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Minireview

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

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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

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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