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african animal trypanosomiasis

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Preface

African Animal Trypanosomiasis

The World Food Conference in 1974 called upon FAO "to launch as a matter of urgency, a long-term programme for the control of African animal trypanosomiasis as a project of high priority". Accordingly, in 1975 FAO initiated the *Programme for the control of African trypanosomiasis and related development* to which very high priority was given. Subsequently, the 10th FAO Regional Conference for Africa held in 1978 confirmed the mandate given by the World Food Conference to FAO.

A five-year preliminary phase of the Programme, in which the necessary technical and administrative structures at international, regional and national levels were to be set up, prior to the development and operation of large-scale projects, is now nearing completion.

The organizational structure worked out will ensure the participation in the Programme of all interested Member Nations and Associate Members of the Organization in Africa, the close association of international organizations and agencies in and concerned with the Programme (especially its financial implications) and adequate technical and administrative support.

Although documents refer to the "FAO Programme", the Programme is, in fact, of and for the African countries and FAO's role is primarily one of coordination in which the Organization will rely heavily on the cooperation and collaboration of OAU, WHO and other organizations.

This means that those African countries wishing to adopt and support the Programme can best do so by initiating discussions with FAO in order to indicate the types of assistance they will be requiring under the Programme.

An indication of the magnitude of the problem of trypanosomiasis in Africa may be gained from the vast area of land, estimated at some 10 million km^2 (a third of the African continent) that is affected. Both humans and animals in this area are affected by this parasitic disease, the causative organism of which, the trypanosome, is transmitted by the tsetse. Of the total area affected some 3 million km^2 are covered by equatorial forest. Much of the remaining area is suitable for either livestock or crop production since it contains some excellent grazing land and large areas of good, virgin agricultural land. This is largely because it has been "protected" by the tsetse from the results of overgrazing and intensive, short-term agricultural exploitation.

Because the need to accelerate pastoral development and to bring more potential farmland into production is becoming increasingly urgent in a number of countries, these are now intensifying their efforts to control the tsetse and trypanosomiasis. The task, however, is so great that coordinated, external technical and financial assistance is essential if these objectives are to be achieved.

While it is hoped that national tsetse and trypanosomiasis control units will be established by those countries that attach importance to the Programme, FAO believes that emphasis has to be placed not only on unilateral tsetse and trypanosomiasis control, but on area development as well. This involves evaluation of agricultural and livestock potentialities and adequate land-use planning of areas to justify the initiation of control measures. Such comprehensive development will help to ensure that the outcome of projects will be successful area and community development rather than the mismanagement of resources freed from tsetse infestation.

Experience in Africa has clearly shown that land use is implicit in the problem of tsetse and trypanosomiasis control and that the costs of the development of land after control has been achieved are likely to be immeasurably greater than the cost of the control of the tsetse itself.

It is most desirable, therefore, that evaluation of the potential resources of an area should precede, or at least accompany, studies of the tsetse that are to form the basis of control plans. Trials to test field control techniques, assessment of stock-carrying capacities, potentialities for water development and irrigation and crop production, etc. have also all to be undertaken before comprehensive or phased area-development can be initiated.

FAO has assured interested governments that it will provide preparatory assistance missions for the purpose of advising them on the formulation *of* policies, programmes and projects aiming at land resource development parallel with progress made in achieving tsetse control.

Governments will, therefore, need to evaluate their plans for the development of areas scheduled for control of tsetse, taking into account national development plans. For this purpose they are being urged to establish national trypanosomiasis control units and to assess their needs in the training field.

In implementing plans for area development and tsetse and trypanosomiasis control under the Programme, FAO is fully conscious of the need to avoid taking any action that may have irreversible, adverse effects on the environment. In rendering advice to governments it will continuously keep this fundamentally important principle in mind.

Trypanosomiasis and tsetse control methods have been greatly improved during the last 25 years and several of these have been applied effectively and economically. These include the use of trypanocidal drugs, vector control by ground aerial spraying of *insecticides,* and selective removal of vegetation forming the habitat of the tsetse. In recent years growing interest has also been shown in the potential use of try-panotolerant livestock as a means of allowing more efficient land utilization in tsetse-infested areas. In addition, research is at present being carried out on the release of sterilized insects and the immunization of livestock.

A series of articles on African animal trypanosomiasis have appeared previously in the *World Animal Review,* a quarterly journal on animal health, production and products published by FAO.

The present publication offers a complete collection of these articles.

African animal trypanosomiasis

PART I. DISEASE AND CHEMOTHERAPY

P. FINELLE *

This is the first of three articles on African animal trypanosomiasis by Dr. Pierre Finelle, who has spent many years in Africa studying this parasitic disease. This first part describes the disease and its occurrence, and the drugs that have been introduced to combat it and their relative merits.

The second part will deal with chemoprophylaxis and the raising of trypano-tolerant livestock, while the third and last article will review vector control as a means of overcoming trypanosomiasis.

Trypanosomiasis is a parasitic disease caused by species of flagellate protozoa belonging to the genus *Trypanosoma* which inhabit the blood plasma and various body tissues and fluids. These parasites are found in many animals but seem to be pathogenic only for mammals, including man.

Animal trypanosomiasis occurs in most of the tropical regions, but only in equatorial Africa does it constitute a major obstacle to the development of animal production. The considerable economic and social repercussions make control of this disease a priority operation for the development of a large part of the African continent.

Trypanosomes

African animal trypanosomiasis can be caused by several species of trypanosomes:

Trypanosoma congolense is found in most domestic mammals: cattle, sheep, goats, horses, pigs, camels and dogs; and also in many wild animals (Figure 1).

T. vivax is a parasite of domestic and wild ruminants and of horses.

T. simiae is found mainly in domestic and wild pigs.

T. brucei is a parasite very close to *T. gambiense* and *T. rhodesiense,* which are the causes of human sleeping sickness. It can be found in practically all domestic and wild animals.

T. evansi is found in Africa only in the Saharan and Sahelian regions where it is primarily a camel parasite, but it may be a parasite of horses, cattle and dogs as well. It also occurs in Asia — where it commonly causes disease in camels and horses, and less commonly in cattle, water buffaloes, elephants and dogs — and in Central and South America. Thus it has a very wide distribution.

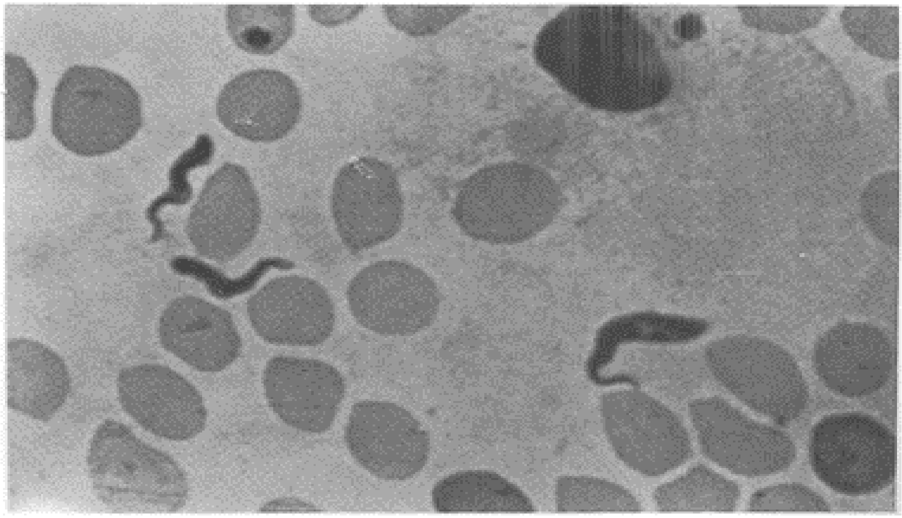


Figure 1. Photomicrograph of a film of blood showing three specimens of *Trypanosoma congolense.*

T. equiperdum is the causal agent of dourine, a contagious equine disease transmitted by coitus, which in Africa occurs only in the north African region and in South Africa. As control of dourine is an entirely different problem from that presented by other forms of trypanosomiasis, it will not be discussed in the present review, which deals only with the African trypanosomiasis transmitted by insects.

Transmission of trypanosomes

Transmission of trypanosomes by insects may be effected by widely different means.

Cyclical transmission, during which the trypanosomes actively multiply in the vectors, occurs through the intermediary of *Glossina* or tsetse flies (Figures 3 and 4). This form of transmission occurs with *T congo-lense, T. vivax, T. simiae, T. brucei,* and the trypanosomes responsible for human sleeping sickness, *T. gam-biense* and *T. rhodesiense. Glossina* spp. are strictly blood feeders living exclusively in tropical Africa. There are about thirty species or subspecies, classified in three groups: *palpalis, morsitans* and *fusca.* Each species has distinct biological characteristics, but in general it may be said that the *palpalis* group consists basically of the species living in forest galleries or in the marginal areas of forests; the *fusca* group consists of large-sized species whose habitat is generally associated with equatorial forests; and the *morsitans* group consists mainly of species living in wooded savanna.

Mechanical transmission is effected by various blood-sucking insects such as flies of the family Tabanidae (horse flies) and *Stomoxys* spp. In the course of a blood meal begun on an infected animal and ended on a healthy one, these insects may carry trypanosomes provided that the interval between the two meals is short. This form of transmission is the rule for *T. evansi,* but may also occur with trypanosomes habitually transmitted cyclically by *Glossina,* particularly *T. vivax* which may therefore be found in regions far from the *Glossina* distribution area (such as Latin America).

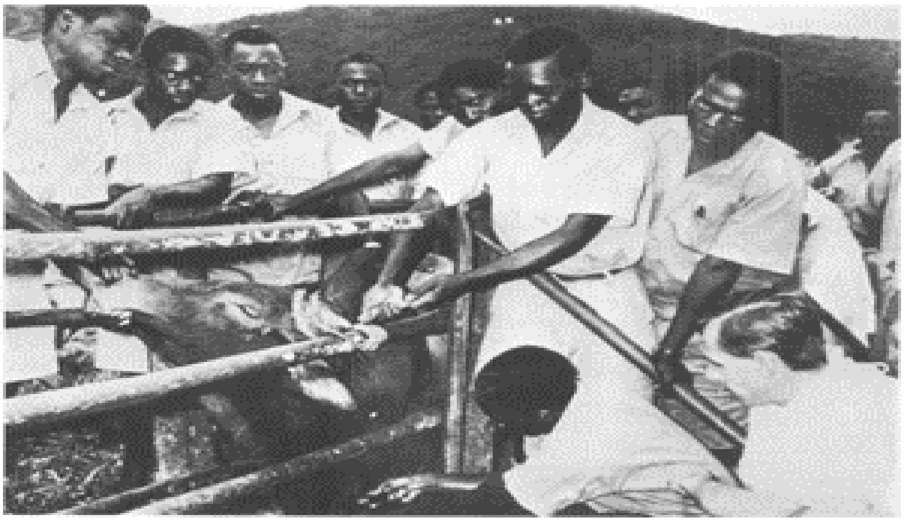


Figure 2. Demonstration of chemotherapeutic treatment against trypanosomiasis by inoculation with a trypanocidal drug in the dewlap.

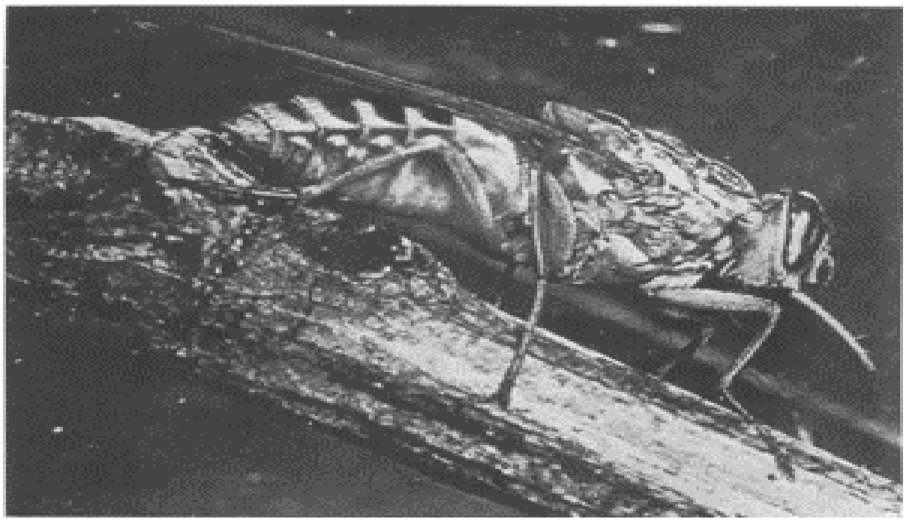


Figure 3. Close-up of a tsetse fly, the insect vector of African trypanosomiasis.

Trypanosomiasis

Trypanosomiasis is generally a chronic evolving disease which is usually fatal if appropriate treatment is not established. It leads to considerable loss of weight and anaemia. Various symptoms are exhibited, including fever, oedema, adenitis, dermatitis and nervous disorders. Because of its protean symptomatology the disease cannot be diagnosed with certainty except through detection of parasites by microscopic examination of blood or by various serological reactions.

The evolution of trypanosomiasis varies widely according to the try-panosome involved and the animal species or breed affected. Trypanosomiasis caused by *T. simiae* in pigs usually assumes a highly acute form leading to rapid death, at least in improved pig strains. *T. brucei* is highly pathogenic for horses and dogs, but in cattle this trypanosome usually causes asymptomatic infection. Zebu cattle are extremely susceptible to infections caused by *T. congolense* and *T. vivax,* but the humpless cattle of west Africa and the Guinean strain of goats show remarkable resistance, enabling these animals to live in areas where other breeds cannot exist.

Biologically-based control of animal trypanosomiasis

In the control of animal trypanosomiasis action is possible on various aspects of the epizootiological cycle of the infection: parasites, host animals and vectors.

ACTION ON PARASITES

This consists of the use of trypano-dal drugs on infected animals. The method aims first at limiting losses caused by the disease, and second at eliminating trypanosome reservoirs. Thus, detection and treatment of infected animals can be considered to be both a curative and a prophylactic procedure.

ACTION ON HOST ANIMALSs

Although immunological responses occur in trypanosomiasis, it has not yet been possible to develop a practical method for immunization. Short of such a method, the use of prophylactic trypanocidal drugs makes it possible in certain conditions to protect animals for several months. Another method consists in raising animals showing natural resistance to trypanosomiasis, such as the humpless cattle of west Africa.

ACTION ON VECTORS

This method applies primarily to *Glossina.* Attempts may be made to (a) destroy the insects, particularly through the use of insecticides; (6) make the environment unsuitable as a habitat, either by altering the vegetation or by eliminating the animal species which constitute the preferred hosts of these insects; (c) reduce their reproductive capacity by the release of sterile males; *{d)* limit their number by using biological control methods. The two latter techniques are still only in the research stage and have not been used so far as a practical control method for *Glossina.*

The various methods will now be considered which can be used in the control of African animal trypanosomiasis, excluding dourine; and the account will be confined to measures for the treatment and protection of cattle, small ruminants, pigs, horses and camels. The measures reviewed include (a) chemotherapy, *(b)* chem-oprophylaxis, (c) breeding of try-panosome-tolerant animals and *{d)* vector control.

Chemotherapy

Since 1938, the date of the discovery of the trypanocidal properties of the phenanthridines, the chemotherapy of animal trypanosomiasis has made great progress and there are several highly active drugs now available which are easy to use. The use of trypanocides has consequently become widespread, and the number of trypanocidal treatments carried out every year in Africa can be estimated at over 6 million, the great majority of them for combating bovine trypanosomiasis.

The trypanocides currently employed are: homidium salts (Ethi-dium-Novidium); quinapyramine sul-fate (Antrycide); diminazene acetu-rate (Berenil); isometamidium (Samo-rin-Trypamidium) and suramin sodium.

Table 1, which gives the data concerning the use of these products, shows that the action of the different trypanocides varies according to the animal species infected and the try-panosomes involved.

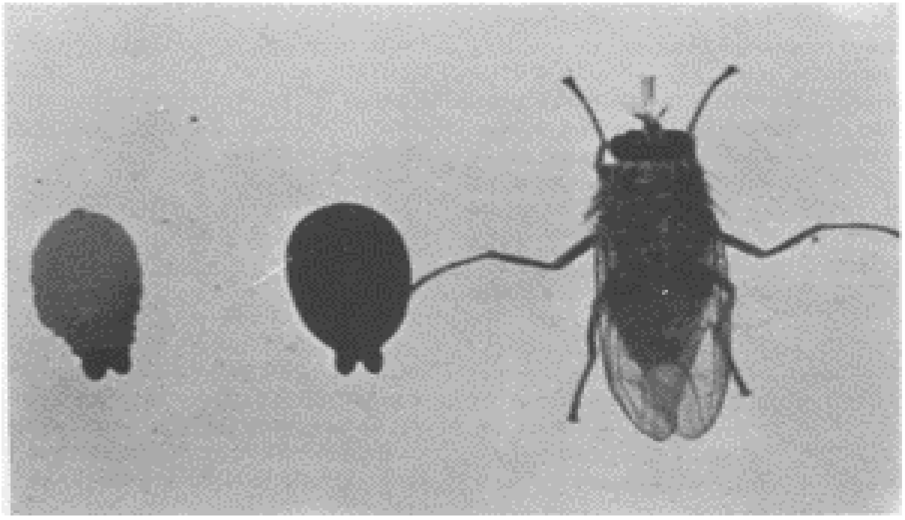


Figure 4. Different stages of evolution of the tsetse fly: larva, pupa and adult fly.

CATTLE TRYPANOSOMIASIS

T. congolense and T. vivax

Cattle infections caused by *T. congolense* and *T. vivax* are by far the most serious, both for frequency and for economic influence. The first really effective trypanocides were the dimidium salts which were widely used during the 1950s. However, their toxic effects, the difficulties involved in their adoption and the frequent appearance of drug-resistant trypanosomes have made the use of more recent trypanocides preferable. Homidium salts have been and are widely used, but a considerable number of cases of drug resistance to homidium have been reported and in many countries it has been necessary to suspend their use. Drug resistance has also been a serious handicap in the employment of quinapyramine sulfate (Antrycide) which is no longer extensively used in cattle for the treatment of either *T. congolense* or *T. vivax* trypanosomiasis.

Diminazene aceturate (Berenil) offers numerous advantages: its high activity against *T. congolense* and *T. vivax,* particularly on those strains resistant to other trypanocides, its very low toxic effects in cattle and its easy utilization make it a practical and safe trypanocide, at least for cattle. Although some cases of resistance were observed early in the use of the trypanocide, it was the accepted view at the time that this was the result of cross-resistance with quinapyramine, and that diminazene did not directly cause resistance because of its rapid elimination through the kidneys, which prevents accumulation of residual subcurative doses. Since 1967, however, strains of trypanosomes directly resistant to diminazene have been found in var-ious countries, notably in the Central African Republic, Chad, Kenya, Nigeria and Uganda, primarily with regard to *T. vivax* but also to *T. congolense.* These strains are fortunately still vulnerable to the phen-anthridine group of trypanocides, particularly isometamidium, leading to the conclusion that in case of failure of a diminazene treatment it is preferable to use another trypano-cide such as isometamidium rather than give further treatment with an increased dose of diminazene.

Table 1. Use of trypanocidal drugs

Trypanocide-laclics	Trade *name*	Method of treatment			Indications		Toxic effects			Treatment of relapses
		Solution	Dosage	Injection 1	Highly active on	Less active on	Good tolerance	Possible local reactions	Possible general reactions	
Homidium bromide	Ethidium 2	*Percent 2* hot	*Mg/kg*	IM	*T. vivax* *T.congolense*		Cattle Sheep Goats	Horses		Diminazene Isometami-dium
Homidium chloride	Novidium 3	2 cold water	1							
Diminazene aceturate	Berenil4	7 cold water	3.5	SC or IM	*T.congolense* *T. vivax*	*T.brucei* *T.evansi*	Cattle Sheep Goats	Horses	Horses Camels	Isometami-dium
Quinapyra-mine sulfate	Antrycide5 (sulfate)	10 cold water	5	SC	*T.congolense* *T. vivax* *T. brucei* *T. evansi*		Cattle Sheep Goats Camels	Horses		Isometami-dium
lsometami-dium chloride	Samorin,3 Trypami-dium6	1 or 2 cold water	0.25 to 1	IM (deep)	*T. vivax* *T.congolense*	*T.brucei*	Cattle Sheep Goats Horses	Cattle		Diminazene
Suramin sodium		10 cold water	10	IM	*T. evansi* *T. brucei*		Camels Horses			Quinapyra-mine

1 im = intramuscular injection: sc = subcutaneous injection.

2 Boots Pure Drug Co. Ltd.

3 May & Baker Ltd.

4 Farbwerke Hoechst A.G.

5 Imperial Chemical (Pharmaceutical) Ltd.

6 Specia.

Isometamidium (Samorin, Trypa-midium) is the most recent of the commonly employed trypanocides. Its main advantage is its effectiveness on trypanosomes resistant to other drugs. At the same time it has the disadvantage of easily creating drug-resistant strains itself; however, these trypanosomes show no cross-resistance with diminazene, which therefore retains *its* effectiveness on such strains. The isometamidium deposit at the injection site can cause a persistent local reaction which may be invisible from outside if deep in-tramuscular injection has been given, as is recommended. This reaction makes the surrounding flesh unfit for consumption and partial confiscation of the carcass is necessary. It is therefore advisable to choose an inoculation site on a part of the body where the meat is inexpensive; the neck muscles are usually recommended.

The two foregoing drugs, diminazene and isometamidium, are currently the preferred treatments for *T. congolense* and *T. vivax* trypano-somiasis in cattle.

T. brucei and T. evansi

Trypanosomiasis in cattle caused by *T. brucei* is of secondary importance as this trypanosome is only slightly pathogenic for cattle. The most active trypanocide against it is quina-pyramine.

T. evansi trypanosomiasis is extremely rare in cattle in Africa, where the disease occurs mainly in camels. It is encountered more frequently, however, both in cattle and in water buffaloes in southeast Asia. The best treatment is quinapyramine.

TRYPANOSOMIASIS IN SMALL RUMINANTS

Sheep and goats are seldom affected by trypanosomiasis and there is little information on treatment. If necessary, the treatments indicated forcattle, with diminazene and isometa-midium, can be used.

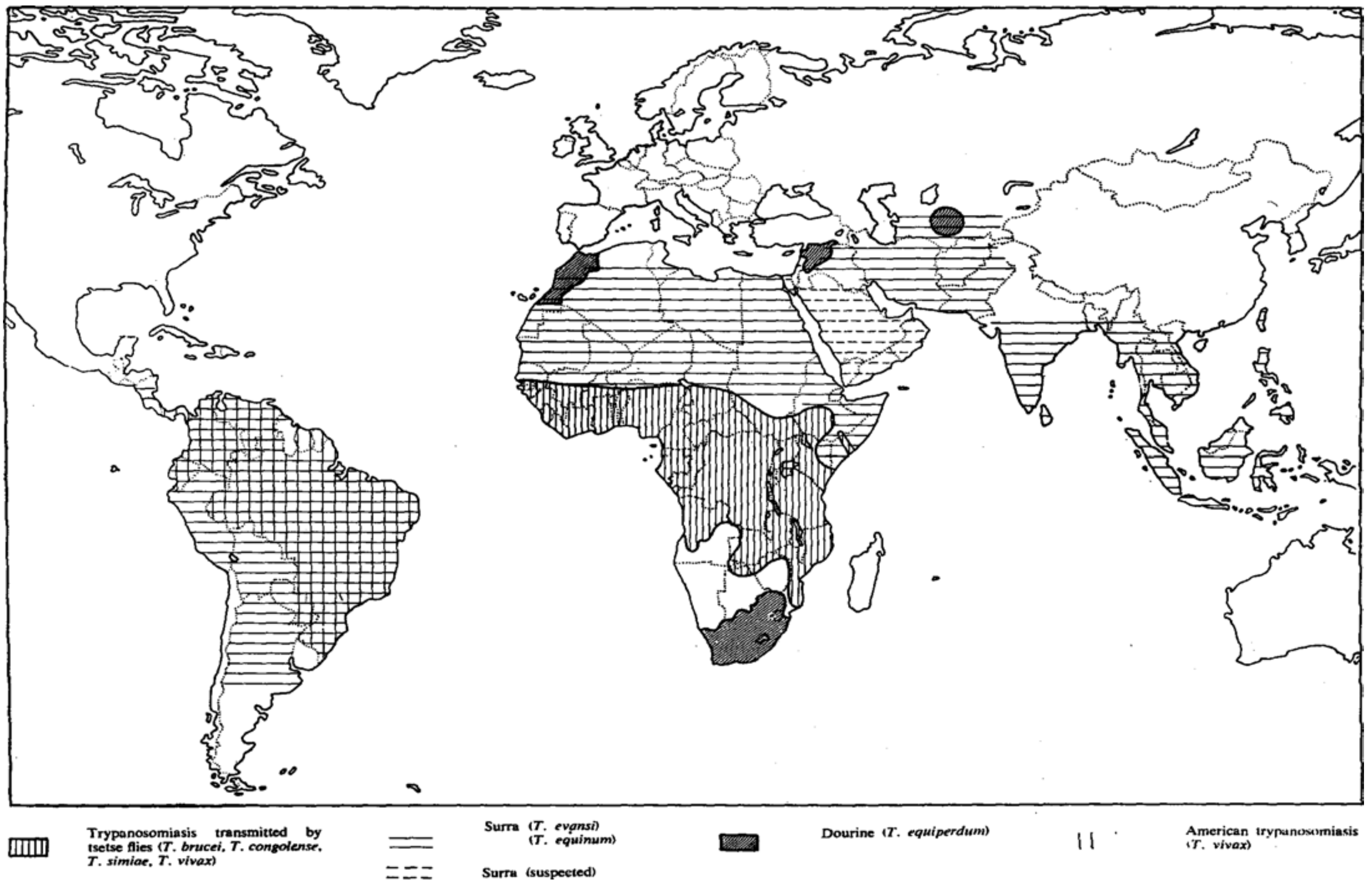


Figure 5. Geographical distribution of animal trypanosomiasis.

TRYPANOSOMIASIS IN PIGS

T. simiae, which is found mainly in domestic and wild pigs, presents a special problem because of its low vulnerability to the various trypano-cides, requiring the application of considerably higher doses than those used against other trypanosomes. Two treatments appear to be effective: an extremely high dosage of isometamidium (12.5 to 35 mg/kg); or a combination of quinapyramine sulfate (7.5 mg/kg) with diminazene (5 mg/kg).

However, the rapid course of this form of trypanosomiasis usually makes any therapeutic action impossible, so that it is necessary to rely on preventive rather than curative treatment.

EQUINE TRYPANOSOMIASIS

T. congolense and T. vivax

Diminazene is not as well tolerated by horses as by cattle. Local reaction and fatal poisoning, with kidney or brain lesions, have been reported. Homidium and isometamidium can be used on horses, although both drugs often cause local reactions; doses should therefore be divided so as to inject no more than 10 milli-litres per injection site.

T. brucei and T. evansi

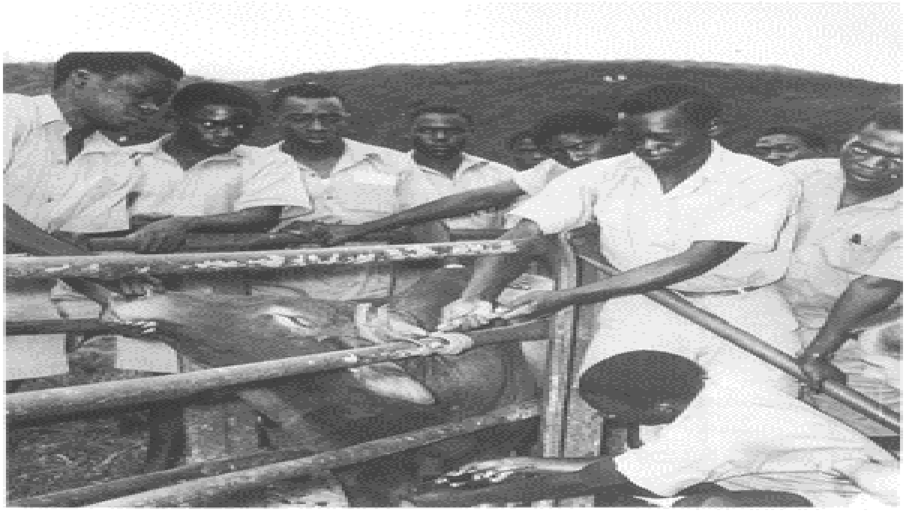
Quinapyramine sulfate is the most effective trypanocide against these two trypanosomes, but this drug is often poorly tolerated and is likely to cause serious local reactions and general disorders. It is therefore advisable to administer the dose in two or three parts at six-hour intervals.

CAMEL TRYPANOSOMIASIS

Quinapyramine sulfate is the preferred treatment for *T. evansi* trypanosomiasis in camels, but suramin sodium is still used in many countries although its cost is markedly higher and cases of drug resistance have been observed. Suramin-resis-tant strains of *T. evansi* remain sensitive to quinapyramine.

Conclusions

Several drugs are now available which are highly effective (except in the case of *T. simiae)* and easy to use; but for each of these products there are specific instructions which must be observed. Care and expert advice must always be taken before any large-scale treatment is started.



Cattle being injected with a drug to control trypanosomiasis

PART II. CHEMOPROPHYLAXIS AND THE RAISING OF TRYPANOTOLERANT LIVESTOCK

P. FINELLE

The first article in this series exam-ined the possibilities afforded by direct action on the parasites responsible for animal trypanosomiasis by the use of trypanocidal drugs on diseased animals. This second paper reviews two other methods of control: protecting susceptible animals by the use of preventive drugs, and making use of the natural resistance of certain breeds of cattle to trypanosomiasis.

Chemoprophylaxis

There are three trypanoprophylactic drugs which can be used: quinapyra-mine prophylactic (Antrycide Prosalt), pyrithidium (Prothidium), and isome-P. Finelle is Animal Health Officer, Animal Production and Health Division, fao, Rome. tamidium (Samorin-Trypamidium). Quinapyramine can also be used in complex forms with suramin, but as this formula is not on the market it must be prepared by the user as follows:

Quinapyramine sulfate	10 g
Suramin anhydrate	8.9 g
Distilled water	q.s. per 200 ml

The methods of using these trypanoprophylactic drugs are shown in Table 1.

CATTLE TRYPANOSOMIASIS

T. congolense, T. vivax, T. brucei

Quinapyramine (Antrycide Prosalt) was the first trypanoprophylactic drug that was sufficiently active for use in common practice. However, it has fallen into disuse because of the frequent appearance of drug-resistant trypanosome strains. Moreover, its prophylactic action, extending over two to three months, is considerably less than that of more recent products. Isometamidium and pyrithidium afford protection ranging from three to six months, depending on the risk. In principle it would be advisable to make a preliminary trial in each case in order to determine the treatment rate. In practice, a four-month cycle may generally be adopted — three injections per year. Isometamidium is most frequently used, particularly because of its lower cost. As in curative treatment, and especially since higher doses are administered for prevention, it is advisable to give the injection in a muscle where the local reaction is not likely to affect the price of the carcass substantially For large animals it is also advisable to divide the dose so as not to inject more than 15 ml per injection site. If trypanosomes reappear before another preventive injection has been given, a curative treatment with diminazene should be administered so as to eliminate theisometamidium-resistant trypanosomes.

Table 1. Use of trypanoprophylactic drugs

Trypanocide-laclics	Trade name	Method of treatment			Indications		Toxic effects		Treatment of relapses
		Solution	Dosage	Injection [1]	Trypanosomes	Length of protection	Good tolerance	Possible local reactions	
Isometamidium chloride	Samorin [2] Trypami-dium[3]	1 to 2 parts per 100 cold water	*Mg/kg* 0.5-1	IM (deep)	*T. vivax* *T.congolense* *T. brucei*	3-6 months	Cattle Sheep Goats Horses	Cattle	Diminazene
Pyrithidium bromide	Prothidium [4]	2 parts per 100 boiling water	2	IM (deep)	*T. vivax* *T.congolense*	3-6 months	Cattle Sheep Goats	Cattle	Diminazene Isometamidium
Quinapyramine chloride and sulfate	Antrycide Prosalt [5]	3.5 g per 15 ml cold water	7.4	SC	*T. brucei* *T.evansi*	2-3 months	Horses Camels Cattle	Horses	Suramin
Quinapyramine-suramin complex		5 parts per 100 cold water	40 (of quinapyramine)	SC	*T. simiae*	young 3 months; adults 6 months	Pigs		Isometamidium 12.5-35 mg/kg

1 IM = intramuscular injection; sc = subcutaneous injection.

2 May and Baker Ltd.

3 Specia.

4 Boots Pure Drug Co. Ltd.

5 Imperial Chemical (Pharmaceutical) Ltd.

T. evansi

In areas where *T. evansi* is prevalent, quinapyramine prophylactic (An-trycide Prosalt) can be used.

PROPHYLACTIC TREATMENT OF SLAUGHTER CATTLE

In Africa, tsetse-free livestock production areas are often located far from the large cities; this means that slaughter animals have to travel a long way to market, often through tsetse-infested zones. These journeys, usually made on the hoof, frequently last for several weeks during which the animals may contract trypano-somiasis that is all the more acute because the cattle come from regions free of infection and therefore have no immunity. Moreover, their resistance is lowered by travel stress. It is therefore necessary that trypano-prophylactic treatment be administered before livestock intended for slaughter enter tsetse-infested areas. Because *(a)* a large number of animals are to be treated at low cost, *(b)* a comparatively short period of protection is required (about one month), and *(c)* drug resistance is unlikely since the animals are to be slaughtered, the following drugs may be used:

— homidium salts, which in regions where drug resistance to this product has not yet appeared give protection for about one month; or

— isometamidium, which in doses of 0.25 or 0.5 mg/kg makes it possible to obtain protection lasting up to two months.

TRYPANOSOMIASIS IN SMALL RUMINANTS

Chemoprophylactic treatment of trypanosomiasis in small ruminants is rare, but it appears that the measures indicated for cattle can be applied equally to these animals.

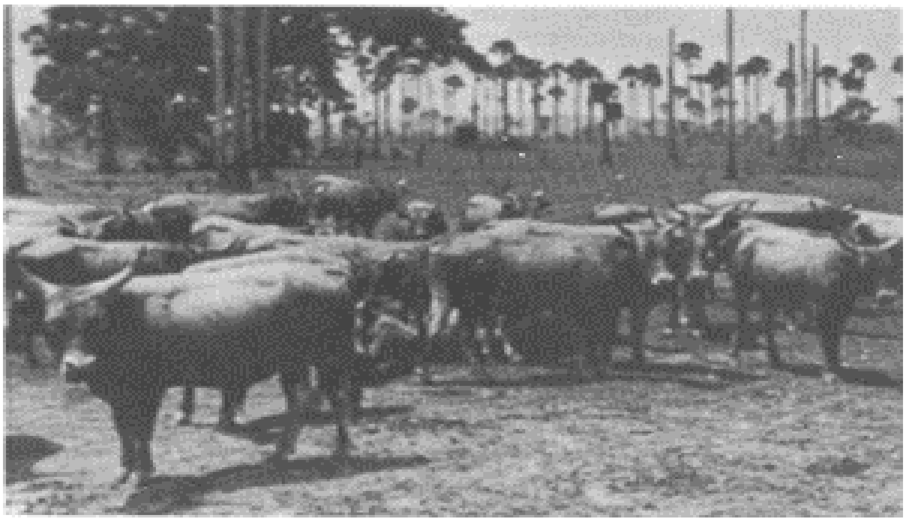


Figure 1. Herd of N'dama trypanotolerant cattle in Ivory Coast. These cattle are humpies s, and their coats are light fawn in colour.

TRYPANOSOMIASIS IN PIGS

For the prevention of *T. simiae* infection in pigs, the following can be used:

— quinapyramine-suramin complex in a dose of 40 mg/kg (quinapyramine sulfate), or 4 ml of suspension for 5 kg liveweight. This product affords protection lasting about three months for piglets and six months for adult pigs;

— isometamidium through deep intramuscular injection into the neck muscles, in doses between 12.5 and 35 mg/kg. This treatment provides protection for about four months.

EQUINE TRYPANOSOMIASIS

T. congolense, T. vivax, T. brucei

Isometamidium and pyrithidium can be used for horses and donkeys under the same conditions as for cattle, although such treatments may cause temporary lameness. It is advisable to administer deep intramuscular injections and to divide the dose if a large amount is to be injected.

T. evansi

Quinapyramine (Antrycide Prosalt) is the most effective, but this product causes serious local reactions in horses. The protection period is from three to four months.

TRYPANOSOMIASIS IN CAMELS

Quinapyramine can also be used to prevent *T evansi* trypanosomiasis in camels.

Drug resistance

The discovery of trypanocidal drugs with preventive action raised high hopes that their use would make it possible to turn subtropical Africa into a flourishing livestock production area. It must be admitted that most of these hopes have not been realized. Although these drugs do provide protection, which in some conditions may last up to six months, all of them frequently give rise to the formation of drug-resistant try-panosome strains. This drug resistance occurs when the'trypanosomes are in contact with a trypanocide administered in a subcurative dose insufficient to ensure the destruction of the parasites. This situation may be due to one or more of the following factors:

a. the application of insufficient doses, due in particular to underestimating the weight of animals;
b. the formation of abscesses followed by partial rejection of the drug;
c. a cyst-forming reaction which prevents the diffusion of the product;
d. preventive treatments at too long or irregular intervals;
e. halting the application of try-panoprophylactics while the animals are still exposed to the risk of infection ;
f. the occasional use of preventive drugs in curative treatments.

Trypanoprophylactic drugs should therefore be used with considerable caution, especially since there is a cross drug resistance between various trypanocides and drug-resistant try-panosome strains which may persist for a long time even after passage through tsetse. In fact, these drugs can be used without danger only on controlled livestock, where it can be certain that the treatment rate and application requirements will be fully observed. These prerequisites sharply limit the possibilities of applying chemoprophylaxis under traditional African livestock production conditions.

Figure 2. Herd of small short-horned humpless cattle in Dahomey. This breed is the second of the trypanotolerant breeds in west Africa, where it is known by different names.

Raising of trypanotolerant livestock

The low susceptibility of some west African cattle breeds to trypano-somiasis has long been known. Early workers observed that such livestock were able to survive and thrive in areas infested with tsetse where other breeds, especially zebu, could not exist.

These trypanotolerant livestock are the small, humpless cattle of west Africa, of which there are two distinct breeds. One is the N'dama, which seems to have originated in the Fouta Djallon massif in Guinea and whose area of distribution covers southern Senegal and Mali, Guinea, northwestern Ivory Coast, and northern Ghana. The horns of these animals are lyre-shaped and the tawny coat is characteristic. The other breed, according to the region in which it is found, is called Baoule, Laguna, Samba, Muturu, Dahomey, and west African short-horned cattle. It is found in Ivory Coast, Ghana, Dahomey, Togo, and in the southern regions of Mali, Upper Volta and Nigeria. These cattle are smaller than the N'dama and more powerfully built; their coats are usually black or piebald black, and they have short pointed horns. The areas of distribution of these two breeds and the zebu are often poorly defined, and many crossbreeds can be found.

There is still very little known about trypanotolerance. It seems to depend on two groups of factors: hereditary and acquired characteristics.

HEREDITARY CHARACTERISTICS

Trypanotolerance is a feature of the small, humpless cattle of west Africa. By studying the behaviour of zebu cios=breds it has been shown that the ujscfjtibility of these animals to trypanosomiasis is intermediate between that of pure humpless and zebu breeds and is approximately proportional to the degree of zebu blood.

ACQUIRED CHARACTERISTICS

Humpless cattle raised in tsetse-free areas have no resistance to trypanosomiasis and behave like those of other breeds; their serum does not contain antibodies and when they become infected the course of the disease is acute and results in death. Trypanotolerance is therefore in part an acquired immunological phenomenon. It is also relative and may break down in certain conditions, particularly in the case of too frequent infections which may succeed in overcoming the animal's immuno-logical defences. Moreover, all the causes capable of affecting the production of antibodies can also reduce it or cause it to disappear. These include malnutrition, overwork, intestinal parasitism and infectious diseases.

The mechanism of trypanotolerance may therefore be explained as follows: the trypanotolerant breeds have a hereditary capacity to produce try-panosome antibodies; but the production of antibodies is set off by infections contracted while the young animal is still protected by the mother's antibodies. Subsequent production of antibodies is maintained and strengthened by subsequent infections, but it can be reduced and even eliminated by all the factors which exert an unfavourable action on the immunological defences.

Introduction of trypanotolerant livestock

The west African trypanotolerant livestock which have been imported into the central African countries have enabled a significant development of livestock production in areas unsuited to the raising of zebu and where there had been no cattle production previously. The number of trypanotolerant livestock in various countries of central Africa can be estimated at about 220 000 head in Zaire, 35 000 in Congo, 15 000 in the Central African Republic, and 5 000 in Gabon.

Two systems for the introduction of trypanotolerant animals can be adopted. In the first, imported breeding stock is assembled on ranches, and the increase in the herd, the offspring, is distributed to the farmers. This permits an effective control of the herd and is perfectly suited to N'dama cattle, which respond well to ranching. The short-horned cattle however, appear to settle better in small herds. In the second system, the breeding stock is distributed directly to the farmers, which has the advantage of immediately involving the village people in the operation. A farmer is given several females and a bull, which are to be repaid in cattle later as the increase in his herd makes this possible. These will be used to start new herds. Whichever system is applied, the operation is faced with technical and human problems.

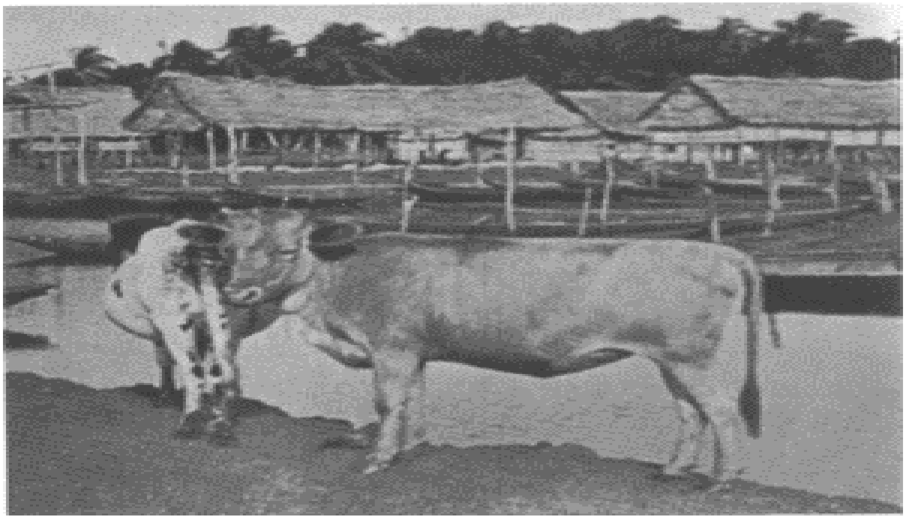


Figure 3. Crossbreeding between N'dama and west African short-horned cattle is frequent. This crossbred Dahomian heifer with short horns and a fawn coat is a good example.

TECHNICAL PROBLEMS

These are primarily the problems connected with any importation of animals, in particular the danger of introducing contagious diseases: rinderpest and contagious bovine pleuro-pneumonia. Since trypanotolerance is related to local strains of trypano-somes, the transferred animals may be susceptible to other strains. It is therefore advisable to ensure strict sanitary inspection during the first *few* months after importation. If necessary, trypanocidal treatments should be given to help the animals overcome trypanosome infections and enable them to adapt their production of antibodies to new strains against which they have no immunity.

HUMAN PROBLEMS

Trypanotolerant livestock are usually distributed in areas where cattle husbandry is a completely new activity. The operation therefore requires considerable organization and resources, at least for the first few years, its success depends on the training of the new stock-raisers. Under prose i': conditions, the introduction of" y anotolerant cattle is one of the most Hxtive methods for developing livestock production in countries where tr/panosomiasis is prevalent. It is costly, requiring considerable personnel, and is slow to start, but these drawbacks are more than offset by the results, which are permanent, whereas the methods considered previously, chemotherapy and *chemoprophylaxis,* must be repeated constantly.

A fourth method, vector control, can also be employed, and will be the subject of the third article in this series on African animal trypano-somiasis.

PART III. CONTROL OF VECTORS

P. FINELLE

Deforestation and bush clearing — an indirect method of tsetse control.

Tsetse flies are the chief vectors of African trypanosomes, and also serve as intermediate hosts in which the parasites multiply actively. Various methods may be used to control these vectors: indirect methods, that attempt to alter the environment so as to make it an unsuitable habitat for tsetse flies, and direct methods — chemical and biological — aimed at destroying the insects or at eliminating their ability to breed.

INDIRECT METHODS

Deforestation

The microclimate that is established by plant cover provides the most suitable combination of temperature and humidity for the tsetse fly because it limits variations in climate to a minimum. The fly concentrates in certain types of vegetation, which vary for the different tsetse species. When this vegetation is cleared, changes occur in the microclimate that may cause the species concerned to disappear. Use of this selective deforestation method therefore requires a very precise knowledge of the biology of the species concerned in the prevailing conditions.

Destruction of the vegetation can be done manually, by felling the trees, or by ringbarking in the case of plant species for which this technique is effective. Mechanical means can be employed with quicker results, but these can only be used in flat country. The use of arboricides has not proved very practical as they are expensive and slow-acting products that do not work well with all plant species.

Regardless of the technique used, the selective destruction of vegetation presents two major drawbacks: it is generally a very expensive operation and it increases soil erosion, which is liable to cause sterility in the cleared land. This method is now seldom employed, except to establish deforested barriers to prevent areas cleared by insecticide spraying from being reinvaded.

Elimination of wild animals

As well as being trypanosome carriers, wild animals are an important source of food for the tsetse fly. Studies of these hosts have shown that the tsetse fly obtains much of its nourishment from a small number of wild animal species, which differ for each species of fly. A control method has therefore been developed with the aim of eliminating the preferred hosts. This method has been employed to a considerable extent in some countries of east and southern Africa with noteworthy results, but at the cost of the massive destruction of big game.

However, the elimination of wild animals, even if restricted only to host species, is not easy to accomplish, especially when it involves destroying small animals like the warthog, the bush pig and the small antelope which are the favourite hosts of many testse species. It has also been observed that the tsetse is not rigidly dependent on specific animal species, and that when the preferred hosts disappear it can feed on other species.

Because of these difficulties, and the increasing concern for wildlife protection, the control of tsetse fly by the selective elimination of wild animals is not to be recommended at present.

DIRECT METHODS

Insecticides

The treatment of tsetse-infested zones with insecticides is currently the most common method of eradication. Insecticides may be applied from the ground or from the air.

APPLICATION FROM THE GROUND

The method consists in applying a persistent insecticide where it has the most chance of coming into contact with tsetse flies, that is, on their most frequent resting places. The insecticide is applied in the dry season, not only to prevent it from being washed off by rain but also because the severe conditions prevailing in this season force the flies to concentrate on certain types of plant which provide a more favourable microclimate. Only one treatment is applied; the insecticide must therefore have sufficiently long persistence, exceeding the maximum pupation period, to act on the newly hatched insects coming from pupae deposited before the treatment.

The insecticides used are usually chlorinated hydrocarbons, chiefly DDT and dieldrin, both of which persist for several months on vegetation. DDT is more frequently used in regions with a Sudanian climate and a long dry season, while dieldrin is preferred in more humid regions with a Gui-nean climate. DDT is applied in the form of wettable powders or emul-sifiable concentrates, diluted to obtain a final concentration of between 2 and 5 percent according to the needs of the region. Dieldrin is used in concentrations varying between 1.8 and 2 percent, obtained from an emulsifiable concentrate. Insecticides can be applied with pressurized sprayers, or motorized or high-capacity vehicle-mounted sprayers. The choice of equipment is essentially a matter of convenience in use, according to the local vegetation and the physical features and extent of the area to be treated.

Ground spraying with portable prepressurized sprayers.

The preferred resting sites of the tsetse fly vary with the different species, the season and local ecological conditions. It is therefore essential to have accurate knowledge of the biology of the species in the region to determine the types of vegetation to be treated. In Nigeria, for example, in the Sudanian regions infested by *Glossina morsitans submorsitans* and *G. tachinoides,* a 2 percent DDT solution is applied exclusively on the supports where the tsetse flies rest during the hottest hours at the end of the dry season. In the case of *G. morsitans,* these supports are shady tree trunks with a diameter of over 20 centimetres from ground level to a height of about 1.5 metres. For *G. tachinoides* it is necessary to treat all tree trunks, visible roots overhanging the banks of streams and woody vegetation near water, all up to a height of about 1 metre. When forest galleries are relatively narrow and well separated from both banks of streams, only 5-metre strips are treated along each bank in the case of *G. tachinoides* and 10-metre strips for *G. morsitans.* If the forest is broader and the banks are not clear, treatment is effected in strips, about 20 metres wide, along the outside edge of the forest and inside the forest galleries in the direction of the stream, at intervals of about 100 metres. In flood plains, where the forest is divided into thickets, only the edges of the thickets and narrow parallel strips inside them, about 20 metres apart, are sprayed. Operations of this kind in northern Nigeria have given highly satisfactory results, and the zones where tsetse flies have reappeared and require further treatment do not exceed 1 percent of the total area treated.

The technique of selective spraying with persistent insecticides using ground equipment has been and continues to be widely and successfully employed in several countries against various species of tsetse fly. It has been most extensively applied in northern Nigeria, where it has led to the clearing of some 125 000 square kilometres, and where the programme is continuing at the rate of about 12 500 square kilometres a year. It is an attractive method because of its effectiveness, its relatively low cost, and because it results in reduced environmental contamination. It should be stressed, however, that it requires thorough prior studies of tsetse fly ecology to determine the conditions for using insecticide, and large, well-equipped and well-trained spraying teams, as well as a dense network of roads and tracks. The method is of real value only in regions where the habitat of the tsetse fly is relatively restricted, at least for part of the year. These various conditions, which cannot often be met, have led to the adoption of aerial spraying, which gives quick results and requires limited personnel.

AERIAL SPRAYING

The first attempts to control tsetse fly by the aerial spraying of insecticide were made in 1948 in Tanzania, and the first large-scale operation was carried out shortly afterwards in South Africa, leading to the elimination, although at a very high cost, of *G. pallidipes* in the Zululand region. Research, particularly in Tanzania, has led to improvements in this technique and to appreciable reductions in its cost. The .insecticide can be applied either as an aerosol without residual action, distributed over the whole infested zone, or as a deposit, with a persistent effect, on the preferred resting sites only.

Ground spraying with portable motorized sprayers.

Aerial spraying.

Aerosol

The aerosol method has been used in various countries, including Rwanda, Kenya and Tanzania, but has been applied most widely in Zambia.

The insecticide is sprayed in the form of fine droplets with a diameter between 10 and 60 *im,* which because of their lightness remain suspended in the air and can penetrate through the vegetation and reach the adult tsetse flies. However, the insecticide is not deposited on the vegetation and has no persistent action, so the treatment must be repeated to reach the tsetse flies which had been in the pupal stage at the time of the first operation.

DDT, BHC, dieldrin, endosulfan, iso-benzan, fenthion and pyrethrum have been used. Light single-engined aircraft are generally employed for these operations, fitted either with heat generators working off the engine exhaus| pipe or with rotary sprayers. In Zambia, heavier two-engined aircraft, which allow more rapid operation, are used successfully. Recent advances in aerial spraying techniques have enabled considerable reductions to be made in rates of application, with highly concentrated insecticides; in Zambia, endosulfan is sprayed at the rate of 30 grams per hectare. Operations are carried out during the dry season, at a time when many trees lose their leaves, and at hours when the meteorological conditions are favourable, at dawn and just before sunset. The aircraft are guided either by ground teams using radio or markers, or by the aircraft's own navigating equipment.

Aerial sprayings are repeated four or five times, at three-week intervals. The conclusion to be drawn from the various, operations for controlling tsetse flies by the aerial spraying of nonpersistent insecticides is that total elimination is possible provided the treated area is suitably isplated from other contaminated regions. In Zambia aerial spraying has led to the eradication of *G. morsitans* from nearly 15 000 square kilometres at a lower cost than spraying with ground equipment. However, the method suffers from several disadvantages: it requires total coverage of the tsetse-infested zone and all that this implies from the point of view of environmental pollution; it requires several applications staggered over about 100 days; the insecticide, which is dispersed in the form of fine droplets, is often carried away by the wind to areas outside those to be treated. Because of these disadvantages the application of long-lasting insecticides is sometimes preferred.

Persistent insecticides

Various tests involving the aerial spraying of persistent insecticides have been made, using an inverted-emulsion insecticide or by selective spraying from helicopters.

Inverted emulsions. In these tests, performed in Kenya under a who/ fao project, dieldrin was used as a water-in-oil emulsion instead of the normal oil-in-water formula. With these inverted emulsions, in which the oil phase is the continuous one, evaporation is limited and the droplets are coarser and less sensitive to atmospheric conditions, so that they reach the target zone with greater accuracy. The vegetation of the region chosen was composed of very dense thicket infested by *G. pallidipes.* Applications were made from aircraft and helicopters, but the latter proved to be more expensive. The results of these preliminary tests proved that the technique was effective in the conditions prevailing in the region, and that its cost was competitive with that of the other methods. The tests should be continued and extended to other species and other types of vegetation.

Selective spraying. The principle underlying the selective spraying of persistent insecticides by helicopter is similar to that of selective spraying using ground equipment: the aim is to treat only the vegetation used as a refuge by the tsetse fly, when weather conditions for the insect are most severe. This method has been successfully employed in northern Nigeria in regions infested by *G. morsitans submorsitans.* A helicopter flying at a low speed (about 40 kilometres an hour) 1 or 2 metres above the treetops sprays (in the dry season) 10 percent dieldrin in the form of droplets with a diameter varying between 90 and 200 (xm, over a width of about 20 metres, at the rate of 1.5 kg of active product per hectare. This technique has turned out to be effective, but expensive if the price is related to the area treated. However, if account is taken of the fact that only 10 percent of the total area is effectively treated, the cost of this method calculated in terms of the cleared area is comparable to that of unselective spraying by aircraft.

PROBLEMS OF CHEMICAL CONTROL

Whatever the technique used, chemical control of the tsetse fly raises several general problems.

Isolation of the cleared region

It is obviously necessary to prevent the cleared region from being reinvad-ed by insects from neighbouring contaminated areas. This can be achieved either by establishing barriers which have been deforested or treated with persistent insecticides and which are sufficiently broad to prevent crossing by the tsetse fly, or simply by re-treating the edge of the already treated zone the following year. It is also necessary to check the movements of vehicles, livestock and possibly of game, all of which can transport tsetse flies over great distances.

Pollution

Chemical control of the tsetse fly certainly raises the pollution level of the area concerned. The insecticides used, usually chlorinated hydrocarbons, are toxic to other insects, including useful species such as bees or predatory insects. They are also very toxic to fish. Their toxicity as far as birds and mammals are concerned is still not very clear, but it is known that they can accumulate in fats.

It must be noted, however, that the levels and quantities of insecticides used for tsetse fly control are much lower than those for controlling crop parasites, and hence account for only a very small part of the general pollution caused by pesticides. Nevertheless, it is highly desirable that new insecticides should be tested with the aim of finding a product with a more selective action and with fewer effects on the environment than the organochlorinated compounds currently used. Biological control methods may also provide a solution to this problem.

Biological control methods

The biological control of tsetse flies is as yet only in the experimental stage. Two methods, which have been proved against other insects, may be considered: the use of organisms pathogenic to tsetse flies, and genetic control.

PATHOGENIC ORGANISMS

Little is known about the pathology of tsetse flies. While there is information concerning insect parasites which prey on tsetse pupae and which in nature certainly play a part in limiting the number of flies, so far there has been no success in breeding these parasites in the laboratory.

Likewise, no work has been done on organisms that are pathogenic to tsetse flies, an approach which has been so promising in the control of other insect species. These matters should receive the very close attention of research laboratories.

GENETIC CONTROL

Research on the genetic control of the tsetse fly has made great strides since it became possible to breed these insects in the laboratory on a large scale. It is now possible to consider methods involving induced sterilization or the transmission of lethal genes. The underlying principle is that as the female tsetse fly generally copulates only once at the beginning of its life, it will produce no progeny when inseminated by a male whose spermatozoids have undergone chromosomal modifications that render them incapable of fertilizing the egg. By releasing a sufficient number of sterile males in a region so that they have a greater chance of mating with the females than the existing normal males, a reduction and eventually an extinction of the population through reduced numbers of progeny can be achieved.

Contact with various chemical products can cause sterility in males, and the gamma irradiation of adult males has the same effect. Laboratory studies have shown that although the longevity of the males is reduced, they live long enough to copulate several times and retain their ability to mate. The advantages of this system are obvious. The species is used to destroy itself, without disturbing the natural biological equilibrium. The males seek out the females and can track them down in places inaccessible to man.

The application of this method requires a large number of males, which is now possible through recent improvements in laboratory breeding techniques. One important problem which remains to be solved concerns the behaviour of the artificially bred insects when they are released in a natural environment. First experiments suggest that after some days of adaptation the sterilized males tend to behave like normal insects, although their longevity is significantly curtailed. However, the practical and economic feasibility of this method can be fully established only after pilot tests have been carried out on the most important tsetse fly species.

The main factor governing feasibility is the size of the natural tsetse fly population. It will certainly be effective to release sterile males after the population has been reduced by treatment with a nonpersistent insecticide. From this point of view, the release of sterile males may be regarded as a supplement to chemical control, opening the way to the complete elimination of the tsetse fly after a brief and nonpolluting insecticide treatment.

Conclusions

The methods of controlling animal trypanosomiasis are numerous and varied; each possesses advantages and disadvantages and these must be assessed in the light of local data and the end results that are sought.

In the fourth and final article in this series, the economic problems raised by animal trypanosomiasis and its control will be considered, in order to assess the relative costs and benefits of the various methods.

PART IV. ECONOMIC PROBLEMS

P. FINELLE

In the previous three articles the methods that can be used to control African animal trypanosomiasis and its principal vector, the tsetse fly, have been examined. However, control of the disease is not exclusively a technical problem because, as the Joint fao/who Expert Committee on African Trypanosomiasis has stated: "The problems caused by the disease should be viewed against the wider background of the general social and economic needs of the countries concerned."

Trypanosomiasis control is expensive. Before large-scale operations are undertaken, an economic analysis is necessary for the region in question to show the extent of the socio-economic losses due to the disease, to determine the priority of trypanosomiasis control in development planning, and to furnish the data needed to estimate the economics of possible control methods by a comparison of their cost with the results that can be expected of them.

Socioeconomic consequences

It may therefore be useful to assess the socioeconomic consequences of African animal trypanosomiasis, and the cost of the different control methods.

INFLUENCE ON LIVESTOCK DISTRIBUTION IN AFRICA

The number of cattle in Africa is assessed at around 160 million head, but distribution is very uneven among the various regions. Two phyto-climatic zones are virtually unsuitable for cattle raising, owing to lack of pasture: the desert or semidesert zone roughly corresponding to the regions where annual precipitation is less than 300 millimetres, covering about 12 million square kilometres, and the zone of dense rain forest, estimated to cover 3 million square kilometres. It can therefore be assumed that of the 30 million square kilometres of the African continent only half carry pastures suitable for livestock raising. These are the areas covered by wooded steppe or savanna. Yet even in these 15 million square kilometres, with their obvious suitability for grazing, livestock production is very unevenly distributed. While the number of cattle exceeds 20 per square kilometre in the most favoured places, there are areas which are completely devoid of livestock despite the presence of good-quality grazing and plentiful water supplies. This anomaly is partly due to animal trypanosomiasis, which occurs in tropical Africa over about 10 million square kilometres. As the infected areas include the 3 million square kilometres covered by equatorial forest, the land suitable for grazing in which livestock raising is limited by animal trypanosomiasis can therefore be estimated at 7 million square kilometres.

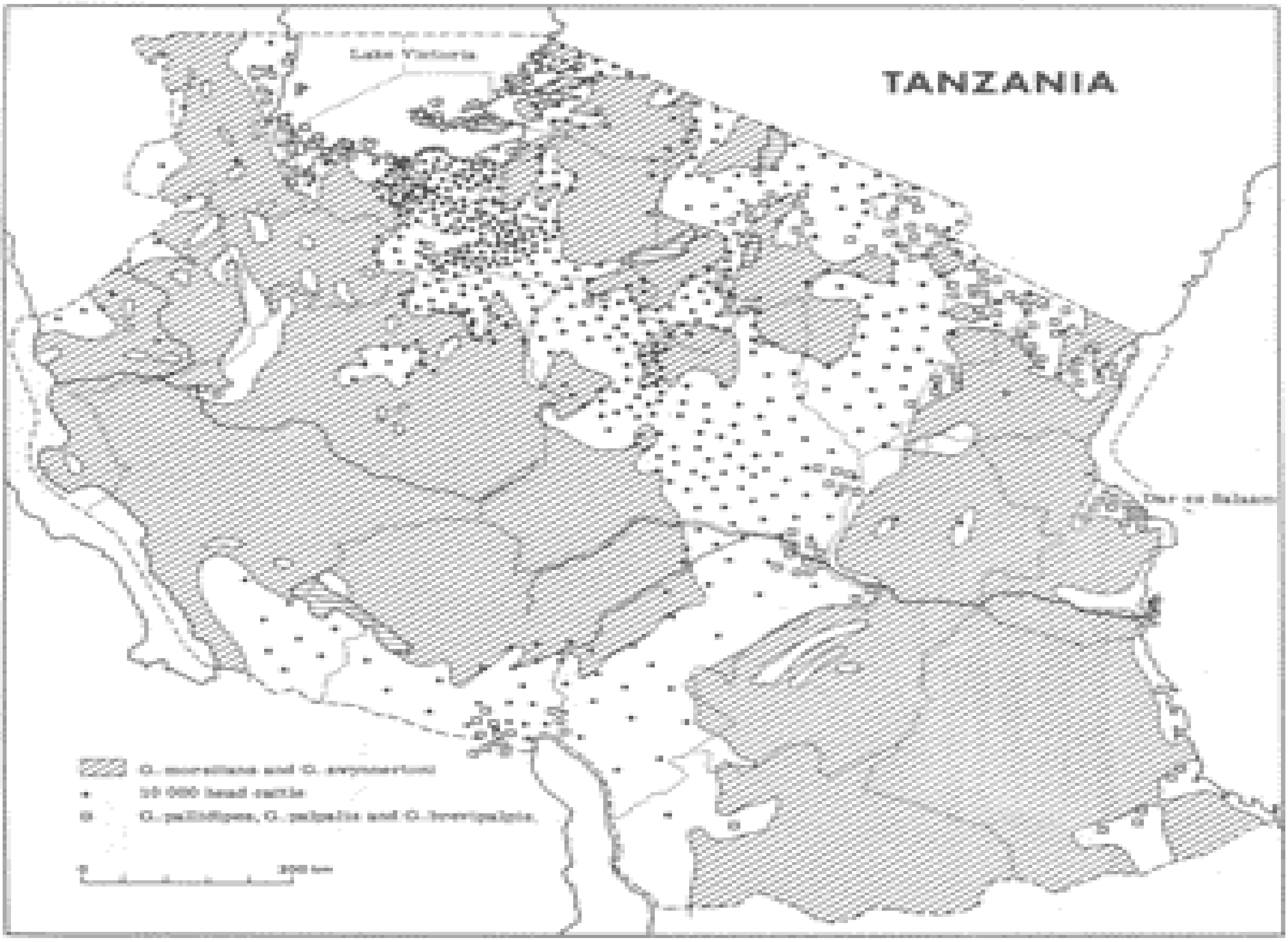
The consequences of animal trypanosomiasis vary in gravity from place to place. Broadly speaking, there are:

— areas where there is virtually no livestock raising;

— areas where only certain livestock breeds, possessing a natural resistance to trypanosomiasis (trypanotolerant breeds), can live;

— areas where, despite the presence of tsetse fly, livestock susceptible to trypanosomiasis can be raised either because of particular local conditions (tsetse flies are limited in number or confined to certain plant types) or because curative or preventive treatment is regularly practised.

In every case, however, trypanosomiasis leads to considerable under-exploitation of natural resources, and to a lower level of animal production than could be achieved if the disease were eliminated.



The influence of the tsetse fly on animal production is nowhere more clearly illustrated than in Tanzania, where the geographical pattern of cattle distribution is almost exactly the opposite of that of tsetse distribution.

ANALYSIS OF SOCIOECONOMIC CONSEQUENCES

The socioeconomic importance of African animal trypanosomiasis is extremely difficult to assess, as the data available are fragmentary and frequently very approximate. In the Present state of knowledge it is possible only to enumerate the various consequences of trypanosomiasis, in the hope that this list can serve as a base for assessments at the local level. Two sets of consequences, direct and indirect, can be identified:

1. *The direct consequences,* represented by the economic losses due to the disease and to the various expenditures incurred in controlling it.

They comprise:

a. mortality;
b. disease, which manifests itself in emaciation, retarded growth, abortion, temporary sterility and various organic lesions;
c. the cost of detection and treatment of infected animals (veterinary service personnel, trypanocidal drugs, equipment, operating expenses);
d. the cost of preventive operations (chemoprophylaxis, tsetse fly control, development of trypanotolerant livestock);
e. the cost of research on animal trypanosomiasis control.

2. *The indirect consequences* of animal trypanosomiasis affect:

a. human health, as the shortage of meat and milk causes protein deficiencies which are particularly harmful to children;
b. agriculture, because the lack of draught animals and manure reduces agricultural output;
c. livestock production: (i) trypanosomiasis limits the possibilities of introducing improved breeds, which are highly sensitive to this disease, thus preventing the upgrading of local livestock by crossing with imported sires; (*ii*) the presence of trypanosomiasis causes livestock to be concentrated in limited grazing areas, which results in their overuse and deterioration; *(Hi)* seasonal variations in the incidence of trypanosomiasis prevent some pastures from being grazed throughout the year and compel herdsmen to practise transhu-mance, which holds them back from integration in the national community;
d. the economy: the deficit in animal production compels countries where trypanosomiasis is rife to resort to imports of meat and dairy products, a practice harmful to their balance of trade.

TENTATIVE ESTIMATE OF DEFICIENCY TO BE MADE UP

While it is impossible to make even a rough assessment of the various socioeconomic consequences of tiy-panosomiasis, one can nevertheless try to estimate the meat production of the regions concerned, if the disease were controlled, on the basis of the following criteria:

— area of the tsetse-infected zone which could be used for livestock raising: 7 million square kilometres;

— average potential density: 20 cattle per square kilometre;

— total potential population of infected zone: 140 million cattle;

— present population: 20 million cattle;

— possibility of increasing the cattle population: 120 million head;

— average productivity in Africa: 12.5 kg per head per year;

— additional meat production: 1.5 million tons per year;

— value of additional meat production (on the basis of 50 cents per kg): US$750 million.

Although very approximate, this estimate shows how animal trypanosomiasis control could contribute to the development of animal production at a time when demand for animal protein, especially beef, is constantly growing and when projections indicate a serious shortfall in the years to come.

Cost of controlling African animal trypanosomiasis

Estimating the cost of controlling trypanosomiasis is no easier than the other estimates of the cost of the disease, as some expenses cannot be accurately quantified. The figures available are not always comparable because they are calculated according to criteria that vary with each country. Therefore, the data given here aim only at supplying an order of magnitude, which will allow an assessment and comparison of the average costs of the possible control techniques.

CHEMOTHERAPY

Approximate cost of a curative dose for a 300-kg bovine animal:

Diminazene (3.5 mg/kg) 15 cents Isometamidium (0.5 mg/kg) 19 cents

The cost of application is difficult to calculate, as it must include a proportion of the costs of the veterinary service and of its budget (peisonnel, equipment and operation) devoted to trypanosomiasis detection and treatment. However, this can be estimated to be around 50 cents. It may therefore be assumed that the cost of curative treatment for a 300-kg bovine animal varies between 65 and 70 cents.

CHEMOPROPHYLAXIS

Approximate cost of a preventive dose for a 300-kg bovine animal:

Isometamidium (1 mg/kg) 38 cents Cost of the opetation 50 cents

As preventive treatments must be repeated on average every four months, the annual cost of chemo-prevention for a 300-kg bovine animal would be about US$2.65.

INTRODUCTION OF TRYPANOTOLERANT LIVESTOCK

An analysis of the cost of importing trypanotolerant livestock was made in 1966[1] following the import into the Central African Republic of 254 animals from Upper Volta and Ivory Coast. The expenditure was broken down into the following percentages:

Purchase of animals	17.0
Transport	35.3

Salaries of purchasing mission personnel	25.3
Miscellaneous	22.4

The average purchase price of an animal was US$40, and its total average imported cost was US$247 (1966).

TSETSE FLY CONTROL

Data on the costs of tsetse fly control are numerous but difficult to compare because they depend on many factors, especially: the evaluation of the area of *the* cleared zone and its relation to the area actually treated, the accounting system used for certain expenses (management personnel, equipment amortization), the expenses involved in preliminary surveys, subsequent surveillance and conservation measures, and the utilization of the cleared zone.

Variations in the parity of the different cunencies involved also make comparisons difficult.

Deforestation

It is impossible to state average costs for deforestation operations because of their great variation. An example is the cost of deforested barriers in northern Nigeria in 1970, which varied between $3 500 and $4 200 per square kilometre.

Ground spraying

Costs vary greatly with the region and the species of tsetse fly. Some recent examples are given in Table 1. *Air spraying*

Table 2 gives the average cost of the various methods based on recent operations.

These data show how difficult it is to forecast the cost of tsetse control operations. Consequently, it would be hazardous to advise which technique would be the most economic in a given area. Recommendations can be made only after pilot trials have been carried out.

Table 1. Cost of ground spraying

Country	Tsetse fly	Average cost per		Remarks
		Treated	Cleared	
		...... *US. dollars*......		
Nigeria, 1971	*G. tachinoides G. morsitans submorsitans*	20-50	10-25	Not including management personnel and equipment amortization
Botswana, 1971	*G. morsitans centralis*	170	18	Insecticide 29 percent; personnel 54 percent; miscellaneous 17 percent
Zambia, 1971	*G. morsitans morsitans*	300	300	

Table 2. Cost of air spraying

Method	Country	Tsetse fly	Average cost per square kilometre, 1971		Remarks
			Treated	Cleared	
			... U.S. dollars ...		
Nonpersistent aerosol	Zambia	*G. morsitans morsitans*	210	210	Insecticide 56 percent; aircraft 29 percent; miscellaneous 15 percent
Persistent insecticide	Nigeria	*G. morsitans submorsitans*	2000	200	Insecticide 52-54 percent; helicopter 36-41 percent
Inverted emulsion of persistent insecticide	Kenya	*G. pallidipes*	218	218	This cost covers only: insecticide 67 percent, flying hours 33 percent

Conclusions

This attempt to analyse the economic problems raised by African animal trypanosomiasis shows that accurate data are so limited that it is almost impossible at present to draw up even an approximate report.

Aware of these significant limitations, fao plans to undertake a two-year study which will include a number of local surveys in carefully selected regions. The study will furnish the basic data for an assessment of the socioeconomic importance of trypanosomiasis and the costs of the various methods used to control it, and should draw the attention of interested governments and assistance organizations to the necessity for a very substantial increase in funds for field operations if the disease is to be controlled to an extent that would allow a significant expansion in animal production.

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A review of the prospects for vaccination in African trypanosomiasis

Part I

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This review of the prospects for developing an immunization procedure against trypanosomiasis explores a number of promising avenues of research. Part I covers variable antigen types (VATs); metacyclic antigens; *In vivo* and *in vitro* attenuation; and molecular and genetic engineering.

Part II, to be included in the next issue of this journal, will cover immunogenicity of subcellular fractions; immunological intervention against the tsetse fly; induction of increased resistance by immunostimulants; trypanotolerance; and infection and treatment. This will be followed by a brief statement of the conclusions reached.

The present methods available for the control of African trypanosomiasis, namely, systematic case detection and treatment, and tsetse control, do no more than limit the disease although both these approaches have been shown to be effective where they have been vigorously applied. The disadvantages attending the use of trypanocidal drugs include lack of availability of effective drugs, drug resistance and, in heavy tsetse fly challenge areas, the frequency with which treatment has to be applied, often to economically unacceptable levels. In the same way, while tsetse flies may be completely eradicated in certain areas by insecticide control, few regions of tsetse infestation have circumscribed boundaries and, unless cleared areas are defended (a costly exercise), reinvasion by the tsetse fly inevitably occurs. Thus there is little doubt that the introduction of an effective vaccine, if used strategically along with established control methods, would make an enormous contribution to the control of African trypanosomiasis, not only by increasing productivity in endemic trypanosome areas but also by opening up for exploitation the vast areas of the African continent largely devoid of livestock because of trypanosomiasis.

The major constraint to developing a trypanosome vaccine is the ability of the parasite to undergo antigenic variation. Murray and Urquhart (1977) reviewed the various attempts made to vaccinate both domestic livestock and laboratory animals and it was obvious from the reported studies that complete protection was readily achieved only if the same variable antigen type (vat) was used for immunization and challenge. When a distinct vat was used for challenge no protection occurred. Therefore, it would appear that an effective vaccine would have to contain all vats, possibly an insurmountable task as the number of vats, although as yet undetermined, is likely to be large. The result is that many workers in trypanosomiasis research consider the possibility of vaccination to be remote. It should be borne in mind, however, that many of these conclusions have been drawn from work on laboratory animals, which invariably succumb to massive parasitaemia. There is evidence to show that under certain circumstances cattle can control parasitaemia and then clinically recover. While this is particularly true for trypanotolerant breeds such as the N'Dama, it can also occur in the more susceptible zebu (Stewart, 1951; Chandler, 1958; Desowitz, 1959; Wilson, 1971; Wilson and Cunningham, 1971 and 1972; Murray *et al,* 1979). The greater capability of the bovine to control parasitaemia creates a new perspective on the question of vaccination. Furthermore, advances in scientific knowledge and technology have opened up several different avenues of research and the present article attempts to explore these.

Variable antigen types (VATs).

Antigenic variation, the major obstacle to developing a trypanosome vaccine, is the process whereby trypanosomes sequentially express a series of surface antigens; it is these antigens that are capable of inducing protective immunity. The immune response against each variant, although rapid and highly effective in destroying any trypanosomes that possess that particular antigen, is invariably *too* late *to* affect that proportion of the population that has altered its antigenic identity. Thus, parasitaemia rises and falls in waves with each parasite population carrying different surface antigens (reviewed by Cross, 1978; Vickerman, 1978). This picture of successive waves of a specific antibody chasing variant trypanosomes has been likened by Goodwin (1970) to a "Tom and Jerry cartoon with a monstrously inept cat pulling the place down in its efforts to pulverize a diminutive and highly resourceful mouse".

What would appear to be required is as complete as possible an understanding of antigenic variation in order that, eventually, it might be possible to produce an effective vaccine by the strategic use of certain trypanosomes or their components. At the population level, the authors' knowledge has been increasing over the past few years, thanks mainly to the concept of multiple cloning in which bloodstream populations are divided into their component parts, namely single trypanosomes, each of which gives rise, in a fresh host, to a defined population that can be frozen as reference material. It is essential that as large a number of clones as possible be isolated, since only then will it be possible to detect some of the subtle immunological and biological differences within and between populations.

This approach has begun to reveal what occurs within a parasitaemic peak, to the level of the individual parasite. It appears that a peak is usually a mixture of vats (Van Meirvenne, Janssens and Magnus, 1975a) with the switch to expression of another type, probably occurring before the appearance of antibody, which is thought to act merely as a selective agent (Van Meirvenne, Janssens and Magnus, 1975a; Le Ray *et al.,* 1977). Examination of sequence of appearance of vats arising within cloned infections has confirmed and extended the observation of Gray, 1965) that there is a tendency for certain types to occur preferentially in the early parasitaemic peaks. Thus, it would appear that vats can be divided into these early "predominant" types and other groups of vats that occur later (Van Meirvenne, Janssens and Magnus, 1975a; Capbern *et al.* 1977).

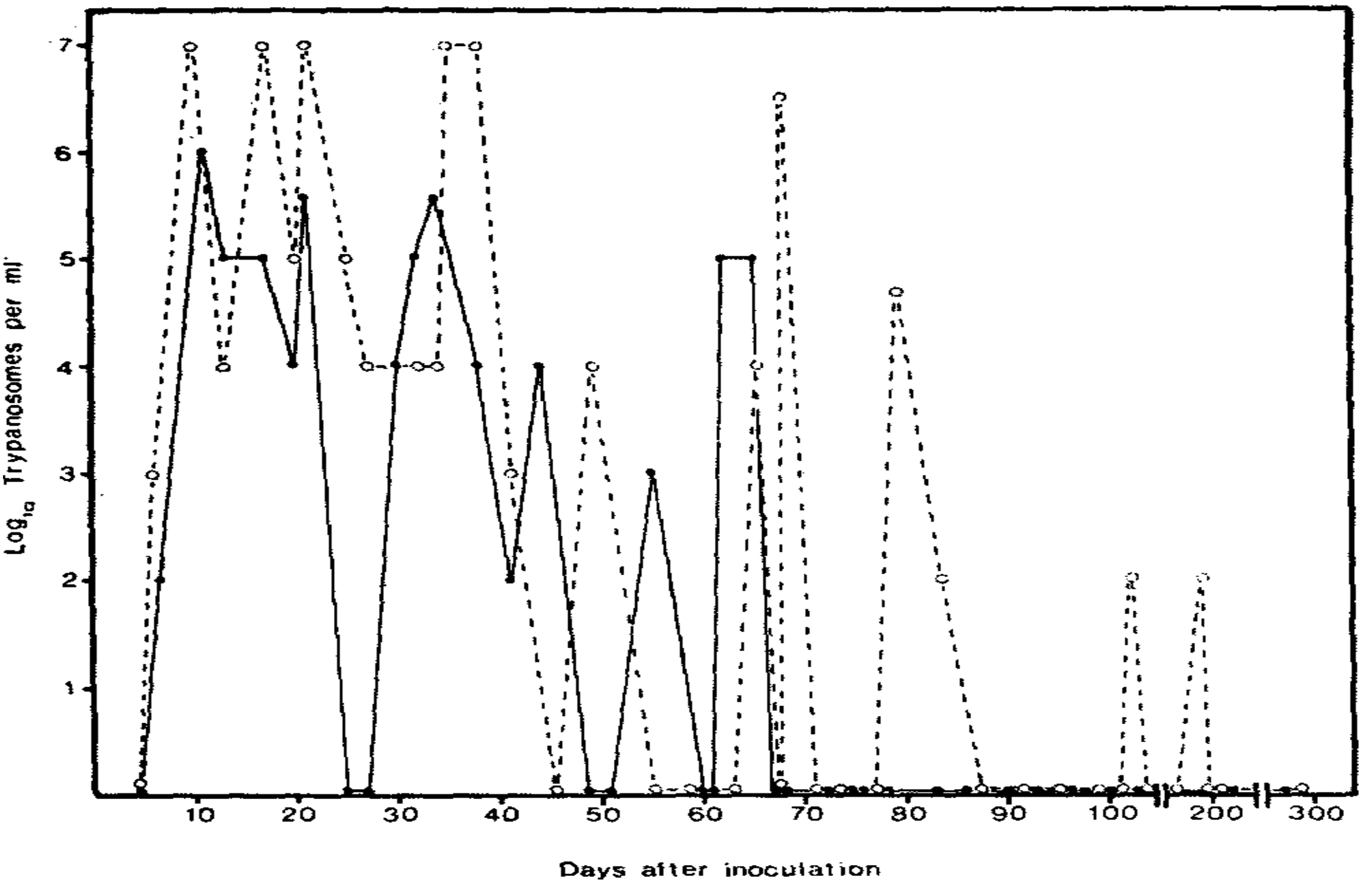

Figure 1 *Parasitaemia profile in an individual four-year-old N'Dama* (•) *and a four-year-old zebu* (o) *inoculated with* Trypanosoma congolense. *Note that the level of parasitaemia is lower in the N'Dama as is the duration of parasitaemia. Both animals were negative for detectable parasites for several months prior to the termination of the experiment and both made a clinical recovery.*

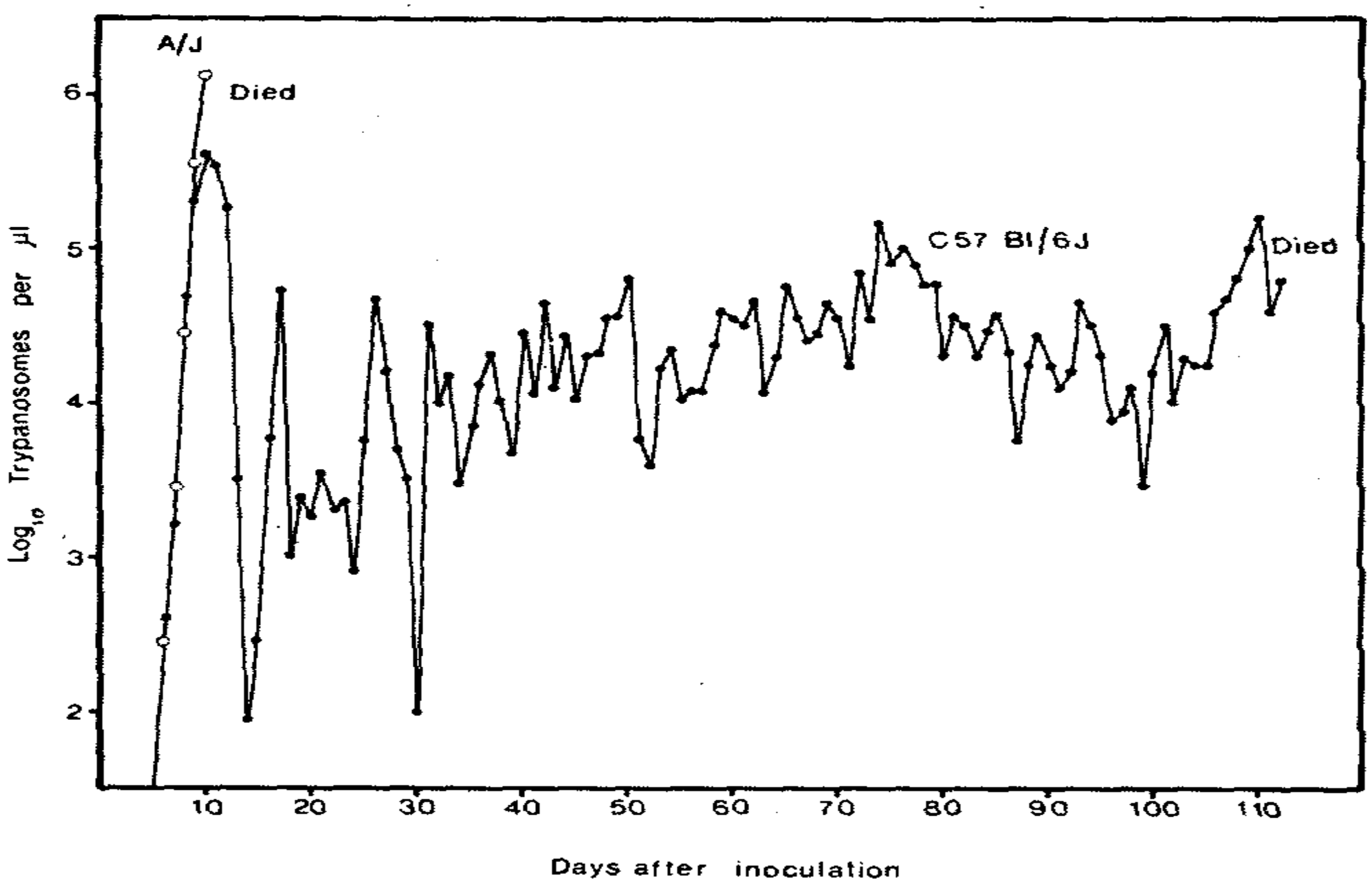

Figure 2 *Parasitaemia profile in an individual C57Bl/6J mouse* (•) *and A/J mouse* (o) *inoculated with* Trypanosoma congolense. *The CS7Bl/6J was able to control and reduce parasitaemia levels to a significantly greater extent than the A/J and as a result was able to survive for over 100 days. Irrespective of breed or strain, cattle were able to control and reduce parasitaemia to a much greater extent than mice. Following infection in mice, death was inevitable, whereas in cattle recovery may occur, particularly in N'Dama animals.*

The total number of vats that a trypanosome can express is known as its "vat repertoire," the full extent of which is as yet unknown although Capbern *et al.* (1977) have been able to isolate 101 vats from one clone of *Trypanosoma equiperdum.* Comparison of vat repertoires from different clones has been initiated (Van Meirvenne *et al.,* 1975b; Van Meirvenne, Magnus and Vervoort, 1977) and has revealed a surprisingly high degree of similarity; in fact, some vats have been found in every repertoire examined. In addition, there is now indirect evidence from serological studies that during an infection certain vats may recur, in some cases within a few weeks of one another. This has been described in cattle infected with *Trypanosoma congolense* (Wilson and Cunningham, 1971) and with *T. brucei* (Nantulya, Musoke, Barbet and Roelants — unpublished results).

As regards vaccination, a rational approach may be successful. Immunization against individual vats is highly effective using such regimes as infection and treatment; irradiated organisms; killed organisms; crude emulsions containing released soluble antigens; formalized whole infected blood or plasma and purified variable antigen glycoprotein (reviewed by Murray and Urquhart, 1977). As little as 3 μg of variable antigen can give protection in mice (Baltz *et al,* 1977). A cocktail vaccine based on predominant vats is likely to be effective against with that repertoire. Investigation of the feasibility or such an approach requires complete analyses of the number of vats, both predominant and otherwise, within a repertoire, of the extent of crossreaction between repertoires and, eventually, of the number of vats that exist within and without given geographical areas.

A word of warning regarding studies on antigenic variation: it is necessary to define not only the parasite but also the host. The parasitaemic patterns produced by a trypanosome will vary with species of host, breed or strain, age, sex, etc. (Figures 1 and 2). In this regard, there is little doubt that exploitation of the *in vitro* culture system, which supports the growth of animalinfective forms of trypanosomes (Hirumi, Doyle and Hirumi, 1977) by eliminating the variable effects of the host, must yield new information on the basis and mechanisms of antigenic variation. Since much of the above work has been carried out with *T. brucei* the authors believe that it is essential that similar efforts be made with *T. congolense* and *T. vivax,* which are regarded as the major pathogens of bovine African trypanosomiasis.

Metacyclic antigens.

Following ingestion by the tsetse fly, *T. brucei* loses its surface coat, which contains the variable antigen. It eventually regains the coat in the fly's salivary gland in becoming the mammalianinfective metacyclic stage (Vickerman, 1969). It has been suggested that all trypanosomes of a particular clone revert to a common "basic" antigen type in the salivary gland (Jenni, 1977, for *T. brucei;* Nantulya, Doyle and Jenni, 1979, for *T. congolense)* akin to the "basic" type arising in the bloodstream after cyclical transmission (Gray, 1965). Vaccination against such types would obviously be of importance. However, there is now evidence to suggest that this is not the case and that *T. brucei* metacyclics arising from the passage of a clone through the tsetse are antigenically heterogeneous (Figure. 3) (Le Ray, Barry and Vickerman, 1978; Barry and Hajduk, 1979; Barry *et al,* 1979b), although it is still the case that there may be only a limited number. A drawback to the potential use of metacyclic populations for vaccination is that they are antigenically unstable (Le Ray *et al,* 1977; Le Ray, Barry and Vickerman, 1978), preventing mass production of antigen and mRNA (see later, molecular and genetic engineering) for potential vaccine preparation. However, these *dfficulties* may be overcome by a recently devised protocol (Barry *et al,* 1979b) whereby antigenically more stable mammalian bloodstream forms with the same vat as metacyclics can be identified and cloned giving rise to populations suitable for bulk preparative procedures. This approach could be pursued to define the vat complement of metacyclic populations with a view to vaccination against trypanosomes of that vat repertoire. Furthermore, it is essential to determine the degree of crossreaction between metacyclics of different repertoires.

Figure 3 *Antigenic heterogeneity among mammalianinfective metacyclic forms in the saliva of a tsetse fly. The fly was allowed to salivate onto a heated glass slide, to which immunofluorescence was applied using specific antiserum against a characterized bloodstream form trypanosome* vat. *Metacyclics with trypanosome* vat *fluoresce strongly, while those of other* vat *display the weak fluorescence of the counterstrain.*

The *in vitro* culture system would also appear to have potential in this area. It has now been shown that "bloodstream forms" of *T. brucei* in culture (Figure 4) can be induced to undergo morphological changes similar to those that occur in the fly, including the eventual production of metacyclic types, by appropriate manipulation of the culture conditions (Hirumi, Hirumi and Doyle, 1978a). As it has now become possible to clone parasites in culture (Hirumi, Hirumi and Doyle, 1978b) this approach might offer a source of metacyclic types of defined antigenic identity.

Figure 4 *Bloodstream forms of* Trypanosoma brucei (*ILR-TbC-221*) *grown* in vitro *for over 31 months. Giemsa's stain.*

In vivo **and** *in vitro* **attenuation.** Another facet of the problem is that, despite the authors' steadily increasing knowledge of antigenic variation, very little is known of how it is linked to the biology of the trypanosome and the hostparasite interaction, apart from the fact that it allows the trypanosome to evade the host's immune response and thus survive. For example, an association between vat and virulence has been proposed (McNeillage and Herbert, 1968; Van Meirvenne, Janssens and Magnus, 1975a) although it is essential that the precise circumstances of such a link are fully investigated (Barry, Le Ray and Herbert, 1979a). It is a common mistake to equate the vat of a clone with all the characteristics displayed by that clone; the vat is just one phenotypic marker. Confirmation of a link between vat and virulence, and the observation that trypanosomes of different vat may interfere with the expression of each other at the population level (Herbert, 1975) conceivably could be exploited to decrease the number of variable antigens required in a vaccine. At a later stage of infection, after expression of predominant vats, it appears that trypanosomes are in some way biologically altered as evidenced by their decreased infectivity and virulence in fresh hosts. The basis of this and whether it is linked to vat or some other characteristic of the parasite remains to be investigated.

Can these changes in behaviour be induced artificially and incorporated into a vaccination protocol ? The possibility now exists of attenuating trypanosomes by continuous passage in culture. In preliminary studies, it has been found that mice infected with parasites maintained *in vitro* by serial subcultivation over 12 months have shown alteration in pathogenicity when compared with noncultured organisms or organisms that have been maintained *in vitro* for less than three months (Hirumij unpublished data). The potential protective effect of attenuated protozoa has already been demonstrated in the control of babesiosis in cattle in Australia (Callow, 1977).

Molecular and genetic engineering.

There is little doubt that the basis of understanding antigenic variation will come from investigations of the molecular biology of the trypanosome. *In vitro* cultivation techniques and recently developed tools in biochemistry and genetic engineering have opened up new horizons. Thus studies of the type carried out by Williams *et ah* (1978) on trypanosomal RNA will provide much essential information on trypanosome biology. Reannealing studies on the nucleic acid coding for the vat repertoire should give an insight into the size of the repertoire, the extent of similarity between different repertoires and the molecular nature of the genes involved. The genetic control of expression of antigenic variation should be studied; artificial restriction of a trypanosome population to expression of only a limited number of its vats might allow effective vaccination.

In any discussion of vaccination, consideration must be given not only to the obvious application of these newly developed techniques to antigen production but also to novel approaches to vaccination. It is possible that in the near future many protein vaccines will be produced from largescale bacterial cultures that contain the gene sequences coding for the appropriate proteins. Recombinant dna technology has already been applied to the largescale production of human somatomammotropin (growth hormone) (Shine *et al.,* 1977), a precious substance that has traditionally been isolated from human placenta.

A further example of the application of recombinant dna technology to vaccine production is the development of a bacterial strain that is capable of producing the native chickalbumin protein at a level of 10 percent by weight of the bacterial cell (Mercereau-Puijalou *et al,* 1978). Thus bacterial strains can be developed to produce proteins for vaccines that normally would be either too expensive to isolate or impossible to purify because of limited amounts of starting material.

In addition to vaccine production in bacteria recent reports describe new techniques that possibly could find application in vaccination procedures. The transfer of specific genes from one genome to another has now been achieved. An example of such a transfer was reported by Wigler *et al.* (1978) where a specific viral gene coding for the enzyme thymidine kinase was purified by electrophoresis and introduced into a thymidine-kinasedeficient tissueculture cell line. Many of the tissueculture cells were able not only to incorporate the dna sequence into their genome but also were able to produce the enzyme at apparently normal levels. It may be possible, therefore, to modify certain tissues during a proliferative stage so as to yield a gene product to correct a genetic deficiency or possibly to produce a foreign protein for use in vaccination.

In other novel procedures recently reported by Dimitriadis (1978) and Ostro *et al.* (1978), differentiated tissue cultures were modified to produce a specific protein for a limited time. In each of these reports, a specific purified messenger RNA (rabbit globin) sequence was encapsulated in a lipid micelle called a liposome. The liposome was introduced to tissueculture cells with the membrane of which the liposome presumably fused. The purified messenger RNA was thereby introduced into the cytoplasm of the cells where it was translated into rabbit globin protein. The messenger RNAS used in such a procedure are degraded at a normal rate and can be modified to delay the cell's normal messenger RNA degradation processes. The normal cell's genome is not permanently modified and would produce the desired protein only for a limited time. In this manner, one could presumably use specific messenger RNAS and specific target tissues to produce the protein required for immunization. The inherent appeal of such a system would be that target tissues could produce sufficient quantities of a specific protein for a limited amount of time, thus allowing immunization to occur. Although such applications of molecular biology to vaccination are presently a dream, there is little doubt of their being a reality in the future. ■

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Part II

M Murray, *J.D. Berry, W.I. Morrison, R.O. Williams, H. Hirumi and L. Rovis*

In Part I of this review of the prospects of vaccination against African trypanosomiasis, contained in the previous issue of World Animal Review, the constraints in developing a vaccine were discussed and current knowledge on the molecular biology of the trypanosome and on antigenic variation with respect to possible future vaccines was evaluated. In this part other possible regimes for immunological intervention, including the immunogenicity and cross reactivity of trypanosome subcellular fractions, reduction of host susceptibility to African trypanosomes by the nonspecific use of immunostimulants or chemotherapy and also the role of trypanotolerant livestock in such approaches, are discussed.

Immunogenicity of subcellular fractions.

Modern biochemical technology has allowed the isolation, purification and characterization of a whole range of trypanosomal subcellular fractions. Thus, the variable antigen, which is responsible for induction of protective immunity, has been shown to be a glycoprotein with a molecular weight of 60 000 to 65 000 daltons, depending on species (Cross, 1975 and 1977 with *T. brucei;* Baltz, Baltz and Pautrizel, 1976, and Baltz *et al.,* 1977 with *T. equiperdum;* Rovis, Barbet and Williams, 1978 with *T. congolense).* While (at least with *T. brucei)* the N minerals of different variable antigen types (vats) differ in amino acid sequence (Bridgen, Cross and Bridgen, 1976), there is now evidence that different vats of the same and also of different species of trypanosomes *(T. brucei/T. congolense)* may have cross-reacting determinants (Barbet and McGuire, 1978). Although it would seem likely that these are hidden from the host's immune response the possibility of vaccination against these determinants must be pursued.

Crossreaction may occur at different levels. For instance, some crossreacting determinants may be found only on vats within one vat repertoire (the total number of vats that a trypanosome can express), while others may be universal. Complete characterization of all determinants, using such techniques as monoclonal antibody production (Kohler and Milstein, 1975), should reveal the structural and functional significance of any crossreacting components. Hyperimmunization against such components may prove effective if manipulated properly.

Most biochemical and immunological studies to date relating to immunogenicity of subcellular fractions have been aimed at analysing the variable antigen of the surface coat It is possible, however, that at some time in the trypanosome's complex lifecycle "weak spots" amenable to immunological control might be exposed. Thus, recent investigations have been made into the purification of a range of subcellular fractions of the trypanosome such as flagellum, membranes and kinetoplast. The biological characteristics and immunogenicity of these fractions have been investigated and compared with those of variable antigen. What the authors have found in studies on *T. brucei* in the mouse is that flagellum and membrane fractions stimulate protection against homologous vat challenge to the same degree as variable antigen (Table 1). It is likely that this is the result of the presence of variable antigen in these subcellular fractions although it is interesting that, per unit weight protein, flagellum is more effective than the purified variable antigen. No protection was achieved on challenge with a different vat although with the membrane and kinetoplast preparations there was significant prolongation of survival accompanied by an alteration in the parasitaemic profile. This was possibly a result of a nonspecific stimulant effect of these fractions (see below, the section on "Induction of increased resistance by immunostimulants").

Using a subcellular fraction of *T. brucei* or *T. rhodesiense* that probably contained a mixture of variable antigen, mitochondrion and kinetoplast to immunize mice, Powell (1976; 1978) found increased survival times and reduced parasitaemias in mice challenged with *T. brucei.* Using *T. brucei* in *C57BI/6J* mice and a similar fraction for immunization, the authors were able to stimulate protection only if trypanosomes of the same vat were used for challenge (Table 1). When another vat was used for challenge protection was not achieved although there was a significant increase in survival time. Of considerable interest is the report of Powell (personal communication) that the use of the above fraction in aluminium hydroxide protected across trypanosome species. Three sheep were immunized in the "feet" with three doses of 1-mg protein fraction of *T. rhodesiense* in aluminium hydroxide. On subsequent challenge with *T. vivax* each of the three sheep developed a transient parasitaemia and then made a complete recovery. All three challenge control sheep became infected and died. These observations now await confirmation.

TABLE 1. **Immunization with various subcellular fractions of Trypanosoma brucei**

Fraction	**Challenge**	
	Same VAT	**Different VAT**
Variable antigen	Complete protection	No effect
Flagella	Complete protection	No effect
Membrane	Complete protection	Prolonged survival
"Powell" fraction	Complete protection	Prolonged survival
Kinetoplast	Increased resistance	Prolonged survival

Immunological intervention against the tsetse fly.

It should be borne in mind that trypanosomes have a complex lifecycle in which there may be "weak spots" susceptible to immunological intervention. For example, stimulation of the mammalian host's response to the tsetse bite or saliva may be such a method. Also, the trypanosomes in the midgut of the tsetse fly are uncoated (Vickerman, 1969) and possess a common surface antigenic identity (Seed, 1964; Barry and Vickerman, 1979). As ingested antibody can retain specific activity for up to four days in the tsetse midgut (Cunningham *et ah,* 1962) it would be of interest to study the effect on fly infection of uptake of high levels of antibody against these common surface antigens (Barry and Vickerman, 1979). Once again, the antigen could be supplied by *in vitro* culture techniques.

Induction of increased resistance by immunostimulants.

The host's immune response to the trypanosome is still poorly understood but there are indications that it is defective. For example, a feature of African trypanosomiasis is the development of a state of immunosuppression (reviewed by Murray *et al.,* 1974) and hypergammaglobulinaemia — involving mainly *igM* (Mattern *et al.,* 1961;

Luckins, 1972), a large proportion of which would appear not to be specific for the trypanosome (Freeman *et al.,* 1970; Corsini *et al.,* 1977). It is possible that the capacity of the trypanosome to survive may be related to the immunologically compromised state of the host. Thus, a complete understanding of the basis of immunosuppression and the relevant immunological effector mechanisms that kill the trypanosomes might allow some form of intervention so that effector mechanisms are stimulated and the host is able to control or eliminate the parasite.

TABLE 2. **Effect of Bordetella pertussis on survival of A/J and C57BI/6J mice challenged with Trypanosoma congolense**

Percentage survival

Days after challenge.	**A/J** 1		**C57BI/6J** 1	
	Control	**B. pertussis**	**Control**	**B.pertussis**
10	68	96	100	100
15	0	43	88	100
20		43	88	96
30		43	88	96
40		39	80	96
50		35	80	91
100		8	26	64
150		0	0	24
Average time to death, in days	11.2±1	26.4±24.6 2	75.4±35.4	113.3±47.8 2

[1] 25 mice per group.

[2] Significant to controls (arithmetic mean ± one standard deviation).

In this regard, the authors attempted to improve the host's immune response, and thus host resistance, by using the immunostimulants *Bordetella pertussis, Corynebacterium parvum* and Bacillus Calmette-Guérin (BCG) prior to or at the time of challenge (Murray and Morrison, 1979). So far this strategy has been successful, at least in mice. It was possible to increase survival times in both susceptible (*A /J)* and more resistant *(C57BI/6J)* strains of mice (Table 2). Thus, following challenge with *T. congolense,* the treated *A/J* strain behaved in a manner much more akin to the more resistant *C57BI/6J.* It should be emphasized, however, that complete protection was never induced by this method. The reduced susceptibility appeared to be ? related to the ability of these immunostimulants, particularly *B. pertussis* and *C. parvum,* to delay the onset of parasitaemia or to reduce the level of parasitaemia (Figures 1 and 2). The best results were achieved when both of these parameters were affected. The possibility that these immunostimulants acted by improving the immune response is being investigated at present.

The strategy of increasing host resistance by nonspecifically acting immunostimulants offers an attractive alternative or additional approach to the complex undertaking of a breeding programme for trypanotolerant livestock. However, whether immunostimulants can be employed effectively in this way in domestic livestock remains to be determined.

Trypanotolerance.

As trypanotolerance was the subject of an earlier review in this journal (Murray *et al.,* 1979), the authors will limit their remarks.

There is now a substantial body of evidence to indicate that certain breeds of cattle, sheep and goats are able to survive and be productive without the aid of treatment in areas of tsetsefly challenge, where other breeds cannot. This attribute is known as trypanotolerance although, as this state is not absolute, it would be better termed as reduced susceptibility. These trypanotolerant breeds are of considerable interest and importance. Not only is there evidence that they are economically exploitable in their own right but they also provide an excellent experimental system for evaluating the important factors that influence host susceptibility to trypanosomiasis. If it is confirmed, as the results of Desowitz (1959) strongly indicate, that the basis of trypanotolerance is the ability to mount a more effective immune response to the trypanosome, it might well be that any immunotherapeutic strategy that may be developed would be more effectively employed if used in trypanotolerant breeds of animals.

Infection and treatment.

Bevan (1928; 1936), working in Southern Rhodesia, was perhaps the first worker to note that bovines that recovered from clinical trypanosomiasis after treatment frequently remained in good health despite reinfection, suggesting that it might be possible to create a "nonsterile" form of immunity. That infection and treatment regimes can achieve this has been confirmed more recently by Wilson and his colleagues working in East Africa (1957 a and b; 1976). Since the method developed is immediately applicable, the authors would like to describe these studies in some detail.

Wilson attempted to evaluate the use of different drug strategies in the development of immunity in young cattle over a period of two to three years. "Immunity" was assessed by trypanocidal drug requirement, development and duration of parasitaemia, ability to maintain normal blood values in the presence of parasites, calving rates in breeding stock and growth rates in a beef herd.

In one experiment a breeding herd located in a high tsetsefly challenge area was managed under the following drug regime. Animals were treated with Berenil, treatment being determined not by the presence of the parasite but on the basis of the development of clinical signs of disease and of packed red cell volume (pcv) below 20 percent (Wilson, Paris and Dar, 1975a).

During the first and second years requirement for treatment did not change; an average of eight treatments was used and animals became parasitaemic about 30 to 40 days after each treatment. However, during the second year there was indirect evidence of reduced susceptibility to trypanosomiasis: for example, the number of live calves born increased and subsequent mortality decreased; abortions, a not uncommon occurrence in bovine trypanosomiasis, also decreased.

Even more promising results were achieved in a later series of experiments in which steers were introduced into an area of medium trypanosome challenge (Wilson *et al.,* 1975b; Wilson *et al.*. 1976). As before, a treatment regime based onappearance of clinical signs or pvc below 20 percent was used in a first group of cattle over a period of 29 months. The period between drug treatments, which was initially between 50 and 60 days, increased to around 130 days by the ninth treatment; at the same time the periods when trypanosomes were present in the blood without great adverse effect had increased from a mean of 11.7 days prior to the first drug treatment to 30.9 days by the ninth treatment. When the drugs were withdrawn from a number of steers six months before the end of the experiment, all survived and the growth rate and pvc values were the same as in the steers with access to therapy, showing that the resistance that developed was not drag dependent.

In contrast, a second group of steers, all of which were treated with Berenil whenever blood infection rather than clinical signs was detected, showed no evidence of developing immunity and they required treatment every 26 days throughout the course of the experiment. When treatment was withdrawn from some of the steers six months before termination of the experiment, their mean weight gains were 58 kg less than those steers in which treatment continued and, in addition, one animal died.

With a third group of steers, Samorin (isometamidium) was used in the same way as Berenil in Group 2, and there was some evidence of the development of immunity. While the need for therapy did not decrease throughout the experiment, pvc values and growth rates were maintained in the animals in which drug treatment was withdrawn six months prior to termination of the experiment, despite the more frequent presence of parasites in this group.

In terms of weight gain there was no doubt that the use of drugs prophylactically on a group basis, particularly Samorin, gave by far the best results. Nevertheless, as Wilson *et d.* (1976) pointed out, the particular advantage in encouraging the development of nonsterile immunity by infection and treatment might lie in the development of lesssusceptible breeding herds over periods of several years, particularly in areas of low to medium trypanosome challenge. This procedure might be even more successful if used with trypanotolerant breeds of livestock. It should be emphasized that drug resistance was not experienced in these studies.

The basis of this form of tolerance or "nonsterile" immunity to the trypanosome awaits investigation. It may be that the host has built up a whole battery of immune responses to the range of metacyclic antigens and vat repertoires that occur in that particular location, or alternatively there might exist a common priming antigen that allows the host to make a series of secondary responses to each vat, thus controlling the infection in the manner of the carrierhapten effect proposed for malaria by Brown (1971). However, it might be related to some nonspecific effect such as expansion and activation of the mononuclear phagocytic system.

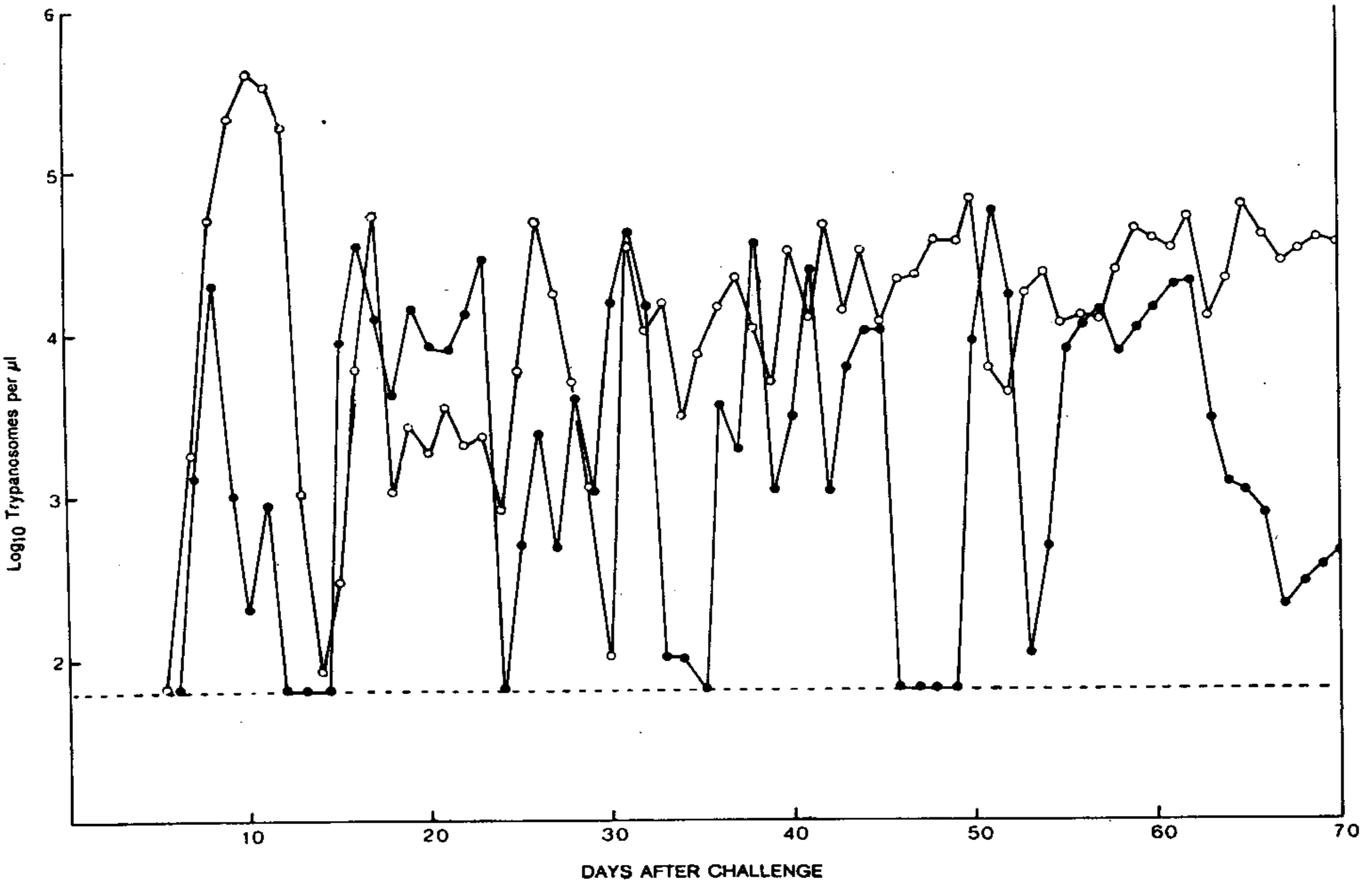

Figure 1. *The parasitaemia profile of a* Bordetella pertussisfreated *C57BI/J61 mouse (•) and a control C57BI/6J mouse (o) challenged with* Trypanosoma congolense. *The broken line just below 2 logio trypanosomes per \il indicates the level of sensitivity for detection of trypanosomes with the haemocytometer technique.*

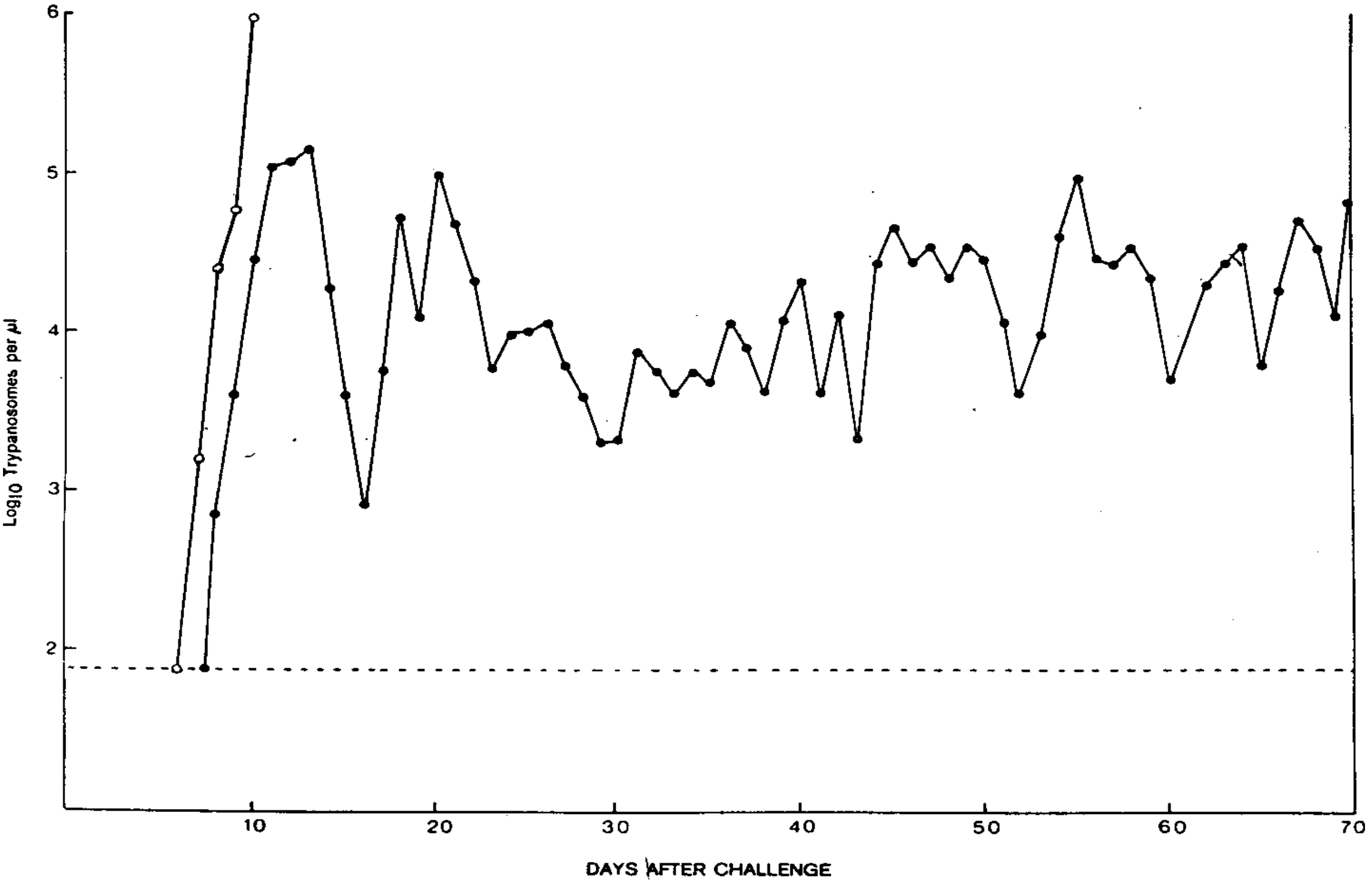

Figure 2. *The parasitaemia profile of a* Bordetella pertussistreated *A/J mouse (•) and a control A\J mouse (o) challenged with* Trypanosoma congolense. *The broken line just below 2 logio trypanosomes per* (i/ *indicates the level of sensitivity for detection of trypanosomes with the haemocytometer technique.*

Conclusions.

While a vaccine against trypanosomiasis is not an immediate prospect, what the two parts of this article have attempted to show is that there are several promising avenues for immunological exploration, namely vat cocktails, trypanosomes attenuated in *in vitro* culture systems, genetic engineering, crossreacting subcellular fractions, intervention against the tsetse, nonspecific induction of increased resistance by immunostimulants, and infection and treatment regimes. It is likely, if any one of these areas is rewarding, that the resulting vaccine will be more successfully exploited, at least initially, in trypanotolerant animals.

The authors would like to emphasize that any immunotherapeutic solution for trypanosomiasis control can come only through a thorough knowledge of the lifecycle of the trypanosome and its basic biology coupled with a comprehensive understanding of the immune response of the finite host. ■

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Trypanotolerant cattle breeds in Zaire

by J. Mortelmans and P. Kageruka

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Cattle were not raised in southwestern Zaire (formerly the Congo Free State) until the early 1880s, when the first animals imported from Angola formed the foundation stock of government stud farms established at Zambi, Kitobola and Dolo to breed draught animals. Later, private stock farms also bred draught bullocks while missions bred cattle both for slaughter and for use as draught animals. At the turn of the century the government farms had about 1 000 animals altogether. By about 1904 the government herds numbered 4000 head of cattle, and in 1907 there were 70 cattle farms with about 5 000 head (Tobback, 1930). At about the same time, the phenomenon of trypanotolerance was noticed among the humpless cattle of West Africa.

The Dahomey breed

In 1904, 50 head of cattle were bought in Benin (formerly Dahomey) by a Mayombe planter (Drousie, 1919; Flamigni, 1939). This breed of cattle appeared shortly afterwards at the Kangu mission and at the Government Livestock Station at Zambi (Van Damme, 1911). In 1912 Van Damme found these cattle very hardy, well adapted to poor regions and useful as slaughter stock. Importation from Benin continued during the period prior to the First World War; the animals multiplied and spread throughout the Mayombe region and other areas of southwestern Zaire. Drousie (1919) described the Dahomey cattle in this region as being small (90 to 105 cm withers height), but with a relatively high dressing percentage (about 50 percent). Because of the breed's hardiness, he suggested it be spread among the African population, especially because its trypanosome resistance allowed it to be raised in the forest zone where no other bovines could survive.

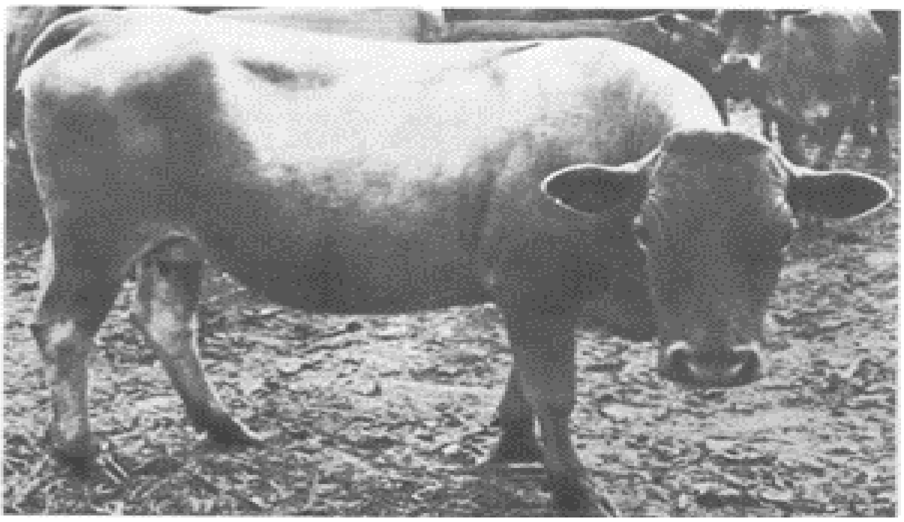
Flamigni (1948) found these animals very hardy and able to live in hot humid countries on semisavanna and in forests, but noted that they need suitable feed to survive; while they require practically no care, they do need good grazing and water. Since Dahomey cattle like to graze at night, they should not be enclosed in paddocks or pens. However, they should be provided with roofs to protect them from rain. These animals like to roam freely in small herds of 3 to 6 head; they live on forest undergrowth and fallow land and seek grazing everywhere, sometimes traversing great distances. According to Flamigni (1948, 1951) the live weight of an adult animal varies from 150 to 200 kg, but may be as much as 200 to 300 kg, while some bulls weigh even more.

The N'Dama breed

The other trypanotolerant breed in West Africa, the N'Daua or Guinean, was introduced into southwestern Zaire in the early 1920s (Tobback, 1930; Flamigni, 1939; Taminiau, 1960). This too is a small breed that is very hardy and capable of tolerating humid heat The climate of the region is characterized by two well-marked dry seasons lasting from a month and a half to three to five months, and a mean annual rainfall of 1 000 to 1400 mm.

N'Dama cattle, first introduced by the large livestock enterprises, have spread into the Kwango-Kwilu region to the northeast Nevertheless, the N'Dama is found primarily on the stock farms of southwestern Zaire, either as a purebred or as a cross bred. On the eve of the Second World War three major stock farms were located in this region: the Kisantu mission with 9 700 head of cattle, the Compagnie des pioduits et frigoriféres du Congo (Isle of Mateba) possessing about 7 000 animals, and the Compagnie Jules Van Lancker at Kolo with some 3 100 head. Six other companies had over 500 head of cattle each and there were 15 smaller farms (Tobback, 1940). By the end of the war, the three major stockraisers owned respectively 9 770, 8 464 and 9 598 head of cattle (Tobback, 1946).

N'Dama cattle have been used to improve the conformation of the Dahomey breed while preserving its hardiness and trypanotolerance, and to impart greater hardiness and trypanotolerance to the larger, heavier and less resistant breeds of southwestern Zaire (e.g. the Angolain, Mateba and zebu).



N'Dama cattle have a latent precocity and reach slaughter weight quickly when raised under good conditions. They have been used to improve the conformation of the Dahomey breed and impart greater hardiness and trypanotolerance to the larger, less resistant breeds of Zaire

However, the resistance of zebu crossbreds has been found inadequate, and since 1946 efforts have been directed toward upgrading them to N'Dama (Tobler, 1961). For these purebred cattle to prosper, it was necessary to give them the right environment, i.e. improved pastures with careful control of brush fires, soundly organized use of the range or pastures and watering points, regular surveillance of stock management, and veterinary care. Several writers stress that it is necessary to maintain high standards of feeding and management if the best results from these anim:.ls are to be obtained (Renier, 1953; Gretillat, 1953; Druet, 1958; Gillain, 1958; Micknevicras, 1959). They also recommend the N'Dama breed for the stocking of the Kwango-Kwilu region and base their recommendations on very encouraging results observed on various farms in the region.

The performance of N'Dama cattle under prevailing conditions in southwestern Zaire has proved excellent, especially in view of their tolerance to trypanosomes in this tsetse flyinfested region. Taminiau (1960) quotes the following average weights recorded at the Mvuazi station: calves at birth, 19 to 25 kg; one-year-old heifers, 127 kg; three-year-old cows, 241 kg; four-year-old cows, 281 kg; adult cows, 290 kg; five-year-old bulls, 430 kg; six-year-old bulls, 456 kg. The slaughterhouse dressing percentage averaged 54 percent (maximum 58 percent and minimum 52 percent). At Gimbi in the trypanosomiasis belt, the average dressing percentage is 50.8 percent. At Gimbi, Flamigni (1959) records live weights of 300 to 325 kg for cows and about 400 kg for five- to six-year-old bulls. Tobler (1961) records for the Kolo stock farm a weight of 280 kg for three-year-old steers, 335 kg for four-year-olds, 345 to 375 kg for five-year-' olds, and 450 to 550 kg for six-year-old bulls. For the same categories in Guinea he quotes 177 kg, 220 kg, 248 to 310 kg and 300 kg respectively from statistics provided by the Ministry of Agriculture of Guinea. In Guinea (their country of origin), the animals attain slaughter weight at 5 to 7 years of age. Tobler was able to slaughter his cattle at the age of 4 years, by which time the animals had reached a greater slaughter weight than in Guinea. Tobler concludes that the N'Dama breed possesses a latent precocity. These animals reach slaughter weight more quickly when raised under good conditions. Selective breeding, good management and above all a satisfactory and reliable source of feed are the key to early maturity.

Good conditions have a favourable influence on trypanotolerance in both the Dahomey and NT>ama breeds. Wellfed animals show a high resistance to trypanosome infections. Their growth curve is not affected by the infection, and the parasites as a rule quickly disappear from the peripheral bloodstream. It has been observed that even calves a few weeks old from healthy cows barely suffer from attacks of *Trypanosoma congolense.*

Current situation

A recent visit to southwestern Zaire has convinced us of the success obtained by a large livestock enterprise which has introduced N'Dama cattle into this region. Starting with 50 N'Dama heifers and two N'Dama bulls in 1927, the enterprise had expanded to 25 000 head by 1950 and stabilized at that level, with some 6 000 head being available for sale annually. Performance at this enterprise shows a 58 percent dressed weight for slaughter stock, an 80 percent annual calving rate, and approximately 100 percent fertility in the breeding units.

Success obtained in southwestern Zaire has led to the extension of the N'Dama breed into Bandundu Province, where enormous land areas are available for the establishment of new pastures. A total of 950 heifers were transferred to Mushie in 1965-68 (400 in 1965, 350 in 1966, 100 in 1967 and 100 in 1968). At the end of 1974 there were 11000 head. Mortality averaged 1.5 percent. The N'Dama cattle in Mushie are purebred; it is one of the few herds where no crossbreeding has been attempted.

Summary

The introduction of trypanotolerant breeds into southwestern Zaire has succeeded extremely well. The Dahomey breed, smaller than the N'Dama, is more readily raised in small family herds, while the N'Dama is excellent because of its precocity and high dressing percentage when raised on medium or largescale stock farms, as has been the practice in the region for nearly 50 years. In 1960, on the eve of the country's independence, there were more than 120000 head of cattle in this area, of which more than 100 000 head were on rather large stock farms (16 with over 1000 head of cattle, 27 with from 200 to 1 000 head of cattle and 107 farms with less than 200 head). Most of the stock on these farms were N'Damas or N'Dama crossbreds. Since then, the herds have continued to multiply and prosper in this region, to the great satisfaction of the stockraisers, the veterinary authorities, commercial firms and government circles.

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Trypanotolerance – a review

M. *Murray, W.L Morrison, P.K. Murray, D.3.* Clifford *and J.C.M. Trail*

It is a wellaccepted epidemiological fact that many West African breeds of cattle are able to survive without the aid of chemotherapy in areas of tsetse fly challenge where the humped zebu cannot (Stewart, 1951). In the same way, it is recognized that some breeds of sheep and goats (E.W. AIlonby, personal communication), many species of wild life (Ashcroft, Burtt and Fairbairn, 1959) and certain inbred strains of mice (Morrison *et al.,* 1978), also exhibit increased resistance to trypanosomiasis. This phenomenon is known as trypanotolerance although in immunological terms this is a misnomer since trypanotolerant animals do become infected with trypanosomes with adverse effects and they do respond immunologically. Thus, while the term trypanotolerance is now widely accepted, it should be understood to mean no more than reduced susceptibility.

The lack of vaccine and the limitations of the present methods of control, namely chemotherapy and tsetse control, have stimulated the desire to develop additional approaches that might allow more efficient land utilization in the vast areas of Africa dominated by the tsetse fly. Thus, there is now considerable interest in the potential use of trypanotolerant livestock. Particular attention has been focussed on the N'Dama breed of cattle because it has a relatively fixed phenotype and can be improved in productivity. Furthermore, published information has consistently confirmed the greater resistance to trypanosomiasis of the N'Dama over the zebu (Chandler, 1952, 1958; Desowitz, 1959; Stephen, 1966; Roberts and Gray, 1972). However, precise comparative information cannot always be obtained from these publications because in some cases the animals under study had previously been exposed to trypanosomiasis and in others their disease history was not known. In addition group numbers were frequently small, the groups were of widely different ages and of mixed sex. Moreover, many of these investigations were conducted on experimental stations where the general husbandry and feeding were of a high standard; as nutrition has a profound effect on the outcome of the disease (Mortelmans and Kageruka, 1976), it is likely that cattle kept on experimental stations will be more resistant to infection than cattle in natural field conditions.

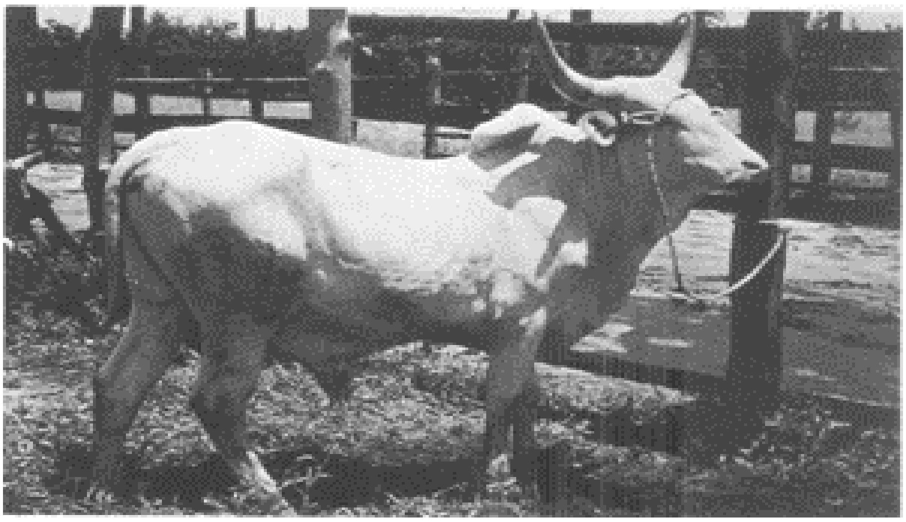

Figure 1. *Zebu. The preinoculation packed red blood cell volume of the zebu in the described experiments was 35 ±4 (standard deviation)*

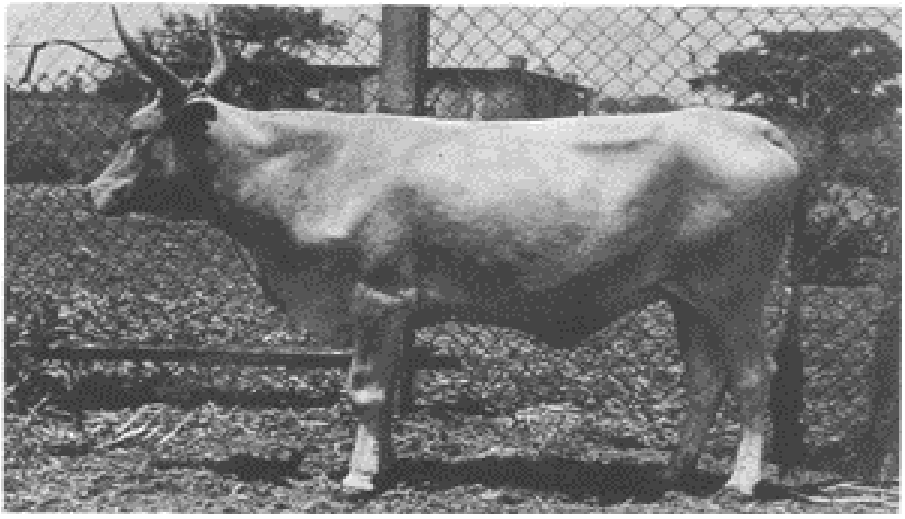

Figure 2. *N'Dama. The preinoculation packed red cell volume of the N'Dama in the described experiments was 35 ±4 (standard deviation).*

Thus, most of the basic questions about trypanotolerance remain to be answered precisely, questions such as, to what extent is inheritance important and how is it influenced by environmental factors; what are the mechanisms underlying increased resistance; and how productive are these breeds under various levels of challenge and in different management and ecological situations. The present article attempts to evaluate the current state of knowledge on these questions, leaning heavily on the authors' own experience with cattle and inbred strains of mice.

Trypanotolerance in N'Dama cattle.

Over the past few years, a series *of* experiments on N'Dama and zebu cattle in The Gambia, West Africa, have been carried out. The objectives of this work were, first, to confirm the existence of trypanotolerance in N'Dama and zebu cattle that had no Previous experience of trypanosomiasis under different types of challenge, second, to compare the progress of the disease and its immunology in the hope of defining the underlying mechanism of trypanotolerance and, lastly, to evaluate the impact on productivity of different levels of tsetse challenge in N'Dama cattle living under natural field conditions. Preliminary results of these studies have been published by Murray *et al.* (1977 b, c, d and e). A complete report is being prepared by Dr P.K. Murray.

Perhaps the most important aspect of this experimental work is the background of the cattle used. The zebu cattle (Figure 1) were from northern Senegal, purchased from a ranch well beyond the northern limits of the tsetse fly belt. N'Dama cattle (Figure 2) were obtained from the Government Agricultural Experimental Station at Yundum, The Gambia, a location considered tsetsefree, although surrounded by areas infested with *Glossina palpalis* and *G. morsitans submorsitans.* All animals studied were clinically, parasitologically and serologically negative for trypanosomiasis. There are divisions of opinion on what constitutes an N'Dama and, unfortunately, there is no genetic definition. The N'Dama used in this work conformed closely to the accepted phenotype in this area of West Africa. Furthermore, blood analysis by starchgel electrophoresis showed a haemoglobin frequency (0.89) similar to that recorded for N'Dama in other parts of Africa.

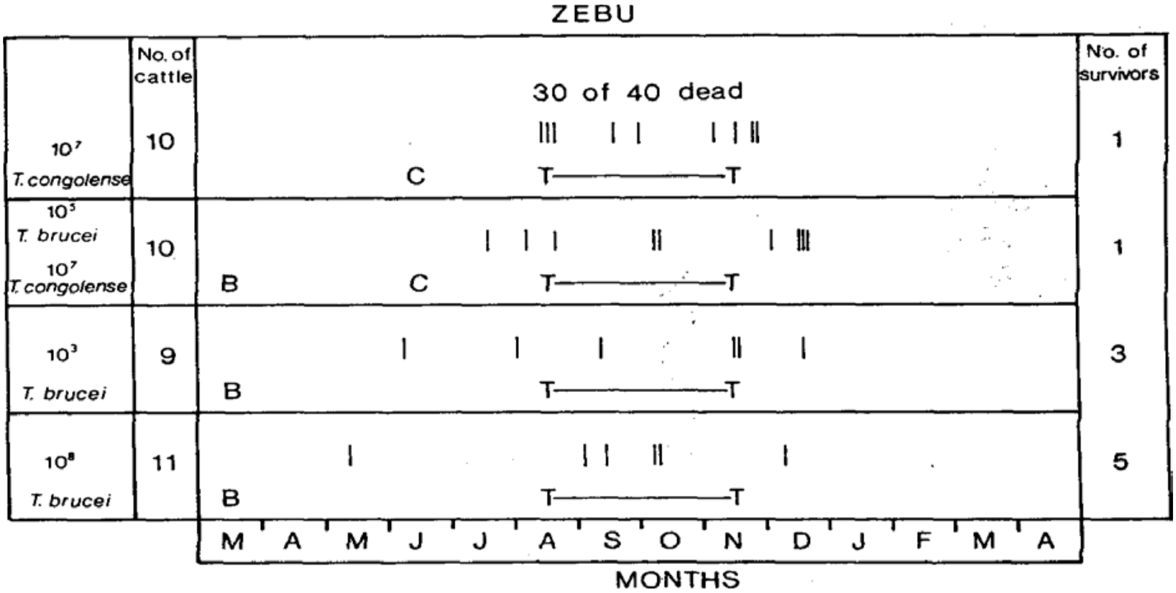

Figure 3. *Experimental design. B = time of* Trypanosoma brucei *challenge; C = time of* T. congolense *challenge;* T—T *=period when the cattle were exposed to* Glossina palpalis.

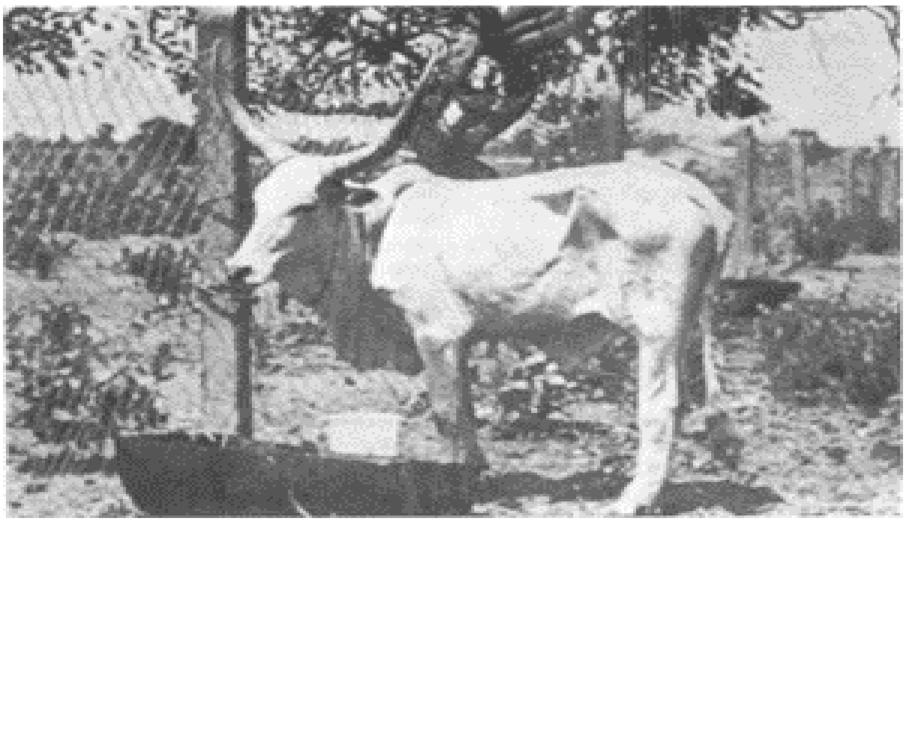

Figure 4. *Zebu suffering from the effects of inoculation with* Trypanosoma congotense.

The design of the first experiment carried out is shown in Figure 3. All animals used were aged three to four years. The 60 zebu were male, whereas of the 61 N'Dama, 34 were female and 27 were male; 8 of these zebu and 9 N'Dama were kept as unchallenged controls. In order to simulate field conditions of nutrition and exercise, the cattle were maintained under such conditions in an area initially thought to be tsetsefree; tsetse traps were set in order to keep the area under surveillance. During the day the cattle grazed extensively, walking up to approximately 27 km and they were tethered at night. No supplementary feed was given.

With the onset of the rainy season in August 1976, the herd came under challenge from *G. palpalis* and this lasted until November. A daily mean of 0.17 flies of both sexes was caught per Malaise trap (W.F. Snow, personal communication). It was estimated that this tsetse challenge commenced 15S days after the needle challenge with *Trypanosoma brucei* and 59 days after inoculation with *T. congolense.* During this time several animals became infected with *T. vivax.*

All 52 inoculated zebu and 52 N'Dama became infected and ill — as judged by deterioration of body condition and the development of anaemia (Figure 4). During the course of the experiment, 12 infected zebu and 15 infected N'Dama were killed for histopathological examination. In the remainder, clear differences in susceptibility emerged between the two breeds. Of the 37 N'Dama allowed to survive, none died, whereas 30 of the 40 zebu died of ?trypanosomiasis; 9 died after needle challenge (3 infected with *T. congolense),* while the other 21 died during or after the fly challenge. These provided the additional histopathological material.

This result was reflected in clear differences in the degree of anaemia that developed in the two breeds. Whereas in both N'Dama and zebu, the onset of the anaemia occurred within a few days of inoculation and was associated with appearance of parasites in the blood, the rate of development and severity of the anaemia was significantly greater in the zebu. This was true for both *T. congolense* and for *T. brucei,* although the severity of the anaemia and the extent of the difference between breeds was much greater in *T. congolenseinfected* animals. Nevertheless, it must be pointed out that the isolate of *T. brucei* employed was pathogenic for both N'Dama and zebu and 3 zebu died as a direct result. It was also obvious that N'Dama and zebu previously infected with *T. brucei* were equally susceptible to inoculation with *T. congolense,* although as before the anaemia became more severe in the zebu (Figure 5).

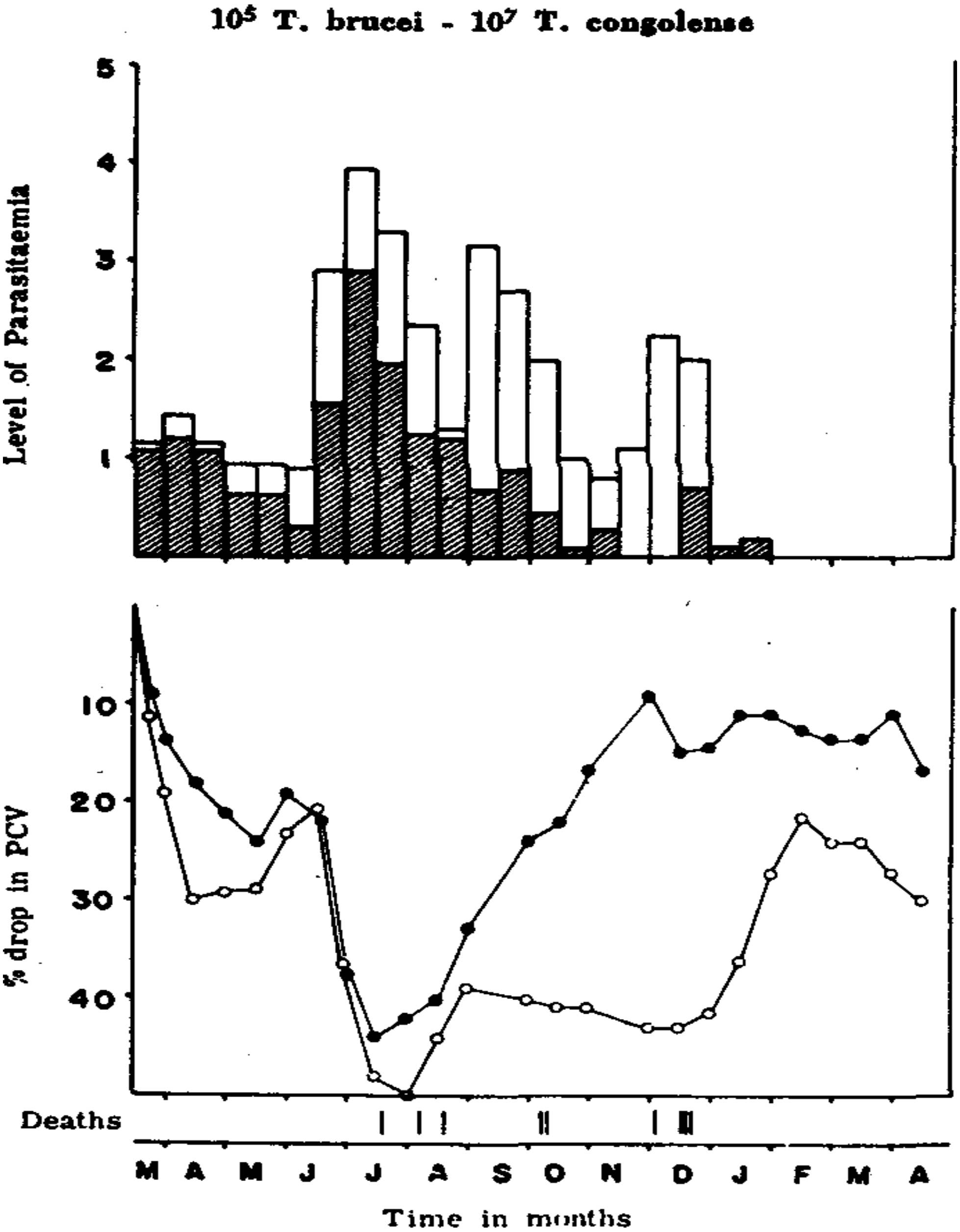

Figure 5. *Average parasitaemia score recorded in N'Dama and zebu inoculated with 10^s* Trypanosoma brucei *followed by 1(P* T. congolense *96 days later. Details of this scoring system have been described by Murray* et al. *(1977a). The level of the first peak of parasitaemia plus one standard deviation is shown. The percentage fall in packed red cell volume* (pcv) is *demonstrated and zebu mortalities are given. The hatched areas of the histogram represent the N'Dama while the open areas represent zebu. Elsewhere N'Dama* = •; *Zebu* = o.

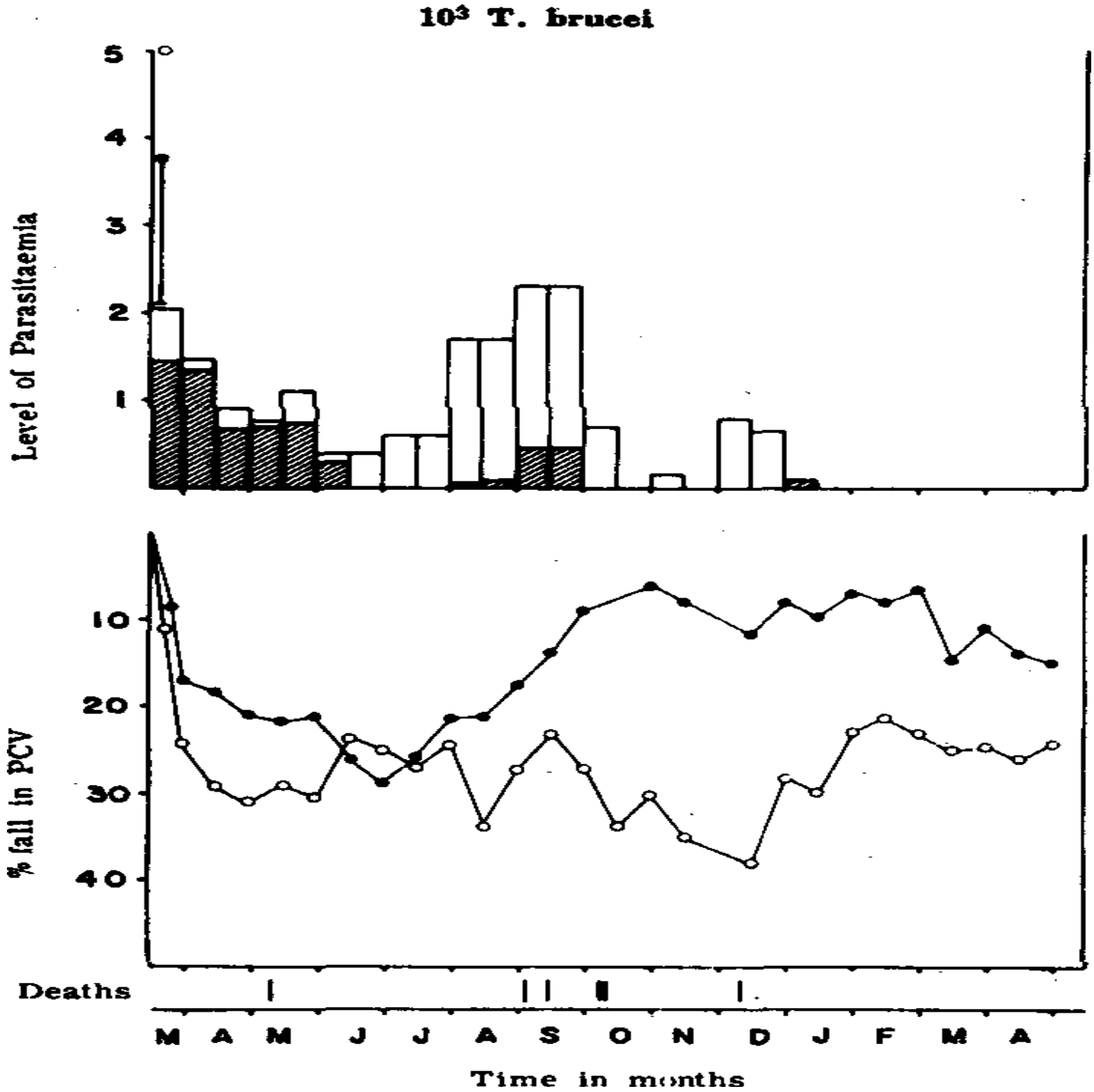

Figure 6. *Average parasitaemia score recorded in N'Dama and zebu inoculated with 10^8* Trypanosoma brucei. *Percentage fall in packed red cell volume* (pcv) *is demonstrated and zebu mortalities are given. The symbols are as in Figure 5.*

During August when there was some indication that animals were recovering from the needle challenge, as judged by levels of anaemia, *G. palpalis* moved into the area and all zebu infected with *T. brucei* except one were reinfected and severe anaemia developed (Figures 6 and 7); a similar situation occurred with the zebu infected with *T. congolense* (Figures 5 and 8). With N'Dama, however, only a few animals became reinfected and even then only transiently. The tsetse challenge appeared to have little effect on the course of the disease.

On examining the parasitaemia of infected N'Dama and zebu, it was immediately obvious that, while the prepatent period was similar, the level of parasitaemia which developed in the N'Dama was consistently and significantly lower than in the zebu. Furthermore, all of the 37 N'Dama allowed to survive and all 10 of the zebu survivors had the apparent ability to eliminate trypanosomes, or "self cure". There was some indication that the duration of parasitaemia was shorter in the N'Dama, but this observation was complicated by the tsetse challenge when most of the zebu, but only a few N'Dama, became reinfected. Nevertheless, from several months after needle challenge onward in most animals and for 90 days prior to termination of the experiment all surviving animals were negative for detectable parasites in the blood and tissues.

Following the disappearance of the parasites from the circulation, 25 of the 37 N'Dama and 3 of the 10 surviving zebu made a slow but complete clinical recovery, as judged by their physical improvement and a return to normal haematological values. However, the remainder did not and, despite the absence of detectable parasites, continued to be anaemic with packed red cell volumes (pcv) approximately 30 to 40 percent below normal. The authors believe this negative anaemic aspect of the trypanosomiasis syndrome to be widespread in the field (Murray, 1979). This outcome should be borne in mind when evaluating Figures 5, 6 and 7, where, by presenting the group mean pcv, a slightly misleading trend is apparent toward the end of the experiment.

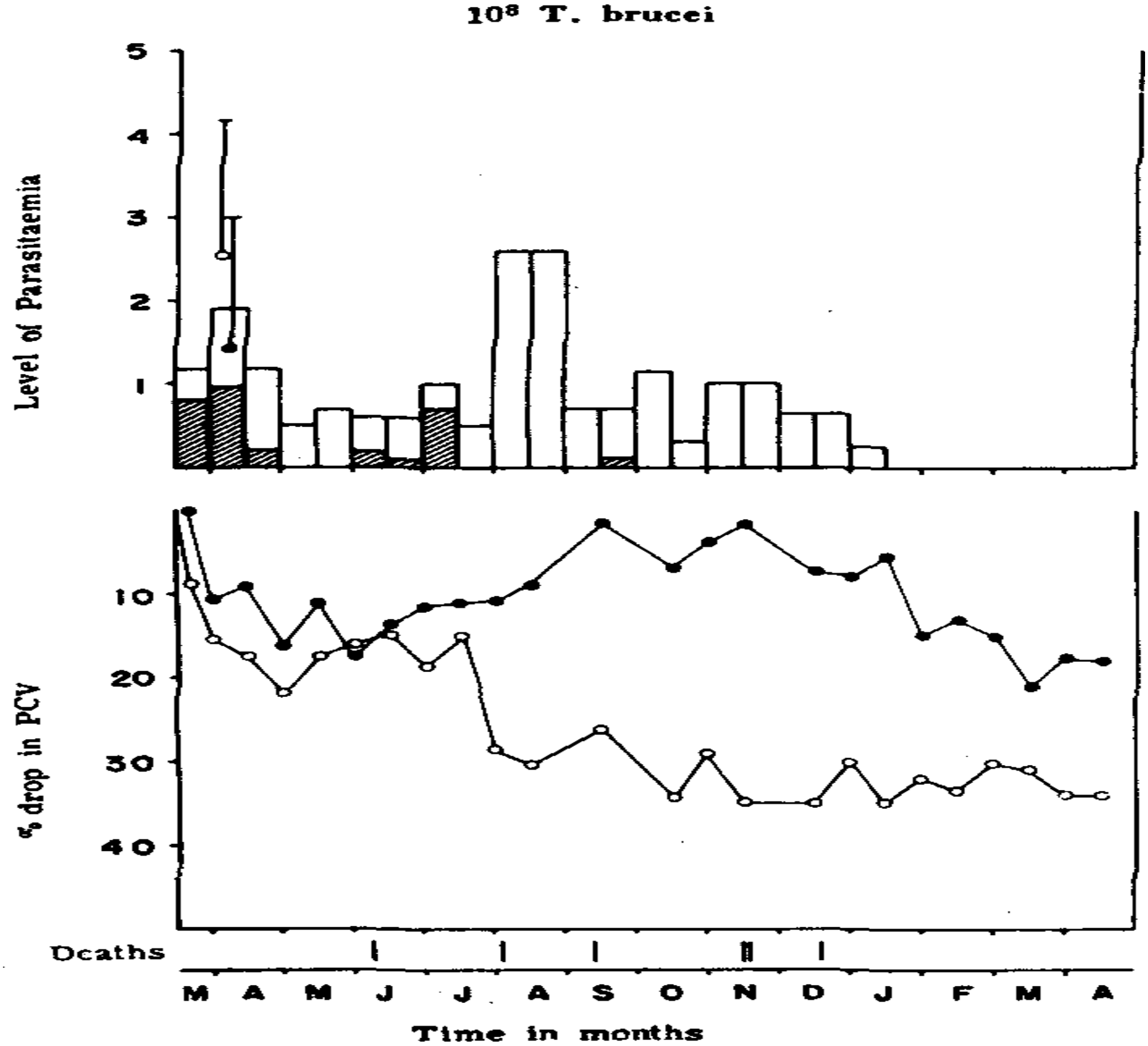

Figure 7. *Average parasitaemia score recorded in N'Dama and zebu inoculated with I0*^{3} Trypanosoma brucei. *The level of the first peak of parasitaemia plus one standard deviation is shown. Percentage fall in packed cell volume* (pcv) *is demonstrated and zebu mortalities are given. The symbols are as in Figure 5.*

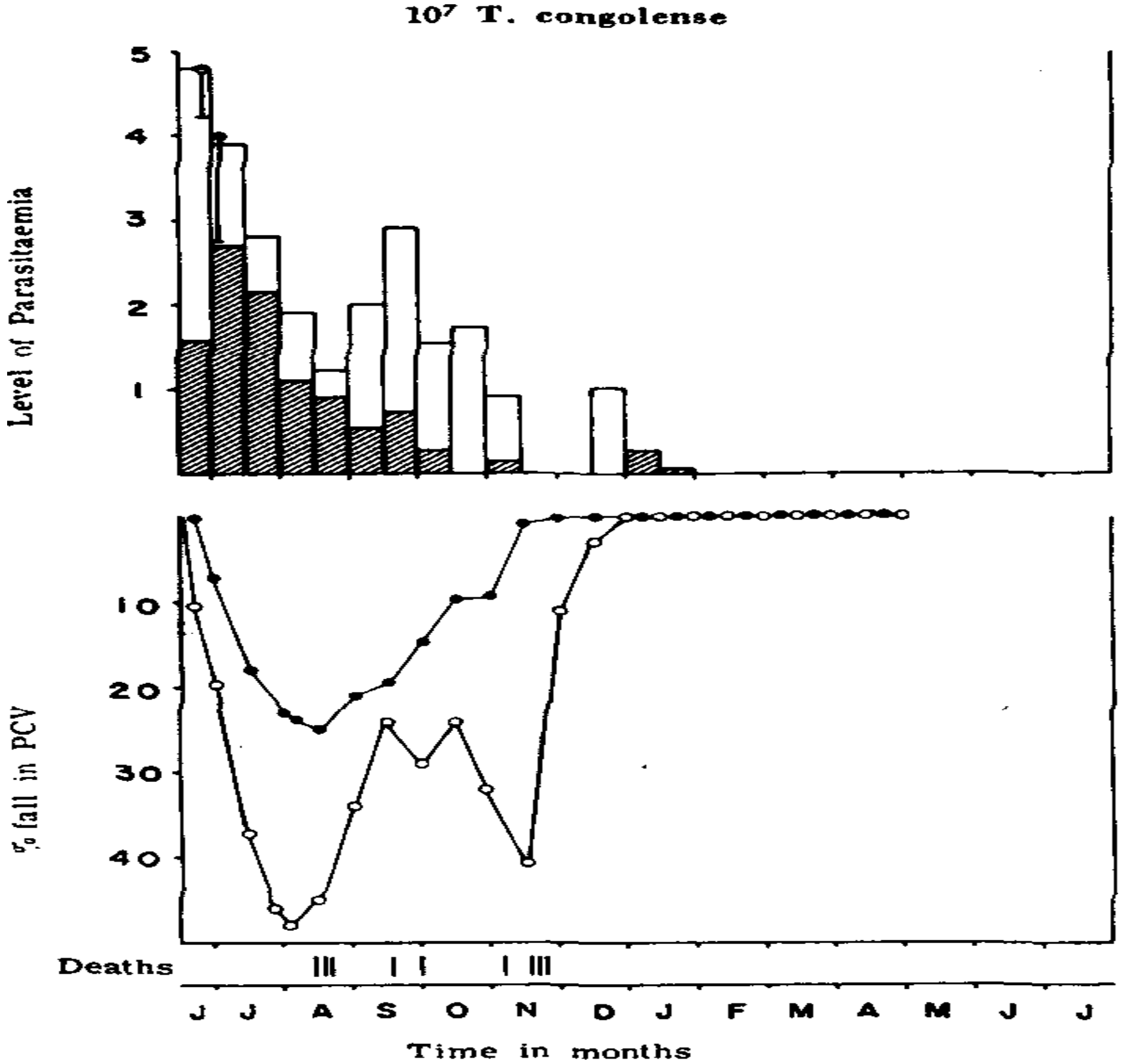

Figure 8. *Average parasitaemia score recorded in N'Dama and zebu inoculated with* 10^7 Trypanosoma congolense. *The level of the first peak of parasitaemia plus one standard deviation is shown. Percentage fall in packed red cell volume* (pcv) *is demonstrated and zebu mortalities are given. The symbols are as in Figure 5.*

Another important finding to emerge from this study was that weight of challenge, as judged by the number of bloodstream forms of *T. brucei* inoculated, had a significant effect on the sequential development of the disease. Both the N'Dama and the zebu that received the heaviest challenge became more rapidly and severely ill and more anaemic than those receiving the lowest dose. The parasitaemic profile was also influenced in that the prepatent period and the level of parasitaemia were lower in the animals inoculated with the lowest dose. In the same way, at least in the N'Dama, it appeared that the dose also affected the period of parasitaemia, the duration being shorter in the group that received the lowest dose; in the zebu, however, this conclusion could not be made because most of them became reinfected during the period of *G. palpalis* challenge. In confirmation of the trypanotolerant nature of the N'Dama breed, but reflecting the quantitative rather than the absolute nature of trypanonotolerance, it was found that the N'Dama receiving the highest challenge, namely, 10^8 *T. brucei,* developed a disease picture of the same order of magnitude as zebu given the lowest dose of 10^3 *T. brucei.* This observation was made only in the initial few months following inoculation and was then complicated by reinfection of the zebu during the period of tsetse fly challenge.

In a further experiment, a group of ten female three-year-old zebu and nine female three-year-old N'Dama were subjected to what was considered a heavy *G. m. submorsitans* challenge. A daily mean of between 20 and 40 flies was caught per Malaise trap (W.F. Snow, personal communication). These cattle had no previous experience of infection. The results were similar to the findings following needle and *G. palpalis* challenge. The zebu developed significantly higher levels of parasitaemia, more severe anaemia and all 10 had died of trypanosomiasis within 242 days of being moved into the challenge area. *At* this time the average pcv of the N'Dama was still above 30 percent; the only N'Dama death was caused by anthrax.

Based on clinical and postmortem findings in the above experiments, death from trypanosomiasis was the result of acute congestive heart failure brought about by a combination of anaemia, circulatory disturbance associated with increased vascular permeability, and myocardial damage. The authors believe that the fact that cattle in this study had to forage for their feed was a contributory factor. Tired, anaemic animals are probably unable to trek the distances necessary to satisfy their nutritional requirements but in their efforts to achieve this they develop cardiac decompensation. It was noticeable that when sick animals were put under intensive care and did not have to forage their clinical condition often improved.

While many aspects of these experiments still await evaluation, what has been established so far is that N'Dama, with no previous experience of infection, were less susceptible than zebu to a variety of challenge situations, including inoculation with *T. brucei* and/or *T. congolense* and to fly challenge with *G. palpalis* and *G. m. submorsitans;* the more virulent the organism the more significant were the differences between the breeds. However, it was found that the trypanotolerant status of the N'Dama was not absolute and was affected by weight of challenge.

Trypanotolerance in other breeds of cattle.

There are several other small breeds of cattle in West Africa that are considered to be trypanotolerant (Pagot, 1974). For example, Roberts and Gray (1973) found that Muturu were less susceptible than zebu but more susceptible than N'Dama; however, Desowitz (1959) found that two Muturu from a herd that had not been exposed to trypanosomiasis for 50 years were highly susceptible and succumbed three weeks after infection. However, in an outbred species such as the bovine it is difficult to draw firm conclusions when such small numbers of animals are involved; clearly more experimental data are required for these breeds.

It is generally considered that the zebu is the most susceptible of the African breeds. However, there is considerable epidemiological evidence that, in some areas, zebu have developed a degree of tolerance; for example, Cunningham (1966) has described how thousands of zebu cattle survive around the shores of Lake Victoria even though they are continuously exposed to tsetse. He reported a 30 percent prevalence of parasites and the presence of neutralizing antibodies in 90 percent of such animals. By definition, these animals must be considered trypanotolerant. It is important that further experimental and epidemiological studies be carried out to evaluate the extent of this situation.

Trypanotolerance in sheep and goats.

As with cattle, it is a well recognized but poorly documented fact that certain breeds of sheep and goats survive in endemic tsetsefly areas without the aid of chemotherapy and must be considered trypanotolerant. There is a paucity of published data on the susceptibility of different breeds to trypanosomiasis under various challenge and ecological regimes. Work in Kenya has confirmed that differences in susceptibility do exist between different breeds of sheep and goats to both needle and fly challenge (E.W. Allonby, personal communication); local breeds are much more resistant than imported ones. It is essential that the extent and basis of this difference be further investigated.

Trypanotolerance in wildlife.

Wildlife have an established reputation for being trypanotolerant or even completely resistant to trypanosomiasis. There is, however, little published information on infection and the clinical course of the disease in experimentally infected wildlife. Surveys involving the demonstration of the presence or absence of trypanosomes in one blood sample on one occasion yield little useful information on susceptibility to the disease of trypanosomiasis. Sequential studies following experimental infections are required where the clinical, parasitological, immunological and pathological parameters are assessed.

In one of the few studies of this type, Ashcroft, Burtt and Fairbairn (1959) examined the susceptibility of various wildlife species to needle challenge with *T. rhodesiense* and *T. brucei.* They found that the animals examined could be considered to lie in two main categories: first, those species such as Thomson's gazelle, dikdik, Blue Forest duiker, jackal, bateared fox, Ant bear, hyrax, serval and monkey, which usually died of the infection: the second category included less susceptible or resistant animals. These could be divided into species that became infected and had parasitaemias of considerable duration, such as the common duiker, eland, Bohar reedbuck, spotted hyena, oribi, bushbuck and impala; species usually infectible but with scanty parasitaemias, such as the warthog, bushpig and porcupine; and the baboon, which was refractory to infection. When the species of game that tsetse normally feed on was evaluated, what was of considerable interest was the observation that the species most susceptible to needle infection were not popular with the tsetse, as judged by blood meals, whereas most of the species of the second group, i.e., the lesssusceptible group, were fed on more regularly, with wild pigs being most popular. This observation would suggest that species in the second group may have evolved by the survival and selection of the more resistant members within each of these species. In a similar but more limited study, Carmichael (1934) also found a range of susceptibility to *T. brucei* between different species of wildlife. Both Carmichael (1934) and Ashcroft, Burtt and Fairbairn (1959) attempted to infect a small number of game animals with *T. congolense.* They found that in most cases the animals tested were not infectible or developed only transient infections and then recovered.

It would appear essential to the authors that such studies be extended. Not only is it important to evaluate the epidemiological role of game animals in African trypanosomiasis but also the fact that certain species are less susceptible or even refractile to trypanosome infection makes them, important subjects for studies into the basic mechanisms of trypanotolerance. It may be, for example, that the resistant wildlife host can "see" antigens in the trypanosome that make the trypanosome more vulnerable; alternatively, these species may have certain blood proteins that are active in a nonspecific way against the trypanosome.

Productivity of trypanotolerant livestock.

There is a lack of scientific data on the productivity of "trypanotolerant" livestock living in the field under natural tsetsefly challenge. As a result, a variety of opinions exists as to just how tolerant and how productive these animals really are under various ecological and management regimes and levels of challenge. The productivity of trypanotolerant livestock is especially called into question on the basis of their small size in comparison with more susceptible breeds. At one extreme is the view that N'Dama cattle are genetically resistant and do not suffer from trypanosomiasis and should be introduced widely into high tsetsefly challenge areas throughout Africa (Pagot, 1974). Other workers feel that further information is necessary before taking such an ambitious step (Stewart, 1951; Chandler, 1952; Roberts and Gray, 1973). At the other end of the scale, Stephen (1966) concluded that the propagation of these breeds, because of their small size, is not to be recommended as a satisfactory means of protein production.

Leastsquares' means and constants for production indices of trypanotolerant cattle breeds under different management systems and tsetse challenges

Item		Number	Index/cow (kg)		Index/100 kg cow (kg)	
			X	constant	X	constant
Overall mean			57.5		28.0	
Total number		30				
Breed						
	N'Dama	21	71.3	13.8	28.4	0.4
	West African Shorthorn	9	43.7	—13.8	27.6	—0.4
System						
	Ranch/Station	16	70.9	13.4	33.1	5.1
	Village	14	44.1	—13.4	22.9	—5.1
Tsetse challenge						
	Zero	3	89.2	31.7	40.0	12.0
	Low	13	66.3	8.8	31.0	3.0
	Medium	10	45.9	—11.6	22.7	—5.2
	High	4	28.6	—28.9	18.2	—9.8

In a recent major survey of the status of the trypanotolerant livestock of West and Central Africa (ILCA, 1979), indices of productivity of trypanotolerant cattle were examined, using all the basic production data that could be found in the region. In 30 herds in the 18 countries studied, sufficient information was available on the main production traits to produce indices. The traits evaluated were reproductive performance, cow and calf viability, milk production, growth and cow body weight. These were used to compute the index of the total weight of calf and liveweight equivalent of milk produced, first per cow per year and finally per 100 kg of cow maintained per year. This final index related these important production traits back to the actual weight of breeding cow that had to be supported, this being closely connected with maintenance costs. The traits and production indices were derived for two basic management systems, village and ranch or station and for four levels of tsetse challenge rather arbitrarily designated zero, low, medium and high. The table indicates the effects of breed groups, management system and tsetse challenge on the two productivity indices.

A tremendous range of productivity levels was spanned by both the N'Dama and West African Shorthorn relative to the different production systems and level of tsetse challenge involved. In both breeds, the range extended from about 15 kg of one-year-old calf and liveweight equivalent of milk produced per 100 kg of cow maintained per year under village conditions in a high tsetsechallenge area, to about 50 kg under improved ranch or station conditions in a low tsetsechallenge area.

The table indicates no significant difference between N'Dama and West African Shorthorn for the major index of "productivity per 100 kg of cow maintained", the actual values being 28.4 kg per annum for N'Dama and 27.6 kg for West African Shorthorn. The only significant differences in individual traits leading to this index were of one-year-old calf and weight of mature cow, the N'Dama group being very much heavier in each case. The higher calf weight led to a higher index per cow for the N'Dama, but the higher maturecow weight resulted in similar indices per 100 kg of cow maintained. The effect of management system was a 38 percent lower productivity index per cow and 30 percent lower productivity index per 100 kg of cow maintained from the village compared with the ranch or station. The performance attributable to zero tsetse challenge was masked by the effect of very intensive feeding and management, thus only low, medium and high can be directly compared. Productivity indices per cow were 30 percent and 56 percent less for medium and high challenge respectively compared with low, while indices per 100 kg of cow maintained were 26 percent and 41 percent less for medium and high respectively compared with low.

Estimates of productivity for 16 zebu and Sanga herds under ranch/station conditions in tsetsefree areas of Africa covering Botswana, Kenya, Mali, Nigeria, Senegal and Uganda, have been built up from the available literature. These averaged 133.4 kg of one-year-old calf and liveweight equivalent of milk produced per cow maintained per year and 37.7 kg per 100 kg of cow maintained per year. Compared with the estimates of 79.7 kg and 36.1 kg for the 30 trypanotolerant groups under ranch/station conditions in light tsetsechallenge areas, these represent a superiority of 67 percent per cow. maintained per annum, but only 4 percent per 100 kg of cow maintained per annum for the zebu and Sanga over the trypanotolerant breeds. This strongly suggests that the productivity of trypanotolerant cattle relative to other indigenous types may be much higher than previously assumed.

A preliminary survey of the impact of trypanosomiasis has been carried out on the N'Dama on The Gambia[1], which live under different levels of tsetse challenge (Murray *et al.,* 1977b; Clifford and McIntyre, 1977). It was found that in heavy *G. m. submorsitans* areas anaemia was widespread and up to 50 percent of the herd could be infected. In areas of lighter *G. palpalis* challenge, the prevalence of trypanosomes was less as was the extent of anaemia. In the heavy challenge areas, while some of the trypanosomeinfected N'Dama died, most N'Dama survived but they often did so in a poor productive state with wasting, stunting (Figure 9), abortion, high calf mortality and with a persistent lowgrade anaemia being manifest. Thus, there is little doubt that trypanosomiasis must be considered a disease of importance in N'Dama in terms of morbidity if not mortality. However, it should be emphasized that many other animals in the same herds were in an excellent productive state, suggesting that a wide range of susceptibility exists within the N'Dama breed. It must be remembered that these results were obtained in areas where zebu could not survive; of 31 zebu introduced in the *G. m. submorsitans* area in June 1977, only one survived until December 1978, and this animal was in poor condition. In the same way, of the 31 zebu studied in the *G. palpalis* area 21 died; the N'Dama in this area were hardly affected.

These N'Dama herds, numbering around 2 000 head, are now double eartagged and have been investigated from a disease and productivity point of view over several years. Detailed quantitative data are at present being evaluated by one of the authors (D.J. Clifford).

Basic mechanisms of trypanotol erance.

While the basic mechanism of trypanotolerance is still to be precisely defined, there is at least circumstantial evidence that the mechanism is related to a hostresponse factor and that it is a heritable trait.

The trypanotolerant nature of the N'Dama and the capacity of certain strains of mice to survive a trypanosome infection longer than others (Morrison *et al,* 1978b) would appear to be related to their ability to limit the level of peaks of parasitaemia and subsequently to control, reduce or even eliminate the parasite. The finding of a similar prepatent period between N'Dama and zebu, and between strains of mice of high and low susceptibility suggested that the initial replication rates in all groups were similar. Furthermore, dose titration studies showed that there was no difference in the infectivity of *T. congolense* for mice of high and low susceptibility (Morrison *et al.,* 1978b). These findings indicated that the different levels of parasitaemia found between breeds of cattle and strains of mice might reflect differences in the nature or quality of the immune response to the trypanosome. This hypothesis requires experimental verification.

Evidence that a more effective immune response might be responsible for the differences in susceptibility between N'Dama and zebu cattle comes from the work of Desowitz (1959). He found that N'Dama with previous experience of trypanosomiasis were able to eliminate trypanosomes more rapidly than their zebu counterparts following a renewed challenge. Employing an *in vitro* test that involved the use of sera from the challenged animals to inhibit trypanosome respiration, it was found that the activity of N'Dama sera was superior to that of zebu sera. Desowitz (1959) concluded that the trypanotolerant nature of the N'Dama lay in its capacity to mount a better secondary immune response. Unfortunately, in these studies the trypanosomal antigenic history of the N'Dama and zebu used was not known precisely. Thus, while the results achieved are indicative of a moreeffective immune response in the N'Dama they require confirmation. Similarly, using a serum neutralization test, Chandler (1958) stated, without supplying details, that the immune response of zebu to the trypanosome was inferior to that of the N'Dama.

A range of susceptibility to *T. congolense* (Morrison *et ah,* 1978) and to *T. brucei* and *T. vivax* (Morrison and Murray, 1979) has been shown to occur in different inbred strains of mice. Following *T. congolense* infection, the *C57BI* was the least susceptible and the *A/J* was the most susceptible of the strains examined. When the spleen lymphocyte populations were studied in these strains of mice infected with *T. congolense,* it was found that there was a marked increase in splenic Blymphocytes and null cells (Morrison *et al.,* 1978). This, allied to the findings of an increase in background plaqueforming cells to sheep erythrocytes, indicated that trypanosome infection resulted in a nonspecific polyclonal activation of lymphocytes, affecting primarily Blymphocytes., Tn the strains of mice that survived longest, the *C57BI* and *AKR,* the increase in Bcells and null cells was less than in the highly susceptible strains. Furthermore, the immunosuppression observed in mice infected with *T. congolense* occurs earlier in the highly susceptible strains. It might be, therefore, that susceptibility is related to sensitivity to polyclonal activation or to immunosuppression induced by the trypanosome infection. Alternatively, differences in the cellular response and degree of immunosuppression might merely reflect differences in levels of parasitaemia observed in the various strains of mice (Morrison *et al,* 1978).

Further support for the hypothesis that trypanotolerance has an immunological basis comes from the effect of immunostimulants on the susceptibility of mice to trypanosomiasis (Morrison and Murray, 1979). The authors found that the administration of *Bordetella pertussis, Corynebacterium parvum* or Bacillus Calmette-Guérin (BCG) prior to or on the day of challenge with *T. congolense* significantly delayed or reduced parasitaemias and increased survival time. In this way, it was possible to change the survival time and parasitaemia levels of the highly susceptible *AjJ* strain to values more akin to the less susceptible *C57BI.* This strategy might have practical significance in rearing domestic livestock.

Further work is now required to define both qualitatively and quantitatively the host's immune response to the trypanosome and to compare this between breeds and strains of animals with different susceptibilities. In this way the important effector mechanisms might be clearly defined and, moreover, it might be possible to potentiate them with the object of increasing host resistance to trypanosomiasis.

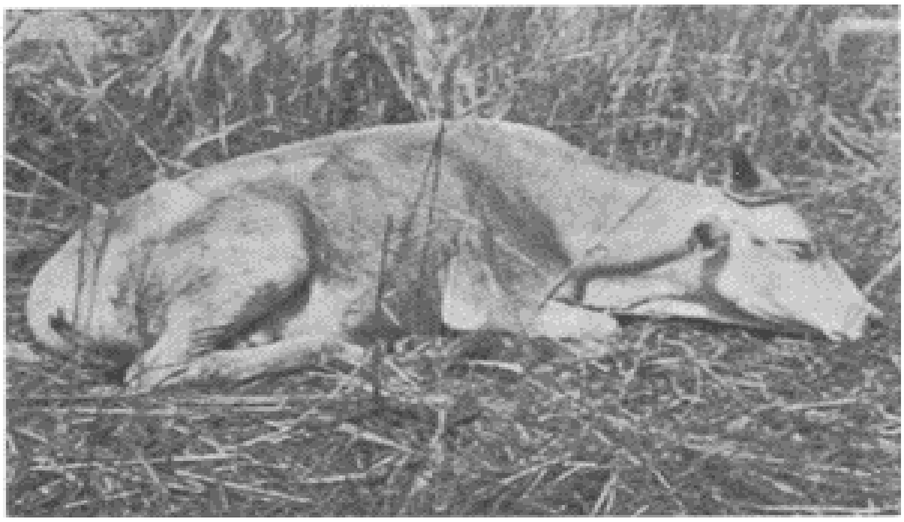

Figure 9. *'The effect of trypanosomiasis on a naturallyinfected N'Dama yearling. The animal is stunted and has a characteristic "nagana" pose.*

It is also essential that possible physiological factors be considered in the construction of the overall picture of the underlying mechanisms of trypanotolerance. As the N'Dama tend to develop lesssevere anaemia than zebu, the authors considered that this might be related to the capacity to mount a more effective erythropoietic response. Thus, a series of *in vivo* pathological studies were carried out in N'Dama and zebu cattle infected with *T. congolense* and *T. brucei;* these studies involved the use of ^{51}Crlabelled red cells, ^{125}Ilabelled albumin and ^{59}Felabelled transferrin (Dargie *et al.,* 1979; Dargie *et al.,* 1979). The findings, however, showed that the anaemia and its underlying processes were broadly related to the number of parasites in the blood and that the superior resistance of the N'Dama lay in their capacity to control parasitaemia rather than their ability to mount a more efficient erythropoietic response.

Nevertheless, it would seem to us that, when N'Dama and zebu are kept under the same conditions and have anaemia of similar severity, the N'Dama always appear to be clinically and physically superior.

Under normal field conditions where nutrition is poor, cattle often have to forage up to about 27 km in a day; perhaps the N'Dama's ability to forage and to digest what it gets is superior to the zebu. Several other physiological mechanisms are also worthy of consideration. The authors have observed remarkable water conservation and heat tolerance in N'Dama; rectal temperatures can range from 34.4°C at dawn to 41.1°C by late afternoon. Furthermore, Pagot (1974) has pointed out that N'Dama can withstand higher levels of humidity than zebu. Zebu appear to have evolved a capacity for conserving water and in East Africa it has been shown that the water requirements of zebu steers is half that of Hereford steers and is as specialized as several species of game animals (EAVRO, 1967). Zebu were found to be better able to conserve evaporative and faecal water than Hereford. Zebu deprived of water stopped eating and metabolised fat consequently reducing urinary and faecal water losses; zebu cattle form faeces as dry as 190 g water/100 g dry matter whereas Hereford are unable to form faeces containing less than 300 g water/100 g dry matter. As a, result, zebu were able to live comfortably without water for two months at an environmental temperature of 22°C or until their fat supplies were depleted, a fact confirmed by field observations on Turkana cattle living under drought conditions. This capacity for conserving water was inherited as a dominant trait in zebu-Hereford F_1crosses (EAVRO, 1967). In possible contrast to N'Dama, zebu would appear to regulate their body temperature within a range of 2°C and neither a periodic heat load nor dehydration had any effect on the range over which zebu regulate (EAVRO, 1967). The greater variation in body temperature in the N'Dama compared with zebu might result in better conservation by N'Dama of water which would otherwise be lost by evaporation. The authors believe that these observations require further investigations to evaluate the possible role played by adaptation of physiological mechanisms in trypanotolerance.

Another aspect that might play a potential role in trypanotolerance is skin physiology, including colour and smell, in relation to attractiveness to the tsetse; skin structure might also be important. In addition the role of nonspecific factors in host susceptibility to trypanosomiasis should be compared between breeds; these factors might include the extent and activity of the mononuclear phagocytic system as well as complement, properdin and conglutinin reactivity. One interesting finding is that the N'Dama breed has a significantly higher level of white blood cells, particularly eosinophils, than the zebu. This observation was made by Oduye and Okunaiya (1971) and the authors subsequently have confirmed their findings.

The genetics of trypanotolerance.

There is now a considerable body of evidence to show that trypanotolerance has a genetic basis. Thus, studies on cattle that have had no previous experience of trypanosomiasis have clearly established that N'Dama are significantly more resistant than zebu (Stephen, 1966; Roberts and Gray, 1973). It is likely that trypanotolerance has evolved in tsetsefly infested areas by natural selection of the more resistant animals within a breed. In this respect (in the authors' experience) a range of susceptibility is found both within groups of N'Dama and zebu cattle. Under such circumstances it is likely that the factors governing the susceptibility have a complex genetic basis.

There have been few breeding studies with trypanotolerant breeds of cattle. Stewart (1951) reported crossbreeding studies, without supplying details, involving the West African Shorthorn, a trypanotolerant genetic mix, and zebu, in which trypanosomiasis resistance was retained in the crossbred offspring. However, Chandler (1958) found that the resistance of N'Damazebu crosses to trypanosome challenge was about half way between the two parent breeds. In an extended crossbreeding trial in the Ivory Coast involving large numbers of N'Dama and Jersey, it was found that the F_1 cross produced an excellent animal as regards growth and milk production (Letenneur, 1978). It was stated that such crosses retained their tolerance although no data were supplied on the level of fly challenge or on the prevalence of trypanosomes. Crossbreds with greater than 50 percent Jersey background appeared to be less hardy and gave equivocal results. The foregoing reports indicate that the trypanotolerant trait is at least partly dominant. However, in using such outbred populations, differences in results on crossbreeding must be expected. Indeed, it is likely that the degree of trypanotolerance observed in first generation crosses will vary widely depending on the individual parental combination. In this respect, any future investigation of the inheritance of trypanotolerance will require the use of large groups of both parental breeds if reliable results are to be obtained. Thus, only by using sufficient numbers of animals will it be possible to determine the feasibility of selection for maximum trypanotolerance along with the retention of the required characteristics of the nontrypanotolerant parent. The main problem in undertaking such a study at present is the lack of genetic markers that would allow monitoring of susceptibility without having to infect all of the animals involved.

It has been proposed that, as N'Dama cattle show almost 100 percent gene frequency for Haemoglobin *(Hb) A,* while zebu are a mixture of *A* and *B,* animals could be selected by *Hb* type. However, the fact that certain exotic breeds such as the Friesian aie predominantly *HbA* (Bangham and Blumberg, 1958) and are highly susceptible to trypanosomiasis, makes it unlikely that *Hb* type will be of value as a marker. With the Tecent upsurge of interest in the major histocompatibility complex (mhc) in cattle and the identification of a series of gene products, the possible association of trypanotolerance with particular mhc products might prove a more profitable avenue of research.

The lack of suitable herds for study, the absence of genetic markers for resistance and the genetic heterogeneity of bovine populations, at present preclude a critical analysis of the genetics of trypanotolerance in the bovine. Thus, the authors have carried out a series of experiments to compare the susceptibility of different inbred strains of mice to trypanosomiasis and to investigate the underlying genetics (Morrison *et al.,* 1978; Morrison and Murray, 1979).

As stated earlier, it was found that strains of mice differed markedly in their susceptibility to African trypanosomiasis. Breeding studies indicated that reduced susceptibility (as judged .by survival times) was inherited as a dominant trait, in that F_1 hybrids between the highly susceptible *A/J* strain and the moreresistant *C57B1J6* showed similar survival times to the *C57BI/6* parents (Figure 10). When these F_1 hybrids were then back-crossed onto the parent strains, the extent of heterogeneity in survival indicated that susceptibility was under polygenic control (Morrison and Murray, 1979).

In recent years, the susceptibility to a number of experimental infections in mice and the prevalence of certain diseases in man has been shown to be at least partially linked to *H-2* hap-lotype (Lilly and Pincus, 1973; Mc Devitt, Oldstone and Pincus, 1974) and with particular *HLA* antigens (Vladutiu and Rose, 1974) respectively. It has been suggested that *H-2* may exert its influence through immune response (*Ir*) genes present in the *I* region of the *H-2* complex. It is thought that immune response genes may also be associated with the *HLA* complex in man. However, the authors' studies on the comparative susceptibility of congenic resistant mice, i.e., mice with a genetic background differing only at the *H-2* locus, have failed to demonstrate a major relationship between *H-2* haplotypes and susceptibility (Morrison and Murray, 1979). So far, the authors have carried out these experiments only on mice of the *C57BI* genetic background and it may be that the genes responsible for reduced susceptibility in this strain override any influence exerted by the *H-2* haplotype.

Despite the lack of precise data there would appear to be overwhelming evidence that susceptibility of cattle to African trypanosomiasis is under genetic control. Nevertheless, there is a considerable body of evidence to support the fact that the innate susceptibility of cattle is decreased by repeated exposure to the same population of trypanosomes in a given area. Thus Desowitz (1959) demonstrated the ability of N'Dama and, to a lesser extent, zebu that had been previously exposed, to mount what could be described as a secondary immune response with the elimination of the parasite. He believed that the course of the disease was dependent not only on the breed of animal but also on the nature of the individual's past contact with the trypanosome. The fact that cattle previously exposed to trypanosomiasis are more resistant was described many years ago by Bevan (1928) and more recently by Wilson *et al.* (1976) who showed that zebu cattle kept under an infection-and-treatment regime did become more resistant.

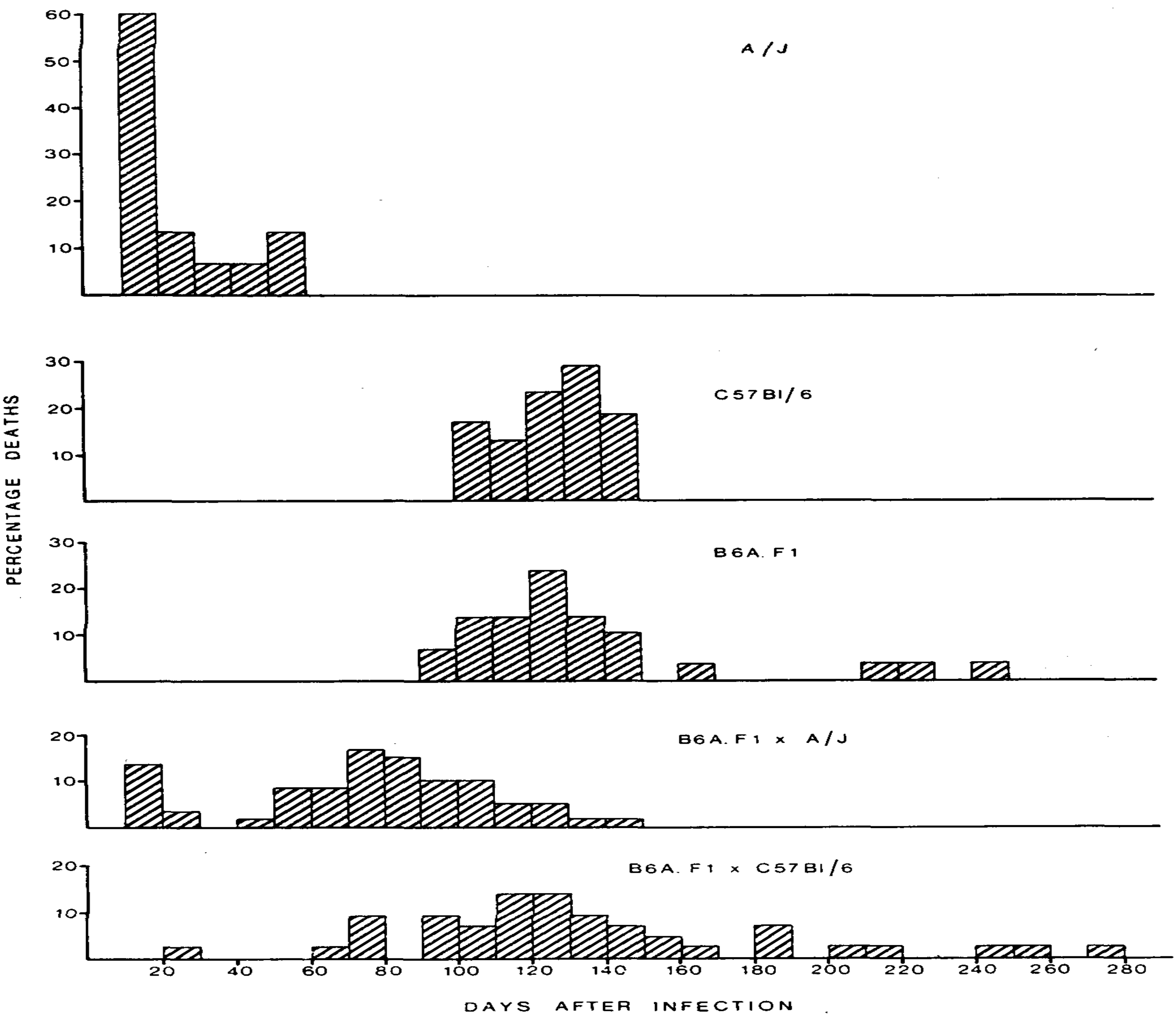

Figure 10. *Percentage deaths in groups of* A/J, C57B1/6J, F_1 *hybrids and backcrosses after infection with* Trypanosoma congolense. Morrison and Murray, 1979

In addition to previous exposure to infection, it is established that other factors, such as weight of challenge, influence susceptibility. Studies have shown that if the dose of inoculum is heavy enough N'Dama can become very ill and may even die (Murray *et al,* 1977 a, e).

In addition, it is essential that the effect on susceptibility of such factors as nutrition, stress, exercise, age of first exposure, effect of colostrum, sex, pregnancy and parturition be fully investigated. The effect of intercurrent disease must also be considered as must the relative susceptibility of trypanotolerant breeds to other infections; it has been reported, for example, that N'Dama are more resistant to streptothricosis (Oduye and Okunaiya, 1971). In addition, the impact of transferring trypanotolerant stock to a distant location must be critically evaluated in order that the conflicting opinions that exist on movement may be resolved; this is obviously one of the most important questions to be answered about trypanotolerance although the successful establishment of trypanotolerant breeds in Zaire and elsewhere would suggest that these breeds do adapt (Pagot, 1974; Mortelmans and Kageruka, 1976).

Conclusions.

There is now a considerable body of evidence, both epidemiological and experimental, to confirm the existence of trypanotolerance. It would also appear that trypanotolerance has a genetic basis although this may be supplemented by repeated exposure to the same population of trypanosomes in a given area. However, trypanotolerance is not absolute and breaks down if the weight of challenge is heavy enough. Further work on the genetics of susceptibility in cattle, sheep and goats and precise information on the effect of environmental factors are necessary.

The productivity *of* trypanotolerant livestock relative to other indigenous types may be much higher than previously assumed; they could well be an economically viable proposition in their own right and be introduced into areas where other livestock cannot exist. Furthermore, it is likely that strategies involving immunotherapy, if and when available, and drugs will be more effective and economically viable if carried out on trypanotolerant stock. Finally, there is little doubt that comparative studies of trypanotolerant and susceptible animals offer one of the best approaches for the understanding of the important immunological mechanisms and physiological factors involved in hostparasite interactions operative in African trypanosomiasis. ■

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The first N'Dama cattle were brought to southwestern Zaire in the early 1920s

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[1] Not all of these herds are pure N'Dama and some are judged to have a component of West African Shorthorn.

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

Part I. Tsetse infestation

K.J.R. MacLennan

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.

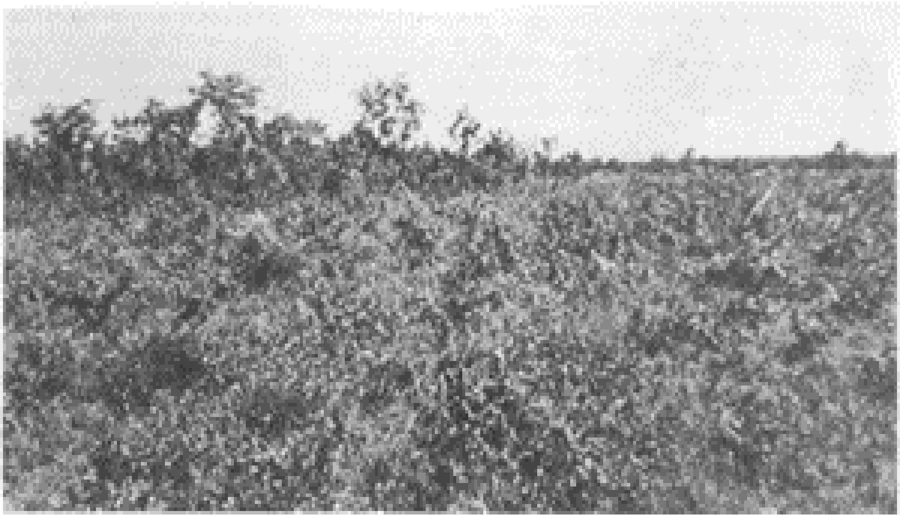
At present most of these constraints, though potent factors in rural development and livestock production, cannot be accurately, or even roughly, quantified in numerical terms. This situation will continue so long as countries lack field facilities to deal with the problems and assemble data on them 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.

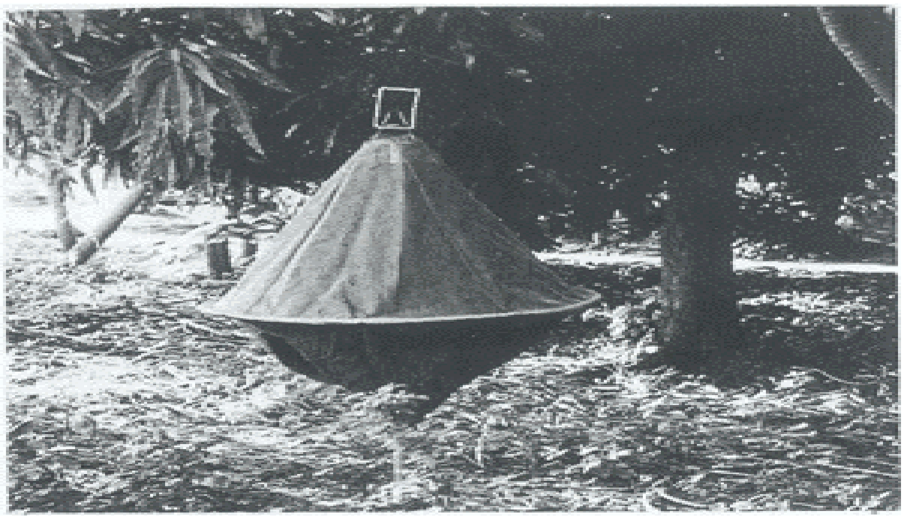
Searching for G. morsitans *with bait, following air spray in Botswana*

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.

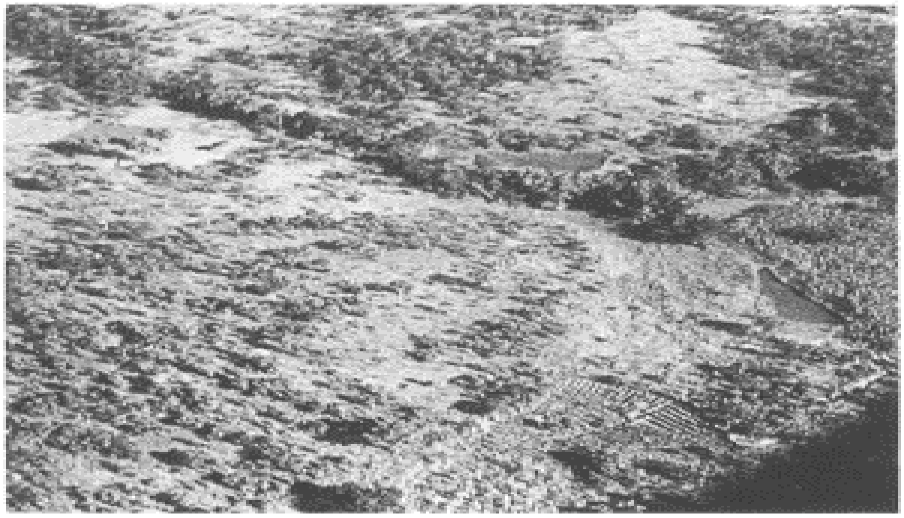
Livestock

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.

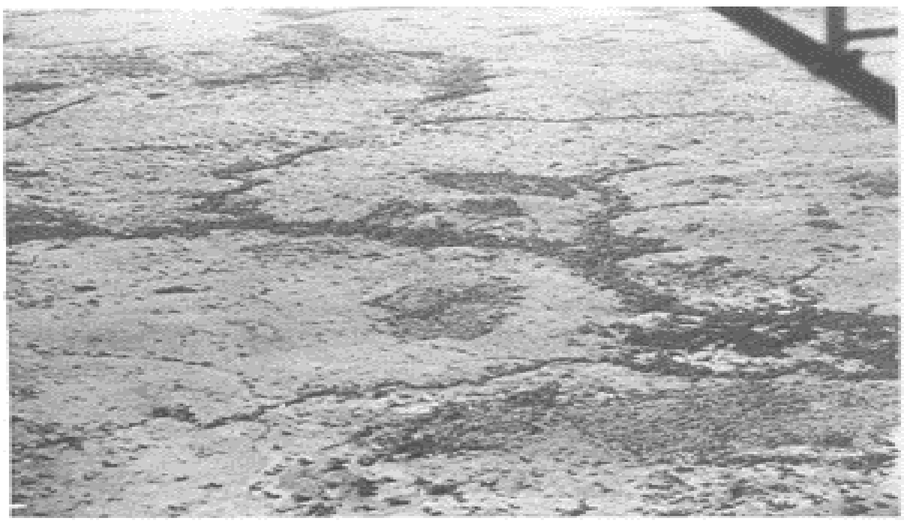
Basically the origin of the cycle of transmission by tsetse flies of trypanosomes pathogenic to livestock is sylvatic (tsetse/wildlife hosts). The relationship of infections in domestic stock to the sylvatic cycle (illustrated in the figure) can be categorized according to whether they are external or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

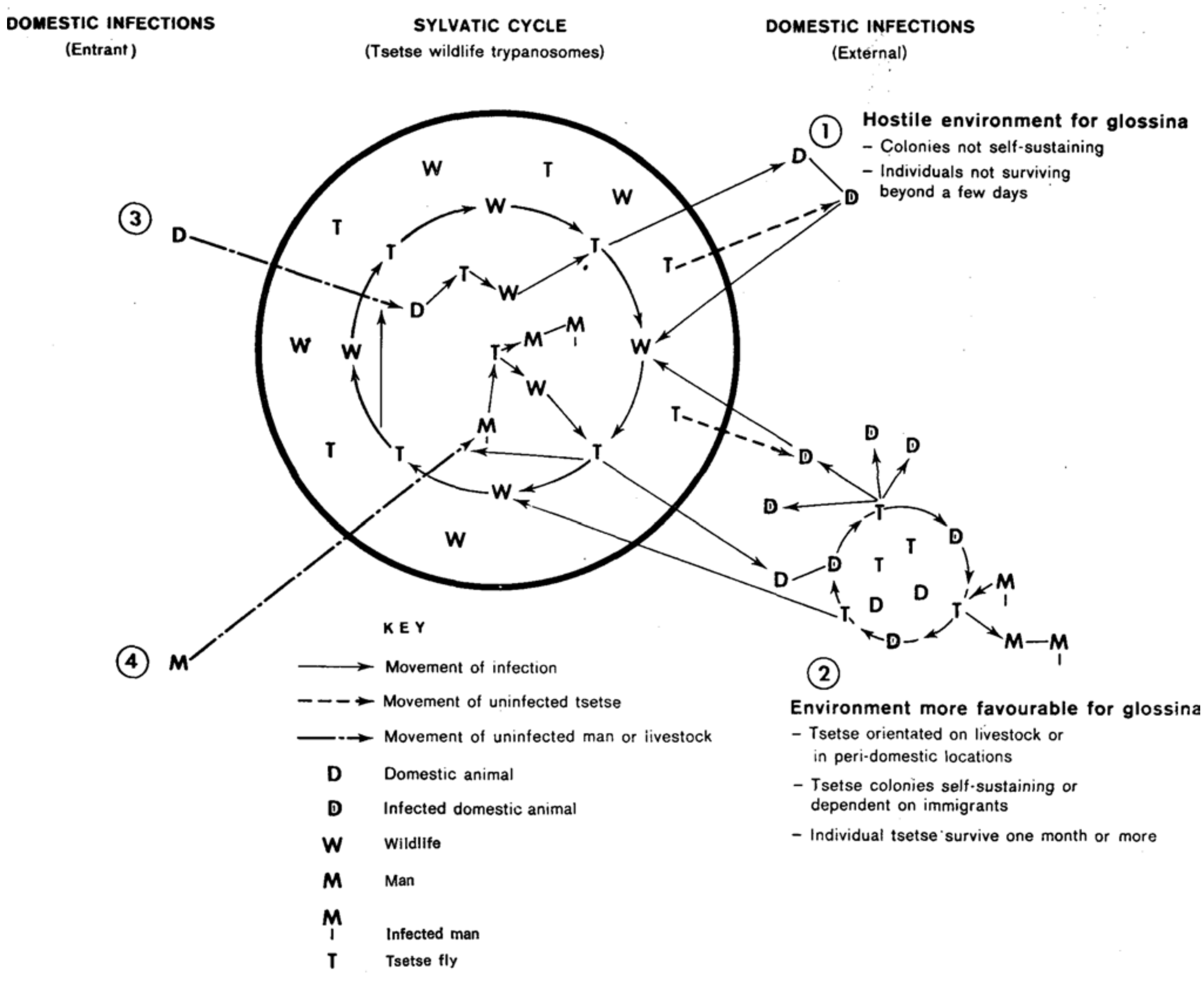
There exist a series of intermediates between the extremes of hostile and favourable environments external to the sylvatic cycle. Ranching projects of an extensive nature will be more vulnerable than those in which bush elimination can be justified economically by increased pasture productivity, a point 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

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.

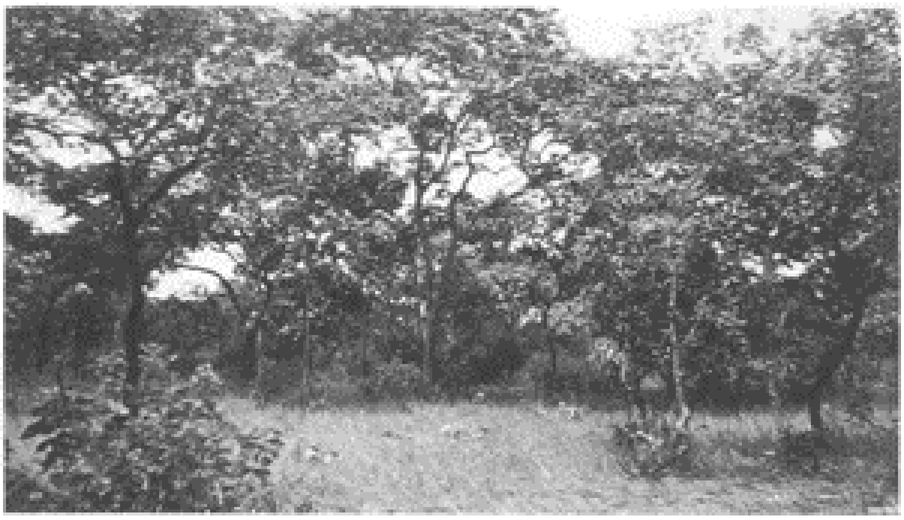
Isoberlinia *woodland infested with* G. morsitans *in the rains*

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.

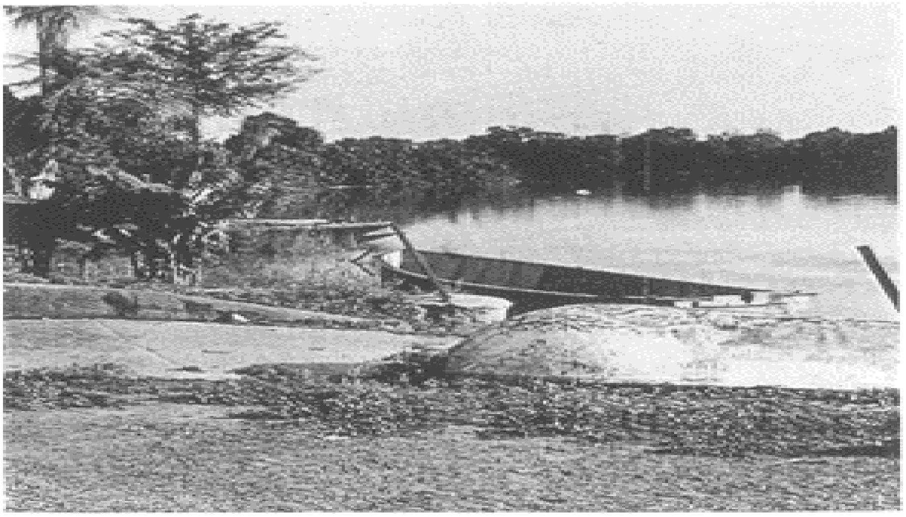
Tsetse infestations are far from being the only basic constraint on balanced utilization of land resources. The most important combination of factors is probably where tsetse infestation and river blindness co-exist. In this situation the elimination of either of the vectors alone will not result in 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.

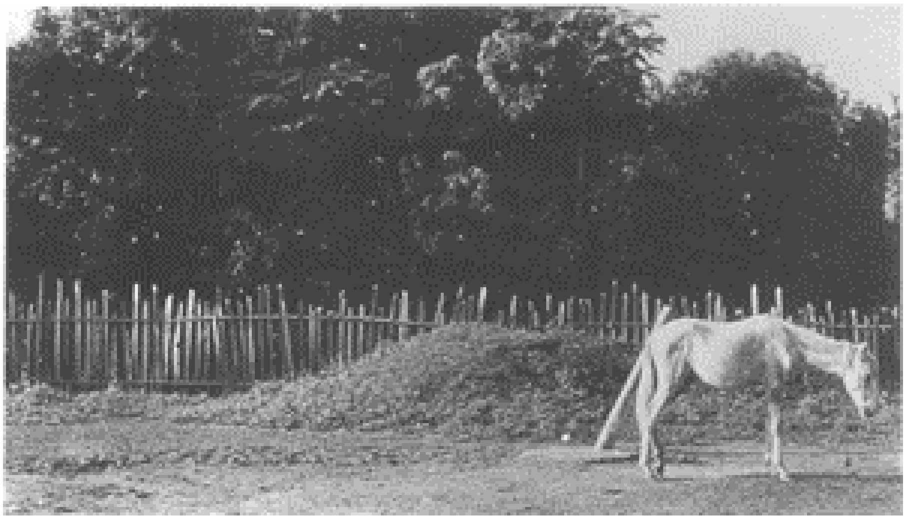
Economic aspects

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.*

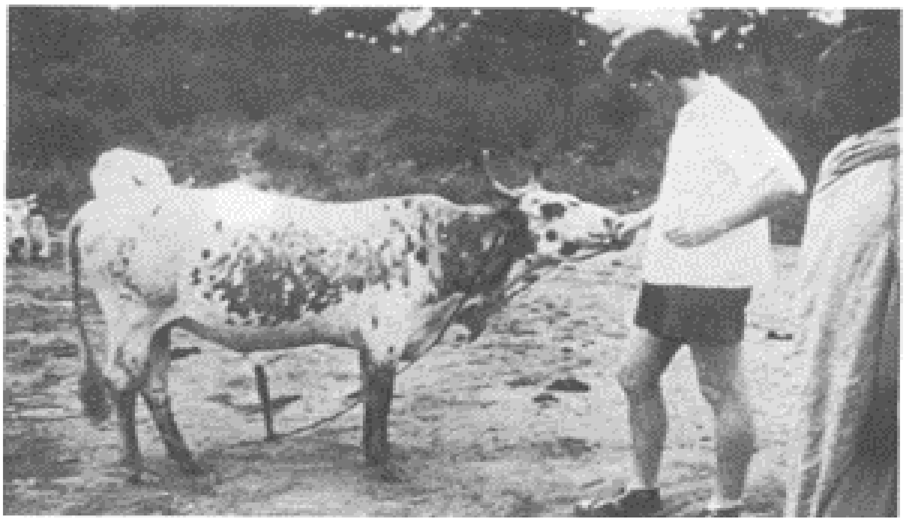
If equations are to be drawn up that meaningfully place the economic impacts of the problem in relation to the cost of countermeasures, it has to be ensured that all components are accounted for and not simply omitted because their significance has not been noticed or quantified numerically. It seems 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

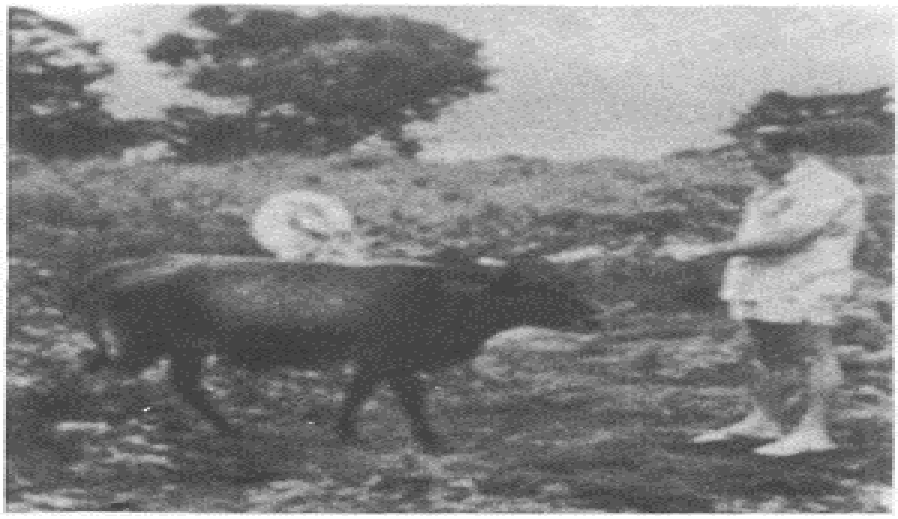
Glossina derives its economic significance solely from its capability to transmit trypanosomiasis to man and livestock. The economic impact is directly related to the risk of contracting trypanosomiasis and, as previously noted, there is a wide range in the degree of trypanosome risk in a variety of 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.

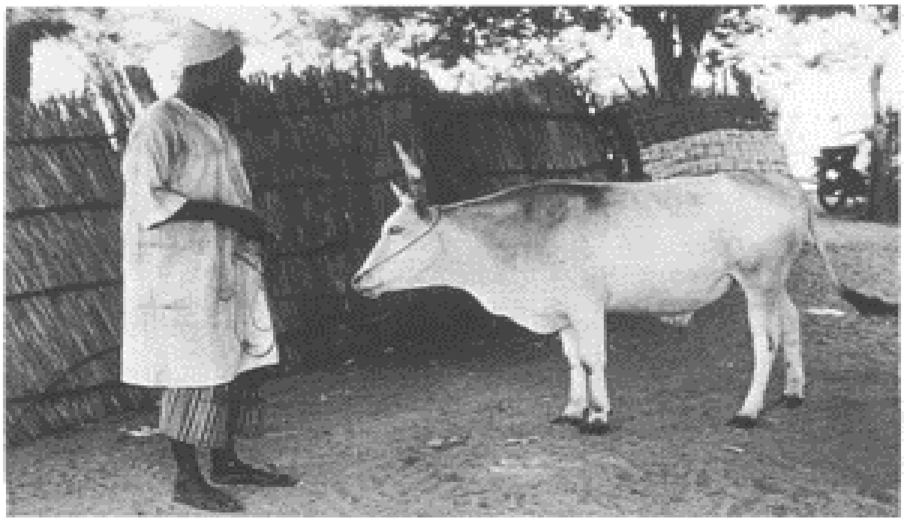
Anti-tsetse objectives are discussed in Part II of this article. There are very important differences in the economics of control compared with largearea eradication (where the latter objective is technically feasible). Examples can be quoted from Botswana, Nigeria and Zambia and from the first such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

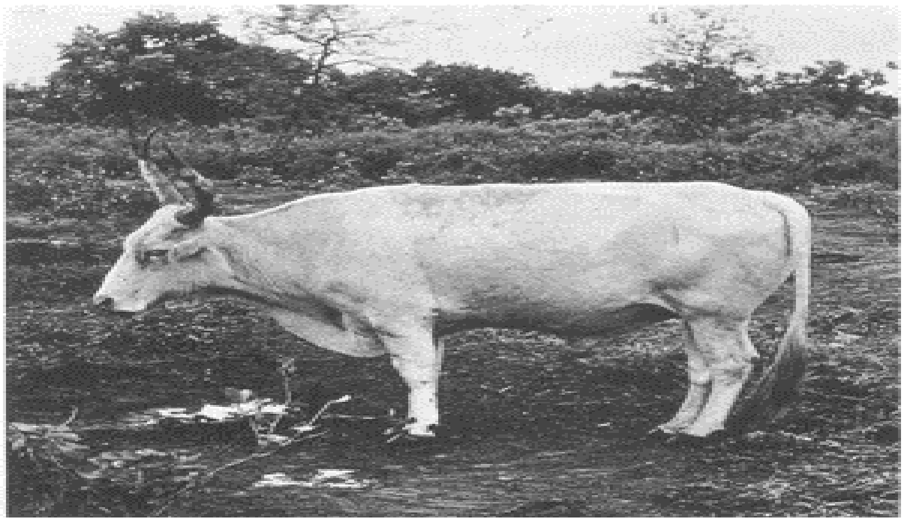
LAND UTLIZATION

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.

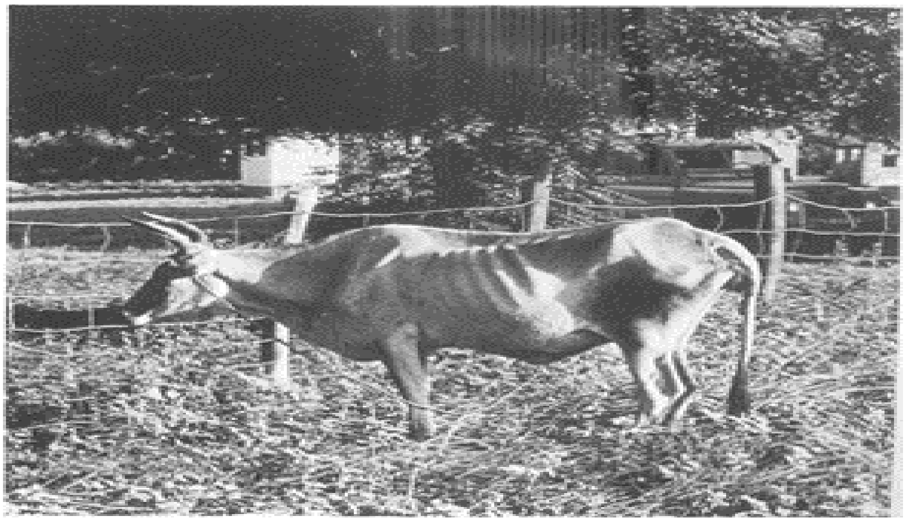
Viewing the tsetse-eradication programme in Nigeria it is evident that it has eliminated considerable direct and indirect problems deriving from trypanosomiasis. For example, tsetse have probably been removed from most of the epidemic sleeping-sickness zone, large *G. morsitans* advances (which had severe 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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Part II. - Techniques in use for the control or eradication of tsetse infestations

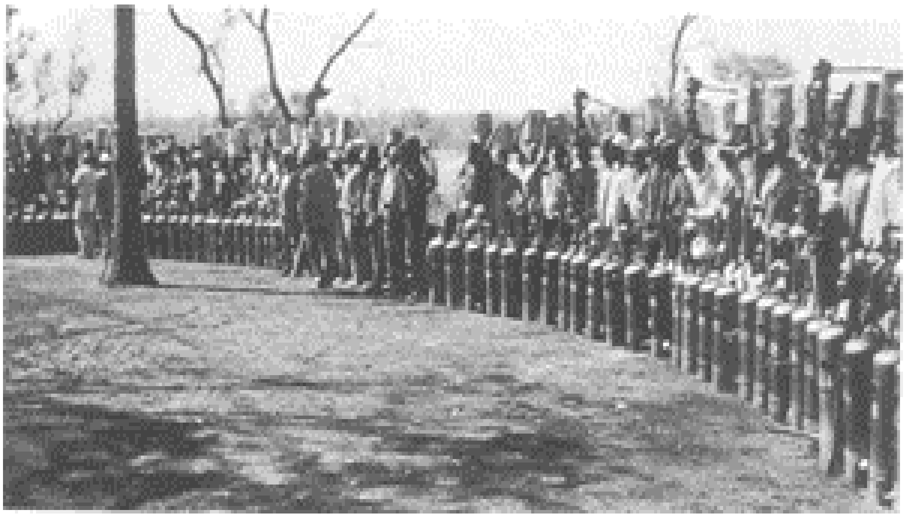
K.J.R. MacLennan

Part I of this article, in World Animal Review *No. 36, dealt in general terms with the problems of tsetse infestations and their effects on rural economies. This part discusses the general principles involved and the techniques in use in the control or eradication of tsetse infestation.*

Successful anti-tsetse activities have included methods such as hand-catching and trapping (Principe, *G. palpalis).* game eviction or destruction (Uganda, Zimbabwe, *G. morsitans, G. pallidipes),* various kinds of tree-clearing and the use of insecticides, or combinations of some of these techniques. Game eviction has been the cheapest method of suppressing savanna tsetse populations (Wooff, 1968), but is repugnant to most thinking people and is now difficult to administer. It is unlikely to succeed in West Africa where savanna tsetse populations thrive on very low game densities and it is not effective against the riverine species. In practical terms most of the anti-tsetse activity in the savanna zones has been by tree-clearing and insecticides either alone, or, more usually now, in combination.

Clearings

Because of the expense of clearing and the considerable maintenance commitment resulting from rapid regenerative growth, clearing activities in recent years have tended to be minimal, although, before modern insecticides became available, clearing operations against riverine tsetse were a major factor in the suppression of the sleeping sickness epidemics in Nigeria in the 1930s *(G. palpalis* and *G. tachinoides).* Though current anti-tsetse activity is mainly conducted through the use of insecticides, clearing still has a place in some sleeping sickness situations, as a means of protection on limited sectors of the perimeter of eradication projects (usually in combination with insecticides) and on the more intensive livestock projects.



Ground spray unit assembled for action in Nigeria. Such a unit can reclaim about 1 600 km^2 (1 000 sq. miles) of G. morsitans *and* G. tachinoides *infested land resource in one dry season operation.*

A variety of clearing objectives are involved, ranging from sheer clearing to selective methods tailored co the habitat and behaviour preferences of particular tsetse species and to climate. However, as with insecticides, selective methods become more difficult to devise and execute in the more humid environments because the habitat relationships of the flies become progressively more diffuse; the flies are more invasive and less dependent on particular components of the tree cover. Selective techniques have proved most successful in the more stressful Sudan and northern Guinea zones (Keay, 1953; Davies, 1964; MacLennan, 1967 and MacLennan and Na'Isa, 1971).

Sheer clearings have an important place on limited portions of the perimeter of insecticidal tsetse eradication areas, which are particularly vulnerable to reinvasion. Mainly because of expense it is not usually feasible now to think in terms of clearings more than 1.6 km (one mile) wide. These are usually supported by periodic insecticidal applications on each side or by buffer zones on the infested side from which infestations are periodically eliminated by insecticidal applications. Sheer clearings can also be important on less-extensive livestock projects where intensive fodder production or pasture improvement leads to the suppression or elimination of woody growth. If only an absolute minimum of shade trees remain, potential tsetse resting places under these can be periodically treated with persisting insecticides and this can ensure that tsetse levels are kept sufficiently low for treatment/prophylaxis to successfully control livestock trypanosomiasis. The economic feasibility of this situation is finely balanced and successful implementation is probably limited to localities of higher quality soil types and favourable rainfall. Furthermore, livestock have to be kept at a reasonable distance from any infested perimeter woodland/forest, or some kind of insecticidal buffer zone created, or else the adjacent area used for arable production rather than for grazing.

The actual technique of clearing that is appropriate depends very much on the circumstances. Selective objectives and the maintenance of the treated area have to be met by hand methods. In practice the performance of motorized saws has been disappointing. In some places large-area sheer clearings have been created by chain-dozing the woodland. The technique may be applicable to the savanna of West Africa though there appear to be no good examples of this. The big problem is again the control of regenerative or successional growth of woody species. Arboricides have performed disappointingly in the subhumid zone though possibly it is worth persevering to discover how to use these agents more effectively. The dozing, windrowing and root-ploughing of woodland or savanna followed by utilization for intensive forage production and intensive grazing possibly offers the best prospect of success provided rainfall and soil characteristics are suitable. The areas that can be handled, however, will be relatively small in relation to overall livestock production needs and the magnitude of tsetse infestation. Sheer barrier clearings are usually done by hand while in riparian associations regrowth is eliminated by piling cut branches on the stumps and eventually burning these, having protected them in the meantime from inadvertent or premature burn and theft of the cut material.

Ground spray of G. morsitans *dry season resting places in the Guinea vegetation zone*

Insecticides

Principles and methods of use. A variety of principles and methods is involved.

Since tsetse flies do not feed on vegetation, and wildlife food sources cannot be systematically dosed, lethal doses of insecticide are acquired by the flies either from the places where they rest, or the surrounding atmosphere while they are in flight or at rest. Methods may be classified according to the duration of lethality of the insecticide emission (transient, or non-residual, as opposed to persistent) and according to the method of dispensing the emission — for example, from the ground or by aerial application. In practice, persistent emissions are applied both by ground spray (usually by knapsack equipment, either hand-pumped, pressure-retaining sprayers or motorized mist-blowers) and by air spray (helicopter) while non-residual emissions are usually dispensed from fixed-wing aircraft or, occasionally, by helicopter. A wide variety of options in equipment and material is available, suited to different circumstances. The situation has been comprehensively reviewed in "Insecticides and application equipment for tsetse control" (FAO, 1976b).

Ground spraying. In recent practice ground spraying has been performed by the relatively precise placement of persisting deposits by teams of carefully supervised knapsack sprayers (Davies, 1964; MacLennan, 1967).

A single placement of insecticide on preferred tsetse resting places is used; the insecticide remains lethal to any adult tsetse that rests on it for a duration at least as long as the pupal period in the ground. An adequate safety margin is required to allow for the fact that in practice all resting places cannot be covered. The deposit is most effective when a lethal dose is picked up and adheres to the feet of the fly after a single contact, but lethal doses can also be acquired through an accumulation of sub-lethal contacts resulting from the daily movements of the flies to a variety of resting places.

Persistence for about eight weeks should be sufficient. However, in locations where reinfestation pressure is continuous *(control* situations) and in buffer zones protecting eradication areas, the duration of persistence should be as long as practicable (Lycklama a Nijeholt, 1965; Mac-Lennan, 1967).

To achieve these degrees of persistence relatively heavy dose rates are necessary but these are applied in a restricted manner developed from a detailed knowledge of the ecology of the target *Glossina* species in the particular environment. The insecticide must be placed where flies will contact it when resting, that is, in the preferred resting places, otherwise it is wasted. Thus blanket applications are ruled out mainly because of the difficulty in distributing such a weight of insecticide, its cost and the impact on non-target organisms.

Two degrees of limitation are practised: first, "discrimination" or dispersal only within tree cover of components known to be frequented by the flies, and secondly, "selection" or limitation within such localities to that stratum of the vegetation and places within it on which flies customarily perch. In certain circumstances the localities are quite specialized and easily recognized once the basic studies of resting behaviour have been carried out. The technology is based on ecological studies initiated by Nash in the early 1930s and continued since then (MacLennan, 1967; MacLennan and Cook, 1972; Scholtz, Spielberger and Ali, 1976). It is most effective when discrimination is of the order of 10-18 percent of the infested area. When the degree of discrimination is 10 percent, a dose rate of 60 g/ha overall in the sub-Sudan zone has achieved extermination, the local application rate being 600 g/ha. Overall dose rates increase with the proportion of the area included in the discriminative application.

The method depends for its success entirely on the acquisition of a sufficiently detailed knowledge of the resting preferences of the tsetse species involved in the particular environment of the project (MacLennan, 1967; MacLennan and Cook, 1972; Scholtz, Spielberger and Ali, 1976). Preferences vary very greatly from species to species and place to place (for example, that which is effective in the drier savannas does not work in the moister zones and that which is required for the elimination of savanna tsetse is very different to that required for riverine species).

Having decided upon the criteria for discrimination and selection and on the dosage rate, one usually applies the insecticide in linear swaths, but only to the vegetational features decided upon. The swath meanders with the vegetational feature and the width varies with local preferences and circumstances but may consist of four sprayers spaced at intervals of about 10 metres advancing in line and following the features decided upon

A single swath may follow both sides of minor drainages and vegetational interzones, particularly ecotones between savanna woodland and tree savanna, or one swath may be needed on each side of larger drainages. All drainages should be followed to their origins. For riparian forest ribbons the swath may be split between the outer and the stream-side margins of the forest and one swath may be needed for each bank. When dealing with savanna species a sharp look-out has to be kept for smaller habitat features such as small tree and thicket clumps associated with termitaria and footslope ecotones that are visible from the swath line and sprayers should be detached to deal with them. If substantial blocks of woodland are not penetrated even by minor drainages or tracks followed by spray groups, swaths should be sprayed at intervals of about 150 metres.

The groups spraying the swaths consist of labourers operating the pumps. Two men may be allocated to each pump and they alternate between actual spraying and carrying insecticide supplies for the man spraying. The groups are directed by trained field staff of the Control Assistant or Scout category, these in turn being supervised by Field Assistants and the whole operation in the field being under the direction of a Control Officer. The terminology varies from country to country but the chain of direction is similar in most places. The Control Officer is very dependent upon adequate maps on which the operation is planned and daily progress is recorded. Usually special maps have to be prepared for this purpose.

To gain access it is necessary to prepare in advance a network of rough motorable tracks and to cut access paths into denser vegetational features. The operation also requires an adequate number of lorries, pick-ups and tractors with trailers to transport personnel, insecticide and water.

The organizational or logistical commitments involved in the treatment of large areas are substantial but an operation unit of manageable size has been able to deal with 1 600 km^2 of *G. morsitarts* infestation in the sub-Sudan zone in Nigeria in one operational season. At that time Nigeria had four such units operational.

As a means of eradicating both *G. morsitans* and riverine tsetse infestations this approach has been highly successful in the Sudan and sub-Sudan vegetation zones but, although successful, it has proved more costly and more difficult to apply effectively in the northern Guinea zone. Much less is known of the relevant aspects of tsetse ecology in more humid locations and there are as yet no indications that similar approaches can be developed for large-area eradication in the southern Guinea or moister areas. Not only are relationships between the tsetse population and the vegetative environment much more diffuse and the tsetse more invasive (Molyneux, Baldry and Fairhurst, 1979) than in areas of greater climatic stress for *Glossina,* but the persistence performance of insecticide deposits is much lower in moister environments. This leads to the use of heavier deposits more generally applied and to sharply rising costs. Even between the Sudan and northern Guinea vegetation zones there exist very important differences in the resting behaviour of *G. morsitans* and in the persistence behaviour of insecticides.

Though further field study may reveal how this method could be applied to the southern Guinea zone and more humid locations for the elimination of tsetse populations, the outlook is not at present encouraging, though clearly the approach is appropriate in control rather than eradication.

The method is technically and financially efficient at levels of discrimination of 10 percent but if more than about 18 percent of the area has to be covered, costs escalate in proportion and there is greater concern about the environmental side-effects of the weight of insecticide being dispensed over wide areas. The annual rate of progress of an operational unit diminishes in proportion to any increase in the percentage of the area included in the discriminative spray.

Helicopter applications. Since the basis of the ground spray technique is the application of insecticide along linear swaths oriented to preferred tsetse habitats it is evident that a similar arrangement could probably be achieved by helicopters and that this would reduce the formidable organizational problems inseparable from large-area ground spray operations. Such a procedure would speed up the rate of reclamation of land resources from tsetse infestation. The concept has been made financially feasible through the development of ultra-low-volume (ulv) insecticide formulations and spray equipment suitable for use on helicopters, reducing very considerably the weight of the payload, which would be prohibitive if conventional insecticide formulations were used (Lee, 1977; Spielberger, Na'Isa and Ardurcahim, 1977).

Small helicopters are used (e.g., the Bell G4A) which follow closely the same localities as those visited by ground spray units. The helicopter flies at a ground speed of 32-40 km per hour (20-25 mph) and 24-32 km per hour (15-20 mph) over forest so that there is an adequate downdraught to achieve a dispersal of insecticide within and below the tree canopy. The machines fly as close as possible to the canopy (1-2 m) and operate from a large number of small temporary clearings made for landing and spaced to reduce non-spray ferrying time to the absolute minimum. The effective swath width in this case is about 20 metres.

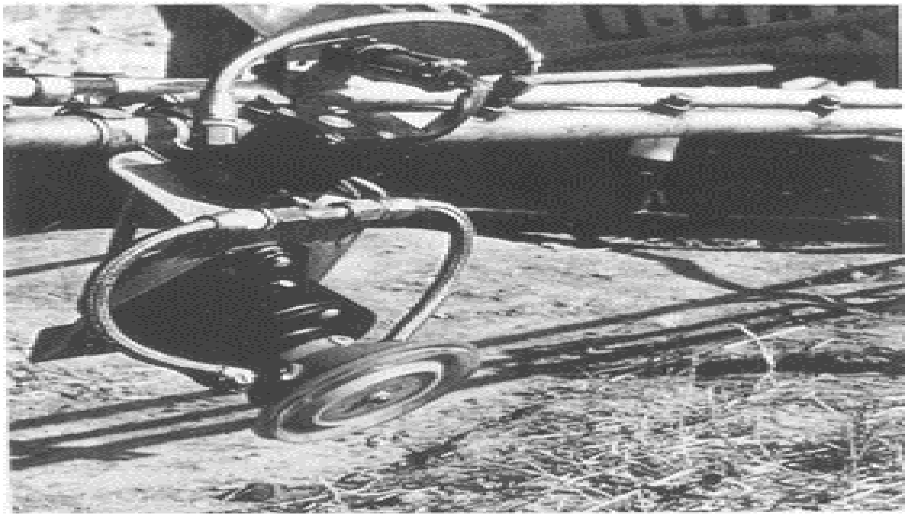
The emission equipment consists of six small, electrically operated and electronically controlled rotary disc atomizers mounted on a 3.2-m transverse boom under the rotor downdraught. Droplet size (determined by the rate of flow and viscosity of the insecticide and the rotation speed of the atomizers) is of crucial importance. Droplets must be sufficiently large to give a deposit with residual activity yet sufficiently numerous to give adequate coverage without being so light that they do not strike. Droplet size is also critical with regard to canopy penetration. Because of this, and the relatively small volumes of insecticide being dispensed, the metering of flow rates and atomizer speeds and the physical characteristics (viscosity, volatility) of the insecticide are of crucial significance to success. Adequate control is achieved through sophisticated electronic control systems and specially designed insecticide formulations. Ground speed becomes a crucial factor also in area insecticide dosage rates. Following any alteration to the several variables it is essential to monitor the droplet spectrum to determine that it conforms to specifications. For this purpose it is as well to seek independent specialist assistance at, or near, the commencement of the spray season.

Above *Motorized knapsack mistblowers in use against infestation in dense habitats*

Right *Livestock at Matyoro Lakes in northern Nigeria, formerly heavily infested* with G. morsitans, G. tachinoides *and* G. palpalis. *Freed of infestation by knapsack spraying of DDT and dieldrin*

The technique is very sensitive to meteorological conditions. After the earth is warmed by the sun a condition of turbulence develops in the lower air, which can carry small droplets upward and disperse them. Ideally a condition of temperature inversion should exist (ground temperatures lower than those at say 7.0 m). Because operations cannot be conducted in darkness, spray activity is effectively restricted to short periods around dawn and dusk. This can be extended briefly by increasing the insecticide flow rate from 4 to 5 litres per hectare, and the droplet sizes by reducing the atomizer rotation speeds. Atomizer speeds of 7 000 rpm will give the generally preferred droplet with volume median diameter of 150 (p.m, while reducing the rpm to 6 500 gives the larger droplet of 170 [pm needed when less favourable meteorological conditions develop. This increases droplet recovery at ground level by 25 percent. However, once turbulence becomes anything but minimal, or if wind speeds in excess of 7 m per second are encountered, spraying can become ineffective. It is emphasized that these figures relate to a particular insecticide formulation and that different criteria will apply to other formulations which will have different physical characteristics.

Left *Helicopter in action returning from spray sortie*



Below *One of six electronically controlled spinning-disc atomizers mounted on helicopter spray boom*

Organizational aspects of deploying and maintaining helicopters in the bush are formidable but, generally speaking, the requirements for labour and transport are much less than for ground spray of a similar area although the cost of helicopter hire more than offsets the saving on labour and transport. A two-machine spray unit can handle about 3 625 km^2 of infested area if the degree of discriminative spray is 10 percent, provided that the unit is smoothly serviced with supplies of insecticide, fuel and spare parts.

The helicopter spray unit requires the same degree of support in regard to pre- and post-spray tsetse surveys, map making and operational planning as does ground spraying and, in practice, it has usually been necessary to protect helicopter sprayed areas by ground spray methods at points where there are particular perimeter re-invasion threats.

In comparison to ground spray, higher local and overall dosages, are required since the element of selection within the swaths, discriminately sprayed, is minimal. As a result of this the impact on non-target organisms is substantially greater. Local dose rates in the Guinea zones are of the order of 800-1000 g/ha. If the degree of discrimination is 10 percent this results in overall dose rates of 80-100 g/ha of infested area. This will be proportionately higher at higher percentages of discriminate spray.

Both ground spray and helicopter applications become progressively less cost effective as the percentage of the area included in discriminative spray rises and, possibly at about 18 percent, is near the upper limit for both methods. At higher rates both cost and environmental aspects give cause for increasing concern. However, where *G. morsitans* advances are in progress or rapid action is required *to* reclaim an infested land resource there is no proven option, at present, other than helicopter spraying, which can be applied in the Guinea zones in cases where there is insufficient time to train, build up and equip the large organizations required for ground spraying.

Helicopter spray techniques have eliminated *G. morsitans, G. tachinoides* and *G. palpalis* infestation from substantial areas (Spielberger, Na'Isa and Ardurrahim, 1977). *G. morsitans* foci have sometimes persisted and have required follow-up applications that have usually proved successful. In practice the method has worked well for the extermination of riverine tsetse infestations in the northern Guinea, sub-Sudan and Sudan zones. Similar limitations on ground spraying exist in more humid areas.

Helicopter applications of non-persistent aerosols, though relatively costly, are feasible technically and could be considered appropriate to certain circumstances (van Wettere *et al.,* 1978).

Fixed-wing aircraft applications. Sequential emissions having a transient effect are blanketed at intervals in time and space over the whole of a project area (MacLennan, 1967). The flies acquire the lethal dose from the surrounding air, not from the surfaces on which they rest, as is the case when using deposits with residual activity. All, or nearly all, adults are eliminated following each application.

The applications have to be carefully timed to ensure that no flies that emerge from the ground following an application live long enough to deposit a viable puparium, and they must be repeated at this interval until the flies are beyond the end of the pupal period in the ground, by which time all puparia deposited before the spray cycles started have hatched. A knowledge of the timing of the reproductive cycle is, therefore, crucial for success. Both the period to first larval birth and the pupal period in the ground vary significantly according to prevailing temperature, becoming shorter at higher temperatures. Usually about five or six applications are required at intervals of about 10 to 19 days for a period of about *two* months. The mean periods can be calculated from average shade temperature to an accuracy of 10 percent (Phelps and Burrows, 1969) from tables compiled by Mulligan and Potts (Glasgow, 1970).

Small, light aircraft are used, of a kind that can take off fully loaded from bush landing-strips located as close as possible to the operational area.

Project areas are preferably rectangular in shape, with the aircraft flight lines oriented transversely to the prevailing wind. The aircraft flies at a speed of about 155 knots, as close as possible to the tree canopy — or about 7.0 m. As in helicopter spraying, a degree of skill and understanding is required of pilots that is of a much higher order than that required for ordinary agricultural crop spraying.

The project is covered progressively by parallel flight lines spaced at intervals of 300 m (sometimes less). The flight lines are controlled at each end from the ground, from cut lines made before the spraying commences and pegged off at the selected flight-line interval by personnel equipped with two-way radios and spotlamps. This personnel is responsible for calling a repeated flight on lines going wider than the acceptable minimum.

Very accurate navigational equipment is required to control both direction and distance. This operates either on the radar-doppler principle or from global, very low frequency radio beacons. If this equipment is sufficiently accurate with regard to direction and distance, a single-ended marking can be adopted, though some reservation has to be expressed regarding a complete lack of monitoring at one end of the flight lines. In some circumstances it is feasible to work from a single, central cut line, but again similar reservations apply.

Meteorological conditions are even more critical in aircraft applications than with helicopter spraying. Normally spraying is restricted to a short period of about one hour around dusk and dawn, while temperature inversion is still present, but, in flatter terrain, the general efficiency of the operation can be greatly increased by night flying, using a special beam-light fitted to the nose of the aircraft. The harmattan wind can be a problem, as in the case of helicopter spraying.

If a single aircraft only is available the operation becomes very vulnerable to any delays resulting from equipment failure. There is little scope for flexibility in timings and if there is slippage beyond the period to first larval birth the whole series of cycles has to start again from scratch.

There is a distinct limitation on flying over broken terrain. Since aircraft have to fly as close as possible to the tree canopy, the operation is best carried out in flatter types of country; it becomes hazardous in more broken country and quite impracticable in hilly country.

The aircraft usually flies at a speed of about 155 knots, emitting insecticide concentrate at the rate of 4-5 litres per minute (depending on the dosage required and the concentration of the active ingredient). The formulation is emitted from a single wind-driven rotary atomizer spinning at about 8 000-12 000 rpm (depending on the physical characteristics of the formulation) to obtain a droplet emission of 30 [pm volume median diameter.

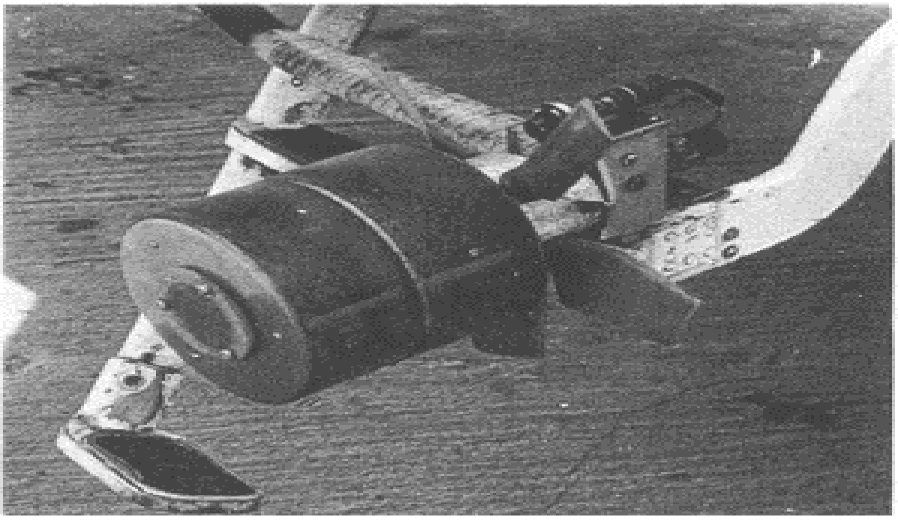
As in helicopter spraying the specifications are critical and careful monitoring of relevant aspects is essential to success. The technology of the emissions has been progressively developed since the early 1950s and is now highly refined, though there is still something to be learned regarding the effects of volatility and drift on optimum flightline intervals. A particularly important feature of the method is the very low dosage of insecticide used: it is of the order of 6-12 g/ha of project area for each spray cycle or 36-72 g/ha in total if six applications are made. The current use of aircraft, both fixed and rotary wing, for anti-tsetse work has recently been reviewed in detail by Lee (1977).

The result of aircraft applications on tsetse populations has been a rapid decline to zero, or something near it, in most instances followed, in some places, by a remarkably slow recovery, the population remaining reduced by about 90 percent for a period of at least three years. Unfortunately, there are no areas of a sufficiently large size that have remained completely free of infestation for long enough for it to be categorically stated that eradication of *G. morsitans* has been achieved by this technique, and there are certainly several locations where eradication has not been achieved. However, there is still scope for much further study on the entomological aspects of spraying by aircraft and a real prospect that further investigation of the survival and drift phenomena will ensure that this method regularly achieves extermination, although this is only possible under suitable conditions of terrain and climate. An additional impact could be produced by reducing the inter-spray cycle intervals to about 10 days, which, recent studies indicate, would ensure that no insemination takes place after the operation commences. There is no experience of the effectiveness of the technique over forest habitats and it would be wrong at this stage to dismiss the possibility of success. The point is of considerable importance since, at present, it is the only approach that can be utilized in these locations that is capable of striking and entering into the moister parts of the sub-humid zone.

However, regarding the current state of knowledge it must be said that the technique has been developed in environments differing in most respects markedly from the moister savannas, and has been used only against *G. morsitans centralis.* The as yet limited experience of the technique against *G. morsitans submorsitans* and *G. palpalis* of the sub-humid zone has been termed "encouraging" but it is still too early to know its actual potential for control or eradication of these species. However, since discriminatory techniques, which are known to achieve extermination, are reaching the limits of their capability in the more humid zone, it is essential to proceed with further development of the fixed-wing spraying technique.

Compounds and formulations. For ground spraying, only ddt and dieldrin have proved fully effective in the field over the years. The former is often used as a wettable powder containing 75 percent active ingredient mixed with water to give a suspension containing 2.5 to 3.75 percent of active ingredient. ddt has the merit of being exceedingly low in its toxicity for humans and it is possibly as a result of the prolonged biological activity at the locations to which it has been very selectively applied that tsetse eradication operations in the Sudan zone have proved so successful. Persistence of activity against *Glossina* can be demonstrated *in situ* for periods well in excess of 12 months (Lycklama a Nijeholt, 1965; and MacLennan, 1967). However, this degree of persistence is obtainable only if it is applied to bark in the dry stage in the Sudan zone and drier parts of the sub-humid zone. Performance falls off rapidly in moister environments where it may fail to achieve results even at much heavier dosages.

Above *Light aircraft being prepared for fixed aerosol spraying in Botswana*



Right *Wind-driven spinning atomizer. One only is required on wing trailing edge inboard of engine.*

In more-humid locations, ground spray operations have used dieldrin in emulsion form at strengths of 2-4 percent derived from 20-25 percent emulsion concentrate. The actual nature of the formulation of the concentrate has been shown to be of importance and, in some countries, a special 18-percent formulation is in use.

In denser habitats, such as swamp forest and thicket, it is sometimes necessary to use motorized knapsack mist-blowers in order to get an adequate dispersal of insecticide within the infested habitat (Koeman *et al.,* 1971). For this purpose a dieldrin emulsion is usually used at a final concentration of 2-4 percent active ingredient derived from 20-25 percent emulsion concentrate.

In helicopter spraying of residual deposits, special ulv formulations of diedrin (18 percent) and endosulphan (25 percent) are used, designed particularly to meet the requirements of anti-tsetse work. It is quite clear that failure will result unless criteria relating to droplet deposits (such as size, volatility, crystalline or surface availability on leaves or bark) are met.

For fixed-wing spraying of aerosols, endosulphan concentrates, sometimes diluted with a suitable solvent, are used at concentrations of 18-35 percent depending on the dosage rate required.

Over the course of the years all potential substitute compounds for these have been tried in the field. In spite of encouraging activity demonstrated in laboratory tests, none (with the exception of some of the new synthetic pyrethroids) has shown any capability of replacing ddt, dieldrin and endosulphan. Certainly, as regards biological effectiveness, there does at last seem to be some prospect of substituting the only compounds that have proved effective over the years with synthetic pyrethroids.

Direct environmental side-effects. These result from the effects of the insecticide emissions on organisms other than *Glossina* and can be immediate or longer term.

The restricted nature of ground spray means that the immediate impact is mainly restricted to organisms that occupy the places to which the insecticide is applied — which, ideally, may be 3-10 percent of the total project area. The fauna that occupies the same niche is affected, particularly insects and insectivores. Animals that are not insectivorous show little if any change and those, including insectivores, that frequent other niches, such as the canopy, are little affected. Some aquatic creatures do suffer an immediate impact. However, the majority of species in the area are not affected, and those which are mostly re-establish themselves from neighbouring unsprayed localities; the rate at which this happens depends on the invasive capability of the animal (FAO, 1977a; and Koeman *et al,* 1971). Two bird species in particular are slow to re-establish, namely the snowy crowned robinchat and the bluebreasted kingfisher. The latter is migratory and its permanent absence can be attributed as much to habitat alteration resulting from changed land use as to the direct effects of the pesticide.

Though it has been searched for, it has not proved possible in Nigeria to find any significant accumulation problem with ddt or dieldrin of a magnitude that would indicate that these compounds are having a significant, deleterious impact in those tsetse eradication areas where the desired result is achieved mainly through a single application of insecticide. It is different in control situations, where application may be required annually, but the number and extent of these are much more limited. It must also be borne in mind that side-effects will be greater in magnitude as the degree of restriction is relaxed, a point favouring fixed-wing application in more humid areas.

In the drier part of the sub-humid zone (the Matyoro Lakes in the sub-Sudan zone) ddt and dieldrin applied in 1961 as a restricted ground spray in a complex of woodland, forest and swamp forest eradicated *G. morsitans* and *G. palpalis* and possibly also *G. tachinoides* (MacLennan and Aitcheson, 1963). Following an investigation in 1970 of immediate and shortterm impacts in a neighbouring area after dieldrin applications, the 1961 area was revisited. All bird species noted to have been affected by the 1961 spray were present and fish were exceedingly numerous (and good to eat) in the small lakes of the system, which have only a very limited seasonal outflow.

The lack of an appreciable accumulation problem can be ascribed to the fact that, in eradication operations of this nature, the result is usually achieved by a single application and to chemical degradation resulting from high ultra-violet values and other features of the tropical environment

The immediate environmental side-effects of helicopter applications are substantially less specific since, although the discrimination is similar to that in ground spraying, the same degree of selection is not, and there is a significant deposition in canopy and aquatic habitats. The immediate impact on non-target organisms is more severe; some heavy mortalities result and some species are slower to reestablish (Koeman *et al.,* 1978). Longer-term accumulation problems are probably not very different to those following ground spraying. The direct impact is mitigated by having ground-sprayed blocks within the helicopter-sprayed area, or adjacent to it, by having unsprayed habitats adjacent to the area and by being careful not to include the whole of any particular type of habitat in the area sprayed (**FAO,** 1977a). Furthermore, the toxicity ranges of dieldrin and endosulphan differ: for example, bees are numerous in endosulphan areas 12 months after spraying while fish are less affected by dieldrin applications. Some reduction in the undesirable impact can be achieved by alternating blocks sprayed by either of these two compounds.

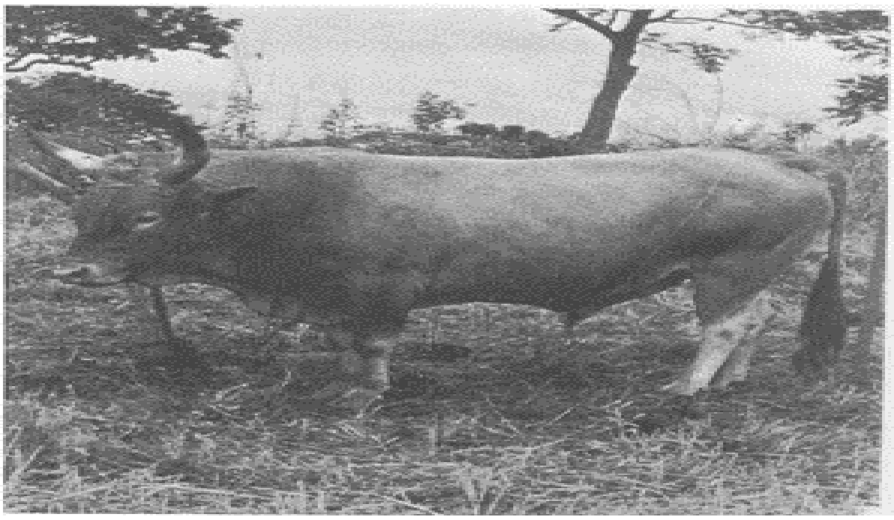
Fixed-wing applications of endosulphan have been studied over a period of three years in the Okavango delta in Botswana. No mortalities directly attributable to the applications have been observed in any species other than *Glossina,* Temporary accumulations of endosulphan, below levels of biological significance, have been observed (Russell-Smith, 1977 - personal communication; and Wood and Turner, 1975) in some species of fish and there is also some indication of transient behavioural responses in some species of fish and ants. The lack of side-effects is possibly not surprising when it is realized that dosages are of the order of 6-12 g/ha per application, much of which does not reach the ground. *Glossina* is particularly sensitive to this compound dispensed in this manner and it is again emphasized that there is no observable mortality of the other numerous Diptera present in sprayed areas, nor of any other animal studied so far.

Usually those engaging in anti-tsetse activity probably rank with the more responsible users of insecticides. Seldom, if ever, have they resorted to large-scale and repeated dispensations of the type that have caused trouble in the USA (Carson, 1961) and in Europe and they have shown no complacency about the continued use of ddt and dieldrin. An overall, balanced judgement is required (Provost, 1972). It is still necessary in some circumstances to use ddt for medical and agricultural reasons and it is not unusual in tropical agriculture to find application rates of 1 000 g/ha, sometimes repeated as many as five times in one growing season and repeated year after year, and to find that compounds such as ddt are a constituent of the applications. Application rates and usage practice in anti-tsetse work have been very different.

The basic objective of large-area anti-tsetse activity is often to facilitate land usage. If this objective is achieved, there is an unavoidable loss of wilderness habitats where these are not specifically conserved. The faunal changes that result from such a development are often of a much greater degree than those arising directly from the application of the insecticides and are of a more permanent nature.

Anti-tsetse techniques are still being improved and new ones developed and at last there is a real prospect of alternatives to the chlorinated hydrocarbons becoming available.

The most promising of the longeracting pyrethroids (decamethrin) has been found to be highly toxic to some fresh-water crustaceans but preliminary experiences show that these are again numerous after 12 months (Spielberger, 1978 - personal communication).



Above *West African N'Dama exhibiting high degree of tolerance to many West African strains of trypanosomes*

Right *West African Dwarf shorthorn (Muturu) cattle. These exhibit a high degree of tolerance to local strains of trypanosomes.*

Control and eradication objectives

There is a considerable diversity in the type of action against *Glossina* that will be appropriate under the different circumstances within the sub-humid zone. This will range from urgent *ad hoc* medical and /or veterinary measures (mainly diagnostic and therapeutic and sometimes augmented by vector control activity) required to contain the immediate consequences of a tsetse infestation affecting established livestock production or resulting in a sleeping sickness epidemic, to longer-term actions designed to eliminate infestation from very substantial areas so that planned development of the land resource can proceed without the serious complications that persisting tsetse infestations can cause. Though continental-scale eradication is not feasible, more local eliminations are feasible in appropriate circumstances and have been achieved in the past.

Anti-tsetse activities have two very different aspirations, namely control or local eradication.

In local *eradication,* a vector-free status is achieved and maintained throughout a large project area. The area is chosen so that tsetse elimination can proceed in a series of annual phases to embrace the entire local tsetse-belt or to take the project perimeter to locations that can be defended for an acceptable expenditure of funds and resources in relation to the area being protected. In *control,* activity is focal, related to specific sleeping sickness or livestock requirements and, since tsetse-free islands dispersed in a sea of infestation are relatively difficult to maintain and defend, a continuing, permanent commitment develops over a large area. This commitment involves vector and disease surveillance and countermeasures as appropriate. When disease episodes occur, the correct course of action is not always easy to formulate since it is often not readily determinable if the episode is due to a tsetse advance, to an occult infestation, drug resistance or maladministration of medicaments. The continuous deployment of scarce technical resources and the substantial supervision commitment are both difficult and expensive to execute and will continue permanently.

In the eradication project the supervisory commitment within the area becomes progressively less until it either takes place at increasing intervals or becomes oriented to the vulnerable sector of the perimeter, if this does not extend to the local limit of infestation. The technical expertise can then be deployed in extension of the fly-free area rather than becoming increasingly embroiled in the supervision of scattered control commitments and the elucidation of perplexing disease outbreaks.

However, the local eradication option can only be exercised where this is feasible in technical and financial terms. In this connection it has to be strongly emphasized that the possibility of formulating an eradication plan cannot even be perceived until a detailed knowledge of tsetse distribution has been acquired and a local field capability exists that is able to do this, collect basic information on habitat relationships and execute, or provide, field support for the anti-tsetse operation. In the absence of this field capability not only do possibilities of action remain obscured but, even if they should be known to exist, they cannot be executed in spite of the availability of financial and technical assistance that could be drawn upon.

It is essential to have an anti-tsetse technique that has been proved to achieve extermination of the particular species in that environment and this is usually developed from control activities or pilot projects. In the absence of a national field capability this experience also cannot be acquired nor can the organization be trained.

The facts of *Glossina* distribution and biology make possible the attainment of an eradication objective over very substantial infested areas of the savanna grazing resources where distribution is not homogeneous. The objective has been attained in several countries, and experience in Nigeria indicates that the objectives can be attained, though not so readily, in the drier parts of the sub-humid zone. The techniques have been developed after many years of field investigation and there is no reason to believe that, after similar expenditure of effort on investigation and technological development (materials, equipment, methods) eradication areas will not be progressively extended, though at present, as has been explained previously, existing, proven technologies are near the limits of their capabilities.

Where eradication objectives are unattainable at present, control situations have to be accepted. In terms of production, that which is feasible in the case of susceptible livestock by treatment or prophylaxis is determined by the degree of risk. As has been explained, higher-level production is usually not feasible except in areas of low risk.

Management

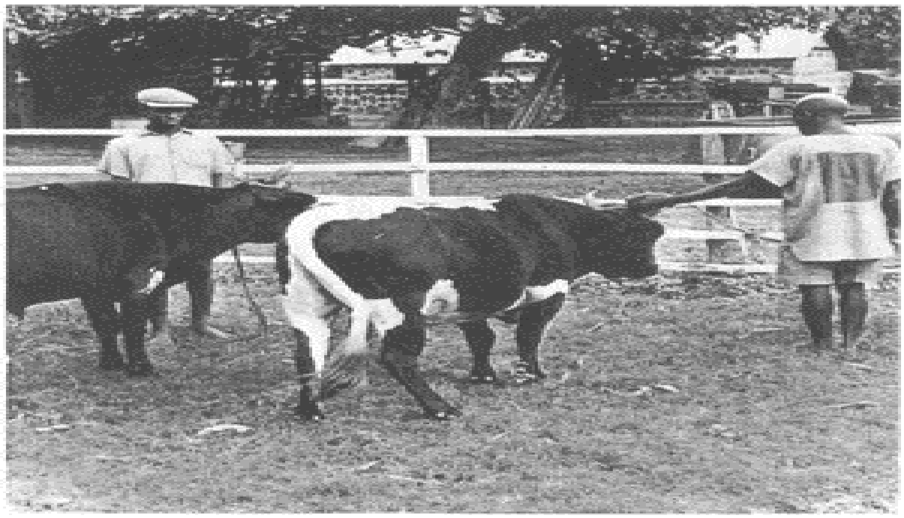
Treatment and prophylaxis. This is appropriate in conditions of low tsetse risk but, in areas of high risk, effective production cannot be ensured by such means unless accompanied by vector suppression (Finelle, 1976).

The difficulties arise from the fact that diagnostic techniques in the individual require a degree of simple laboratory support, that techniques are not completely reliable, and that they require the handling and bleeding of animals. The diagnosis of a trypanosomiasis problem is more readily made on a herd basis and the whole herd dealt with as appropriate.

Drug resistance can be an economically significant problem under static management systems dependent for success on a specific level of production. Repeated treatment in the presence of infestation, particularly if it is livestock-oriented, favours the development of a resistance problem. However, there is still some scope in situations of low tsetse risk, through the alternation of appropriate trypanocides, of reducing the impact of resistance even though, by now, crossresistance to several trypanocides is widespread. It seems that the unstable nature of the resistance phenomenon might soon lead to greater degrees of crossresistance between the currently available trypanocides. No new compounds are available to counter this, most of those available can be significantly toxic to one class of animal or another and there is no generally suitable trypanocide for *T. simiae* infections in pigs (even if there were one it would usually not be possible to administer it in time to save the lives of the animals).

It has been the usual experience that block treatment of entire groups of cattle at appropriate intervals gives better results than waiting for an individual positive diagnosis or until a percentage of the group becomes positive (this latter procedure should not be practised). Surveillance for infection of the entire group on a fixed management system is essential at regular intervals. The treatment of individual trypanosomiasis cases as they arise works in practice only in situations where tsetse risk is minimal, accurate diagnosis is swift and effective treatment follows promptly. The practical difficulty and cost of doing this, as, for example, on extended range, or on a ranch, or in servicing a dispersed group of smallholders with work-oxen, should not be underestimated, nor should the degree of technical expertise required to handle both animal health and the entomological aspects. Pastoral transhumants can accept greater risks and lower levels of production than is practicable under more static management systems. Properly controlled, closely supervised, mass curative treatment and strategically timed prophylaxis have done much to mitigate annual losses from trypanosomiasis and to increase the dry season utilization of infested areas. However, since drug resistance is of widespread occurrence, this practice has to be used with great care and also to ensure that treatment is not just encouraging owners to linger in high-risk areas. Thus, it can be appreciated that the careful supervision and management in the "control" situations require levels of expertise in the animal health and entomological aspects that are either not readily available or can only be deployed in relatively limited areas. Indeed, breakdowns resulting in serious disease outbreaks are not unusual even on very high level management projects. It is also evident that the needs of transhumants are not being fully met in a number of countries for a variety of reasons. These are some of the realities that have to be faced when deciding whether to proceed with the establishment of tsetse eradication areas where these are technically feasible or a control commitment where eradication is not feasible.

Though the difficulties involved have been emphasized, the trypanosomiasis problem can be adequately countered provided the risks have been correctly assessed as being of an acceptable degree and the animal health and entomological expertise is available to carry out the required countermeasures against the disease and, when necessary, against the vectors.



West African shorthorn in Ghana. These exhibit a high degree of tolerance to local strains of trypanosomes.

Tolerant and non-susceptible livestock. Stock that are exotic to the tsetse zone in origin are particularly susceptible to trypanosomiasis but, within the zone, there are breeds of cattle (Pagot, 1974), pigs, sheep and goats, horses and donkeys that exhibit degrees of tolerance of infection. As with treatments/prophylaxis the degree to which the phenomenon can be utilized to achieve effective production is related very significantly to the severity of the risk from *Glossina.* Constant exposure to high-risk situations and the intervention of "stress" periods (Stephen, 1966) can lead to clinical breakdown and sometimes death. Furthermore, it is usually the case that, until they have become infected and the immune defences activated, these animals are about as vulnerable to infection as any other animal (Roberts and Gray, 1973).

Trypanotolerant cattle, once adjusted to the local trypanosomes, produce meat effectively where fully susceptible animals would die. Daily weight increase and time to maturity of selected types under good management and negligible or unspecified degrees of tsetse risk can be impressive (Pagot, Coulomb and Petit, 1972; and Roberts and Gray, 1973). However, the working and milking capabilities of the cattle are usually low and animals reach optimum average slaughter weights at a size and time when the average zebu is near the rate of peak daily weight gain. There is still much to be learned about the production and reproductive capability of these animals (Stephen. 1966) under conditions of moderate and high tsetse risk, and there is no straight comparison available of the production per unit area from closed herds of zebu and tolerant breeds under comparable conditions in which *Glossina* is absent. All this information is essential to any assessment of the extent to, which the use of these animals can mitigate the trypanosomiasis problem or rather whether it would be better to pursue actions that make possible production from susceptible stock. There is much to be learned but though there is clearly an important potential for the appropriate use of tolerant animals under certain circumstances, it cannot be suggested that they provide a complete solution in situations of high trypanosomiasis risk. Their ability to cover ground is less than that of the zebu, though they appear to be much more resistant to streptothricosis. In any case these animals are in short supply.

There appear to be no livestock capable of producing meat that are not susceptible to tsetse-transmitted trypanosomiasis, other than poultry, fish and, in practice, rabbits.

Housing. Under zero-grazing systems susceptible livestock can be isolated from risk by keeping them in fly-proof accommodation when this is practical and economically feasible (as might be the case in pig production units and certain dairy units).

Methods under development

Sterile male release. The method is still under development and has the important advantage that it becomes more efficient, in the biological sense, at lower tsetse densities and has no detrimental direct side-effects on other organisms. However, efficient breeding colonies of each of the *Glossina* species to be eliminated have to be established and, though real progress is being made on colonization techniques, the individuals to be released are still costly to produce. Natural males have to be outnumbered 3:1 by sterile males, which can cost about US$ 1 to produce. Natural savanna tsetse populations have first to be reduced by non-persistent insecticide applications. In the sub-humid zone it is possible that the method may be applied more readily to the riverine species. However, regardless of the species, sterilized males have to be released regularly throughout the area for a period of several months, which, in some circumstances, could prove a major obstacle in areas of low human population density. This aspect, however, could prove no more difficult than the deployment of ground spray teams. A considerable logistic support, as in ground spraying, would, of course, be required.

Growth-regulating hormones. Compounds are available that have been shown to affect, for example, maturation of the puparium. Until such time as a powerful attractant is available for use on *Glossina* there exists an insurmountable problem in applying the compound.

At tract ants. There is as yet no powerful, long-range attractant though some promising advances in developing one are being made. The availability of such an agent would greatly improve the efficiency of survey and detection methods, would make possible the sterilization of natural populations rather than having to produce individuals from colonies and would make possible other channels of attack such as the use of hormones. In the present state of knowledge the availability of an effective attractant that could be used in the field would contribute more than anything else to our ability to deal effectively with the tsetse problem. ■

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Crossbreeding N'Dama and Jersey cattle in Ivory Coast

L. Letenneur

The low productivity of tropical cattle is one of the reasons for the imbalance in the worldwide meat market. The developing countries possess 70 percent of the world's cattle and buffaloes, yet produce only 34 percent of the beef; thus, the productivity per head of cattle is 4.5 times lower in the developing countries.

The coastal countries of the Sudan-Guinean zone have only small national herds. It is estimated that the national herd of trypanotolerant cattle in Ivory Coast is 380 000 head; 320 000 of these belong to the so-called "Baoul*é*" breed, but in fact most of them are, to a greater or lesser extent, crossbred with either zebu or N'Dama. The remaining 60 000 are humpless N'Dama, which are located in the western part of the country and bred on the Aboukouamekro and Sipilou ranches. To this population should be added 100 000 zebu, most of which came north at the time of the great drought in the Sahel.

Jersey bull used in Jersey x *N'Dama crossbreeding programme.*

Almost 90 percent of the cattle spread out north at the eighth parallel in the Sudan-Guinean zone, grazing the natural savanna in a low productivity system. However, as a result of the work of the Société pour le développement des productions animales and of the research on forage and fodder crops conducted by the CRZ,1 the technical transformation of various stock farms is being accelerated through sound management of the savanna, livestock upgrading techniques, the intensive production of forage and fodder crops outside the scheme of crop rotation, and seed production. In each of these various fields there are definite and important possibilities, and it should also be noted that Ivory Coast has an abundance of agroindustrial by products useful for feed.

The major problem is one of obtaining cattle breeds that are genetically adapted to the climate, sufficiently trypanotolerant, and capable of converting these enormous feed resources into livestock products in a way that is economically feasible and suits the facilities of the stock farmer.

Selection among local breeds is done to increase the number and performance of cattle. This work is indispensable and must be pursued and intensified, but will not alone meet the need for rapid development of beef production.

Crossbreeding, however, does offer a great potential but it also involves great risks. This article examines its potential for increasing individual production and herd numbers, as well as for determining the limits of the resistance of cattle to the difficult Sudan Guinean climate and their tolerance to trypanosomiasis, by presenting a ten-year record of experimentation of Jersey X N'Dama crossbreeding.

Choice 1 of animals.

Of the breeds available in Ivory Coast the N'Dama first caught the attention of breeders due to its larger size, its carcass quality and its trypanotolerance. The CRZ, which had started a selective breeding programme of the N'Dama in 1955, possessed by 1964 a rather homogeneous N'Dama herd with known individual performance that could be used as foundation stock for crossbreeding. That same year, in compliance with directives from the Minister of Agriculture and in view of the encouraging results obtained at the Centre d'élevage (Animal Breeding Centre) of Bingerville, the committee in charge of research programmes in animal husbandry and veterinary medicine invited the CRZ to undertake an experimental project for the upgrading of N'Dama cattle by introducing the Jersey breed. As previous trials had shown that it was possible to raise N'Dama cattle throughout Ivory Coast (including the coastal zone), it would be feasible to do extension work on crossbreeding if this experiment were also to give positive results. The Jersey breed was chosen for reasons of physiology and husbandry and because of the goals of the first phase of the desired upgrading.

Owing to the poor results obtained in the past in trials with artificial insemination of trypanotolerant cattle, natural mating had to be employed and a bull selected that was compatible in size with the N'Dama cow. Moreover, physioclimatological work had shown that the larger size obtained by crossbreeding might upset the heat regulation process through alteration of weight/body size ratio.

The aims of the crossbreeding were: (i) to improve milk production in the vicinity of the large urban centres of Ivory Coast; and (ii) to test the extent to which the introduction of genes for milk production into the N'Dama genotype would make it possible to obtain earlier maturing beef cattle through the better nutrition of calves during the suckling period.

The milk production of the N'Dama cow is generally sufficient to feed the calf up to a certain stage of growth; animals crossed with large sized beef breeds would, if natural suckling were allowed, have to go through an initial stage of improvement of their milk production. Furthermore, it was also considered advisable to test not only the adaptation of the various crossbred progeny to the environment, but also their disease resistance.

The crossbreeding plan.

Trials were designed for the breeding and testing of animals of the following grades:1/2, 3/4, 7/8 and 5/8 Jersey.

The decreased hardiness observed in 3/4 Jersey animals led, in 1971, to the proposal to abandon the upgrading process and to try to produce 3/8 Jersey-5/8 N'Dama animals instead. Thus a type of animal better adapted to the more usual stockraising conditions in Ivory Coast was sought, which would be used to breed early maturing beef cattle, particularly through the combined effects of heterosis and better feeding of calves, while at the same time allowing a small amount of the milk to be marketed (provided that this did not adversely affect the growth of the calves).

Males and females with different proportions of Jersey and N'Dama breeding were obtained as follows: 192 halfbreds, obtained by mating Jersey bulls with N'Dama cows; 343 3/4-breds, obtained by mating Jersey bulls with F_1 cows (256), or by the interbreeding of the 3/4-breds themselves (87); 236 3/8 Jerseys, obtained by mating N'Dama bulls with 3/4-bred cows (39), or by mating 3/4-bred bulls with N'Dama females (182), or by interbreeding the 3/8-breds (15); 112 5/8-breds, obtained by mating 3/4-bred bulls with F_1 cows.

Rearing conditions.

Parallel with the genetic improvement project, the CRZ conducted a programme for the intensive production of forage and fodder crops, thus providing a basis for the feeding system.

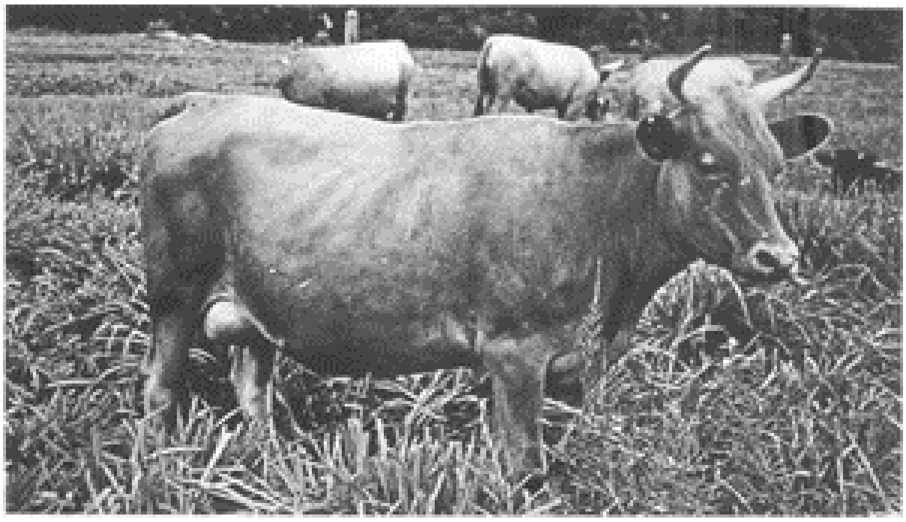
The conditions of calf rearing were closely linked to the genetic level of the dams. Lactating mothers were put out to graze either on the natural or improved savanna while calves of N'Dama cows or 3/8-bred cows were raised by natural suckling up to weaning at about 8 months of age. Calves from other crosses were separated from their dams at birth, fed colostrum, and were then subjected to a standard feeding practice using whole milk, concentrates and hay; they were weaned at 4 months of age.

TABLE 1. **Liveweight gains (kg) of N'Dama and Jersey x N'Dama crossbred males**

	N'Dama	**F_1**	**3/8**	**3/8**	**3/4**	**3/4**	**5/8**

			N'D ♂ X 3/4	**N'D ♂ X 3/4**	**J X F**	**3/4 X 3/4**	**3/4 X F_1**
At birth	n = 111	n = 76	n = 13	n = 60	n = 100	n = 24	n = 41
	17.6 ± 0.6	19.3 ± 1.8	20.0 ± 1.8	17.4 ± 0.9	20.9 ± 0.6	18.1 ± 1.5	21.5 ± 0.8
3 months	n = 197	n = 84	n = 14	n = 84	n =100	n = 24	n = 34
	55.1 ± 1.5	58.1 ± 2.0	66.9 ± 4.8	64.9 ± 2.8	65.0 ± 2.2	54.9 ± 4.1	62.0 ± 4.5
6 months	n = 190	n = 84	n = 14	n = 82	n = 104	n = 23	n = 33
	89.8 ± 2.5	98.5 ± 3.1	100.6 ± 8.1	115.8 ± 3.9	105.1 ± 3.2	84.6 ± 5.6	89.9 ± 5.3
12 months	n = 163	n = 84	n = 14	n = 79	n = 87	n = 13	n = 25
	129.7 ± 3.6	143.1 ± 5.1	153.1 ± 10.2	177.4 ± 4.9	167.1 ± 5.1	129.8 ± 14.4	127.4 ± 8.0
18 months	n = 134	n = 78	n = 11	n = 45	n = 68	n = 10	n = 18
	176.6 ± 5.4	182.4 ± 6.1	221.5 ± 9.7	261.2 ± 6.1	222.1 ± 5.7	202.4 ± 23.7	200.0 ± 13.3
2 years	n = 111	n = 71	n = 7	n = 35	n = 54	n = 5	n = 9
	227.4 ± 5.5	227.7 ± 8.0	253.0 ± 11.0	318.9 ± 10.2	275.9 ± 8.0	246.8 ± 50.2	259.7 ± 16.0
3 years	n = 65	n = 22	n = 2	n = 22	n = 28		
	311.2 ± 10.1	312.7 ± 16.4	297.5	395.6 ± 14.7	378.8 ± 12.6		
4 years	n = 20	n = 4		n = 4			
	328.6 ± 18.8	407.2 ± 3.8		432.8 ± 23.3			

The weaners were grazed rotationally on night and day pastures of *Brachiaria ruziziensis, B. brizantha* or *Stylosanthes guianensis* and, in addition, were given a concentrate feed. This phase, the most critical one, lasted, on an average, 41/2 months. When the animals had reached 100-120 kg liveweight, they were included in the bull calf or heifer herds. Their feeding remained much the same at this stage, but the energy and protein supplement was restricted to 1 kg of rice bran or cottonseed and given during the dry season only. Once the animals had reached 210 to 230 kg liveweight, they were incorporated in the herds of adult males and breeding cows.



Jersey X *N'Dama crossbred cow on* Panicum maximum *pasture.*

TABLE 2. **Liveweight gains (kg) of N'Dama and Jersey x N'Dama crossbred females**

	N'Dama	**F_1**	**3/8**	**3/8**	**3/4**	**3/4**	**5/8**
			N'D ♂ X 3/4	**N'D ♂ X 3/4**	**J X F**	**3/4 X 3/4**	**3/4 X F_1**
At birth	n = 119	n = 69	n = 15	n = 50	n = 90	n = 12	n = 49
	16.7 ± 0.5	17.7 ± 1.2	17.4 ± 2.0	16.1 ± 1.0	20.5 ± 0.6	17.5 ± 2.2	20.4 ± 0.8
3 months	n = 198	n = 78	n = 9	n = 77	n =93	n = 12	n = 48
	5.14 ± 1.4	55.0 ± 1.5	61.4 ± 3.1	61.6 ± 2.3	62.8 ± 2.1	51.3 ± 3.3	62.9 ± 1.9
6 months	n = 189	n = 75	n = 9	n = 75	n = 107	n = 12	n = 48
	84.3 + 2.2	94.2 ± 2.4	90.8 ± 9.3	108.1 ± 4.2	102.3 ± 3.0	78.5 ± 6.7	87.0 ± 3.3
12 months	n = 158	n = 75	n = 9	n = 73	n = 101	n = 6	n = 33
	120.7 ± 3.2	137.9 ± 3.2	131.6 ± 16.2	165.2 ± 4.8	158.2 ± 3.8	121.5 ± 16.9	128.8 ± 7.1
18 months	n = 139	n = 74	n = 9	n = 53	n = 94	n = 6	n = 23
	154.2 ± 4.3	185.4 ± 5.5	193.3 ± 9.1	225.5 ± 5.9	212.8 ± 4.9	179.0 ± 14.8	192.7 ± 6.1
2 years	n = 128	n = 70	n = 8	n = 47	n = 81	n = 3	n = 12
	190.9 ± 4.9	216.7 ± 6.9	235.9 ± 13.2	257.0 ± 8.0	258.3 ± 6.5	157.0 ± 7.6	240.8 ± 15.9
3 years	n = 44	n = 40	n = 6	n = 31	n = 58		
	259.8 ± 8.4	308.4 ± 8.7	276.0 ± 15.2	306.6 ± 11.0	287.9 ± 9.2		
4 years	n = 34	n = 12		n = 18			
	286.7 ± 8.4	344.0 ± 16.9		336.1 ± 10.8			

The males were then subjected to more intensive feeding on improved pastures, with supplementary feeding during the dry season (1.5 kg of cottonseed or rice bran). In fattening trials, however, some of the animals were raised on intensively grown forage crops (irrigated *Panicum maximum)* from June 1973 to July 1974.

The females were maintained on *Stylosanthes* pasture from 1968 to 1971; from then on they had *Panicum maximum* available to them. In view of the uses to which they were to be put and their performance, the 3/8-bred cows were kept on natural or improved savanna. During milking, they consumed on an average 2 kg of rice bran as a supplementary energy source to the basic ration.

Preventive treatment was provided against contagious diseases such as rinderpest, bovine contagious pleuropneumonia and anthrax. Treatment for helminths and ticks was of the type that is standard in the Sudan-Guinean zone. No preventive or curative treatment was used against trypanosomiasis, except for the herd of 3/4-breds; for the latter, two annual injections of trypamidium were given until 1973, but thereafter a curative medication with Berenyl (N.D.) was given as required, the risks of infestation having diminished.

Performance

Liveweight gain.

Owing to the nature of the experiment, animals of the various breeding groups could only be produced successively. Consequently it was not possible to make any contemporary comparisons of performance.

Comparisons were therefore limited to liveweight gains which are presented in Tables 1 and 2. It may be concluded that the 1/2-, 3/4- and 3/8-breds have very good rates of weight gain.

When the herds were maintained on irrigated pastures of *Panicum maximum* for one year, the 3/8-bred bull calves exhibited greater gains than did the 3/4-breds or the N'Dama.(439, 409 and 355 g/day respectively).

In some of the breeding groups distinct differences appeared to be linked with the manner in which they were produced. The weight gain of the 3/8-breds obtained by mating 3/4-bred males to N'Dama females was superior to that of 3/8-breds from reciprocal matings. As for 3/8-bred bull calves obtained by the *inter se* mating of 3/8-bred parents, too little data were available to make a comparison possible.

The progeny of *inter se* matings of 3/4-bred parents gave poorer results than the F_1 . The maximum weights attained were 640 kg for 10-year-old F_1 draught oxen. F_1 cows are at present the heaviest of all crossbreds; the heterosis effect is particularly marked.

Productivity of females.

The average age at first calving was 37 months for the N'Dama, 39 months for the F_1, 31 months in the 3/4-breds and 27 months in the 3/8-breds.

The 3/8-bred females appeared to be very precocious. Their age at first calving is on an average one year less than that of N'Dama females. This same aptitude did not appear in the F_1; however, the latter were bred at the age of 27 months on the basis of observations previously made among the N'Dama.

It may be noted that one 3/8-bred heifer that was accidentally mated at an early age did calve at 141/2 months. Her calf, which she suckled, weighed 110 kg at 9 months. The rather extraordinary sexual precocity observed among the 3/8-breds confirms similar observations made elsewhere on Jersey crossbreds. This characteristic would serve the goal of increasing herd size rapidly and could be a useful trait in the humid tropics. With adequate nutrition, it therefore seems perfectly feasible to obtain calving at the age of 24 months.

Average calving intervals were slightly less than one year for the various crossbred progeny. Compared with 410 days for the N'Dama, calving intervals among the F_1, 3/4-breds and 3/8-breds averaged 355, 363 and 352 days respectively.

The maximum number of conceptions under natural mating conditions occurred at the end of the dry season for all animals, with the corresponding peak number of births in October, November and December.

Milk production.

Almost all F_1 and 3/4-bred cows let down their milk even when their calves were not present at milking time. They also showed good aptitude for complete hand milking. On the other hand, there was great difficulty in hand milking the 3/8-breds; it is therefore concluded that these females should be kept as suckler cows, with the eventual possibility that some surplus milk may become available for sale.

Table 3 shows the milk yields of the F_1 and 3/4-breds in different lactations. Expressed as fatcorrected milk (fcm), the average milk yields (total and per day) of the F_1, increased progressively from the first to the sixth lactation (i.e., from 1 284 to 2 038 kg, which correspond to an average daily yield of 5 to 7.3 kg). The butterfat content was high; in the first lactation it was 5.76 percent, but declined thereafter to 5.47 percent in the sixth lactation.

The milk production of the 3/4-breds was on average higher than that of the F_1. The yields increased substantially from the first to the fourth lactation (i.e., from 1 375 kg to 3 227 kg). The peak of the lactation curve was at the end of the first month. The persistency coefficient among the F_1 was 0.97 from the first to the second month and 0.92 from the second to the sixth month; thereafter, there was a drop to 0.87 in the seventh month and to 0.82 in the eighth and ninth months. Among 3/4-breds the corresponding figures were 0.96 during the first three months and 0.87-0.94 from the third to the sixth month, depending on the length of the calving interval.

TABLE 3. **Recorded milk production in halfbred and 3/4-bred animals**

Lactation number	**Level of upgrading**	**Number of observations**	**Length of**	**Total**	**Butterfat**	**Milk**	**Daily**
			Days	*Kg*	*Percent*	*. . . Kg FCM . . .*	

2nd	1/2	72	255	988	5.76	1 284	5.0
	3/4	53	263	1 136		1 375	5.2
1st	1/2	69	256	1 175	5.66	1 456	5.7
	3/4	23	287	1 332	5.36	1 603	5.5
3rd	1/2	59	255	1 271	5.59	1 569	6.2
	3/4	9	290	1 792	5.13	2 095	7.2
4th	1/2	36	251	1 435	5.52	1 749	7.0
	3/4	2	464	2 694	5.32	3 227	6.9
5th	1/2	10	268	1 611	5.44	1 942	7.2
6th	1/2	5	278	1 664	5.47	2 038	7.3

The average lactation period was 255 days among the F_1. It was longer among 3/4-breds, in which group it varied from 263 to 464 days. The average length of the dry period was 100 days.

The highest milk yield recorded among the F_1 cows was 2 663 kg fcm in 276 days, corresponding to a daily average of 9.7 kg.

Behaviour of lactating cows.

Seven F_1 cows had to be withdrawn from the dairy herds because they could not be handmilked. They were placed in the N'Dama herd and used for selective breeding. This herd was kept under the most primitive conditions of the station, namely on natural or improved savanna.

The 3/4 N'Dama-1/4 Jersey calves obtained from these F_1 females showed markedly superior growth during the first six months to their N'Dama halfsibs (30 kg more for males and 36 kg more for females). Despite the limited number of progeny (five males and eight females), the difference is sufficiently great to be taken into account. The average daily milk yield during the first four months of lactation, estimated on the basis of the calf weight at four months of age, was 5.14 litres; this yield is close to that of the F_1 when milked by hand but kept under definitely better conditions.

F_1 and 3/4-bred cows thus had good milk yields and an aptitude for complete hand milking, whereas the 3/8-breds had to be kept as suckler cows. Their performance is similar to that observed in Ghana.

Meat production potential.

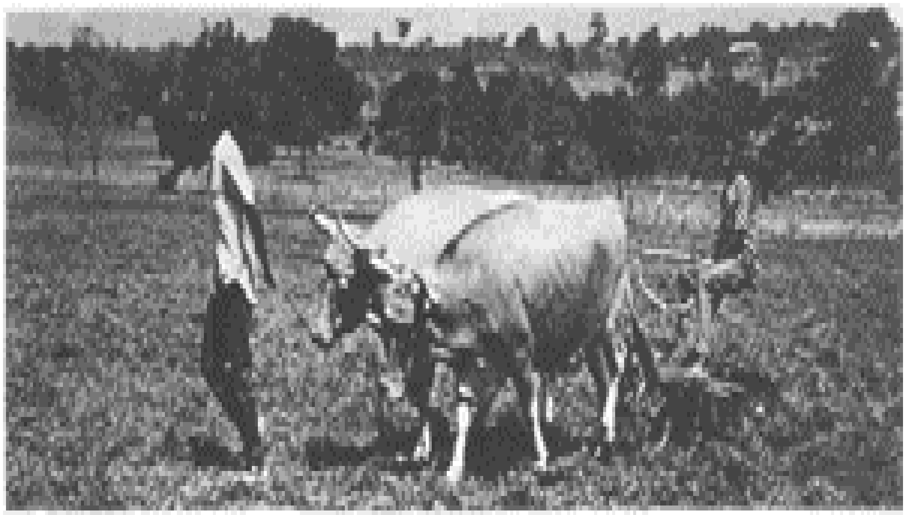
This was analysed almost exclusively on the F_1 males, since most of the 3/4-bred males had been used for reproductive purposes and the 3/8-bred males had been employed as draught cattle.

During intensive fattening trials the average daily gains observed on 37-month-old animals which grazed on *Panicum maximum* and received a concentrate ration (based on cottonseed and rice bran) were 896 g in the first month, 604 g in the second and 263 g in the third.

The carcass weights averaged 211 kg, with a dressing percentage of 57.8; the highest carcass weight was 241 kg, representing 61.3 percent of the live-weight. The conformation of the carcasses was generally good and the fat quality index satisfactory. The tender, juicy and finely marbled meat from these carcasses has always been greatly valued by consumers.

Health.

The health of the F_1 and 3/8-breds under conditions at the CRZ, which was comparable to that among the N'Dama, was excellent. In particular, according to clinical observations they retained their trypanotolerance which is an essential quality of the N'Dama. Table 4 gives in summary form the percentage mortality recorded at the CRZ in each age class.



Jersey X *N'Dama bullocks used for ploughing.*

Among the 3/4-breds, however, mortality figures were particularly high, indicating that these animals are not very hardy. The main causes of death were rickettsiosis, pasteurellosis, trypanosomiasis, piroplasmosis and calf diarrhoea. The animals lost their trypanotolerance and after an initial observation period a wholesale treatment with trypamidium was practised. This was however discontinued in 1973 when the glossina became rare as a result of various measures taken at the station.

This general lack of hardiness of the 3/4-breds in all age-classes was attested by a poorer adaptation to the climate than that of the F_1 and 3/8-breds and caused, in particular, a reduction of their grazing period; the practice of not allowing the herds to go out except during the hotter hours of the day was catastrophic for the six 3/4-bred bulls loaned to local farmers. By contrast, in the same environment the F_1 and 3/8-bred steers gave complete satisfaction; the few deaths reported were attributable not to lack of hardiness among the animals but to accidents or to a lack of minimal care and to inadequate nutrition.

Conclusions

The overall balance is very favourable for the F_1 and 3/8-bred Jersey X N'Dama crosses. The 3/4-breds, however, lack hardiness, and this limits their potential future use in the humid tropics.

The 3/8-breds would do perfectly well under the care of trained stockmen. Their hardiness, their suitability as draught animals, their high growth rate — definitely superior to that of the N'Dama — along with their sexual precocity (making calving possible at slightly over two years of age), the eventual possibility of partial milking (a difficult habit to change, because it is the regular source of income from most local herds and would result in catastrophic consequences for the calves) should make 3/8-breds the choice animals in a general programme for rapid development of meat production. Moreover, considering its ease of calving, this type of animal could be used as the stock for a more ambitious genetic upgrading programme. Nevertheless care has to be taken not to reach the 3/4-bred level.

TABLE 4. **Percentage of mortality in different breed groups**

	3/8	**F_1**	**5/8**	**3/4**	**N'Dama**
	. . . . *Percent*				
Bull calves and heifers	5	7.6	22	28.6	8
Yearlings and 2-year-olds	3	4.3	4.6	14.2	
2-year-olds to 3-year-olds	1	1		16.8	
Adult cows		2		16.2	
Bulls				3.2	

In making a summary report on overall performance the F_1 could be readily ranked as the best; it combines hardiness and high liveweight, good carcass quality, excellent aptitude for use as a draught animal, and a good milk yield, with the possibility for complete hand milking. This type of animal should be popularized among middlesize farms that practise a minimum of intensive production of forage and fodder crops, and also among surburban improved stock farms which have trained manpower at their disposal and which market their milk. F_1 females are, in fact, capable of giving a gross monetary value seven times greater than N'Dama cows and have much better fitness characteristics; the males are choice beef or draught animals. In any case, extreme prudence in selecting a breeding programme is essential. The results obtained for the 5/8-breds are still too incomplete to recommend production of this type of animal, and the risk of segregating genetic traits by crossbreeding of the F_1 has not been assessed, so further experimentation is needed. Other genetic avenues that permit maximum benefits from heterosis, such as two-stage crossing and rotational crossing, remain to be explored, but it would be worth while seeking out parent stock adapted to the tropics.

Under present conditions, the production of 3/4-breds is not recommended; indeed, it is to be avoided. Commercial crossbreeding, involving the slaughter of F_1 females, is also not advised, because this would be contrary to the important policy of increasing herd size. The use of F_1 animals for breeding should be looked at in relation to the end use of the progeny. If they are to remain in the farm sector, backcrossing to the N'Dama may be recommended; the resultant animals exhibit excellent hardiness and are superior in performance to the N'Dama.

The mating of 5/8-bred bulls with F_1 females probably presents the minimum risks for medium-sized enterprises or dairy farms on the outskirts of towns with trained manpower and improved pastures. A return to a policy of two-stage crossing might also be considered, provided that the greatest caution is exercised in the choice of the third breed which would, in any case, be of minimum hardiness. The 3/4-breds are not to be recommended in the various production settings.

The question that remains is: what policy should be adopted for a large-scale crossbreeding programme in the humid tropics in the light of these ten years of experience with Jersey X N'Dama crossbreeding in Ivory Coast?

Apart from the necessity of carefully identifying the best stock farming areas, ascertaining the level of technical knowledge of stock farmers, and investigating possibilities for intensive production of forage and fodder crops and for using agroindustrial by-products as feed, it is important to adopt an appropriate method for reproduction, whether it be natural mating or artificial insemination. Widespread natural mating is only feasible with 3/4-bred bulls on N'Dama cows or 5/8-bred bulls on F_1 cows, while the production of 3/4-bred bulls should be organized in specialized centres prior to their use in a few stud farms, where the sires would be under close surveillance. This could be facilitated by a well-controlled lending scheme to herds run by trained stockmen in favourable regions, in particular, in natural savanna regions with heavy soils where draught animals are used, or in stock farming regions where trained stockmen are implementing a forage improvement programme. The use of 5/8-bred bulls in mediumsized enterprises or in suburban stock farms with trained manpower and improved pastures presents much less difficulty.

Recourse to artificial insemination does not seem a Utopian dream and is favoured by the current practice of community raising of large herds. In any case, two prerequisites, at present the subject of research, should be mentioned: a good knowledge of the sexual physiology of local humpless cattle, and the development of artificial insemination techniques through oestrus synchronization.

Whichever method of reproduction is chosen, extension work to popularize a policy of crossing requires the establishment of specific breeding facilities, such as a centre for multiplication of sires with a high percentage of Jersey blood (over 50 percent), a stud farm, and an artificial insemination centre.

The establishment of such facilities is largely a prerequisite for the popularization of the Jersey X N'Dama cross, which offers the potential of a 50 percent increase in meat production as compared with the local N'Dama cattle. Taking also milk yield into account, the gross production value of each halfbred cow could be increased fivefold and the enormous forage potential of the countries in the humid tropics could be utilized profitably. Moreover, the maternal qualities of F_1 and 3/8-breds open the way to more ambitious genetic programmes. ■

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[1] The project for crossing of Jersey X N'Dama cattle conducted at the Center de recherches zootechniques (CRZ, Animal Husbandry Research Center) of Bouaké-Minankro was launched in 1965. It was executed by J. Coulomb and R. Cadot from 1965 to 1970; and by L. Letenneur, J.C. Mathon, J. Charray, G. Roberge, J.L. Messanger, L. Glattleider, B. Carino and L. Hermitteau from 1970 to 1976.

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