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The role of game animals in the maintenance of endemic and enzootic trypanosomiases in the Lambwe Valley, South Nyanza District, Kenya

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Rhodesian sleeping sickness and bovine trypanosomiasis were endemic in the Lambwe Valley of western Kenya, where the vector of both diseases was a tsetse fly Glossina pallidipes. *Since a large resident population of game animals also inhabited the valley, a programme was designed to assess the relationships between game animals, tsetse, and trypanosome populations and the results were collated with some aspects of local human ecology and the general epidemiological situation in the valley. Of 134 game animals examined for trypanosome infections, 16.4% were found to be positive. This overall infection rate was similar to that found in cattle in the same area.* T. brucei *was the commonest trypanosome found in game animals, but the isolation of* T. rhodesiense *from a reedbuck (*Redunca redunca*) was of greater interest. Altogether, 90% of the bushbuck (*Tragelaphus scriptus*) examined were infected with animal trypanosomes; this is particularly significant since bushbuck was the preferred host of* G. pallidipes *and greatly influenced the distribution pattern and behaviour of the tsetse. It was concluded that the association existing between bushbuck and* G. pallidipes *was extremely important in creating disease foci and that the spread of infections to man was largely a result of poaching activities.*

An important factor in the ecology of both trypanosomes and tsetse flies is the presence of so-called " game " animals, and these animals are therefore of considerable significance in the epidemiology and epizootiology of the trypanosomiases. This is, however, only one factor in the complex transmission patterns of these diseases.

The term " game animals " is a convenient description for communities of large, nondomestic mammals, including ungulates, carnivores, and, to a lesser extent, primates. The role of each game animal population within any community may differ, and the roles may be reversed within a similar community in a different environment.

The results of investigations conducted in the Lambwe Valley, Kenya, are described in this article. The investigations were designed to establish the incidence of trypanosomal infections in game animals in the area, to assess the role of these animals in the maintenance and local transmission of pathogenic trypanosomes, and to determine the relative significance of game animals in the epidemiology and epizootiology of the trypanosomiases.

STUDY AREA

The studies reported here were conducted in the Lambwe Valley, South Nyanza District, Kenya. Descriptions of the area, including accounts of the game animals and the tsetse and trypanosome populations, have been given by Allsopp & Baldry (1972) and Baldry (1972).

MATERIALS AND METHODS

Incidence of trypanosome infections in game animals

During the period from June 1970 to May 1971, 134 animals of 10 game species were examined for trypanosome infections in the Lambwe Valley. A substantial number of the animals were obtained by Kenya Game Department staff during control operations in the locality.

Fresh blood taken from the heart of each animal immediately after death was inoculated into laboratory rats and mice. Initially, injections were either

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subcutaneous or intraperitoneal, but for most investigations only the latter route was employed. The number of laboratory animals used for each blood sample was generally 2 rats and 4–6 mice.

Serum samples were also taken and 90 of them were examined for trypanosomal antibodies (see Binz & Allsopp, 1972) by the latex agglutination test (LAT) as described by Binz (1972). Thick and thin blood smears and gland smears were made for preliminary surveillance.

All *Trypanosoma brucei* subgroup infections were subjected to the blood incubation infectivity test (BIIT) (Rickman & Robson, 1970) for a specific identification of the parasite.

Distribution and density of game animals

The area showed 3 major vegetation types—namely, grassland, isolated thicket clumps, and dense continuous thickets.

The density of game animals was assessed in grassland by means of periodic total counts undertaken largely by volunteers. In isolated thicket clumps the population density was estimated by periodic counts in 3 quadrats of 0.64 km^2, using beaters to drive animals out of the area and recorders around the perimeter to determine the number of each species seen to leave. No attempt was made to estimate densities of game animals in dense continuous thickets. A more detailed description of these methods has been given by Allsopp et al. (1972).

Epidemiological and epizootiological data

Data on trypanosome infections in man, livestock, and tsetse are taken from the findings of Baldry (1972), England & Baldry (1972), Robson & Ashkar (1972), and Watson (1972). Other relevant information was obtained from local residents and Kenya Game Department staff and by personal observations.

THE HISTORY OF TRYPANOSOMIASIS IN THE LAMBWE VALLEY

T. rhodesiense was first recorded in Nyanza Province, Kenya, in 1953–54, although there had been a serious outbreak of disease in south-east Uganda, adjacent to Central Nyanza District, in 1940. From that time onwards, conditions progressively worsened until the disease reached epidemic proportions in the Alego location in 1964. South Nyanza District had a history of *T. gambiense* infections before the 1955–57 insecticide campaign (Glover et al., 1958) when it was eradicated, but *T. rhodesiense* sleeping sickness was discovered in the district only in 1959–60.[1]

Prior to the 1959 settlement scheme in the Lambwe Valley, the area had been virtually devoid of cattle, mainly on account of the high incidence of trypanosomiasis. Even after this time it was still necessary to treat cattle regularly with trypanocidal drugs.

THE DISTRIBUTION OF PATHOGENIC TRYPANOSOMES IN RESERVOIRS OTHER THAN GAME ANIMALS

In man

During the period 1968–70, *T. rhodesiense* infections were discovered in 56 people out of the total valley population of about 6 000 (Watson, 1972). The incidence of infection during this 3-year period declined from 0.48% to 0.18%. Altogether, 75% of the adult cases were in males.

Serological tests showed that some persons who exhibited no parasitological evidence of trypanosomiasis nevertheless produced a positive reaction to the LAT, indicating the presence of circulating trypanosomal antibodies and suggesting that the incidence of this disease was in fact greater than that estimated parasitologically (Binz, 1972). The rate, was, however, still low.

In domestic animals

A total of 3 695 cattle, 402 sheep, and 2 287 goats were examined for trypanosomes during the period 1968–70, the infection rates being 17.0%, 5.0%, and 2.1%, respectively. The trypanosomes found most frequently in cattle were *T. congolense* (9.7%), *T. vivax* (6.6%), and *T. brucei* (4.8%) (Robson & Ashkar, 1972).

Of the 133 *T. brucei* subgroup infections in cattle reported by Robson & Ashkar (1972), 14 (10.5%) were identified by means of the BIIT as being caused by *T. rhodesiense*. One strain of *T. rhodesiense* was isolated from a sheep and an " intermediate " strain from a goat.

It is significant that the overall infection rates given above were greatly exceeded in areas such as Otuok, where the rate in cattle was 65% for the animals examined; the trypanosomes present were *T. brucei* (39.0%), *T. congolense* (38.4%), and *T. vivax* (23.2%) (Robson & Ashkar, 1972).

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[1] Willett, K. C. et al. (1965) *Trypanosomiasis and tsetse in the Nyanza Region, Kenya,* Unpublished WHO working document TRYP/INF/2.65. See also Baldry (1972).

In Glossina pallidipes

Between 15 April and 11 May 1970 a total of 652 tsetse flies from the Otuok–Rari area were dissected and 20% were found to be infected with trypanosomes; 81% of the infections were caused by organisms of the *T. vivax* group, 16% by the *T. congolense* group, and 1.5% by the *T. brucei* subgroup. No *T. rhodesiense* infections were identified (England & Baldry, 1972).

Repeated collections in the same general area during May–September 1970 produced an infection rate of 30.9% from 1 000 flies, 74% of the infections being caused by the *T. vivax* subgroup, 23% by the *T. congolense* subgroup, and 2.2% by the *T. brucei* subgroup. Of the 7 *T. brucei* subgroup isolates, 1 was identified as *T. rhodesiense* by the BIIT (England & Baldry, 1972).

In wild rodents

A total of 690 wild rodents were examined for trypanosomes and 11 were found to be infected with *T. lewisi*. No other pathogenic trypanosomes were identified (Robson, 1972).

THE DISTRIBUTION OF PATHOGENIC TRYPANOSOMES IN GAME ANIMALS

Of the 134 animals examined for trypanosomes, 22 (16.4%) were infected, *T. brucei* being the most common pathogen (Table 1). Bushbuck (*Tragelaphus scriptus*) had the highest incidence of pathogenic trypanosomes, 9 of the 10 animals examined being infected. The only uninfected animal was a juvenile. The trypanosomes found were *T. congolense* (50%) and *T. brucei* and *T. vivax* (25% each). *T. brucei* was also isolated from reedbuck (*Redunca redunca*), waterbuck (*Kobus defassa*), and hyaena (*Crocuta crocuta*), and *T. congolense* from oribi (*Ourebia ourebi*) and reedbuck. *T. vivax* was found only in bushbuck, while *T. rhodesiense* was isolated from a single adult male reedbuck. No pathogenic trypanosomes were isolated from bushpig (*Potamochoerus porcus*), duiker (*Sylvicapra grimmia*), roan antelope (*Hyppotragus equinus*), or topi (*Damaliscus korrigum*).

The infections found in hyaena were a cause for speculation since these carnivores were particularly nocturnal in the Lambwe Valley and rested in underground dens during the day. Unless the infections resulted from the bites of tsetse entering the dens during the day, as might occur if female flies were searching for breeding sites, or from the ingestion of infected animals, then these observations suggest nocturnal activity by *G. pallidipes*, particularly since this species of tsetse has been noted elsewhere to be active after dark (Chorley & Hopkins, 1942).

Some of the 90 sera from game animals examined by the LAT gave positive reactions, although the

Table 1. The frequency of trypanosome infections in game animals in the Lambwe Valley, 1970–71

Game animal	No. examined	Pathogenic *Trypanosoma* infections					Total		Nonpathogenic infections	
		vivax	*congolense*	*brucei*	*rhodesiense*	*congolense/ brucei*[a]	Actual	%	*theileri*	%
bushbuck	10	3	3	0	0	3	9	90.0	0	0.0
bushpig	3	0	0	0	0	0	0	0.0	0	0.0
duiker	10	0	0	0	0	0	0	0.0	0	0.0
hyaena	6	0	0	3	0	1	4	66.6	0	0.0
impala	11	0	0	0	0	0	0	0.0	0	0.0
oribi	28	0	2	0	0	0	2	7.3	3	10.0
reedbuck	57	0	1	3	1	0	5	9.1	5	9.1
roan antelope	2	0	0	0	0	0	0	0.0	0	0.0
topi	2	0	0	0	0	0	0	0.0	0	0.0
waterbuck	5	0	0	2	0	0	2	40.0	1	20.0
totals	134	3	6	8	1	4	22	16.4	9	6.6

[a] Mixed infection.

animals were parasitologically negative (Binz & Allsopp, 1972). This suggested that the overall infection rate was in fact greater than the 16.4% indicated by parasitological examination alone (see Table 2).

Table 2. Immunological investigation of sera from some Lambwe Valley game animals for trypanosome infections [a]

Game animal	No. examined	Parasitologically positive		Positive LAT [b]
		Pathogenic	Non-pathogenic	
bushbuck	9	8	0	7
bushpig	3	0	0	0
duiker	10	0	0	1
hyaena	4	2	0	0
impala	6	0	0	0
oribi	17	0	2	2
reedbuck	36	3	4	13
topi	2	0	0	0
waterbuck	3	0	1	1
totals	90	13	7	24

[a] Data from Binz & Allsopp (1972).
[b] LAT, latex agglutination test.

THE DISTRIBUTION AND DISPERSAL OF GAME ANIMALS IN THE LAMBWE VALLEY

The Lambwe Valley has well-defined vegetation types, which profoundly affect the resident species of game animal. These animals can be broadly defined as bush-dwelling and plains-dwelling species; the former group includes bushbuck, bushpig, duiker, waterbuck, and buffalo (*Syncerus caffer*); the latter group comprises Jackson's hartebeest (*Alcelaphus bucelaphus jacksonii*), oribi, topi, and roan antelope. Impala (*Aepyceros melampus*) and reedbuck tend to occupy both habitats.

The Lambwe Valley is virtually enclosed within the surrounding hills, and on account of this geographical factor in conjunction with human settlement game animals could not disperse into surrounding areas during times of stress caused by climatic extremes but were confined within the valley.

Within the valley the total numbers of plains species remained stable but there were seasonal changes in the patterns of distribution. Population estimates for plains species in the Lambwe Valley Game Reserve are given in Table 3. Being more susceptible to climatic changes in the exposed grasslands, plains species tended to concentrate in the more densely wooded and thicketed areas during prolonged dry periods. During such times the grassland cover was greatly reduced both by the climatic conditions and by habitual fire-raising activities of the local people. The interstitial grasslands of the thicket clumps and woodlands were less prone to encroachment by fire and therefore retained more herbaceous cover.

Table 3. Population estimates for plains game in the Lambwe Valley Game Reserve, August 1970 to May 1971

Game animal	Mean/census	Mean/km²
impala	390	7.80
Jackson's hartebeest	78	1.56
oribi	263	5.26
reedbuck	311	6.22
roan antelope	93	1.86
topi	243	4.86
totals	1 378	27.56

Bush-dwelling species, living in a more buffered environment, did not exhibit this change in distribution. Among the bush-dwelling species, bushbuck and duiker had small home ranges and were the most sedentary species. Bushpig tended to leave their daytime retreats to feed on cultivated land after dark, and to some extent all bush-dwelling species showed nocturnal activity. Waterbuck had relatively large home ranges and, although generally considered to be a sedentary species, they covered far greater areas than either bushbuck or duiker. Buffalo seldom remained in the same place for long periods, but continually changed their location within the thicket belt; this may have been a direct result of intensive poaching activities.

Reedbuck and impala occupied both the grasslands and the peripheral thicket areas. Little is known about the size of the home range of the former species, but observations in the valley suggested that it was fairly small. Although no attempt was made to identify individual animals, the repeated sighting of groups of a similar size in the same area suggested that herds, including as many as 20 animals, sometimes occupied a limited range. Impala, like waterbuck, were also sedentary animals, but with relatively large home ranges.

In addition to ungulates, the valley also had a small community of carnivores. Leopard and hyaena were the larger species, with serval, civet, mongoose, and genet also present. Nothing is known of the population dynamics of the leopards or whether they carried trypanosomes. They were quite frequently seen after dark, which suggests that they were relatively common. Hyaenas were not often seen, but it appears that they fed after dark while visiting local farms. The stomachs of those collected contained exclusively goat.

ASSOCIATIONS INVOLVING BUSH-DWELLING GAME SPECIES AND MAN

The approach of game animals to man

Many of the bush-dwelling species of game animal left their daylight shelter after dark, and were attracted to cultivated land where they fed on and among crops such as maize and beans. Bushbuck and duiker fed on the small forbs at ground level that are characteristic of recently tilled soils, while bushpig destroyed large areas of mature maize crops by breaking down the plants and digging among the roots.

The approach of man to game

People in and around the Lambwe Valley existed largely on subsistence farming and, nearer the lake, fishing. In such poorly developed areas, where family incomes were very low, many of the day-to-day requirements were obtained from the land and there was a regular traffic, carried out almost exclusively by women, between homesteads and woodland where wood for fires and building was collected.

Since cattle are kept as convertible assets for buying wives or use in emergencies, the diet of maize or bananas has to be supplemented with fish or meat. Game animals may, therefore, have constituted an important part of the diet of the people, and the very large number of snares found in the valley substantiated this view. Many of the homesteads, particularly those that were somewhat isolated, had as many as 10 snares set on game paths or in gaps through thicket patches around the settlement.

Poaching was probably the most significant aspect of human approaches to bush-dwelling game. It was obviously widely practised and, since snare lines had to be checked daily, a segment of the population, usually male, was in repeated contact with thickets, bush-dwelling game animals, and tsetse.

The influence of the distribution of man on that of game animals

The 0.64-km^2 quadrats used in the Otuok area to determine the distribution of bush-dwelling game animals were sited in relation to human settlements and herds of cattle.[1] Ot. 1T was near a human settlement only, there were no human settlements or cattle in the immediate vicinity of Ot. 2T, and Ot. 3T was near a human settlement with cattle.

With the exception of duiker, which were fairly uniformly distributed, and buffalo, the various species of game animal appeared to be attracted to human settlements (see Table 4), conforming with their habit of feeding on cultivated land. A secondary factor was the proximity of the dense continuous Otuok thicket block, and the lower densities of some species observed in Ot. 3T were possibly the result of the relative isolation of the quadrat from this highly significant factor.

Buffalo were most frequent in Ot. 2T, reflecting their tendency to avoid contact with man.

ASSOCIATIONS BETWEEN PLAINS SPECIES OF GAME ANIMAL AND MAN

The approach of game to man

Local people were continually occupied in setting fire to the grasslands, an activity that was not fully understood. Peripheral areas of new growth may have been used for grazing cattle or setting snares, but these uses were out of proportion to the frequency and extent of the burning-off observed throughout the valley. There was a tendency for burning-off to occur most frequently in the vicinity of human settlements, although it was by no means confined to such areas.

With the notable exception of roan antelope, plains game animals were strongly attracted to recently burned areas and were therefore seen close to human habitations. It was not unusual to observe oribi or topi grazing alongside cattle, particularly when, as was often the case, the herds were either unattended or watched over by a young child from a considerable distance.

[1] See Fig. 1 in Allsopp et al. (1972).

Table 4. Distribution of game animals and *Glossina pallidipes* between quadrats Ot.1T, Ot.2T, and Ot.3T, and density estimates of game animals for the Otuok isolated thicket clump vegetation type

Game animal	Mean/quadrat/census			Percentage distribution between quadrats			Density/km²
	Ot.1T	Ot.2T	Ot.3T	Ot.1T	Ot.2T	Ot.3T	
bushbuck	6.1	3.2	3.1	49.19	25.81	25.00	6.59
reedbuck	6.2	9.3	14.4	20.73	31.10	48.16	15.41
duiker	5.1	5.0	3.2	38.34	37.59	24.06	6.96
impala	0.7	0.2	1.0	36.84	10.52	52.63	1.00
waterbuck	3.6	0.0	0.7	83.72	0.00	16.28	2.34
buffalo	0.2	0.7	0.0	22.22	77.77	0.00	0.45
bushpig	0.6	0.1	0.6	46.15	7.69	46.15	0.67
oribi	1.9	1.1	2.2	36.45	21.15	42.31	2.73
others	0.4	1.5	0.7	15.38	57.69	26.92	1.34
totals	24.8	21.1	25.9	34.54	29.39	36.07	37.49
G. pallidipes				67.2	28.0	4.7	

The approach of man to game

Gangs of poachers with dogs and spears may occasionally have hunted plains game animals, but this activity appeared to be far less frequent than trapping.

ASSOCIATIONS BETWEEN GAME ANIMALS AND DOMESTIC LIVESTOCK

The association of game animals with cattle or other domestic livestock depended on human activities. Areas occupied by bush-dwelling game animals were generally infested by tsetse and were, consequently, avoided by people with livestock. Therefore, domestic livestock seldom came into contact with bush-dwelling game animals and the only times when such contacts might have occurred were during the nocturnal excursions of game animals into settled areas. Another possible source of contact occurred when cattle were watered each day. Although this took place in the evening when fly activity was assumed to be minimal, some flies were undoubtedly still active.

The associations of game animals with man or domestic livestock could be of significance in the transmission of trypanosomiasis only when tsetse fed on all three. The behaviour of the flies was therefore of fundamental importance and the nocturnal wanderings of game animals could have had no epidemiological or epizootiological significance unless the tsetse were also nocturnal and remained in the vicinity of human settlement after feeding on game animals during the night.

Similarly with plains game animals, unless the tsetse moved away from the primary and secondary habitats to feed in open grasslands, the association between these game animals and man or cattle could have had little effect on the transmission of disease.

The associations having the greatest epidemiological significance were those involving regular visits by man to thickets—e.g., during poaching activities. The watering of cattle in tsetse-infested areas, even when the flies were not very active, was probably potentially the most dangerous association epizootically.

ASSOCIATIONS BETWEEN GAME ANIMALS AND TSETSE

The associations have been discussed at some length by Allsopp et al. (1972) and although their results were obtained mostly from the Otuok area of the Lambwe Valley, there is no reason to suspect that the situation was significantly different in other parts of the valley.

Allsopp et al. (*op. cit.*) observed that the degree of availability of different species of game animal to *G. pallidipes* varied considerably, as did the host preference of the flies. These authors classified game animals in respect to their relationships with *G. pallidipes*, as follows.

(1) *Host species available and highly preferred* included bushbuck and possibly bushpig. Bushbuck were definitely selected by *G. pallidipes* even when the density of other species was greater. In the Otuok area there was a positive correlation between the distribution of bushbuck and of *G. pallidipes*, i.e., the tsetse distribution pattern corresponded to that of the preferred host (see Table 4).

(2) *Host species highly preferred but seldom available* included buffalo and roan antelope. Behavioural characteristics—namely, the transitory nature of the former and the preference of the latter for open grasslands—brought them into only sporadic contact with stable tsetse populations. This category had no effect on tsetse distribution.

(3) *Unsuitable hosts* included most of the remaining species of game animal. In spite of their greater availability, other species were preferred as food. These species had no effect on tsetse distribution. The considerably greater availability of some unsuitable species, notably reedbuck, may have outweighed the effects of species preference, inducing *G. pallidipes* to feed on them occasionally, thus accounting for the trypanosome infections in these species.

TRANSMISSION CYCLES AND THE MAINTENANCE OF ENDEMIC AND ENZOOTIC TRYPANOSOMIASES

Disease transmission and the maintenance of endemic conditions were dependent on numerous factors, the most important being host–vector contact, host susceptibility, and trypanosome distribution in the vector population.

Host susceptibility is a field that still requires further study. Most species of game animal found at Lambwe appeared to be capable of supporting trypanosome infections, as indicated both by the infections discovered in the Lambwe Valley and by studies made elsewhere (see Joint FAO/WHO Expert Committee on African Trypanosomiasis, 1969). The length of time that an infection could survive in a host was also significant and long-lasting infections observed during laboratory experiments (e.g., by Ashcroft et al., 1959) may not exist in nature, where hosts are continually subjected to different stress factors and the parasite is frequently challenged by other species of trypanosome.

The distribution of trypanosomes throughout the vector population is also significant but, at least in the Lambwe Valley, it was not known. It is unlikely that infections were randomly or uniformly distributed throughout the fly population; they were most probably aggregated in areas of greater contact with man, cattle, or game animals.

The game–tsetse cycle

From an evolutionary point of view, and since some game animals occurred naturally in *G. pallidipes* habitats, it is reasonable to assume that the cycle between game animals and tsetse was fundamental to the transmission of the trypanosomiases.

The three categories of game animal described above exhibited different roles in connexion with infection. The most important species in the maintenance of high endemicity were those, such as bushbuck, that were constantly available to tsetse and were selected for feeding. Such species ensured a continual interchange of trypanosomes between host and vector and maintained a high parasite level within the populations, irrespective of their capacity for survival.

The challenge of one trypanosome species by another is of possible significance in the cycle involving preferred species of game animal. Where there was continual tsetse challenge there must also have been considerable trypanosome involvement, the effects of which could have determined the ultimate infection rate in the game animal population. It has been suggested by Robson & Ashkar (1972) that *T. congolense* infections in livestock reduce host resistance to trypanosome challenge and enable *T. brucei* to become established in detectable proportions. It is perhaps significant that *T. brucei* were found in bushbuck only in mixed infections with *T. congolense* (Table 1).

With a sedentary fly population feeding on a sedentary game animal population there was a possibility of localized increases in the trypanosome level, leading to the creation of " foci ". Bushbuck were most likely to be involved in the formation of such naturally occurring foci.

Species such as buffalo and roan antelope that were preferred by *G. pallidipes* but were only sporadically available were of less consequence in the localization of trypanosomiasis, but they would tend to promote the dispersal of the infection.

Roan antelope may leave the fly habitats completely for long periods and the maintenance of infection, without repeated tsetse challenge, would depend to a great extent on the ability of the parasite to survive in this host. Buffalo, although transitory in habit, generally remained within major fly habitats. Infections in this species were therefore probably less dependent on the survival capacity of trypanosomes than on the distribution of the parasite throughout the fly population. If the trypanosomes were uniformly distributed, which is unlikely, a high level of parasitaemia could have been maintained. Conversely, if they were distributed unevenly, infections would depend on the survival of trypanosomes in buffalo and on the relative time spent by these animals in areas of high and low infection rates. Since high endemic areas were probably associated with human settlement, it is unlikely that they were much frequented by buffalo.

The role of this category of game animal was consequently less important than had previously been thought. Species in this category may, however, have carried the disease to nonendemic areas or may possibly have introduced new strains into established foci, thus invigorating the local trypanosome population.

The final category of game animal, designated as unsuitable, were undoubtedly of least significance in the maintenance and transmission of trypanosomiasis. They possibly formed peripheral reservoirs around major foci, thus buffering these zones against the areas of low endemicity.

The game–tsetse–man cycle

As mentioned above, the approach of man to the habitat of game animals and tsetse was probably of greatest significance in the epidemiology of sleeping sickness. Poachers and woodgatherers entering the sphere of influence of a transmission cycle involving game animals and tsetse would have been exposed to contact with the disease. For the cycle to be maintained through all three phases, the contact with man would have to be regular and poaching activities would be most likely to fulfil this requirement. Once *T. rhodesiense* became introduced into such a cycle, whether from a game reservoir or by being brought from an external source by man, the level of the disease within the cycle could rise substantially, depending on the regularity of contacts and the length of time before the human recipient succumbed to the disease. Such a situation would have arisen when sedentary populations of game animals were involved, since there was unlikely to be regularly maintained contact between man and transitory species of game animal.

The game–tsetse–cattle cycle

This cycle again depended on the introduction of a third element into an established game–tsetse cycle. Regular watering or grazing of cattle in areas occupied by *G. pallidipes* would create such a situation, but cattle owners often took obvious precautions to prevent it. Laxity in such preventive measures, perhaps during new settlement, might result in such a cycle. The encroachment of human habitation into previously unpopulated areas, particularly where these were within the tsetse belt, might produce such circumstances. Unfamiliarity with an area or the need to use oxen for clearing thickets and woodland could bring cattle into closer contact with the game-tsetse cycle.

G. pallidipes feeds essentially on game animals, and analyses of blood meals from flies caught in the Lambwe Valley indicated that cattle were relatively infrequently bitten (England & Baldry, 1972). If the numbers of game animals became reduced in any area, as might occur after large-scale human settlement, there could be a shift in the feeding habits of the tsetse. This would be enhanced by the effect of climatic factors on the fly population if settlement took place during the wet season, i.e., when the flies were more dispersed and less dependent on the shade provided by dense vegetation. During such times, the less important game species such as reedbuck and waterbuck might become more involved in transmission cycles.

Transmission cycles not involving game animals

Two types of transmission cycle in which game animals are not involved can be recognized—namely, man–tsetse–man and cattle–tsetse–cattle. In the Lambwe Valley there was little evidence that man–tsetse–man cycles occurred since those areas not occupied by at least some species of game animal were free from tsetse. Tsetse infestation of settled areas not in the immediate vicinity of fly habitats has not been observed, and the low incidence of human sleeping sickness corroborates this. There may, however, have been an exception in the Opuch–Nyakiya area where a sudden outbreak of sleeping sickness occurred in 1971 (see Baldry, 1972) under circumstances that strongly suggest close man–tsetse contact.

Since the distribution of cattle was tied to that of the human population, the conditions pertaining to the man–tsetse–man cycle also apply to cattle–tsetse–cattle cycles. It is therefore considered that such cycles were absent from the Lambwe Valley.

DISCUSSION

The Lambwe Valley was an area of low *T. rhodesiense* endemicity but there was a high frequency of trypanosomes pathogenic to domestic livestock. The overall distribution of pathogenic trypanosomes was similar in cattle (17%) and game animals (16.4%) although there were local foci in which the cattle reservoir greatly exceeded that in game. Otuok was a case in point, the frequency in cattle being 65% compared with only 12% in game animals. The overall frequency of *T. rhodesiense* was greater in game animals (0.7%) than in cattle (0.4%) or *G. pallidipes* (0.01%). However, the number of game animals examined was relatively small and this comparison could be misleading.

Various aspects of the ecology of several species of game animal have been investigated with particular reference to their involvement with man, domestic livestock, and tsetse. A comprehensive appraisal of the part played by game animals in the epidemiology and epizootiology of trypanosomiasis cannot be attempted since pertinent data on human ecology and local practices in animal husbandry were lacking. In addition, samples for trypanosome investigations could not be obtained from all the species of game animal in the Lambwe Valley Game Reserve and thus none from buffalo and Jackson's hartebeest, and only two from roan antelope, were examined.

In view of these limitations the assessment made here is basically that relating to natural host–vector biology, and the variations caused by behavioural traits in the hosts. Casual observations and information from local people were the basis on which this assessment was subjectively expanded to include human and livestock elements.

It has long been known that some game animals are natural reservoirs for trypanosomes. The extent of this reservoir depends on behavioural characteristics of both the species of game animal concerned and the vector. It is reasonable to assume that those species most regularly bitten by tsetse would support the greatest density of trypanosomes, and this is in fact the case with bushbuck in the Lambwe Valley; this species is constantly available to *G. pallidipes* and is a highly preferred host. The frequency of trypanosome infections in bushbuck was the highest rate found in all the potential hosts examined, including domestic livestock. Of the 10 bushbuck collected, 9 were infected; the single exception was a young animal. The infecting trypanosomes were *T. congolense* (50%), *T. brucei* (25%), and *T. vivax* (25%). Although *T. rhodesiense* was not found, it has previously been isolated from bushbuck by Heisch et al. (1958).

This particular host–vector relationship appears to be of great importance in maintaining endemic and enzootic conditions. Such a close association between two sedentary species creates ideal conditions for the localized build-up of disease foci (see also Willett et al., 1965). Such foci could be amplified by changes in environmental conditions, such as temporary associations with transitory game animals, man, or domestic livestock. These contacts might raise the overall parasite level within the basic game–tsetse cycle and, by introducing new strains of trypanosome, could invigorate the established parasite population.

Continued contact between man and a natural focus, as might result from activities such as poaching, could cause an expansion of the cycle to include man, in which case human pathogenic trypanosomes might eventually become consistently involved. Similarly, regular approaches of livestock to this focus might result in the evolution of a game–tsetse–cattle cycle. Such cycles are instrumental in initiating epidemic or epizootic conditions.

The species of game animal preferred by *G. pallidipes* but only sporadically available probably constitute a natural dispersal mechanism for pathogenic trypanosomes. However, being confined within the Lambwe Valley ecosystem, these species are probably less important in this respect than man and domestic livestock whose freedom of movement is very much greater.

The recurrent peaks in the number of cases of sleeping sickness diagnosed in the Lambwe Valley between 1961 and 1970 (Watson, 1972) (see Fig. 1) may have been the result of an intrinsic periodicity in the trypanosome population. Alternatively, they could have been caused by environmental changes, perhaps induced by climatic variations. During the prolonged period of dry weather that occurred most severely between January and March 1971, there was a tendency for both game animals and tsetse to concentrate in the relatively buffered environment of the thickets and woodlands. Game–tsetse contacts would consequently have increased

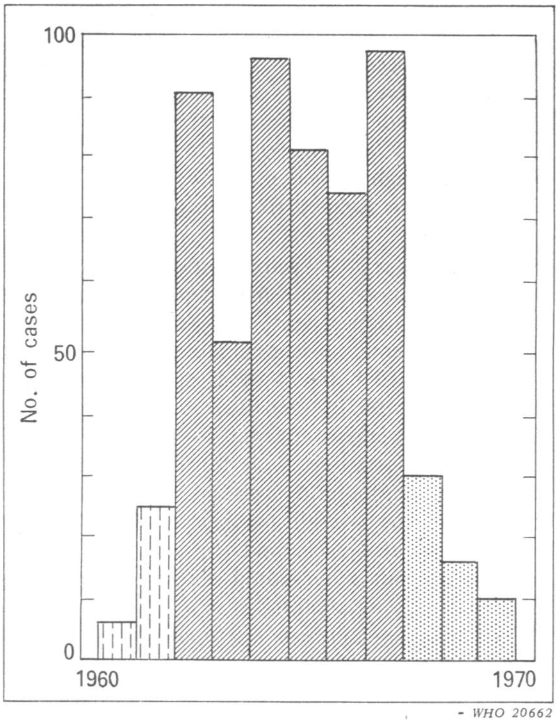

Fig. 1. Frequency of *T. rhodesiense* sleeping sickness in the South Nyanza District, 1960–70. Vertical shading, low endemicity: *T. rhodesiense* first recorded in 1959-60. Diagonal shading, high endemicity, subject to annual fluctuation. Dotted shading, progressive decline in endemicity concomitant with Project activities and Game Department enforcement of Lambwe Valley Game Reserve (1968) by-laws.

in these areas, and there would have been more prolonged associations between tsetse and transitory species of game animal. With the possibility of social stress within a population of game animals lowering their resistance to infection, this situation could potentially be one in which the level of infection throughout the game animal and tsetse populations might increase.

Contacts between man or domestic livestock and tsetse during or following a period of stress would more easily result in the establishment of infections and the spread of disease would be facilitated by the dispersal of tsetse during the wet season when their movements would no longer be restricted to sheltered habitats and their life expectancy would be greater.

The seasonal distribution of human sleeping sickness in the Lambwe Valley area (Watson, 1972) does in fact show peaks in April–May and November, which correspond to the bimodal rainfall distribution characteristic of the area (see Fig. 2). It is worth noting that the 1971 Opuch–Nyakiya sleeping sickness outbreak reported by Baldry (1972) was detected in mid-May.

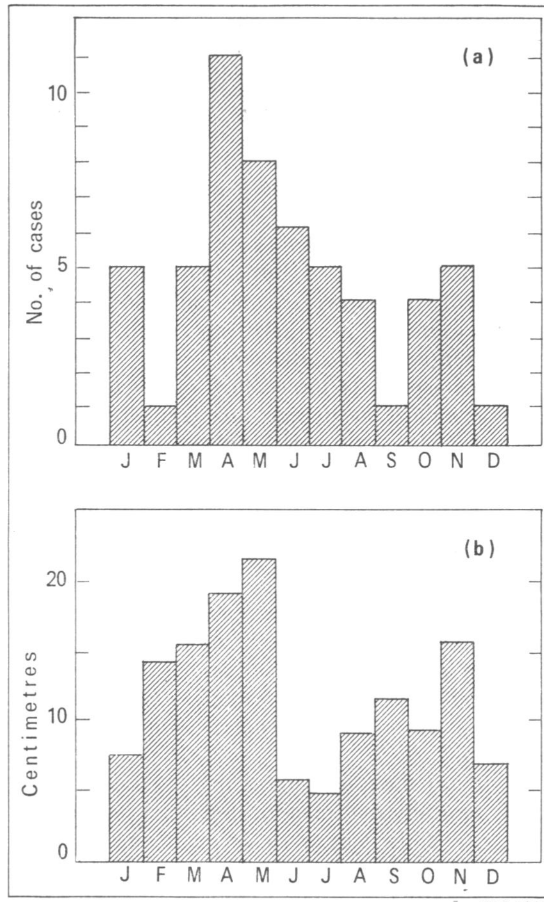

Fig. 2. Monthly frequency of *T. rhodesiense* sleeping sickness in South Nyanza District in relation to rainfall, 1968–70. (a) Cases of sleeping sickness; (b) mean monthly rainfall.

CONCLUSIONS

This study suggests that the game–tsetse cycle was of fundamental importance in the maintenance of the trypanosomiases. Contact between man or cattle and this basic host–vector association could result in transmission of the disease. Such contacts could be avoided by destruction of the basic cycle, and in various ways this has been the approach commonly adopted by tsetse control authorities. Transmission could, however, be averted by isolating the cycle, and in the Lambwe Valley, where *G. pallidipes* and its primary game animal hosts are found mainly in a contiguous belt of thicket and *Acacia* woodland, this might be a more satisfactory approach to disease control.

Such a form of tsetse and trypanosomiasis control has already been suggested by Ford (1969), who concluded that eradication is often an expensive, short-term approach that will fail unless the reclaimed areas are immediately and continuously occupied. Ford (*op. cit.*) proposed multiple land-use practices, involving a reduction of the tsetse–trypanosomiases problem to a level that would encourage development of the area.

An important step towards isolating the game–tsetse cycle has already been taken in the Lambwe Valley by the creation of a partially fenced game reserve. To achieve complete isolation, however, a number of objectives must be realized. (1) Game animals and tsetse must be contained within the game reserve. The former could be restricted to the reserve by the erection of selected additional fencing and they would be encouraged to remain within the area by the creation of a permanent water supply. To contain the fly, the reserve boundary could be extended to include all the major thickets, i.e., Riamkanga and Nyaboro. Selective barrier clearings would also be necessary. (2) Contact between the game–tsetse cycle and man or domestic livestock would have to be prevented.

It would be necessary to prevent poaching within the reserve but to achieve long-term results an alternative source of meat would have to be provided. Cattle ranching in areas separated from the reserve by a zone of cultivated land in which livestock would be prohibited, to produce livestock to be sold for consumption and not for herding, might achieve this aim. Woodgatherers could be given an alternative supply of wood by the afforestation of the Kaniamwia Escarpment and parts of the Gwasi hillside.

Local travellers who continually pass through the Lambwe Valley should receive primary consideration when internal and access roads are planned for the reserve; such roads should not be constructed solely for the convenience of tourists. Where the roads pass through or near to thickets, wide clearings should be made and there should be selective applications of a non-persistent insecticide. These measures would also improve potential for viewing game animals. By reducing man–tsetse contact, the already low level of *T. rhodesiense* in the natural hosts would probably remain below a level that might endanger the health of tourists.

Although a game reserve was created on land originally destined and surveyed (Makin & Nyandat, 1965) for agricultural development, there is no reason why areas adjacent to the reserve should remain at a subsistence level of economy. A multiple land-use programme involving tsetse control, tourism, cattle ranching, forestry, and arable farming would benefit the people of South Nyanza, not only by the economic return but also by its intrinsic approach to the prevention of trypanosomiasis, which has been a serious problem in the Lambwe Valley area for so many years.

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RÉSUMÉ

LE RÔLE DES ANIMAUX SAUVAGES DANS LA PERSISTANCE DES TRYPANOSOMIASES ENDÉMIQUES ET ENZOOTIQUES DANS LA VALLÉE DE LA LAMBWE (DISTRICT DU NYANZA DU SUD, KENYA)

Les animaux sauvages (ongulés, carnivores, primates) sont des réservoirs potentiels de trypanosomes; dans les régions infestées par les glossines, ils peuvent jouer un rôle capital dans la transmission de trypanosomes patho-

gènes à l'homme et aux animaux domestiques. De juin 1970 à mai 1971, les populations animales de la vallée de la Lambwe ont fait l'objet d'une enquête visant à déterminer leur degré d'infection par les trypanosomes et à étudier les rapports entre ces populations, *Glossina pallidipes*, l'homme et le bétail qui interviennent dans l'épidémiologie des trypanosomiases.

L'examen parasitologique d'échantillons de sang prélevés chez 134 animaux appartenant à 10 espèces a montré une infection par des trypanosomes dans 16,4% des cas. Neuf céphalophes sur 10 (90%) étaient infectés par *Trypanosoma congolense* (50%), *T. brucei* (25%) ou *T. vivax* (25%). Ce dernier trypanosome n'a été trouvé chez aucune autre espèce. *T. brucei* a été aussi isolé chez des antilopes-chevreuils, des hyènes et des kobs; *T. congolense* chez des antilopes-chevreuils et des oribis; *T. rhodesiense* chez une antilope-chevreuil. L'examen immunologique de 90 de ces sérums a donné un taux d'infection légèrement plus élevé que celui fourni par les recherches parasitologiques (16,4%). Ce dernier taux était comparable à ceux trouvés chez le bétail (17%) et chez *G. pallidipes* (20%). *T. rhodesiense* a été décelé plus fréquemment chez les animaux sauvages (0.7%) que chez le bétail (0,4%) et chez *G. pallidipes* (0,01%).

Les espèces animales étudiées peuvent, grosso modo, être classées en espèces de brousse et en espèces de plaine. L'antilope-chevreuil et l'antilope impala se rencontrent dans les deux types d'habitat. A l'exception du buffle, qui parcourt des distances considérables, les espèces de brousse se déplacent peu pendant le jour, mais sont fréquemment observées sur les terres cultivées dès la tombée de la nuit. Les espèces de plaine sont moins sédentaires et, à l'exception de l'antilope rouanne, occupent de préférence les zones herbeuses. On trouve en outre dans la vallée de la Lambwe des léopards et quelques hyènes, aux activités surtout nocturnes.

Le rôle des animaux sauvages dans la transmission des trypanosomiases à l'homme et aux animaux domestiques est fonction des rapports qui s'établissent entre ces divers groupes et de l'intervention de *G. pallidipes*. Cette glossine a en tout temps la possibilité de se nourrir sur les céphalophes auxquels vont ses préférences trophiques. Elle prélève aussi ses repas de sang sur les buffles et les antilopes rouannes qui ne sont pourtant que des hôtes occasionnels.

Certaines activités comme la chasse, surtout, et l'approvisionnement en bois sont l'occasion de contacts fréquents entre l'homme et les animaux sauvages; si ceux-ci sont du type « de brousse », le risque existe pour l'homme de contracter la trypanosomiase. Le bétail est habituellement tenu à l'écart de la végétation infestée par les glossines et il n'a que peu de contacts avec les animaux sauvages de brousse. Il est cependant exposé à l'infection par des trypanosomes lors de l'abreuvage ou lorsqu'il est utilisé pour le défrichement de nouvelles terres. Partout où des contacts entre l'association de base animaux sauvages/tsé-tsé et l'homme (ou le bétail) sont établis avec une régularité suffisante, des cycles de transmission s'installent et assurent la persistance des trypanosomiases endémiques et épizootiques.

Sur le plan pratique, cette démonstration du rôle des animaux sauvages dans la transmission des trypanosomiases implique la nécessité de rompre les cycles animaux sauvages/tsé-tsé/homme (ou bétail). Aux méthodes classiques de lutte contre le vecteur il faut préférer, dans le cas de la vallée de la Lambwe, le recours à un programme à fins multiples d'utilisation des terres.

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