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Tsetse-transmitted Trypanosomiasis: Variations on a Theme*

by

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Keywords. — Tsetse; Trypanosomiasis; Epidemiology; Impact.

Summary. — Tsetse-transmitted trypanosomiasis is an important disease of livestock and people in large parts of sub-Saharan Africa. It occurs in various epidemiological settings driven by the encroachment of people and livestock into tsetse-infected areas. Each epidemiological setting represents a particular host-vector interaction. Of particular veterinary importance is the situation where the livestock (mainly cattle) have become the main host of tsetse flies and the main reservoir of trypanosomes. This change from a sylvatic to a domestic transmission cycle seems to result in a reduction in the prevalence of highly pathogenic trypanosome strains and thus a reduction in the disease impact. The creation and maintenance of such trypanosomiasis endemic areas may constitute an additional tool in the control of the disease in livestock.

Trefwoorden. — Tseetsee; Trypanosomiasis; Epidemiologie; Impact.

Samenvatting. — *Door tseetseevliegen overgedragen trypanosomiasis: variaties op een thema.* — Trypanosomiasis is een belangrijke ziekte voor mens en dier in sub-Sahara Afrika. De epidemiologie van ziekte kan verschillen afhankelijk van de interactie tussen de gastheer en de vector en is het gevolg van de introductie van mensen en vee in gebieden waar tseetseevliegen aanwezig zijn. Vooral de situatie waar de tseetseevlieg en de parasiet in hoge mate afhankelijk zijn van vee is van diergeneeskundig belang. De overgang van een sylvatische naar een domestische transmissiecyclus heeft tot gevolg dat de proportie van zeer pathogene trypanosoomstammen vermindert en tegelijkertijd ook de impact van de ziekte op dierlijke productie. Het creëren en onderhouden van zulke endemische situaties is mogelijks een bijkomend middel voor de bestrijding van dierlijke trypanosomiasis.

Mots-cles. — Tsé-tsé; Trypanosomiase; Epidémiologie; Impact.

Resume. — *La trypanosomiase transmise par la tsé-tsé: variations sur un thème imposé.* — La trypanosomiase transmise par la tsé-tsé est, en Afrique subsaharienne, une grave maladie affectant le bétail et les gens. Différents profils épidémiologiques sont

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décrits, selon l'importance du rôle joué par la faune sauvage. Chacun de ces profils se caractérise par une relation vecteur-hôte distincte. D'un point de vue vétérinaire, la situation est particulièrement intéressante lorsque le bétail (surtout bovin) sert d'hôte principal à la tsé-tsé et aux trypanosomes. En effet, la transformation du cycle de transmission sylvatique en un cycle domestique paraît associée à une diminution de la prévalence des souches de trypanosomes hautement pathogènes et donc à une diminution de l'impact de la maladie. Promouvoir de telles situations endémiques pourrait s'avérer utile au contrôle de la trypanosomiase animale.

Introduction

Trypanosomiasis is a disease of humans and livestock caused by hemoparasites of the genus *Trypanosoma*. In livestock, *Trypanosoma congolense* is considered as the most pathogenic trypanosome species. In sub-Saharan Africa, these parasites are mainly transmitted by vectors called tsetse flies (genus *Glossina*). About thirty-seven African countries lying within the tsetse belt are affected by the disease. Of the estimated hundred and sixty-five million cattle found in Africa, about fifty million are kept in tsetse-infested areas and their production is normally low. If not controlled, the disease can induce important losses in livestock production. Furthermore, the disease causes important economic losses by limiting crop production due to less efficient nutrient cycling, reduced access to animal traction, lower income from milk and meat sales and reduced access to liquid capital. The total loss due to this disease is estimated to about 4.75$ billion every year (Swallow 2000).

Epidemiological Settings in Livestock Trypanosomiasis

Previous studies on livestock trypanosomiasis conducted throughout the tsetse-infested areas of Africa have shown that the disease can present itself in various epidemiological situations with differing impact on livestock production. The development of appropriate integrated control strategies requires a good understanding of the factors contributing to these epidemiological situations. The four epidemiological circumstances that can be recognized in the southern African region are (*i*) areas where livestock are absent; (*ii*) zones where livestock have been introduced in game areas but where game is still abundant and constitutes a major source of food for tsetse; (*iii*) areas where, often because of human interference, the density of game animals is low and livestock constitute the main source of food for tsetse; (*iv*) areas where livestock occur at the edge of tsetse-infested wildlife zones (game/livestock interface) (Van den Bossche 2001) (fig. 1). These epidemiological settings represent different levels of interaction between tsetse flies and domestic and/or wild hosts. Although the various

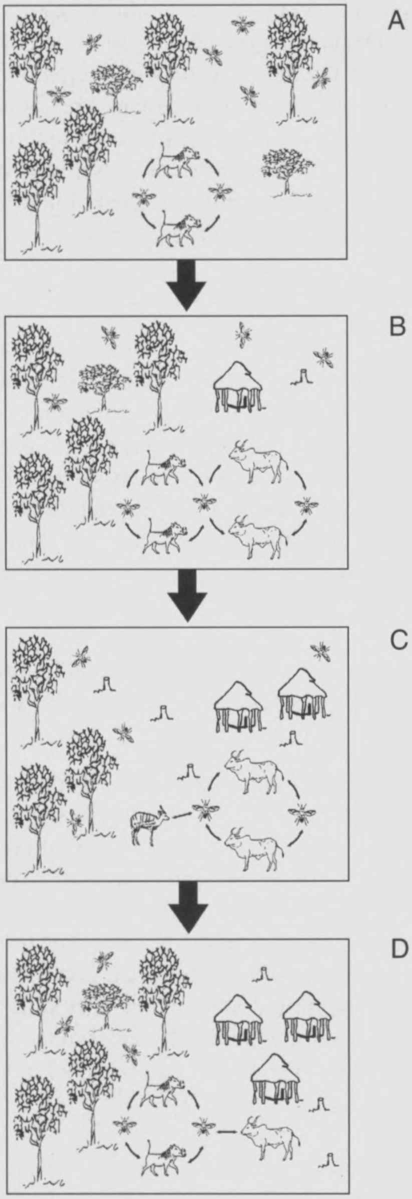

Fig. 1. — Trypanosomiasis epidemiological situations in southern Africa: (A) areas where livestock are absent; (B) areas where livestock have been introduced in game areas but where game is still abundant and constitutes a major source of food for tsetse; (C) areas where the density of game animals is low and livestock constitute the main source of food for tsetse (endemic trypanosomiasis); (D) areas where livestock occur at the edge of tsetse-infested wildlife zones (interface trypanosomiasis) (*Source*: VAN DEN BOSSCHE 2001).

epidemiological settings occur in geographically different areas or have an important spatial dimension, they are the result of one overriding process, *i.e.* the encroachment of people and their livestock into tsetse-infested wildlife zones and the subsequent alteration of the environment as a result of anthropogenic changes (*e.g.* clearing of vegetation for settlements, agriculture). Such changes have significant repercussions for the density of tsetse, wildlife and domestic animals and hence for the interaction between those important components of the epidemiology of tsetse-transmitted trypanosomiasis.

Tsetse-infested Game Areas where Livestock are Absent (fig. 1A)

Although tsetse-infested game areas where livestock are absent do not constitute an economic problem, they do represent an important reservoir of flies and trypanosomes. Indeed, trypanotolerant game animals are excellent reservoirs of trypanosomes independent of the trypanosome's species and its pathogenicity. A survey conducted in the tsetse-infested Hluhluwe-iMmfolozi Park in the KwaZulu-Natal Province of South Africa revealed that almost 20 % of the buffalo sampled were infected with *T. congolense*, a trypanosome species that is the cause of most of the bovine trypanosomiasis cases in southern Africa (Van den Bossche, pers. comm.).

Areas where Livestock have been Introduced in Tsetse-infested Game Areas but where Game is still Abundant and Constitutes a Major Source of Food for Tsetse (fig. 1B)

The introduction of people and their livestock into a tsetse-infested area has been the cause of severe livestock trypanosomiasis epidemics in extensive parts of Africa. The presence of tsetse flies has indeed slowed down the exploration and invasion of large parts of the African continent. Even today, the introduction of cattle into tsetse-infested areas of northern, central and southern Mozambique as part of the restocking exercise after the civil war results in serious problems with livestock trypanosomiasis (Sigauque *et al.* 2000). Similarly, the introduction of livestock in the tsetse-infested areas of the Rift Valley in Ethiopia, as a result of overgrazing in the tsetse-free highlands, has resulted in important trypanosomiasis outbreaks and the decimation of large livestock populations (Slingenbergh 1992).

Areas where the Density of Game Animals is Low and Livestock Constitute the Main Source of Food for Tsetse (fig. 1C)

In large parts of tsetse-infested sub-Saharan Africa the progressive clearing of natural vegetation for cultivation, the introduction of domestic animals and the almost complete disappearance of large game animals have had important repercussions for the distribution and density of tsetse flies. In Malawi, for example, the distribution of tsetse is almost confined to protected areas where vegetation remains undisturbed. Outside those protected areas, the extensive clearing of natural vegetation has resulted in the almost disappearance of tsetse flies and the disease they transmit (Van den Bossche *et al.* 2001). It can be anticipated that in the years to come similar environmental changes in parts of Africa where the human population is high will result in a similar decline in the distribution and density of the tsetse population and the trypanosomiasis prevalence. This process of gradual reduction in tsetse density may in certain areas ultimately lead to autonomous, anthropogenic clearing of tsetse and thus the disappearance of the disease (Bourn *et al.* 2000). However, before tsetse flies have been cleared completely an intermediate epidemiological setting seems to develop where the disease reaches a level of endemicity with high morbidity but low mortality.

Endemic Livestock Trypanosomiasis

Although not restricted to eastern Zambia, the plateau area of eastern Zambia constitutes a prime example of the epidemiological situation where livestock trypanosomiasis has such an endemic character. The Eastern Province is located between latitude 10-15 ºS and longitude 30-33 ºE and covers an area of about 60,000 km^2. After the Rinderpest epizootic of the 1890s, killing a large proportion of the wild host population, eastern Zambia was largely free of tsetse and cattle were reared successfully in the Luangwa Valley (Vail 1977). However, the quick regeneration of the wildlife population and the protection of game resulted in a concomitant increase in the density and distribution of the tsetse population. At the same time, game and tsetse (*Glossina morsitans morsitans*) were spreading out of the Valley, south and east onto the eastern plateau, resulting in the first outbreaks of bovine trypanosomiasis on that plateau area. In the following decades, both game (mainly elephants) and tsetse spread across the plateau and severe trypanosomiasis outbreaks stimulated the Zambian Government into embarking upon an extensive programme of bush clearance and game elimination together with resettlement programmes to induce bush clearing and, at a later stage, ground and aerial spraying to reduce the density and spread of the tsetse population. Currently, tsetse flies are found in most of the areas of the plateau. However, extensive farming with an estimated farming population of 151,300 families, a total crop area of about 250,000 hectares of which 58 % is ploughed by hand and a cattle population of about 10 animals/km^2 have resulted in a high level of tsetse habitat fragmentation and the disappearance of large game animals from the plateau. Currently, in the absence of large game animals, livestock constitute the main source of food for the tsetse population on the plateau (Van den Bossche & Staak 1997).

The outcome of a study conducted on the plateau area of eastern Zambia, in an area representing a gradient of tsetse habitat fragmentation starting from a zone with high levels of habitat fragmentation and ending in an area where livestock and people are almost absent, showed a clear relationship between levels of habitat fragmentation and the density of tsetse flies. In fact, the density of tsetse was low in areas with high levels of habitat fragmentation compared to areas where vegetation was undisturbed (figs. 2 & 3). Surprisingly, habitat destruction and the concomitant decrease in tsetse population density seem to have limited impact on the incidence of livestock trypanosomiasis on the plateau of eastern

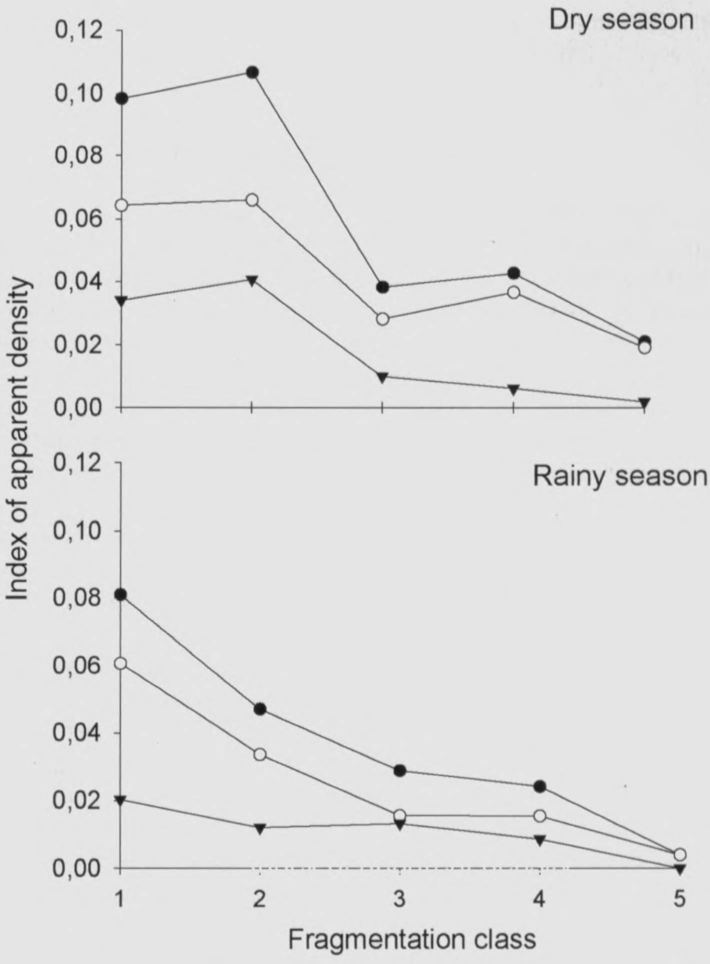

Fig. 2. — Index of apparent density of tsetse flies (*Glossina morsitans morsitans*) in areas of increasing habitat fragmentation or destruction (1 = low level of fragmentation and 5 = high level of fragmentation) on the plateau of eastern Zambia.

Fig. 3. — Clearing for agriculture results in the fragmentation of tsetse habitat in large parts of tsetse-infested sub-Saharan Africa (Photo: P. Van den Bossche).

Zambia. Indeed, notwithstanding the significant differences in tsetse density, the monthly incidence of livestock trypanosomiasis in highly fragmented areas differs little from the incidence observed in areas where the density of tsetse flies is high and the level of habitat fragmentation low (fig. 4). The reason for this high level of challenge at low tsetse densities is to a large extent explained by the high infection rates of tsetse flies in areas with high levels of habitat destruction. The reason for such high infection rates still requires further studies but it could be due to a higher level of stress experienced by tsetse flies in such fragmented areas and the subsequent increase in their susceptibility to trypanosomal infections (Akoda *et al.* 2009).

Human settlement and habitat fragmentation also have direct effects on the population density of large game animals. In fact, in most of the settled areas of southern Africa and probably elsewhere in Africa, big game animals have disappeared and the tsetse population is getting increasingly dependent on livestock for its survival. Although the livestock population consists of a range of host species, studies in settled areas of the plateau of eastern Zambia have demonstrated that tsetse flies prefer to feed on cattle rather than on goats or pigs (Simukoko

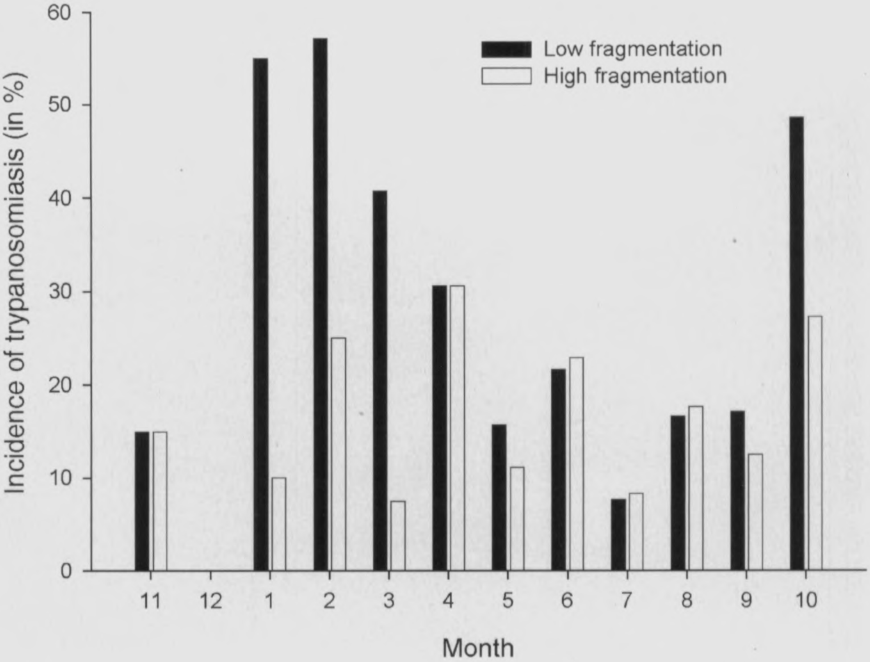

Fig. 4. — Monthly incidence of bovine trypanosomiasis in areas of low and high tsetse habitat fragmentation.

et al. 2007a). This preference for cattle and more specifically the preference for the biggest animals in a cattle herd, with large oxen receiving a tsetse challenge that is about six times higher than calves (SIMUKOKO *et al.* 2007b), is in accordance with the entomological findings on the attractiveness of different age categories and sex of cattle to tsetse flies (fig. 5). In fact, according to TORR *et al.* (2006) and TORR & MANGWIRO (2000), tsetse flies are attracted significantly more by the odour of big animals (*i.e.* oxen) and animals that show less defensive behaviour and are attracted least by calves. This high challenge of cattle by tsetse flies must result in high prevalences of trypanosomal infections in the cattle population. In the tsetse-infested areas of the plateau of eastern Zambia, for example, about 30 % of the cattle are infected with pathogenic trypanosomes (SIMUKOKO *et al.* 2007a). However, this does not imply that in the absence of cattle tsetse flies will not feed on other domestic animals such as goats or pigs. In fact, in the heavily tsetse-infested Luangwa Valley of Zambia where cattle are absent goats undergo significant tsetse challenge affecting their productivity (BEALBY *et al.* 2000). The observed heterogeneity of incidence or individual variation in exposure to tsetse or trypanosomiasis challenge, in particular, or vector-borne diseases, in

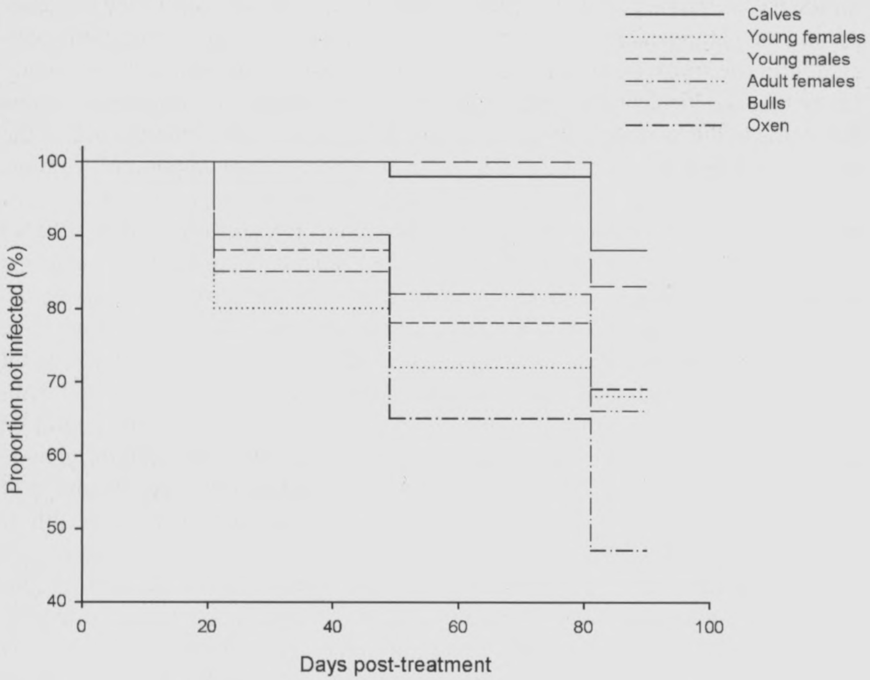

Fig. 5. — Kaplan-Meier survival curves for infection with *T. congolense* of cattle of different ages and sex on the plateau of eastern Zambia demonstrating the different levels of challenge in cattle of different ages and sex (*Source*: Simukoko *et al.* 2007b).

general, is a well-known phenomenon and may have repercussions for the optimal design of disease control programmes (Woolhouse *et al.* 1997, Kelly 2001).

Notwithstanding the high prevalence of trypanosomal infections in the cattle population of the eastern plateau, the impact of bovine trypanosomiasis on cattle productivity is relatively low (Doran 2000). This is surprising considering the devastating impact trypanosomiasis can have on susceptible livestock. Such a situation with high morbidity but low mortality in a trypanosomiasis endemic situation is of particular veterinary interest. Understanding the reason why such a situation develops and how it can be maintained may have substantial repercussions for developing appropriate trypanosomiasis control strategies.

Although the development of a level of trypanosomiasis tolerance within the livestock population cannot be excluded, the main reason for this trypanosomiasis endemic situation is attributed to the important role cattle have as reservoirs of trypanosomes in such a trypanosomiasis endemic area. The change from a trypanotolerant game reservoir, in which infections can develop without affecting the reservoir's health, to a susceptible livestock reservoir must have repercussions for the trypanosome population present in the area. This was confirmed by determining the pathogenicity of the trypanosome strains circulating in the cattle population in the trypanosomiasis endemic area of eastern Zambia. In fact, a study comparing the virulence of thirty-one genetically different *T. congolense* strains belonging to the Savannah subgroup and isolated from cattle at eleven sites on the plateau revealed significant differences in virulence. More importantly, almost 80 % of the *T. congolense* strains circulating in the cattle population were of moderate or low virulence whereas the remaining trypanosome strains (20 %) were highly pathogenic (Masumu *et al.* 2006a). This is in contradiction with the observation that highly pathogenic trypanosome strains have higher transmissibility and should thus dominate in the trypanosome population (Masumu *et al.* 2006b). On the other hand, a susceptible host population (such as cattle) cannot maintain highly pathogenic trypanosome strains. Indeed, cattle infected with such highly pathogenic strains would either die as a result of the infection or be given a curative treatment with trypanocidal drugs. It thus seems that the change from a wild to a domestic host has resulted in a gradual selective advantage of trypanosome strains of low pathogenicity with minimal impact on the health of the infected animal. Nevertheless, it remains questionable how under such endemic circumstances 20 % of the trypanosome population can be highly pathogenic. Immunological studies have revealed that even though sterile immunity can only be achieved with strains belonging to the same serodeme (Nantulya *et al.* 1984), interference in trypanosomes occurs in some combinations of heterologous strains (Morrison *et al.* 1982). A study determining the importance of this interference phenomenon in a trypanosome population in the endemic area of eastern Zambia revealed that interference did occur between genetically different strains but also between strains with different virulence (Masumu & Van den Bossche, unpublished results). In fact, the outcome of experimental infections showed that a primo-infection with a low virulent strain protected the infected animal against the adverse effects of co-infection with extremely virulent strains. Consequently, considering the high prevalence of strains with low or moderate virulence in the trypanosome population, a large proportion of the cattle population will be infected with such low virulent strains and thus be protected against the adverse effects of infection with highly pathogenic strains. This interference between strains of different pathogenicity explains the persistence of the highly pathogenic strains in a susceptible host population.

Conclusion

The findings summarized above stress the importance of understanding the particularities of the relationship between the host, the vector and the parasite in tsetse-transmitted trypanosomiasis but most likely also in other vector-borne diseases. More specifically, the findings show how the impact of livestock trypanosomiasis can change substantially as a result of changes in the interactions between the host, the vector and the parasite and how under particular conditions the disease can acquire an endemic nature with little impact on production despite high morbidity. Moreover, the outcome of the studies also suggest that disease impact is not a static feature but can change over time as a result of changes in the environment that directly or indirectly affect the interactions between host, vector and parasite. In the context of disease control or disease management it is therefore important to recognize those drivers of change and at the same time appreciate the possible impact of those changes on disease impact and its control.

The major drivers of change contributing to the development of an endemic livestock trypanosomiasis situation, as observed on the plateau of eastern Zambia, are associated with the encroachment of people and their livestock into inhabited areas and the subsequent alteration of the environment mainly because of human settlement and cultivation. Such interferences have direct repercussions for the distribution and density of the vector but will also gradually affect the proportion of wild and domestic hosts. In fact, much of the decline in the density of big game animals in sub-Saharan Africa can be attributed to human interference. Large populations of wildlife are currently confined to protected areas such as game reserves and national parks. This situation is unlikely to improve since livestock will continue to play an important role in the livelihood of about 70 % of the world's poor. Hence, it is likely that in the foreseeable future the importance of livestock will increase even more. The repercussions of those findings for the epidemiology of tsetse-transmitted trypanosomiasis in particular and perhaps for vector-borne diseases in general is that livestock will become increasingly important for the survival of the vector (serving as host) and for the survival of the parasite (serving as reservoir). Parasite transmission is thus gradually changing from a dominant "sylvatic" to a dominant "domestic" cycle.

Although the repercussions of the domestication of the transmission cycle are not fully understood, our observations already draw the attention to some important effects on the parasite population and its phenotypic expression. In fact, the change from a trypanotolerant reservoir to a trypanosusceptible reservoir implies that highly pathogenic trypanosome strains are difficult to sustain. Currently it is not known what part of the trypanosome population circulating in trypanotolerant game animals is highly pathogenic. However, the high transmissibility of the more pathogenic strains puts them certainly in an advantage over low pathogenic ones. It is thus likely that a substantial proportion of trypanosome strains transmitted in the sylvatic transmission cycle constitute a severe threat to livestock. The effects on livestock of an exposure to those "sylvatic" strains can, for example, be observed at the edge of tsetse-infested game reserves where the impact of trypanosomiasis on livestock productivity is usually high (Doran 2000).

It is difficult to estimate the time it takes before a highly epidemic situation changes into an endemic situation where low virulent strains with lower impact on production prevail. Nevertheless, the creation of such an endemic situation could perhaps be encouraged by reducing the interaction between livestock and game animals in tsetse-infested areas. In this respect, the creation of private game reserves in large parts of southern Africa may ultimately constitute a threat for livestock since those game animals can become reservoir of trypanosome strains that cause severe disease in livestock. If, however, such trypanosomiasis endemic situation can be created and/or maintained, their creation or maintenance may constitute an additional tool contributing to sustainable trypanosomiasis management by establishing an environment in which livestock owners can "live with the disease".

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