Tsetse-transmitted trypanosomiasis in relation to the rural economy in Africa

Part I. Tsetse infestation

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Previous issues of World Animal Review *have contained articles on African animal trypanosomiasis. This article concentrates more especially on problems of tsetse fly infestation and the techniques used in the control or eradication of the fly. Part I in this issue covers the former aspects and Part II (to be included in the next issue) will cover the latter.*

Primarily the rationale for action against tsetse infestation reflects the increasing need to develop the rural economy in the affected areas and the impact and constraints which trypanosomiasis has on the utilization of land resources.

Looked at in general terms the significance of the tsetse-transmitted trypanosomiasis problem derives from the necessity for most African governments to provide an adequate food supply for a rapidly increasing human population that is requiring a better quality diet. Most governments are therefore seeking to increase overall food production and also to increase the availability of animal protein, which in many densely populated areas and particularly in the humid zone is notably deficient. Rapidly increasing human populations are evident in most countries because the more general epidemic diseases have either been controlled with varying effectiveness or may have been eliminated, e.g., smallpox, and remedies are available for many of the debilitating endemic diseases (though often not on an adequate scale). Birth rates are generally high, since infant mortality rates are declining, life expectancy has increased and, although civil strife and war are still, unfortunately, occasional features of grave local import they do not account for significant reductions in overall human population growth. Their economic consequences, however, have been severe in the short term and they are a significant impediment to concerted action against tsetse populations in several localities.

Looking to the future it seems reasonable to take a general 10-year (and preferably 20-year) perspective of land resource requirements in relation to the need to provide a rapidly expanding human population with a diet adequate in quantity and improved in quality. Furthermore, developing economies require an ever-increasing urbanization to serve both industrial and governmental activities and this, in several lightly populated countries (e.g., Zambia, with nearly 30 percent of the population urbanized — MacLennan, 1975) through depletion of traditional food-producing manpower, can give rise to situations where remaining food producers are no longer able to satisfy the needs of the community.

In other circumstances it is the production of commodities such as coffee, rubber, cocoa, palm oil, groundnuts, cotton and sugar for local usage and export that is competing for rural manpower and land resources. Such commodities are often of prime importance to national economies. There is no doubt that the increasing arable utilization of the land resource for some of these objectives is bringing about a diminution in the extent of relatively safe pasturage for dry season transhumance and ruminant production.

For various conservation objectives discussed later it is necessary to take a perspective longer than 20 years of future land requirements. Thus the need for dietary improvement and the facts of population growth combine to exert a multiplying effect on food production targets while cash crop and conservation objectives have also to be accommodated. Since the available land resource is mostly tsetse infested (Ford and Katondo, 1973) the significance of the tsetse problem will escalate sharply rather than diminish with time.

Since historic times tsetse infestation has been a fundamental factor in the interaction between man and his environment, having a basic and deleterious impact on rural and national economies. For a variety of reasons the impact has become more pronounced since the advent of European influences affected both the efficiency of current production and the development of underutilized land resources. Moreover, this factor has had major repercussions on conservation objectives and landuse planning.

Impact of trypanosomiasis on utilization of land resources

The incidence and severity of trypanosomiasis in man and livestock are closely related to the species of *Glossina* present in the area. The flies can be classified taxonomically in three major groups; the vegetative communities usually, though not exclusively, preferred by the majority of species in each group correspond to the riverine, forest or savanna. It must be emphasized, however, that in highrainfall areas (including the subhumid zone) circumstances may be such that it may be quite usual for riverine tsetse (Baldry, 1964, 1966a and b, 1968, 1969a and b, and Page, 1959) not to be dependent on riparian vegetation and to be found in woodland up to about 6.5 km away while some members of the forest group are exceptional in their independence of forest. However, G. *fusca* is occasionally present in the subhumid zone in forest relicts in Nigeria and more extensively in the countries west of 3?E (Ford and Katondo, 1973 and U. Spielberg, 1978 — personal communication). *G. medicorum* is also found extensively in forest relicts of the zone in Ghana, the Ivory Coast and Upper Volta (Ford and Katondo, 1973 and Unesco, 1959). The usual classification of the tsetse subgenera is given in the table, which indicates the main habitat preferences. The geographical distribution has been mapped by the Scientific and Technical Research Commission of the Organization of African Unity (OAU).

Feeding preferences of tsetse flies, trypanosome infection rates, the virulence of transmitted infections and relationships to vegetative habitats vary widely between the subgenera, the species within the subgenus and even within the species, from one locality to another. Recent knowledge of these matters is summarized in articles referred to at the end of the article by MacLennan (1974).

In general terms (there are notable exceptions to practically any general statement about tsetse flies) it can be said that all tsetse communities harbour trypanosomes pathogenic to susceptible livestock. The actual infection rate in livestock at risk varies within very wide limits. Very low levels of infestation by solely riverine species (Jordan, 1961 and Page, 1959) give rise to a trypanosomiasis situation, even in highly susceptible exotic breeds, which can be relatively easily contained by surveillance and treatment (e.g., on the University campus at Ibadan and Yaounde"), whereas heavier infestations by flies of the riverine group give rise to increasingly severe trypanosomiasis problems. In the case of the waterside species *G. fuscipes* a high density of this fly does not appear to play a significant role in cattle trypanosomiasis transmission (J. Le Roux — personal communication). Flies of the savanna group give rise to severe trypanosomiasis problems in susceptible stock even when present in low, or barely detectable, densities (Jordan, 1961 and Leeflang, 1975). Some members of the forest group (G. *fusca* and *G. medicorum)* undoubtedly feed on cattle if they have the opportunity and can very probably be the cause of a serious disease problem (Jordan, 1962 and Jordan, Lee-Jones and Weitz, 1961). Others (G. *brevipalpis)* can be poor transmitters of infections they harbour (Wilson, Dar and Paris, 1972) and yet others seldom have the opportunity to feed on cattle or might not be attracted to them.

In fundamental contrast all tsetse communities do not harbour trypanosomes pathogenic to man. The pathogenic human trypanosomes have a focal distribution with substantial fluctuation in the actual areas involved over the course of time. Rhodesiantype sleeping sickness (which is not prevalent in the West African region) is transmitted mainly by flies of the savanna group (G. *morsitans* and *pallidipes)* and infection is not infrequently derived from wildlife origins (Heisch, McMahon and Manson-Bahr, 1958) with man-to-man transmissions taking place by savanna or riverine tsetse in epidemic situations (Onyango, 1969). It has been shown that domestic livestock harbour the trypanosomes in certain circumstances (Van Hoeve *et al.,* 1967). Gambian-type sleeping sickness (the

form of the disease prevalent in West Africa) also perhaps sometimes arises from reservoir hosts other than man — possibly domestic animals (Molyneux, 1973) — but usually man is the source of infections transmitted by flies of the riverine group (notably G. *palpalis* and close relatives and G. *tachinoides).* Though it is believed that savanna tsetse do not transmit this disease there is lack of precise information on this point in areas of mixed infestation. However, there is no doubt that riverine tsetse alone are usually responsible for human infections of the Gambian type.

Livestock trypanosomiasis

As already noted, susceptible livestock, in contrast to human beings, are at continuous risk wherever tsetse are present, the severity of the problem varying within very wide limits. Some of the mediating factors involving the vector are described above. The picture is also affected by factors involving the animal, notably type, breed, previous experience of infection, therapy, and "stress" factors such as parturition, lactation, inadequate nutrition, and the exertions of traction. The morbidity rate varies within very wide margins, according to the degree of tsetse risk. The clinical manifestation in the animal also varies and can be exceedingly acute, when it is usually rapidly fatal. Frequently it is more chronic in type giving rise to a debilitating illness also often fatal if not treated. Apparent, and occasionally actual, selfcures are sometimes observed in certain livestock and cures can be effected in many animals by therapeutic measures. Animals that have been severely ill (other than for a short period) may, however, suffer permanent damage from the experience; such animals have an impaired productive capability. Losses, therefore, take the form of mortality and depressed productive capability, be it of meat, milk, reproduction or traction, for reasons amply explained by what is known or being learned of the pathology of the disease.

Many livestock projects are basically marginal in financial terms and the occurrence of a trypanosomiasis problem can mean that they easily become unprofitable. The cost of arranging regular surveillance by blood sampling, adherence to a strictly timed and accurately dosed drug regimen required to prevent drug resistance, coupled often with the need to finance periodic activities to reduce the numbers of tsetse present, ensure that projects otherwise successful become loss-makers. In high tsetse-risk areas the disease may become unmanageable but in some locations of low tsetse risk there are several examples of successful production and development, sometimes through the use of trypanotolerant livestock.

Cattle ranch in G. morsitans-infested Guinea savanna woodland. Suppression of regrowth through intensive or improved pasture production. Infested woodland in distance.

Though tsetse flies are not the only vectors of pathogenic trypanosomes to livestock it is tsetse-transmitted trypanosomiasis that is the most serious constraint because of the variety of infections being transmitted and because, during the course of a cycle of development by the trypanosome, the vector itself becomes infected and remains infective for a period of time, in contrast to the ephemeral nature of infectivity in vectors other than *Glossina* capable of noncyclical transmission. The latter problem, should it develop, is relatively easily contained or even eliminated by simple therapeutic measures. It is a very different matter in the case of tsetse-transmitted trypanosomiasis.

Regarding therapy, the general impression that emerges in the field is one of escalating demand for treatment and, in many areas where antivector measures are either not undertaken or have only been partially successful, of rising infection rates in livestock with a widening gulf occurring between demand for treatment and treatments actually administered. Indeed some countries are failing increasingly to satisfy the demand for treatments, mainly in the traditional livestock sector, but also, significantly, on government and parastatal livestock projects. Reliable numerical data are difficult to obtain because of the immensity and diffuse nature of the trypanosomiasis problem, the inadequacy of techniques for the determination of infection in the individual, and because of the administrative and logistical problems of deploying specially trained junior staff on such activities. Not only is there a gap between what is needed and the treatments officially made available but there is no attempt at control in some countries while in others there is a significant amount of illicit treatment administered. Drug resistance is widespread and probably increasing. The extent and significance of the problem cannot be specified since most countries lack the facilities to study it.

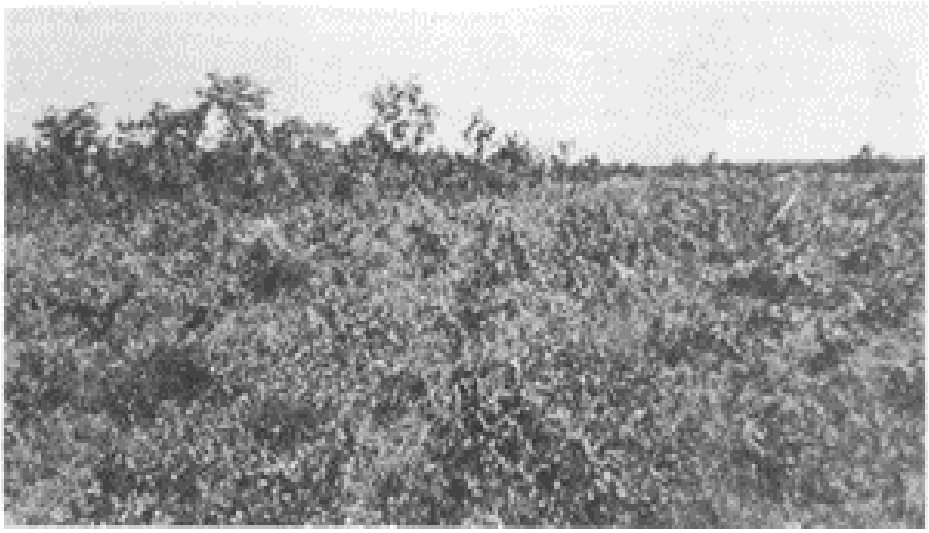
At present most of these constraints, though potent factors in rural development and livestock production, cannot be accurately, or even roughly, quantified in numerical terms. This situation will continue so long as countries lack field facilities to deal with the problems and assemble data on them or, as is sometimes the case, do not adequately deploy and supervise the staff resources which they do have. The fact that the problems are not adequately quantified in numerical terms does not mean that they are not significant.

Natural instabilities in trypanosomiasis situations

SEASONAL ALTERATIONS IN TSETSE DISTRIBUTION

There are important seasonal variations in the degree of risk to which livestock are exposed in areas that have pronounced variation between wet and dry seasons. In more equable climates the variation is much less. During pronounced dry seasons there is a general regression in the distribution of tsetse particularly if the dry season is also hot. The burning, usual in the savanna lands of Africa, accelerates the diminution in the extent of suitable tsetse habitats.

Pastoralists having susceptible livestock take advantage of these developmerits to make seasonal use of the huge grazing resources present within tsetse-infested savanna lands where infestation is mainly from riverine species or where savanna tsetse density is low or is from flies dispersed from the main tsetse belt. They are, however, unable to utilize successfully, even seasonally, the interior of savanna tsetse belts except where sizeable cultivated enclaves have developed as a result of human settlement. These tend to be used rather briefly so long as the supply of the valuable fodders derived from the farming activities is available. In localities of low risk from riverine tsetse only, pastoralists and some settled cultivators with livestock can be found permanently within the tsetse zone. They can manage and accept the levels of trypanosomiasis that ensue, the pastoralist moving away, if necessary, an option that is not open in areas of higher levels of husbandry and on fixed livestock projects such as ranches.



Kapid regeneration at same location as in the facing photo, following felling and periodic slashing of suckers and seedlings. Vitalization of native grasses favours rapid regeneration of woody species.

The genus Glossina

Fusca group (subgenus *Austenina*):	Forest tsetse
Rain forest species:	*G. tabaniformis, G. nigrofusca, G. haningtoni, G. nashi*
Forest-edge species:	*G. fusca, G. medicorum, G. fuscipleuris, G. schwetzi, G. severini, G. vanhoofi*
Others:	*G. brevipalpis, G. longipennis*
Palpalis group (subgenus *Nemorhina*):	Riverine tsetse
	G. palpalis, G. fuscipes, G. martinii, G. quanzensis, G. caliginea, G. pallicera, G. tachinoides
Morsitans group (subgenus *Glossina*):	Savanna tsetse
Savanna:	*G. morsitans, G. swynnertoni, G. longipalpis*
Savanna and thicket:	*G. pallidipes*
Evergreen thicket:	*G. austeni*

LONGER TERM FLUCTUATIONS IN TSETSE DISTRIBUTION AND DENSITY

The most dramatic instability involves the savanna group. This takes the form of longer term fluctuations either in local density within the infested area or of major fluctuations in the margin of the infested area. Over periods of 11 or 12 years it is quite usual for tsetse densities to fluctuate between the very heavy and the barely detectable, a fact that greatly complicates the assessment of risks to which livestock development projects are subject. The territorial expansions in areas of savanna tsetse infestation have been prodigious and are still continuing. When these have moved into unoccupied land resources the immediate consequences have been minimal but where livestock have been present the result has been devastating. Very high mortalities in all classes of mammalian livestock cause the evacuation of the affected area or the impoverishment of the people who remain. Only in countries where *Glossina*

distribution has been adequately mapped and regularly updated can the full extent of such developments be known. Past changes have been described in detail by Ford (1971) — though not everyone would agree with some of his interpretations, the facts of the situations are meticulously described. Brief examples of some of the more important recent events are as follows. Since 1952 the advances of *G. morsitans* in the central and eastern parts of northern Nigeria have led to the occupation of at least 25 900 km^2. Since 1950 in the central part of Cameroon an advance of *G. morsitans* has occupied about 20 860 km^2 and, unless halted, will proceed very probably to occupy a further 9 000 km^2 of valuable and extensively utilized land resource. Since 1953 *G. morsitans* in Zambia has occupied 11 700 km^2 in the southwest and lesser advances are taking place at other locations (MacLennan, 1975).

In all these examples the effect on the rural economy has been grievous, resulting in evacuation, in the case of mobile pastoralists, or the impoverishment of those farmers unwilling to move. The impact in southwest Zambia has been particularly serious because the people there lack the mobility of West African pastoralists and depend on cattle sales for the purchase of the foodstuffs that the land cannot provide. Initially this advance moved into an unoccupied land resource that was later converted into a National Park. It proved impossible to contain the advance within the limits of the park, and trypanosomiasis in cattle in the adjacent land resource, which had previously been nil, required 118000 treatments in 1974. However, this was not sufficient to prevent heavy losses among the 37 000 head of cattle most exposed to risk. In the Cameroon example there have been similar consequences with the further complication that greater mobility of the livestock owners has contributed significantly to an everincreasing overstocking and degradation of tsetse-free pasturages. In Nigeria the advances have also occupied very important pastoralist grazing resources and here, as in Cameroon, therapy could not ensure the continued utilization of the fodder resource.

The full extent of advances of the fly in Africa is not known. In addition to the examples mentioned, notable advances are known to have taken place in Botswana, Zimbabwe, Uganda, Tanzania, Ethiopia and very probably in eastern Senegal and western Mali. The largest and most active advance of modern times is probably proceeding in southeast Angola. The problem is not limited to *G. morsitans;* there have also been some notable advances by *G. pallidipes.*

Very large scale regression of infestation took place in the early 1890s following on the elimination of natural tsetsefood sources by the rinderpest panzootics. Most of this country has since been reoccupied. Smaller scale local regression of infestation is presently taking place as a result of cultivation and hunting.

FLUCTUATIONS IN INFECTIONS IN TSETSE FILES

Instabilities in the species of trypanosome prevalent in tsetse populations (and in its virulence) are also evident. This is most apparent in the case of *T. vivax* in *G. morsitans* deriving its blood meals mainly from cattle. On cattle trek routes (e.g., Dorin to Oyo in Nigeria) infection rates in both cattle and flies can escalate remarkably (Baldry, 1969a and b; Ferguson, 1964; Riordan, 1971; Yesufu and Mshelbwala, 1973). The same thing can happen on cattle ranches and farms as on the Mokwa Ranch and the Shika Farm. Domestic pigs may contract relatively mild infections due to *T. congolense* or *T. brucei* until *T. simiae* is introduced into the relationship, when a fulminating outbreak of fatal trypanosomiasis is the usual consequence, even when tsetse density is exceedingly low. It seems likely that, once introduced by an infected tsetse fly, conditions in piggeries favour rapid mechanical transmission of *T. simiae* by other haematophagous flies (stomoxys).

A very important trypanosome in fection fluctuation in the case of *Glossina* is that of the human pathogens. Fortunately these are not often present in tsetse populations and, apart from the inconvenience of bites, human communities, though freely fed upon, live unharmed by tsetse infestations, until such time as the human pathogen is introduced resulting in serious epidemics or continuing endemicity. Serious outbreaks of sleeping sickness can result in the abandonment of valuable land resources.

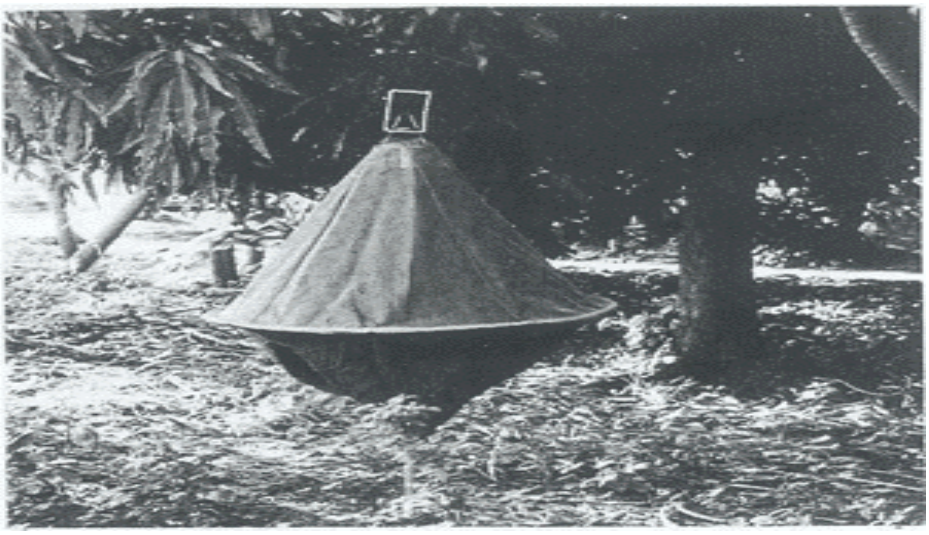
Searching for G. morsitans *with bait, following air spray in Botswana*

Land use

BALANCED LAND USE

A balanced utilization must assign parts of the land resource, in varying proportions according to topographic, climatic and edaphic considerations, and community need, to the following usages: (1) conservation of readily degradable areas; (2) conservation of an adequate wildlife resource; (3) conservation of adequate tree cover; (4) provision for forestry plantations; (5) provision for extensive rangelands; (6) provision for village or community pasturage and ranches; and (7) provision for a truly balanced, mixed arable agronomy.

The major objective of increased production is attained principally through item (7) to which items (5) and (6) contribute directly since by a balanced, mixed agronomy is meant food and cash crop production integrated with livestock that consume the byproducts of cultivation and fallows as well as the savanna pasture and browse resources. Items (3) and (4) satisfy vital community needs for fuel, building materials, wild fruits and other items of diet and medicines.



Biconical trap in garden of young mango and banana trees

Tsetse infestations are basically a feature of the wilderness and will persist within infested land resources assigned to objectives (1) to (3) or perhaps invade them if they are not already infested. They will also either persist within or disperse widely into areas assigned to objectives (4) to (7) if these contain the necessary habitat and food sources. Areas devoted to objectives (5) and (6) may not, at the time assigned, harbour detectable infestation but developments within them, i.e., fluctuation of tsetse densities, or favourable environmental or crop situations can cause an escalation of the tsetse problem or else the project can be engulfed by a tsetse advance.

River floodplain habitat of G. morsitans *and* G. tachinoides in *northern Nigeria. Infestations were later removed by ground spraying.*

"Settlement schemes", if they result in a sufficiently extensive modification of vegetation and fauna, can result in the areas becoming untenable for resident tsetse populations. Suppression of trypanosomiasis by this means is more easily achieved from infestation with savanna tsetse and when livestock are not involved in the development. For reasons explained earlier, i.e., varying infection rates, factors involving the animal, infrequency of human pathogens in tsetse populations, livestock trypanosomiasis persists as a problem at tsetse densities that do not give rise to a serious sleeping sickness problem.

Some of the riverine tsetse species persist in natural vegetation present in areas of densest human settlement, as, for example, in the rural environment of Tiv country and Ibo land and around Kano city in Nigeria, or in urban areas such as Bida in Nigeria and Bamako in Mali, and cause trypanosomiasis in livestock and periodically in humans (Baldry, 1964,1968, and 1969a and b; Challier, 1973; Touré, 1974).

Wholesale modification of the environment in a manner that renders it uninfestable is impossible since the land resource is not homogeneous in its nature (a variety of land usages have to be accommodated) and because it would be physically, financially, technically and administratively impossible to exert the type of comprehensive control over landuse activity on the scale that would be required.

Viewed in this light it seems that the sound, balanced land utilization that is required to meet the needs of a rapidly expanding human population as described earlier, though it can lead to changes in the *Glossina* species present and in levels of infestation, will, in many circumstances, ensure the perpetuation of the trypanosomiasis problem except where specific measures are successfully undertaken to eliminate infestation and maintain tsetsefree areas. As mentioned earlier the problem will increase in importance in the future.

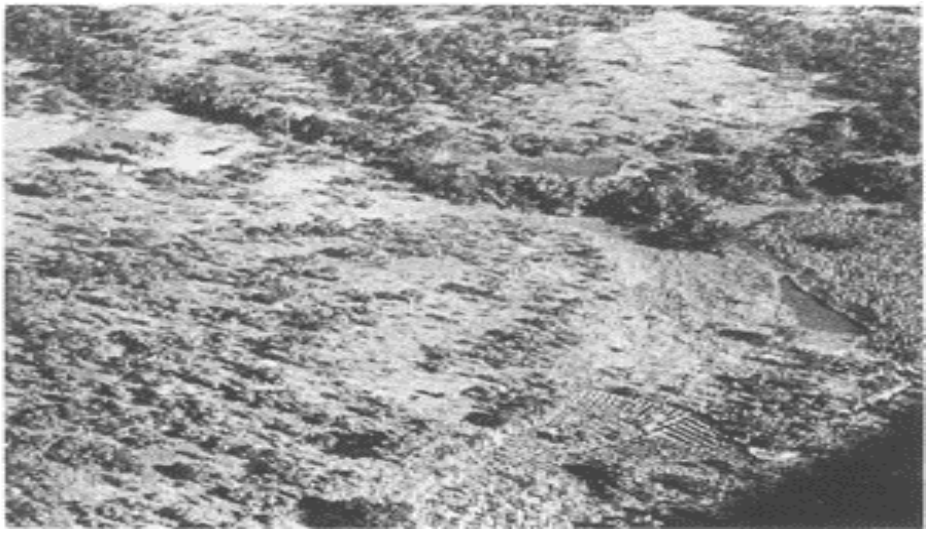
Livestock

Cattle are important converters of the abundant grazing and browse resources of the savanna lands. However, the introduction of cattle into areas apparently free of savanna tsetse infestation has, on frequent occasions, brought to light, through an incidence of trypanosomiasis, the existence of infestations previously present at levels below detection or it has resulted in an escalation in the actual level of infestation or has enabled tsetse colonies to exist where previously this was not possible.

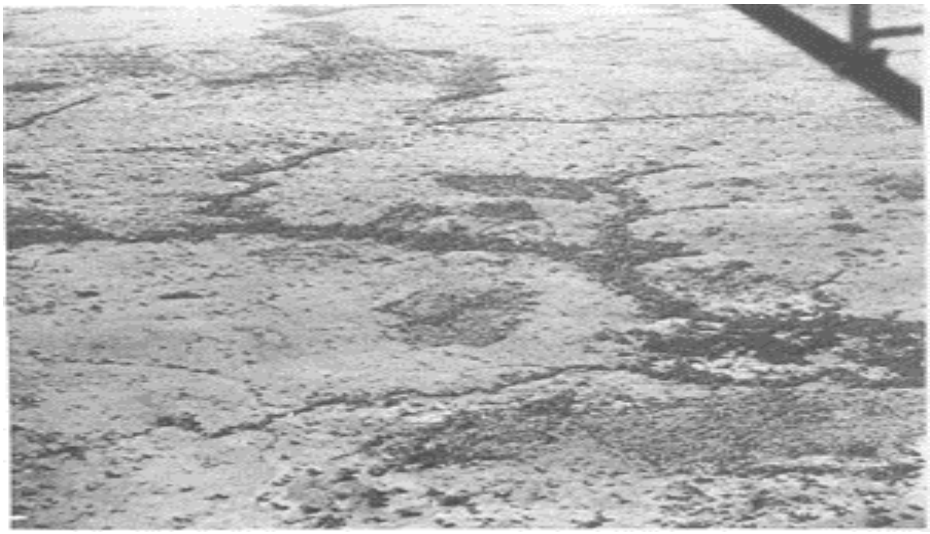
Basically the origin of the cycle of transmission by tsetse flies of trypanosomes pathogenic to livestock is sylvatic (tsetse/wildlife hosts). The relationship of infections in domestic stock to the sylvatic cycle (illustrated in the figure) can be categorized according to whether they are external or internal to it.

OMESTIC INFECTIONS EXTERNAL TO THE SYLVATIC CYCLE

Environment hostile for Glossina. Such a situation would exist, for example, on a cattle ranch from which all tsetse-breeding habitats and most of the shaded resting places have been eliminated. Occasional livestock infections can be caused by infected tsetse flies dispersing or being carried into the *project* area and, before they perish, biting a susceptible animal.



Aerial view of G. morsitans *and* G. palpalis *habitats in Guinea savanna*



Aerial view of persisting network of riparian G. palpalis *habitats in Guinea savanna zone*

In the true savanna zones the risk is relatively light if only riverine species of *Glossina* are involved. Though dispersal by these species takes place more readily in subhumid and humid areas, tsetse densities and infection rates are sometimes low. If the risk is from *G. morsitans* it is known from experience that no project is safe from infection if there is a primary focus of these flies located within a radius of about 16 km. Individually dispersed tsetse can be exceedingly difficult to detect, and may not be found even following repeated searches. Such a situation encourages the belief that mechanical transmission by other haematophagous insects is responsible (Kirby, 1963; and Wells, 1972). However, sooner or later tsetse are usually detected, and if the source population is removed trypanosomiasis infections cease (Kirby, 1963). *G. longipalpis* has somewhat less ability to disperse but is a very effective vector.

If environmental conditions are a little less hostile for *Glossina* and dispersed flies live for more than five days, they can themselves acquire *T. vivax* infections derived from infected livestock and, if the dispersed flies are mainly dependent on the livestock as a food source, a progressively more intense transmission cycle of *T. vivax* develops the longer the flies survive. Thus a small number of flies can cause a high incidence of trypanosomiasis in livestock (MacLennan, 1974; and Leeflang, 1975). Furthermore, with the sylvatic cycle it becomes possible for a fly to acquire drug-experienced infections from livestock and return with them to the sylvatic cycle.

Environment favourable to Glossina. Some cattle-development projects have been sited following repeated tsetse surveys that, though the vegetation seemed suitable, indicated the absence of infestation. On some, either a *G. morsitans submorsitans* advance has later approached the project, or there was sufficient cover on the project to enable dispersed tsetse flies to survive for a significantly longer period because of the constantly available food source in the form of cattle. Breeding tsetse populations have established themselves where previously this was not possible. As the flies live longer a cyclical proliferation of *T. congolense* and *T. brucei* develops in addition to *T. vivax.* A very intense transmission cycle rapidly escalates and may become so severe that therapeutic and prophylactic agents are powerless to prevent serious losses. This happened on the Shika Stock Farm, the Mokwa Ranch and on the Kontagora settlement scheme in Nigeria. An extreme example of the manner in which infestation and infection can escalate is provided by the slaughter cattle trek route described earlier (Riordan, 1971). In this latter instance it is significant to note that the development took place in an environment not hitherto thought suitable for infestation by *G. morsitans submorsitans,* and located outside the normal sylvatic associations of this species (Baldry, 1969a and b).

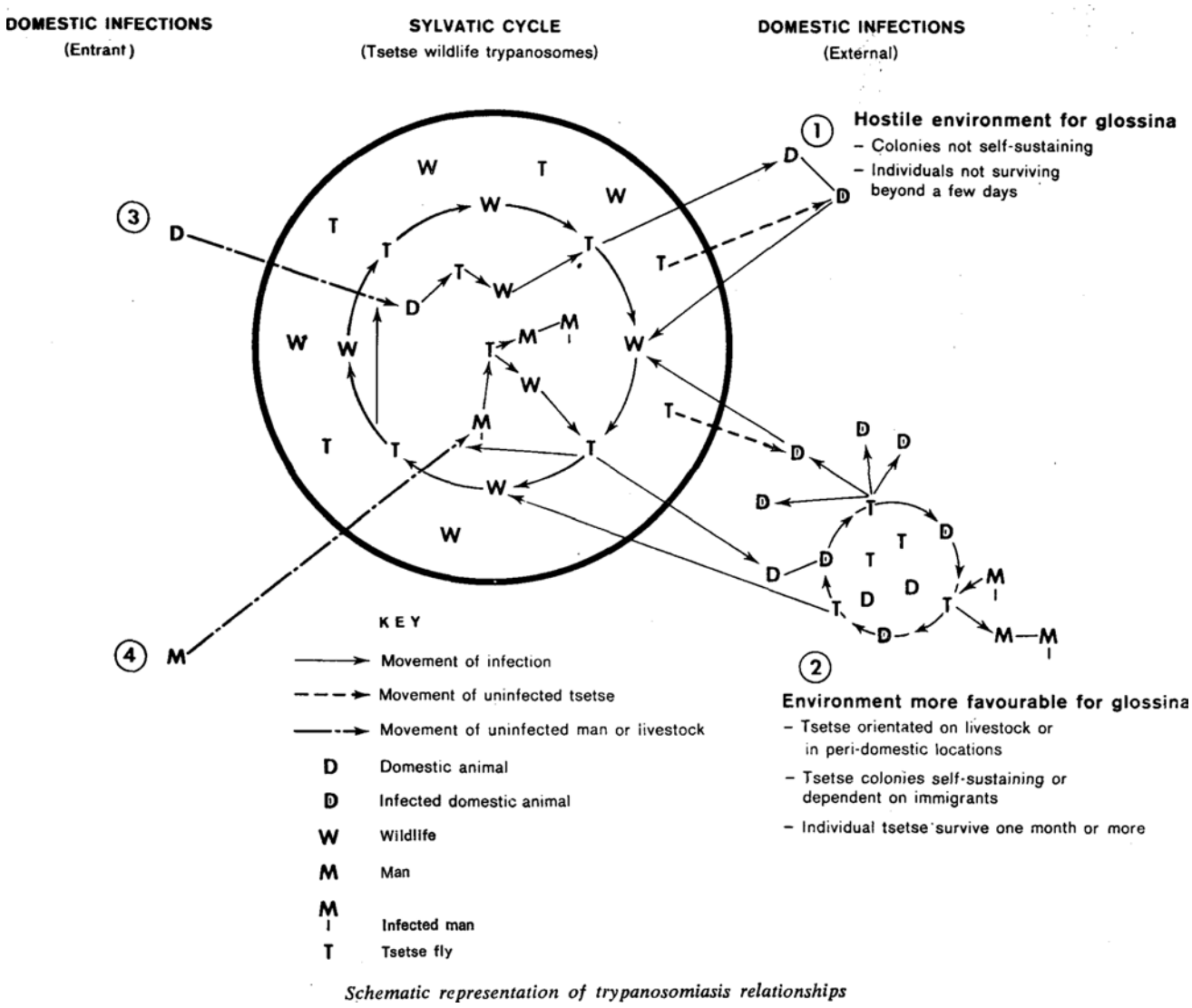
There exist a series of intermediates between the extremes of hostile and favourable environments external to the sylvatic cycle. Ranching projects of an extensive nature will be more vulnerable than those in which bush elimination can be justified economically by increased pasture productivity, a point of special significance for projects located in the southern Guinea and derived savanna zones (Keay, 1953).

Epizootiologically, the return of domestic infections to the sylvatic cycle through the movement of either infected tsetse or livestock is of considerable importance, since the strains of trypanosome are livestockoriented and will have frequently experienced chemotherapy and may have an enhanced level of drug resistance. Drug-resistant strains are readily transmitted by tsetse flies, and can be serially passaged through wildlife hosts by tsetse flies with no diminution in the level of drug resistance (Gray and Roberts, 1971a and b).

The proliferation of habitats favouring savanna tsetse is favoured by the utilization of the grazing resource in areas of fire subclimax. The less severe the annual fires become the greater the grazing intensity, and this favours the densification and proliferation of woody growth. In localities of heavy usage this change progresses remarkably rapidly and provides increasing shelter for tsetse dispersal or for resident satellite tsetse-colonies. A rapidly escalating trypanosomiasis situation can then result and it is only when densification has advanced to the stage that the grass has been suppressed that such localities sometimes become vegetationally unsuited for savanna tsetse.

This is an important aspect affecting beef production in the subhumid zone, which favours intensive fodder production from artificial lays etc., and is a point to be considered when making economic evaluations.

Domestic pigs particularly, but also sometimes cattle, that are maintained by family groupings and villages, support satellite colonies of *G. tachinoides* (Baldry, 1964 and 1968) and sometimes of *G. palpalis* (Challier, 1973; and Touré, 1974). The situation is particularly prone to develop in the southern Guinea and derived savanna zones (Keay, 1953). Trypanosomes are constantly transmitted to domestic stock by these infestations, which, in some locations, are also involved in troublesome sleeping sickness outbreaks. Habitat associations are de scribed later on in this article under the section on crops.



Schematic representation of trypanosomiasis relationships

DOMESTIC INFECTIONS INTERNAL TO THE SYLVATIC CYCLE

Livestock entering the territory of the sylvatic cycle. The most important example we have of this is the system of pastoral transhumance used to maintain most of the domestic beef supply in West Africa. As northerly grazing areas dry out and grazing resources are consumed, pastoralists move their livestock southward. The progress is a leisurely one, and much time is spent in consuming the farm byproducts and in manuring the farms of the settled

farmers. Where possible, savanna tsetse infestations are avoided, and the climatic influences described earlier moderate the general risk of contracting trypanosomiasis. However, heavy risks cannot always be avoided and some serious trypanosomiasis outbreaks do occur, apart from the lower general incidence of trypanosomiasis resulting from some exposure to the riverine group of *Glossina.* The tendency is for the pastoralist to escape from areas of heavier risk as soon as possible and, with the advent of sufficient grazing and surface water in northerly locations, the mass movement northward of several million head of cattle is completed in about 10 to 14 days. This accounts for the fact that in the six northern provinces of Nigeria 86 percent of the counted cattle population is located during the rains in the tsetsefree or lightly infested portion amounting to 46 percent of the former Northern Region.

Though it seems fashionable to use adjectives such as "primitive", "wasteful" and "inefficient" to describe this system of husbandry, it can be said that it affords a seasonal respite for overgrazed northerly pastures; makes possible the seasonal exploitation of some tsetseinfested grazing resources; uses up farm byproducts that would otherwise be wasted; and sometimes returns at least some fertility to the cultivated soil. In the present state of knowledge and experience it seems doubtful whether the major part of beef requirements, consisting of some 790 000 head per annum of cattle of Nigerian origin, could be economically and practically provided by any other method.

The subhumid zone is not completely evacuated by pastoralists with zebu stock in the wet season; a small proportion remain. The White Fulani breed in particular appears to possess a degree of trypanosome tolerance that permits allseason utilization of some areas where risk is light and confined to riverine tsetse only. However, this does not indicate that such places are suitable for mixed farming activity by settled cultivators or for higher level husbandry systems.

Regression in areas infested by savanna tsetse is making possible an increased exploitation of the southern Guinea and derived savannas by pastoralists, but adaptations by tsetse populations to domestic circumstances are also taking place. These vegetation zones and the forest zone provide a more favourable environment in which such adaptations can occur.

Isoberlinia *woodland infested with* G. morsitans *in the rains*

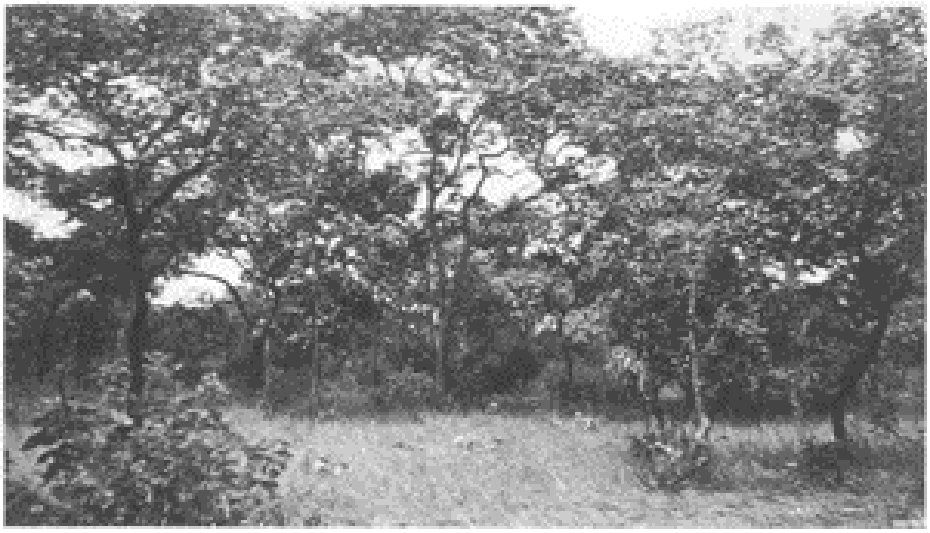
Another case arises when trypanosometolerant livestock (Pagot, 1974) live within the sylvatic cycle. Three factors seem important in determining whether this will be successful. First, the introduction to risk should be in such a way that the animal has the opportunity to adjust to it or has earlier acquired some tolerance through exposure. Second, the level of husbandry is important since malnutrition and other stress factors may be followed by clinical

breakdown. Third, a sustained and very heavy challenge in the laboratory can lead to stunted growth and retarded sexual development (Stephen, 1966). There is some evidence that this also happens in the field though in other locations these cattle are in good bodily condition despite being at quite heavy tsetse risk.

Arable agriculture

Some examples can be quoted of the relationship between crops and tsetse infestation under various circumstances. The examples are not exhaustive and it seems probable that the full extent of such association has not been revealed by current experience. The developments have usually not been foreseen and the infestations have to be dealt with in retrospect and arise from activities that otherwise are highly desirable.

The occupation of mango groves by *G. palpalis* and *G. tachinoides* (Baldry, 1969a and b; Challier, 1973; and Touré, 1974), leading to troublesome sleeping sickness outbreaks and persistent livestock infections, is probably the best known example. The problem can become an urban one. Infestations can also persist in sacred groves, which are of vital significance to the local community. Other actual or potential riverine tsetse habitats can result from guava, cashew, coffee, cocoa, banana and sugar cane plantings. In some areas tree plantings around family groupings harbour *G. tachinoides* and *G. palpalis.* Hedging, particularly lantana, although not only this species, harbours peri-domestic *G. fuscipes* infestations in Nyanza in Kenya and other riverine species in West Africa (Baldry, 1966a and b). *G. tachinoides* utilizes cocoyam cultivations in the densely occupied land resource of Ibo and in the derived savanna in Nigeria (Baldry, 1968). In this locality, this important vector of sleeping sickness elsewhere is not at present transmitting this disease since the tsetse are feeding mainly on pigs, to which they are transmitting livestock trypanosomes, whereas in Tiv land, in the subhumid zone, sleeping sickness is also transmitted. In some of these examples the tsetse colonies appear to be self-sustaining but in other situations they might be dependent on recruitment from natural populations.



Isoberlinia *woodland infested with* G. morsitans. *Hot season following bush fires (see facing photo).*

Another relationship with arable farming is seen in areas where farmers are also cattle users. Family groups are less efficient in producing a marketable surplus if they do not possess effective work oxen for ploughing and for getting the produce to market. It has been stated that possession of work oxen increases the production of the family group sixfold.

Pressure-retaining knapsack sprayers in use on G. tachinoides *resting places in a Sudanvegetation zone*

Most of the subhumid zone of West and Central Africa is tsetse infested and in this area cultivators are not usually using draught oxen. It has been the usual experience in this area that, if cattlekeeping for draught purposes is encouraged, losses mainly attributable to trypanosomiasis are frequent. In areas of light risk it should be possible to mitigate these losses by treatment but often the risk is a continuous one and the individuals are dispersed over a wide area and therefore difficult to service with treatments as soon as these are required. In such static situations not only does frequent treatment favour the development of drug resistance but anaemia and myocarditis result from trypanosomiasis. Thus heart failure in infected animals (if they possess sufficient strength to be worked) under work stress is not uncommon. The risks are considerable and, generally speaking, it would be wrong to encourage a farmer to get into debt for the purpose of purchasing work oxen in tsetseinfested areas. Tractors are not the complete answer to this problem since, compared with, animals, they cannot use the freely available grazing resources; do not provide byproducts (milk, manure); cannot be eaten; have no financial reserve significance; have as yet no social importance; do not reproduce; and are even more difficult to maintain.

Conservation

As noted previously, the unhomogeneous nature of the land *resource* and the necessity to conserve substantial portions of it for particular purposes interact with livestock production, and particularly with the utilization of the abundant grazing and browse resource of the subhumid zone, through the shelter that the conserved resource provides for the continuation of the sylvatic origins of livestock trypanosomiasis.

The most extreme example of this situation is the wildlife reserve, which, so long as it remains infested, provides a permanent source of tsetse flies and pathogenic trypanosomes. It is of interest to note that motivation for the first successful large-area tsetse-eradication operation using insecticides, completed in 1952 in South Africa, arose from the dispersal of *G. pallidipes* from the Umfolozi, Mkusi and Hluhluwe game reserves and the resulting impact that this had on livestock production in the surrounding land resource of Zululand (Du Toit, 1954). It is probably correct to state that all game reserves and national parks within the subhumid zone are tsetse infested and that the increasing utilization of the surrounding land resources and, in some places, the advancement of tsetse-eradication projects, will give increasing prominence to this situation. This implication for the future has seldom been considered when such reserves have been established.

Tsetse infestations are no protectors of wildlife resources. Wildlife decimation has proceeded and is still proceeding in areas of the densest infestation. Wildlife resources can only be protected through the will of the people and the law of the land. Nor do tsetse infestations preserve the land resource from lowlevel exploitation by cultivators who are not dependent on livestock. They do, however, restrict utilization for any mixed agronomy by cultivators to whom cattle are important and inhibit its utilization by pastoralists. To argue that the continuation of tsetse infestations is essential for the conservation of the land resource is a singularly negative and erroneous position to take up, interfering as it does with the balanced and efficient utilization of the land resource. It is a position not accepted by most national governments. Abuse of the land resource is not a problem peculiar to areas freed of infestation but tsetse eradication does provide a unique opportunity for sound, balanced development.

Rice farm development behind the riparian forest of the river trees

Forest reserves have also in fact provided for the perpetuation of tsetse infestations in Nigeria and these have expanded into more recently conserved areas. Not only, for example, has a very large scale tsetse advance used reserves as stepping-stones, into and through the Anchau Corridor, disrupting the pastoral utilization of a large portion of the subhumid zone in northern Nigeria but, in the Shika area, a similar development gave rise to uncontrollable trypanosomiasis in the higher level management area of the Shika Stock Farm (Kirby, 1963).

Another conservation aspect is involved in statements that have recently been published to the effect that tsetse and trypanosomiasis control have been major factors causing the degradation of the Sahel and that continuation of this activity will result in similar changes in the savanna zone.

However, the fundamental urge in pastoralists is to find new grazing lands. Overutilized areas are avoided as far as possible. Under the transhumance regime pastoralists remain in the savarma grazing resource when it is safe for them to do so. The overutilization of fragile areas such as the Sahel undoubtedly accelerates degradation but, contrary to the statements that have recently had considerable publicity, it is not tsetse and trypanosomiasis control and/or eradication that have resulted in the overexploitation of Sahel grazing land; a multitude of other factors have been responsible. The Sahel grazing land is not used by the large pastoralist community based in the savanna zones. However, the extent of safe savanna grazing resources there is diminishing at a remarkably rapid rate through the pressure to grow food and commercial crops, and to tsetse advances. The consequence is that there is now developing a shortage of safe, common grazing land in the savanna zone. This increases any trend toward pastoral overexploitation and makes less grazing available also for transhumance from the Sahel, making it even more difficult to maintain the seasonal relief that is the fundamental feature of the transhumance system. Thus it can be suggested that, far from contributing to the degradation of the Sahel, tsetse eradication and trypanosomiasis control provide a substantial relief to the overgrazing problem.

Purely pastoral exploitation in the savanna lands of West Africa seems unlikely to lead to changes similar to those that have taken place in the Sahel, which, in the main, is not a fire subclimax. In the fire subclimax of the savannas the heavy utilization of the fodder resource leads in fact to the densification and proliferation of woody species and the area becoming progressively less attractive to pastor alists. Many examples of this kind of succession are to be seen, such changes taking place most rapidly in the subhumid zone. Here, it is cultivation practices that have been responsible for major degradations of the land resource.

Tsetse infestations as a constraint on livestock production in the subhumid zone

The previous sections have described the impact of tsetse infestations on balanced utilization of land resources. These directly or indirectly relate to the need to improve the efficiency of the agronomy in areas of current utilization or to expand the area of utilized land.

Tsetse infestations are far from being the only basic constraint on balanced utilization of land resources. The most important combination of factors is probably where tsetse infestation and river blindness co-exist. In this situation the elimination of either of the vectors alone will not result in long-term, trouble-free development. There are many other factors not related to disease, as well as other diseases (most notably streptotrichosis in zebu cattle in the subhumid zone) that are restraints on rural development. But within the tsetseinfested land resource it is tsetse infestation alone, unless accompanied by river blindness, that is the fundamental constraint in a large area of tropical Africa having the basic capability for balanced development.

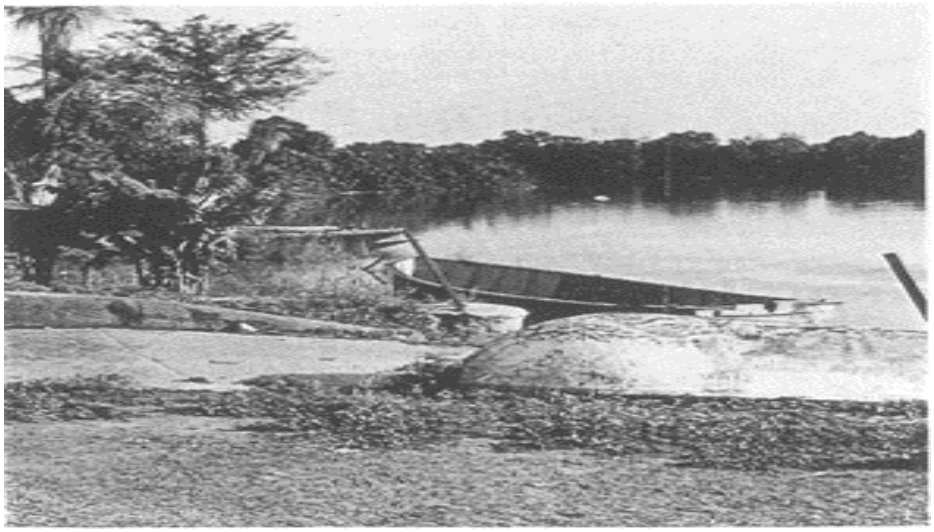
It is sometimes said that some of the tsetse-infested land resources are incapable of supporting arable agriculture and/or pastoral usage. But against this it must be pointed out that much of the best-watered and mostfertile land resources are tsetse infested. Similarly it is said that much of the underutilized savanna forage resource of Africa (estimated in total to cover 7 million km^2) cannot be utilized with out very great expenditure on infrastructure, such as the provision of water points and possibly not even then. In this case also it is necessary to stress that a very large proportion of good grazing, most notably that of the subhumid zone. could be utilized at once by pastoralists using existing cattle herds and with practically no capital, expenditure other than that required to remove tsetse infestations. It is true that shortages of meat in some areas are due more to offtake/marketing problems than to shortage of stock or grazing. In other very substantial regions of the continent, however, again

most notably in the subhumid zones, there is a great human need for more meat, which existing national herds could more effectively supply if available grazing resources were to be freed of tsetse infestation.

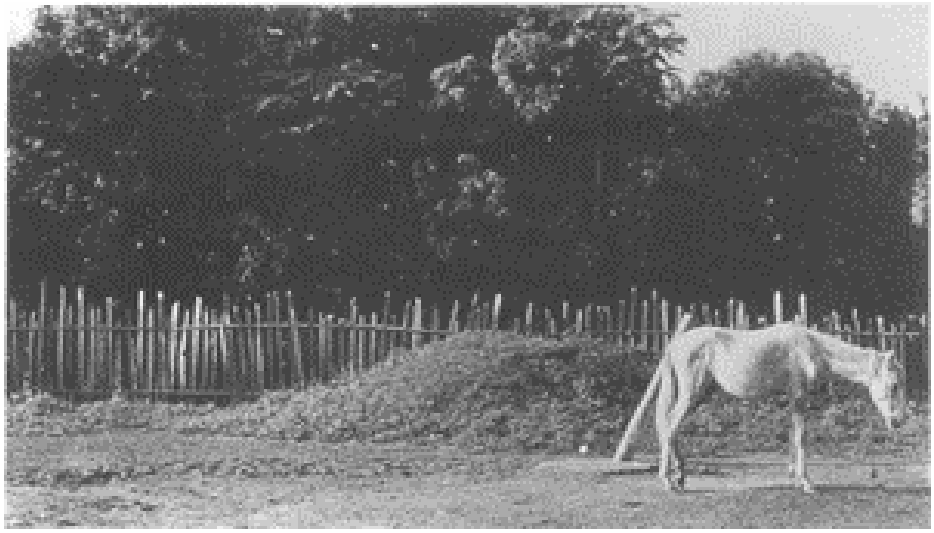
Economic aspects

Aspects relevant to the economic assessments of the tsetse problem are the economic impacts of tsetse-transmitted trypanosomiasis, the cost and technical effectiveness of counteractivities and the value of the resulting benefits.

Each of the individual items of the complex of effects and interactions described above has an economic connotation. Often this is fundamental, sometimes it may be slight. Some effects are not easily quantified in monetary terms, yet they may have a fundamental economic significance. Not infrequently numerical data are not available or are inaccurate, yet the aspect to which they refer is of major economic significance (as, for example, actual infection rates, mortality rates, production losses and incidence of drug resistance in pastoralist stock presented for treatment) and may be substantial in numerical terms.



Jetty, oho used for bathing and washing clothes, within about 20 metres of the infested mango garden in the photo above. Riparian forest G. palpalis *habitats in background.*



Garden of young mango trees, papaya, banana, etc., infested with G. palpalis. *Horse showing chronic trypanosomiasis.*

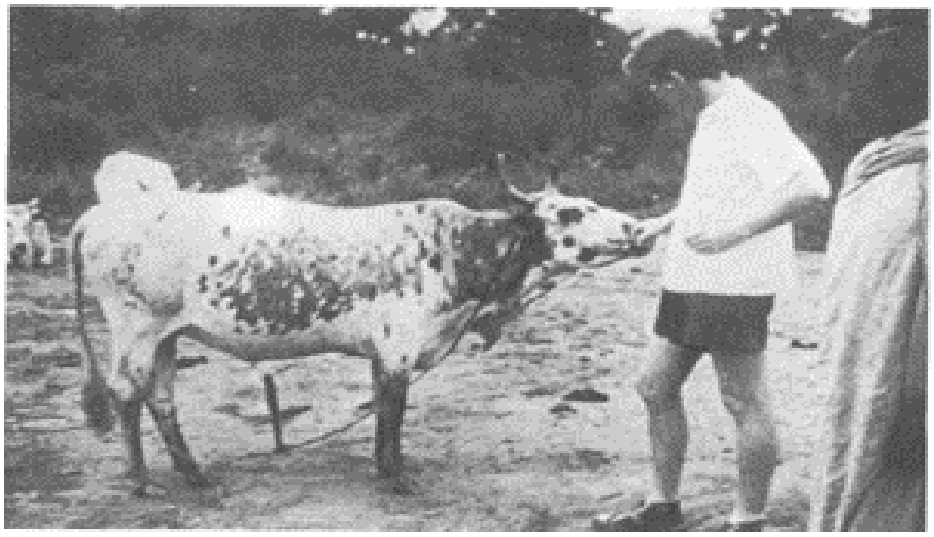
If equations are to be drawn up that meaningfully place the economic impacts of the problem in relation to the cost of countermeasures, it has to be ensured that all components are accounted for and not simply omitted because their significance has not been noticed or quantified numerically. It seems important that the negative impacts of infestation on balanced land use be adequately assessed. In regard to the problem of trypanosomiasis it is easier to be more precise about the costs of counteractivities than it is to measure the costs resulting from the disease.

TRYPANOSOMIASIS INFECTIONS

In purely economic terms trypanosomiasis infections can be of little account where tsetse densities are low, where livestock infections arise from flies with low infection rates, not primarily oriented on livestock and where facilities for diagnosis and treatment are readily to hand. This is exemplified in the forest zone in places where the risk from *G. palpalis,* and where savanna species (G. *longipalpis)* and forest species (particularly *G. fusca* and *G. medicorum* and possibly some others), are not present. This is the case in some areas of relatively high human population density.

In these circumstances cattle, exotic to the tsetse zone (zebu and temperate breeds) can be maintained and trypanosomiasis can be one of the lesser and more readily treated problems to be countered. Facilities for the diagnosis and treatment of trypanosomiasis must, however, be available. Usually they are provided from the general background of services and supervision that such projects require for reasons other than trypanosomiasis. The availability and cost of the facilities have to be considered in the economic assessment. Though characteristic of specific locations in the forest zone this situation may occasionally be encountered in the savannas, but will be inherently less stable and there will, therefore, be the need;' for a greater risk component to be included in the economic assessment. Furthermore, no risks can be assessed without repeated surveys being carried out by a specialized tsetse field unit under the control of a specialist entomologist. Both the availability and cost of this requireihent have also to be considered.

The other extreme relating to the disease exists in areas of moderate or high densities of savanna tsetse where the incidence of the disease, despite the availability of therapeutic agents, is such that continuous production from susceptible livestock, even from low-level husbandry systems, is impossible. The severity of the economic impact in relation to production from susceptible livestock is complete, as exemplified in areas overtaken by tsetse advance and described earlier. This situation exists over much of the subhumid zone.



Trypanotolerant West African shorthorn (Muturu). Dense G. morsitans *infestations in vicinity (Nigeria, Katska type).*

Intermediate situations exist where treatments, accompanied when necessary by vectorsuppression activity, or periodic withdrawal of stock from risk (as in transhumance), can make livestock production possible. A point to be considered is that large numbers of pastoralists can be serviced relatively easily at fixed treatment points, which they readily attend. It is much more costly and difficult to service similarly a scattered community of smallholders or ranches. In practice it has on occasions proved impossible to provide the degree of service necessary to prevent losses, resulting in livestock projects becoming uneconomic. Small projects are more readily serviced in the physical sense but at higher cost per animal unit and they are not likely to contribute greatly in alleviating national beef deficits, though any step in the direction of the development of a balanced, mixed agronomy is to be encouraged. Higher level husbandry projects can be more vulnerable than basic pastoralism.

TSETSE FILES

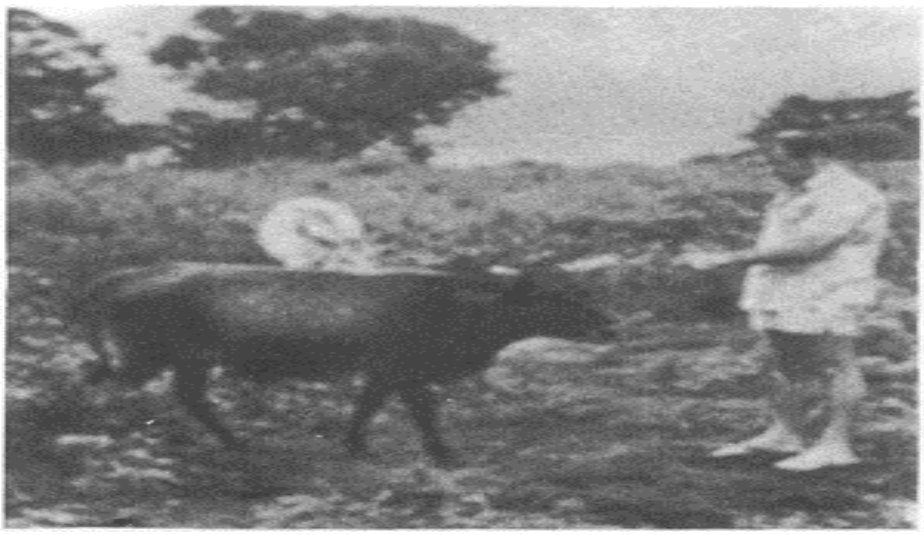
Glossina derives its economic significance solely from its capability to transmit trypanosomiasis to man and livestock. The economic impact is directly related to the risk of contracting trypanosomiasis and, as previously noted, there is a wide range in the degree of trypanosome risk in a variety of circumstances. Essentially, economic aspects concern: the necessity to know which tsetse species are present and their density, what are trypanosome infection rates in the flies, and what is the relationship of the infestation to man and livestock; and what is the cost of the antitsetse activity required.

An essential component, is the availability and cost of a specially trained field organization, adequately serviced with transport and travel allowances under the control of a specialist entomologist performing repeated surveys and compiling records of tsetse distribution over the course of time. Single surveys can reveal a degree of the economic risk but cannot fully assess the instabilities discussed previously. Livestock projects that are developed in the subhumid zone in the absence of adequate information on *Glossina* run a high risk of failure. Unless the circumstances are sufficiently favourable in regard to the *Glossina* risk they cannot be protected so as to ensure adequate levels of production at a cost that can be justified in economic terms. In more extreme situations, adequate protection is not feasible in purely technical terms. Additionally there is the cost of arranging trypanosomiasis surveillance and treatment in livestock (and possibly humans) and the actual cost of antitsetse activities that may be required.

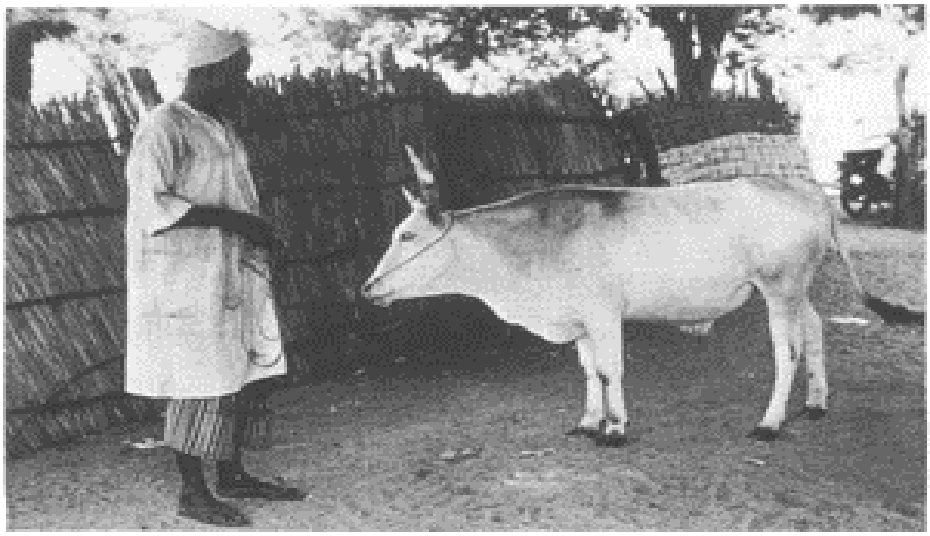
Anti-tsetse objectives are discussed in Part II of this article. There are very important differences in the economics of control compared with largearea eradication (where the latter objective is technically feasible). Examples can be quoted from Botswana, Nigeria and Zambia and from the first such operation, ever completed in South Africa (Du Toit, 1954).

In Botswana, taking the annual cost of containing *G. morsitans* infestation and excluding any other costs, the annual expenditure following a successful eradication becomes substantially less by the third year. On generous assumptions the maintenance of the eradication situation settles down at half the annual cost of control. The major expenditure on the eradication is recouped by the fifth year (Negrin and MacLennan, 1977).

It must be emphasized, however, that for this expenditure the area of the eradication operation would be 3.7 times that of the area over which control is currently exercised and that the value of the land resource freed of infestation has not been included in the economic equation. The continuing expenses of diagnosis and treating livestock trypanosomiasis inherent in the control situation, the constraints on balanced land utilization and the effects of human trypanosomiasis have also not been taken into consideration.



Trypanotolerant N'Dama of Fonta type (Guinea)



Trypanotolerant N'Dama (Hamitic longhorn) work ox. Dense G. morsitans *infestations in vicinity (Gambian type).*

The other significant aspect is that it is impossible technically to develop an extermination operation of smaller size because of the necessity of reaching a defendable perimeter. The fact that half the area reclaimed would not be put to "productive" use but would be assigned to conservation objectives does not detract significantly from the economic advantage of effecting eradication though the inclusion of this area is essential in reaching that objective. A more extreme example of this aspect is provided by the Zululand operation and the current problem in southwest Zambia.

In the Zambia example (MacLennan, 1975) a *G. morsitans* advance overtook the southwest corner of the country with the consequences described earlier. The cumulative cost of vectorcontrol activities, which proved far from effective in providing complete protection to the livestock, over a six-year period of containment, was more than double the estimated cost of eliminating the entire infestation (on the assumption that current airspray techniques achieve extermination). The annual cost of maintaining the eradicated area free from reinvasion on the vulnerable perimeter would be less than the present running cost alone on the "holding lines" of game and stock fences supported by clearings and game eviction. Again, the value of the land resources available for production and the benefit of eliminating other constraints inseparable from infestation are not taken into consideration.

In Nigeria anti-tsetse operations developed from the need first, to control very serious sleeping sickness epidemics (most active in the Sudan and subhumid zones) and later, to deal with the consequences of *G. morsitans* advances on the pastoral utilization of the land resource in several areas. The presence of the disease resulted in the abandonment of valuable land resources, much of it the more fertile and better watered portions (as, for example, the alluvial floodplains). From the vectorcontrol activities it proved possible to develop substantial extermination areas within a longterm programme of eradication. By 1977, 194 532 km^2 in a programme covering 259 000 km^2 had been completed. The removal of disruptive effects on the rural economy, particularly on pastoral and arable utilization and on conservation activities (especially those in connection with forestry and the reservation of pasture resources) had very important economic connotations.

LAND UTLIZATION

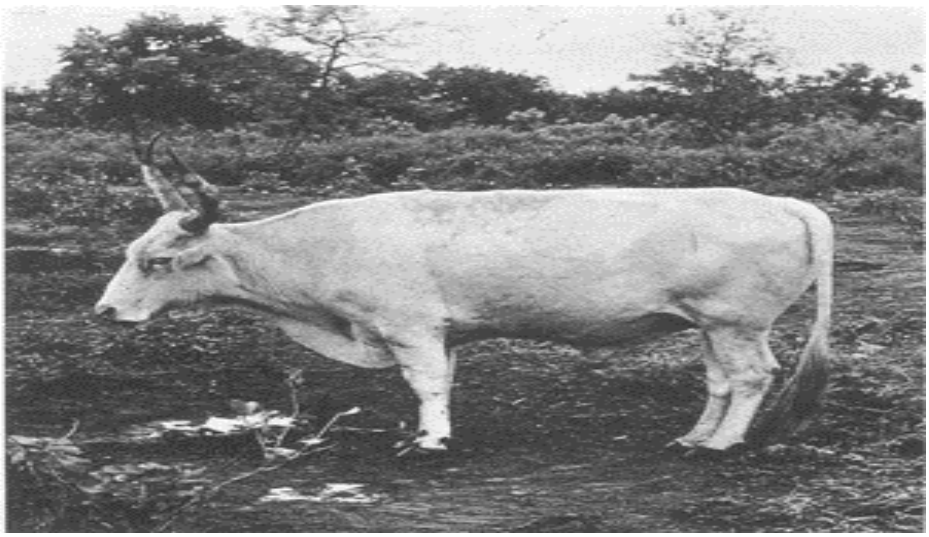
It has frequently been observed that, in development, the cost of eliminating tsetse infestations (where this is technically feasible) is a small part of the total cost of development. The most recent example, quoted from Nigeria (Jordan *et al.,* 1977), indicates that, in a proposed grazing development, the tsetse-eradication component amounts to 1 to 2 percent of total investment or 9 to 17 percent of investment (less the cost of livestock). However, in an alternative "low key" proposal for the same location, eradication costs would amount to 26-42 percent of infrastructure costs. It has to be stressed that the calculation is dependent on the project falling within a large extermination area. At the proposed location it cannot be suggested that periodic tsetse suppression (as opposed to eradication) would ensure an economically viable project or that an eradication "enclave" could be maintained for a reasonable cost. In the control situation it is unlikely that each suppression operation would cost significantly less to execute than a single effective eradication. Recoveries in *G. morsitans* populations following air-spraying in Botswana, which fell short of eradication, were slow but were rapid in areas where livestock were located and this caused a significant incidence of trypanosomiasis within 12 months of spraying. It is doubtful also whether repeated ground-spraying of large areas, without achieving eradication, could be accepted over the years (assuming largely unaltered tsetse habitats within the project and primary *G. morsitans* infestations within a radius of about 16 km), because of the cost, environmental aspects relating to persistent insecticides in current use, the transmission capability of lowdensity *G. morsitans* populations and their orientation on cattle.

Viewing the tsetse-eradication programme in Nigeria it is evident that it has eliminated considerable direct and indirect problems deriving from trypanosomiasis. For example, tsetse have probably been removed from most of the epidemic sleeping-sickness zone, large *G. morsitans* advances (which had severe impacts on utilization of the grazing resources) have been halted or reversed and, in addition, a large area, hitherto unusable. or only partially utilizable, has been freed of infestation.

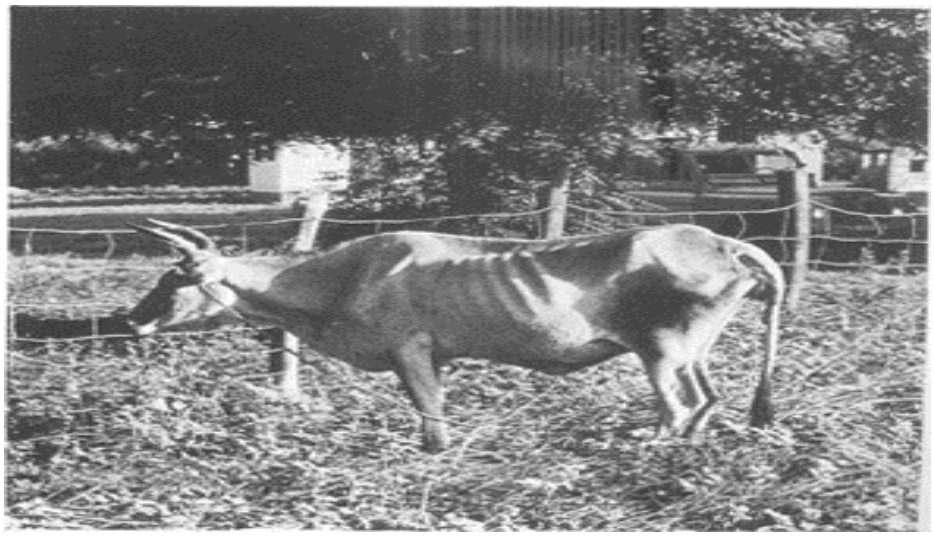
In effect this has provided some compensation for the loss of grazing resources resulting from population growth and food/cash crop production. In the absence of a "land budget" it is not known what is now happening or what will be required in the future, but even by 1973 it appeared that the transhumance system was under severe stress and that a major reason for this was the progressive loss of safe grazing areas and dry season "survival" grazing areas.

Though much of the tsetse eradication area was on occupied land resource substantial areas of new grazing have been made available at a cost in 1973 of about Naira 200 per 2.59 km^2 (US$ 117 per km^2). This represents the actual operational cost of one eradication unit for one year achieving eradication over 16 000 km^2 and including all unit personnel and labour charges, allowances, all materials, depreciation on all transport and equipment, and assuming that the proportion of the area included in discriminative spraying was 10 percent. Since that time there has been a severe inflation and, in the subhumid zone, discriminative spraying has increased possibly to 18 percent with a proportionate increase in cost and a reduction in the rate of annual progress. The equivalent cost today, in intermediate situations in the subhumid zone, could be estimated to be about 2.5 times the 1973 costs, bringing the

cost up to US$ 293 per km^2 or something near US$ 3 per hectare. This would still seem a cheap way to create usable grazing. Over much of the eradication area this has been the only development charge, since the livestock already existed and was simply re-accommodated. Specific infrastructural support that did not already exist has been minimal or nil.



Trypanotolerant Gambian N'Dama showing some zebu blood



Trypanotolerant Gambian N'Dama. Old female with chronic trypanosomiasis

It appears that, in Nigerian conditions, the most important follow-up activity is to secure the appropriate portions of the land resource for conservation and grazing objectives based on land use, capability assessments and on community need. If the situation is not stabilized in this manner it is only a question of time before problems that have developed in tsetse-free areas are seen again in the eradication areas.

Traditional methods of land use will, however, have to continue to be the main method of land utilization. Not only do higher level developments have to be technically feasible but, on the scale required to make a significant impact, they require a very large investment. They also have to be fostered by a body of technical expertise that knows exactly what it is about and the activities have to be acceptable and enforceable in the administrative and political senses. It seems that, in actual production terms and in relation to the needs of the larger human

populations, production by traditional methods will have to provide what is required during the lengthy and difficult transition to more advanced practices where these are appropriate.

The problems of ensuring sound and balanced land utilization are common to tsetsefree and to infested locations and are certainly not confined to Africa. Tsetse eradication provides scope and space for the attainment of objectives that were not previously available in the Sudan and subhumid zones. Toooftenrepeated dicta to the effect that tsetse eradication activity should only proceed where the whole land resource can be put to productive use immediately and that settlement of the land resource will prevent reinfestation have little meaning in the West and Central African context. The former is inconsistent with balanced land use and in meeting future population needs and the second has no basis in fact in this region. ■

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