal contact with insecticides applied to the surface of the target (Vale, 1993), or by heat or starvation after being guided to a non-return cage (Brightwell et al., 1991). The method aims at exerting an additional daily mortality of 2–3% to the female segment of the population. The attractiveness of the devices can be enhanced, especially for savannah type species, by using potent odour attractants and these bait methods (Green, 1994), when applied at the appropriate densities, can suppress these tsetse fly population to low numbers in a few months (Takken et al., 1986). The technique is more efficient when the targets/traps are impregnated with insecticides like pyrethroids, as only 20% of the attracted flies are generally entering the device (Rayaisse et al., 2010).

Although the technology is considered relatively low cost and unsophisticated, there are several technical aspects essential for its efficient application i.e. the importance of trap/target deployment and siting, the maintenance requirements of traps and targets, their periodic replacement, the periodic replenishment of the odours, the use of cloth material with an appropriate reflectivity pattern, insecticide deposits degrading by UV light and the use of the most suitable trap/target in relation to tsetse species and geographic distribution (Vreysen, 2001).

In addition, landscape fragmentation, especially in West Africa, also needs to be taken into consideration. The efficiency of traps and targets is correlated with tsetse dispersal capacities, and it has been shown that dispersal for riverine species of tsetse decreases with increasing landscape fragmentation (Bouyer et al., 2009a). Any decrease in tsetse dispersal should be compensated by an increase of target density to obtain the same effect. Moreover, tsetse dispersal is likely positively correlated with their density, which might explain why this technique is more suitable for suppression than for eradication (Kagbadouno et al., 2011; Bouyer et al., 2010b). As an example, traps and targets have been used with great success to suppress populations below the transmission threshold in sleeping sickness foci (Challier, 1984), but to date, eradication has never been achieved using this technique against riverine tsetse species in West Africa.

Recently, it was demonstrated experimentally that a reduction of a blue–black target to 1/16th of its original size, resulted in a concurrent reduction of only half the catch size of *G. f. fuscipes* suggesting a better cost-effectiveness (Lindh et al., 2009). To get the same end effect however, the target density per unit of surface area needs to be increased as the costs of deploying the targets were not considered in the above study. Moreover, its efficacy still needs to be tested under operational conditions of a control programme.

An alternative to the use of insecticides would be traps or targets impregnated with growth inhibitors that prevent reproduction (i.e. causing abortion) without killing the flies instantaneously (Langley et al., 1990). It has been hypothesised that male flies that had been contaminated could transfer the chemical through mating to females that had not been into contact with the targets and thus extend the action range of the targets; but this assumption has never been confirmed. For the moment, this approach has remained experimental and has not been applied at an operational scale (Hargrove and Langley, 1990).

Stationary attractive devices are very suitable for localised deployment by farmer communities to protect small areas, but the high target densities required against certain species and in certain dense habitats make the use of these devices over large areas uneconomic (FAO, 1992b; Kappmeier et al., 2007). The beneficiary farmer communities also experience difficulties adopting this technique in the long term, as it is generally considered a public good (Kamuanga et al., 2001).

A derivative of this technique is the deployment of an insecticide-impregnated fence around cattle pens or corals, that uses the animals as live attractive devices (Bauer et al., 2005). This technique was recently used very effectively around pig enclosures in Guinea (Kagbadouno et al., 2011), but its use is restricted to those situations where animals are confined to small surface areas which is often the case in semi-urban areas.

5.3. Live bait technique

This method is based on insecticide treatment of livestock and exploits the blood sucking behaviour of both sexes of tsetse. Tsetse flies, attempting to feed on cattle or other treated domestic livestock are killed by picking up a lethal deposit of insecticide on the ventral tarsal spines and on pre-tarsi whilst feeding (Leak, 1998). The success of the method depends on a relatively large proportion of feeds being taken from domestic animals (Gouteux et al., 1996) and a sufficient proportion of the livestock population being treated. Pour-on formulations have the advantage over other techniques that no sophisticated equipment is needed, and the insecticide application is rapid and easy. The use of persistent insecticides on livestock has proven to have a suppressive effect on certain tsetse populations in those areas with a high density of cattle and where adequate expert support was present, e.g. in Zimbabwe against *G. pallidipes* (Thomson and Wilson, 1992), in Burkina Faso against *G. m. submorsitans* and *G. p. gambiensis* (Bauer et al., 1995) and in Ethiopia against *G. f. fuscipes* and *G. pallidipes* (Leak et al., 1995). Species of the *G. palpalis* group are more opportunistic feeders, and suppression of the population is often followed by a new equilibrium of the population at low densities (Bauer et al., 1995). Eradication of a riverine tsetse population has to date not been demonstrated using this technique mainly due to a certain proportion of the target population feeding on alternative hosts like reptiles, and, at least in the case of *G. p. gambiensis* due to the tendency of the fly to return to a similar host as encountered during the first blood meal (Bouyer et al., 2007a).

Unlike with stationary attractive devices, the technique is less prone to theft and does not suffer from maintenance problems. However, several issues such as the required cattle density, the proportion of the herd that requires treatment, and host preference of different tsetse species require further research. Other disadvantages are the high treatment frequency, the high cost of the insecticides, insecticide residues in cattle dung, sustainability in the motivation and participation of farmers and the potential development of resistance to the insecticides in both tsetse and ticks.

Recently, it has been proposed to limit the application of the insecticide to certain areas of the host that are preferred biting sites (lower parts of cattle) for riverine (Bouyer et al., 2007c, 2009b) and savannah species (Torr et al., 2007) using partial spraying or insecticide footbaths, first developed to control the tick *Amblyomma variegatum* (Stachurski and Lancelot, 2006). This method reduced the amount of insecticides used and treatment time by 90%, with a subsequent reduction of their environmental impact (Vale et al., 2004). However, external support especially is required for very traditional farmer communities that have poor developed socio-technical networks. In case were farmers are grouped in more dynamic farmer associations, the period needed to provide external support can be significantly shortened (Bouyer et al., 2011).

5.4. Sterile insect technique (SIT)

The SIT relies on the production of large numbers of the target insect in specialised production centres, the sterilisation of the males (or sometimes both sexes), and the sustained and systematic release of the sterile males over the target area in numbers large enough in relation to the wild male population to out-compete them for wild females. Mating of sterile insects with virgin, native female insects, results in no offspring (Dyck et al., 2005). With each generation, the ratio of sterile to wild insects will increase and the technique becomes therefore more efficient with lower population densities (inversely-density dependent) (Vreysen and Robinson, 2011).

The SIT is non-intrusive to the environment, has no adverse effects on non-target organisms, is species-specific and can easily be integrated with biological control methods such as parasitoids, predators and pathogens. There is no evidence of development of resistance to the effects of the sterile males provided that adequate quality assurance is practised in the production process. Unlike the inundated releases of predators or parasitoids, sterile insects cannot get established in the released areas (Vreysen, 2001).

The theoretical model of Knipling (1979) clearly demonstrates one of the major advantages of the SIT i.e. the control effort becomes more economical and efficient as the natural population declines and increasing ratios of sterile to wild males are achieved. This is in contrast with conventional methods of killing insects, e.g. with insecticides. Here, the continued use of the same treatment will result in the same or a reduced percentage effect as the natural population declines (Kagbadouno et al., 2011). The sequential, phased use of techniques that are effective at high population densities followed by techniques effective at low population densities would therefore result in maximum efficiency throughout the intervention phase (Van der Vloedt et al., 1980; Vreysen and Robinson, 2011).

The sterile insect technique is only effective when the target population density is low, it requires detailed knowledge on the biology and ecology of the target pest, and the insect should be amenable to mass-rearing. Specifically in the case of tsetse flies, their low reproductive potential makes the rearing of large numbers challenging and there is a potential danger of disease transmission in case the sterile male insects are released as pupae. In addition, the SIT necessitates efficient release and monitoring methods, which have to be applied on an area-wide basis (Vreysen, 2005).

Sterile males should only be released as part of an area-wide integrated pest management (AW-IPM) (see below) approach in view that mated wild females immigrating into localised control areas are immune to the presence of sterile males. The SIT has been successfully used in combination with other control tactics to eradicate, suppress, or contain pest populations of Diptera, Coleoptera and Lepidoptera i.e. eradication of the New World screwworm fly *Cochliomyia hominivorax* in the USA, Mexico, Central America and Libya (Wyss, 2000; Lindquist et al., 1999), containment of the pink bollworm *Pectinophora gossypiella* in California (Henneberry, 2007) and the Mediterranean fruit fly *Ceratitis capitata* in Guatemala/Mexico (Villaseñor et al., 2000) and suppression of the codling moth *Cydia pomonella* in Canada (Bloem et al., 2005) and *C. capitata* in South Africa, Israel/Jordan (Barnes et al., 2002; Cayol et al., 2002).

Initial studies in the 1960s in Zimbabwe and in the 1970s in Chad and Burkina Faso already indicated the potential of using the SIT against both riverine and savannah tsetse species (Cuisance and Itard, 1973; Dame and Schmidt, 1970; Van der Vloedt et al., 1980). A first full-scale project was implemented from 1977 to 1979 and aimed at evaluating the SIT against *G. m. morsitans* in a 195 km^2 savannah area in Tanzania. After suppression of the population by two aerial applications of endosulfan, sterile males were released for 15 months at an average sterile to wild male ratio of 1.12:1. Despite this low ratio, sufficient sterility was induced in the native female population to maintain the population at 5% of the pre-control level (Williamson et al., 1983).

From 1981 to 1984, two riverine species of tsetse, *G. p. gambiensis* and *G. tachinoides* were eradicated from 3500 km^2 of agro-pastoral land in Burkina Faso by integrating the release of sterile males with insecticide-impregnated screens (Politzar and Cuisance, 1984). In a similar effort in Nigeria (1979–1988), 1500 km^2 of agro-pastoral land was cleared from another riverine species, *G. p. palpalis* using insecticide impregnated targets and traps followed by the release of sterile males at a sterile to wild male ratio of 10:1 (Oladunmade et al., 1990; Takken et al., 1986).

All these projects demonstrated that (i) the SIT is a powerful and robust technique and is very effective against riverine and savannah tsetse flies (in certain ecological settings), (ii) tsetse flies can be successfully mass-reared in Africa, (iii) a prolonged deployment of traps and targets in dense riverine vegetation does not lead to eradication, and (iv) none of these SIT-based projects were applied according to the area-wide concept (see below) and were therefore soon re-invaded by surrounding tsetse populations and thus not sustainable.

One of the most critical aspects of the SIT is the quality of the released insects. To be successful, the released sterile insects must intermingle rapidly with the wild insect population after release and mate at the same rate as their wild counterparts (Vreysen, 2005). The quality of the insects can be impaired by factors in the rearing e.g. crowding, rearing procedures, diets, insect pathogen load, deterioration of the strain, laboratory adaptation, genetic drift, etc., or through handling, irradiation, packaging, release methods, etc. (Simmons et al., 2010). Quality of the released insect should have priority over quantity in the production process, and the frequent monitoring of this quality in the field should be routinely established in operational programmes. Data from the sterile male *Glossina austeni* release programme on the Island of Unguja indicated that sterile and wild male flies congregated in the same ecological niches, showing that both the sterile and the wild insects responded in a similar way to environmental cues (Vreysen et al., 2011). Similar observations were made with *G. p. gambiensis* in Burkina Faso, even after the colony had been cultured for more than 35 years (Sow et al., 2012).

6. Tsetse population control strategies: area-wide integrated pest management (AW-IPM)

Tsetse fly populations can be managed using a field-by-field (localised) or an area-wide approach. Both strategies have merit but they have completely different goals and hence outcomes and economic balance sheets. In a field-by-field approach, control tactics are used in a localised area and the goal is to temporarily alleviate the burden of trypanosomosis over an area that is of direct interest to the farmer. The only way this strategy can be sustained by the beneficiaries is to reduce the control costs as much as possible. The area-wide approach aims at the sustainable removal of an entire tsetse fly population within a delimited geographical area (Klassen, 2005). Using simple mathematical models Knipling (1972) showed the importance of total population control and emphasised the damage that small relic populations from where individuals can be recruited into the cleared areas, could do to the entire control effort. From this, the principle of total population control was deducted: "uniform suppression of an entire population of an insect pest will achieve greater suppression than a higher level of control on most, but not all of the population, each generation".

In AW-IPM, the focus is on preventive pest management and the approach is pro-active i.e. control the pest before it reaches damaging proportions and it addresses all members of the pest population throughout the ecosystem. This strategy usually requires several years of planning and in view of its complexity, requires an organisation dedicated exclusively to the control effort. It also tends to use advanced technologies such as geographic information systems (GISs), population genetics, remote sensing and aerial release techniques (Klassen, 2005; Vreysen, 2006).

Field-by-field insect management is a reactive approach and the farmer typically reacts defensively when the pest population has reached damaging levels – or in the case of tsetse/trypanosomosis when the vector-borne disease prevents cost-effective cattle production. The goal of this strategy is to defend a valued entity (crop, livestock) and, as the control tactics are implemented by the individual, requires minimal planning. The control tactics and the time of application are chosen and implemented by the farmer irrespective of the actions or intentions of his neighbours. The farmers are usually not part of a special organisation and use most often 'low tech' control tools (Klassen, 2005; Vreysen, 2006).

An earlier example of the successful application of total population control (i.e. the AW-IPM concept – although the term was not coined yet in those days) against a tsetse population resulted in the sustainable eradication of *G. pallidipes* from Zulu Land, South Africa. The programme was implemented from 1945 to 1952 and integrated the use of insecticides sprayed by fixed wing aircraft with game destruction, bush clearing and extensive trapping against the entire *G. pallidipes* population. During the 7 years of the programme. *G. pallidipes* was cleared from 11,000 km^2 (du Toit, 1954) and Zulu Land remains to date a zone free of *G. pallidipes*.

Another, more recent example of a successful AW-IPM campaign was the creation of a *G. austeni*-free Island of Unguja, Zanzibar (1994–1997). The island, situated 35 km of the east-coast of Tanzania harboured only one species of tsetse that was responsible for high prevalence rates of trypanosomosis in livestock. The direct losses caused by the disease to the livestock sector were estimated at USD 2 million per year and 4000 head of cattle had to be imported every year to satisfy the demand in meat. The fly population was suppressed using the live-bait technology in the agricultural zones of the northern half of the island (that had high cattle densities) and by deploying insecticide-treated blue cotton screens in the dense forested areas. These suppression phases were followed by the aerial dispersal of sterile male flies over the entire surface area of Unguja Island, including the small offshore islands (Vreysen et al., 2000). The last indigenous *G. austeni* fly was trapped in September 1996 and Unguja Island has remained free of tsetse and AAT ever since (Saleh et al., 1999).

The success on Zanzibar created once again hope in Africa and incited African Governments to re-think their commitment to the tsetse and trypanosomosis cause. The African Heads of State and Government, at the 36th Ordinary Session of the Organisation of African Unity (OAU) summit meeting in Lomé, Togo (July 2000) called for renewed efforts to control tsetse in Africa, which culminated in the establishment of the Pan African Tsetse and Trypanosomosis Eradication Campaign (PATTEC). The PATTEC initiative was approved at the OAU's meeting in Lusaka, Zambia in 2001 and officially launched in Ouagadougou, Burkina Faso later in the same year.

In East Africa, data derived from old tsetse distribution maps, from satellite-derived remote sensing (Hay et al., 1996; Rogers et al., 1996) and from population genetics studies (Krafsur, 2003) has indicated that tsetse fly populations are not distributed along a continuous large belt but often in distinct pockets. Hence, sustainable tsetse-free zones could be created in Eastern and Southern Africa mainland using area-wide management principles (Vreysen, 2006).

West Africa, however, is characterised by complex ecological zones that are correlated with a distinct north–south humidity gradient. Over a distance of 2000 km, the landscape changes from extreme arid in the north (Sahara desert) to very humid (tropical rainforest) in the south along the coast. It has been hypothesised that this is reflected in the distribution of tsetse flies, i.e. limited in the north band to distinct fly pockets in local riparian vegetation patches, progressing southwards towards linear distributions along the river systems in the sub-humid savannah area (middle band) towards an ubiquitous distribution in the humid south band (tsetse not only being restricted to the river systems but also present in the surrounding humid woodland, mangroves and forests) (Hendrickx et al., 2004). These different ecological settings will obviously have consequences for the implementation of AW-IPM programmes.

G. p. gambiensis that thrives for most of the year in the riparian forests that line the beds of the major rivers and its tributaries in the sub-humid savannah of West Africa (middle band) is a case in point. These vast hydrological networks create favourable habitat conditions for this tsetse species and these ecological particularities were originally not considered a drawback for the application of AW-IPM approaches. As riverine tsetse populations are confined to the riverbeds of the various river systems which are organised in river basins it was proposed to use the "river basin" as a unit of operation of AW-IPM in West Africa (Hendrickx et al., 2001). This assumed that each primary river basin (and possibly also secondary and tertiary) contained riverine tsetse populations that were geographically isolated from those belonging to adjacent river basins.

Population genetic studies, initiated in various parts of West Africa have however indicated considerable gene flow between *G. p. gambiensis* populations belonging to different river basins and that these populations cannot be considered isolated (Bouyer et al., 2010a; Koné et al., 2011; Marquez et al., 2004). A release recapture study in Mali confirmed the population genetics data and showed the potential of these flies to cross the watersheds of adjacent river basins (Vreysen et al., submitted for publication). The fact that riverine tsetse are able to navigate the savannah areas between river basins indicates that implementing a tsetse eradication campaign using AW-IPM principles in West Africa will require establishing efficient buffers to prevent re-invasion or to use the rolling carpet principle in case of an eradication strategy (Hendrichs et al., 2005).

7. The phased-conditional approach

AW-IPM programmes in general and especially those that incorporate an SIT component are very complex and management intensive undertakings and success cannot be taken for granted. A series of technical and managerial prerequisites have been identified that need to be addressed for these programmes to be successful. The technical prerequisites include: the availability of high-quality baseline data to develop an appropriate strategy, adequate competitiveness and mating compatibility between the strains used for release and that of the target population, persistence of the quality of the release strain, and sound monitoring. The managerial prerequisites include: commitment of all stakeholders, adequate funding, a flexible and independent management structure with dedicated full-time staff, independent peer reviews and consistency in the implementation of critical programme components taking into account differences in local ecological, socio-economic and political conditions (Vreysen et al., 2007).

To facilitate the planning and implementation of AW-IPM programmes and to increase its chances of success, the FAO/IAEA recommends a strategy that is based on the phased conditional approach (FAO/IAEA, unpublished report). This systematic approach entails that progress towards a particular next phase is conditional to completion of all activities in the previous phase. The different phases are: (1) policy and strategy development, long term commitment and management structures, (2) base-line data collection and technical feasibility assessment, (3) preparatory and pre-operational activities, and (4) operational implementation of AW-IPM measures.

7.1. The tsetse project in Senegal – an example of the phased-conditional approach

The Niayes area is located north of Dakar and is characterised by vestiges of Guinean gallery forest comprised of oil palms in low lying areas, which contain small marches (Toure, 1974). The region

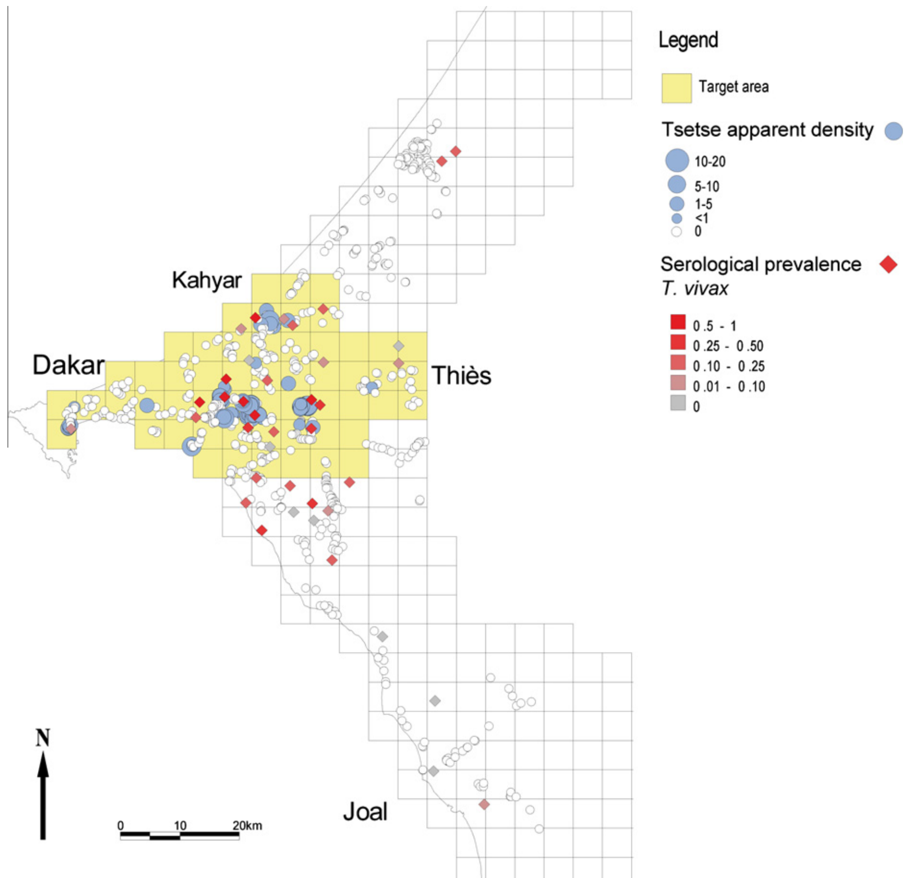

Fig. 1. Serological prevalence of *Trypanosomosa vivax* and apparent density (no flies per trap per day) *of Glossina palpalis gambiensis* in the Niayes area of Senegal. Yellow area demarcates the selected target zone for the eradication (figure compiled from data presented in Bouyer et al. (2010b) and Seck et al. (2010)).

has a coastal microclimate favourable to the rearing of exotic cattle breeds for milk and meat production but its ecological conditions are also favoured by *G. p. gambiensis*. In the 1970s attempts were undertaken to eradicate the *G. p. gambiensis* population from the Niayes using ground spraying with dieldrin (Toure, 1973). Although these control efforts did alleviate the burden of AAT, the fly was detected again in 1998 and its presence confirmed by field surveys in 2003 (Stephen Leak, unpublished report to the IAEA). In 2005, the Government of Senegal embarked on a feasibility study to assess whether the *G. p. gambiensis* population could be eradicated from the Niayes in a sustainable way and which strategy would be most suitable.

For the implementation of the project, the Government of Senegal and its local and international partners adhered to the phased conditional approach. The Government of Senegal official policy with respect to tsetse control was confirmed with its subscription to the PATTEC initiative. This was strengthened with the creation of the "La grande offensive agricole pour la nourriture et l'abondance (GOANA)" (http://www.gouv.sn/IMG/article_PDF/article_777.pdf) project, which aims at improving food production in Senegal, and includes the artificial insemination of local dairy cattle using sperm of exotic breeds.

As part of the second phase, a comprehensive entomological base line data survey was conducted using a stratified sampling strategy. The study revealed that the suitable habitat was extremely fragmented, that flies could be present in very small pockets but at high densities, and that the total infested area was limited to 525 km^2 (Bouyer et al., 2010b). A survey of AAT showed a mean parasitological prevalence of 2.4% for *Trypanosoma vivax*, and a serological prevalence of 28.7%, 4.4%, and 0.3% for *T. vivax*, *Trypanosoma congolense* and *Trypanosoma brucei brucei*, respectively (Fig. 1). The area were resident infected cattle but no tsetse were sampled will be included in the final eradication zone (Seck et al., 2010). A population genetics study using microsatellites, mitochondrial DNA and geometric morphometrics of the wings as markers revealed that the *G. p. gambiensis* populations of the Niayes were genetically isolated from the nearest known population in the east of the main tsetse belt of Senegal (Solano et al., 2010a). These data confirmed that the creation of a zone free of *G. p. gambiensis* in the Niayes is likely to be sustainable without any risk of re-invasion from the eastern tsetse belt in Senegal. These studies were followed by a socio-economic survey to be able to make an ex ante benefit-cost analysis of the campaign and an environmental study to assess the potential impact of the eradication campaign on biodiversity and the ecosystem.

Based upon these data, the Government of Senegal and its partners adopted a strategy of eradication using an AW-IPM approach to create a sustainable *G. p. gambiensis*-free zone in the Niayes. A combination of insecticide pour-ons, insecticide-impregnated Vavoua traps, insecticide-impregnated fences and insecticide foot baths (the latter two only in cattle farms) were selected as suppression tactics, which would be followed by the SIT as the final eradication component in view of the extreme fragmentation of the habitat.

A series of preparatory and pre-operational activities were carried out after completing the base line data collection phase i.e. the establishment of a field insectary in Dakar to receive the sterile flies or pupae from Burkina Faso, the collection of flies from the

Niayes area for the establishment of a Senegal colony at the FAO/IAEA Insect Pest Control Laboratory in Seibersdorf, Austria, an assessment of mating barriers between the Senegal and Burkina Faso strains, development of pupal handling and transport protocols, ground trial releases in different releases sites, development of a new aerial release machine, testing of the suppression strategy, etc. The outcomes of all these activities will allow the project to advance to the operational phase.

8. Conclusions

Despite the availability of very effective control tactics against the tsetse fly, both for the localised use by farmer communities to suppress tsetse populations below an economic or disease-transmitting threshold, and for use in AW-IPM approaches that have adopted an eradication strategy, there are few examples where these projects have been sustained or where the results (eradication) have been consolidated (less than 0.3% of the total infested area). Whereas in the case of localised farmer-based suppression programmes, the reasons for the limited successes are socio-economic and cultural, in the case of eradication programmes, the reasons are more managerial and strategic. Programmes that do not adhere to area-wide principles have very little chance of becoming sustainable.

The AW-IPM programmes in Zulu Land, Okavango, Nigeria and Unguja Island have shown that tsetse-free zones can be created and sustained. These successes are however no guarantee that any AW-IPM programme will be successful as they are no ‘turn-key’ operations. They are complex and management intensive and success cannot be taken for granted, but enormous benefits are possible if proper attention is given to the defined prerequisites.

Disclosures

The authors Marc J.B. Vreysen, Momar Talla Seck, Baba Sall, and Jérémy Bouyer report no conflicts of interest to be declared.

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