Paper 5: Tsetse, trypanosomiasis and cattle in a changing environment

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Abstract

The Nigerian environment is undergoing profound and widespread changes induced by human population growth and agricultural expansion. As land suitable for cultivation becomes increasingly scarce in the more highly populated areas, particularly to the north and south of the country, the relatively underutilized regions of the Nigerian subhumid zone are becoming more extensively exploited.

As a result of these artificial changes in the environment, natural vegetation is being transformed into farmland, and wildlife populations are being hunted out. Consequently, the natural habitats and hosts of tsetse (Glossina spp.), the vectors of animal and human trypanosomiases, are tending to disappear.

Coincident with the expansion of human settlement and cultivation, and the declining importance of trypanosomiasis, there has been a southward spread in the distribution of cattle. Recent population estimates, based on low intensity, low-level systematic aerial surveys, indicate that the subhumid zone supports some 4.5 million head of cattle, and that the overall population size does not change significantly with season. A seasonal redistribution appears to take place within the zone, but in general terms cattle distribution remains closely associated with cultivation and human settlement.

Introduction

Nigeria possesses the largest and most diverse human population of any country in Africa. The population has been, and still is, growing rapidly. As a result, there has been a progressive expansion of agricultural land which has inevitably affected the natural environment. Many of these effects are being felt in the subhumid zone, as defined by ILCA (1979). It is the purpose of this paper to identify the interrelationships between some of the major changes that have taken place and the distribution of the national cattle population, particularly in relation to the incidence of tsetse and trypanosomiasis.

Tsetse and trypanosomiasis

Tsetse (Glossina spp.) are the primary vectors of animal and human trypanosomiases, and as such have been the subject of many years of intensive scientific study. Although Nigeria has had a long history of tsetse control and eradication through the application of insecticide, operations within the subhumid zone have been relatively limited (Putt et al, 1980). Much of the eradication programme has taken place outside the zone (Davies, 1964; 1971), and the effects within have been confined to adjoining regions to the north and northeast. Various localized tsetse control operations have been mounted within the subhumid zone, largely as protective measures around ranches and areas of residual human sleeping sickness.

Recently, alternative control methods have also been used. The Federal Department of Pest Control Services (FDPCS), in conjunction with the International Atomic Energy Agency and the Food and Agriculture Organization of the United Nations, has initiated a Project for the Biological Control of Tsetse in the Lafia area, which employs a novel form of control, utilizing the sterile male release technique in place of conventional insecticide application.

Of the eleven recorded species of Nigerian tsetse (Davies, 1977), six have been found within the boundaries of the subhumid zone. Each of the main species-groups is represented: G. morsitans and G. longipalpis of the 'savanna' dwelling group; G. palpalis and G. tachinoides of the 'riverine forest' group; and G. fusca and G. haningtoni of the 'forest' dwelling group. The latter two species are exceptional for the subhumid zone in that they are basically rain forest species and records have been confined to atypical forest outliers. Essentially, therefore, four species predominate within the zone.

Nigerian tsetse distribution maps (FDPCS, 1980; and map 16.13 in Nord, 1982) show G. morsitans occurring in a series of discontinuous belts scattered across the northern two thirds of the subhumid zone. The other savanna species, G. longipalpis, has been recorded over a wide area of central and southwestern portions of the zone. The two riverine species occur throughout the zone, G. palpalis being absent from the extreme northeast, and G. tachinoides absent only from limited areas on the southern boundary.

As with any genus, a variety of complex interacting factors and species-specific requirements determine tsetse distribution and abundance The availability of suitable habitats and hosts are two determinants of primary importance, both of which, in the course of time, have been greatly influenced by human activity.

Human population is increasing throughout Nigeria, particularly in the north and south. Both central and northern Nigeria have also absorbed significant numbers of both pastoralists and agropastoralists who have moved southwards, away from the drought-affected semi-arid and arid zones further north. The consequent pressure on land resources has led to an accelerated agricultural expansion within the relatively underpopulated subhumid zone. Such expansion has been facilitated, and its direction channelled, by Nigeria's rapidly developing road network. As a result, a wide variety of natural tsetse habitats have been transformed by the combined processes of land clearance and wet-season cultivation of upland savanna; removal of riverine forests for dry-season cultivation; firewood collection; and extraction of valuable timber. In addition the demand for bushmeat and associated heavy hunting pressure has greatly reduced, and in many areas eliminated, the natural hosts of tsetse. The net result of these artificial environmental changes has been to reduce the availability of both the habitats and hosts favoured by Glossina spp., which in turn has caused an overall decline in the distribution and abundance of tsetse populations (Bourn, 1983).

The savanna tsetse species are most susceptible to the impact of agricultural expansion. As wildlife hosts are hunted out and natural woodland vegetation is turned into farmland, the distribution and abundance of G. morsitans and G. longipalpis are bound to decline. The fragmentary nature of G. morsitans belts, in an environment which would otherwise be suitable, is itself evidence of the impact of long-term human activity on the availability of suitable hosts and habitats. Various advances and recessions of G. morsitans have been documented in the past (MacLennan, 1958; Wilson, 1958; and Ford 1971), but an balance the overall trend has been one of general contraction and, eventually, local extinction (Putt et al, 1980; and also compare published and revised tsetse distribution maps 6.13 and 6.14 in Nord, 1982).

However, the more dense riverine forest/thicket vegetation is more difficult to transform into farmland than is woodland. It is also a naturally very patchy habitat. As a result, the primary habitat of riverine tsetse species is, initially at least, more likely to remain intact. Thus G. palpalis and G. tachinoides tend to persist even in very confined habitats surrounded by extensive areas of cultivation. Under these circumstances, however, in the virtual absence of wildlife, cattle and people are likely to become the major hosts, with tsetse populations concentrated at regularly used forest crossings or at cattle and village watering points.

As land-use intensity continues to increase, even the remaining riverine forest will be encroached upon by cultivation, logging, palm wine collection and fire. Suitable habitats for riverine species of tsetse are therefore also likely to dwindle and ultimately, in extreme cases, to disappear.

Thus, under the generally prevailing conditions of declining tsetse populations, disappearing wildlife reservoirs of trypanosomes, and the increasingly sedentary nature of livestock husbandry in more southerly locations, both Putt et al (1980) and Bourn (1983) concluded that there must have been a fundamental shift in vector-host-parasite relationships, and that the very nature and importance of the disease had changed. In part at least, this is reflected in the rise and fall of various government-sponsored disease control measures shown in Figure 1.

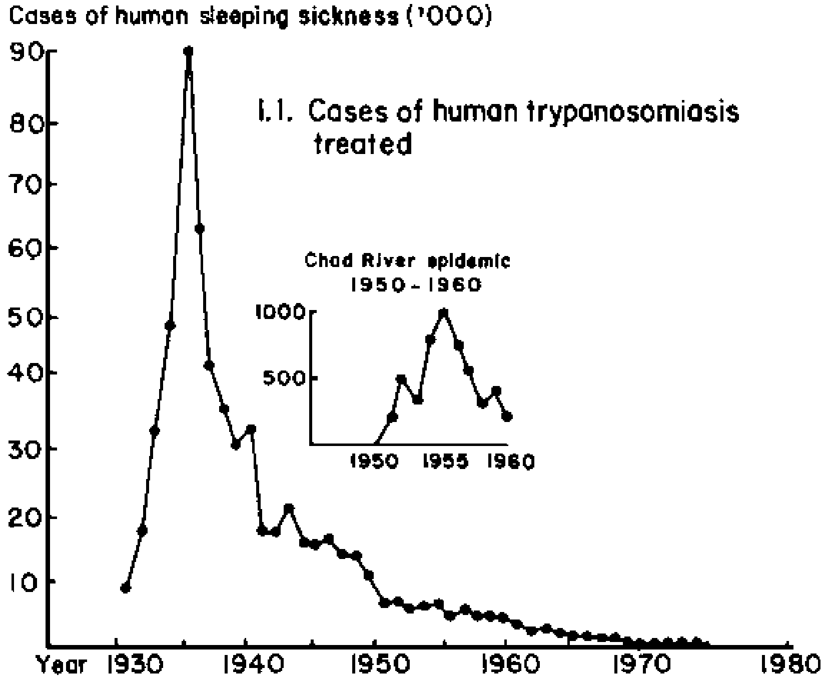
Cattle

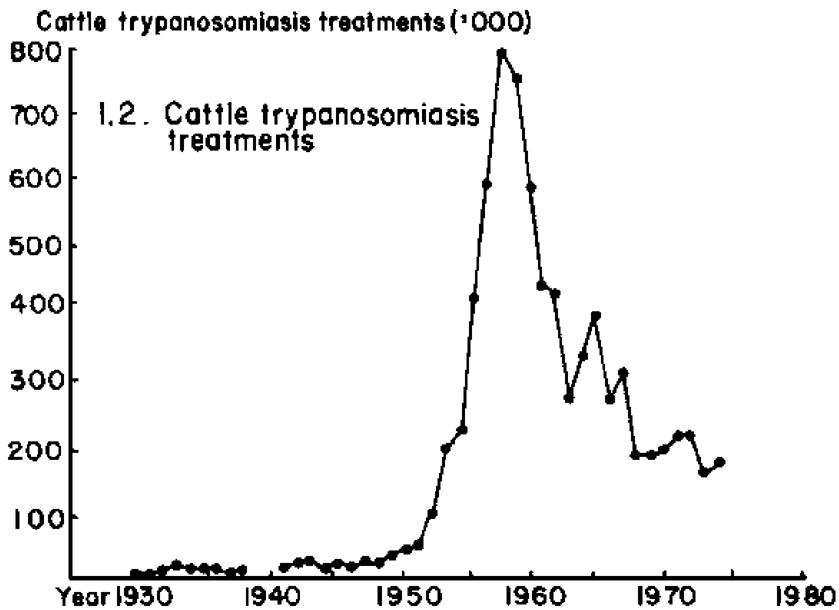
How many and where are they?

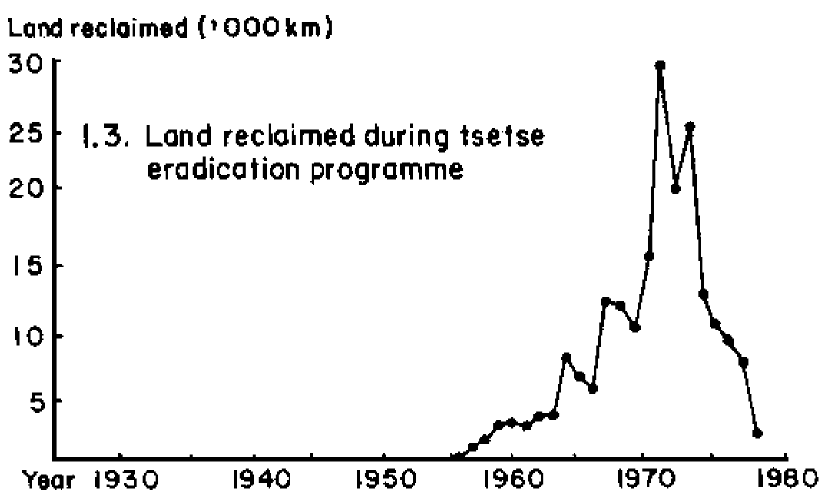
The size and distribution of Nigeria's cattle population has long been a subject of debate and partially informed guesswork. Various indirect population estimates have been derived on the basis of cattle tax (jangali) returns, offtake rates, hide and skin exports, the numbers of trade cattle passing from the north to southern markets, and vaccination returns. The accuracy of the estimates obtained of course depends on the validity of the underlying assumptions: the degree of tax evasion, the measure of herd productivity, the proportion of animals imported into the country, and the efficiency of the vaccination programmes. Nevertheless, despite the inherent uncertainty, it is generally believed that the size of Nigeria's present cattle population is in the range of 10 to 15 million, the majority of which are humped zebu owned by the Fulani people.

In addition to zebu cattle, there are an estimated 300 000 head of the more trypanotolerant cattle (ILCA/FAO, 1980). Their distribution is largely restricted to the derived savanna and forest regions south of the Benue and Niger rivers. Three major breeds are recognized: 150 000-180 000 Keteku (Muturu x White Fulani Zebu); 100 000-120 000 Muturu (Dwarf West African Shorthorn); and some 15 000 N'Dama. No clear boundary can be defined between the distribution of zebu and trypanotolerant breeds, but as mentioned earlier, with the southward drift of zebu cattle into southern Guinea and derived savanna vegetation zones, there is likely to be a significant, and increasing, degree of overlap.

Figure 1. Trypanosomiasis treatments and land reclamation.







Traditionally, the Fulani pastoralists were regarded as living a primarily nomadic existence. The bulk of the cattle population was considered to inhabit the northern part of the country in the wet season, and to move southwards into the 'Middle Belt', or subhumid zone, during the dry season. This nomadic, or extensively transhumant, life-style was believed to reduce the risks of contracting trypanosomiasis in more southerly tsetse-infested regions during the wet season. In the dry season the distribution and abundance of tsetse were greatly restricted by adverse climatic conditions, and cattle owners took advantage of the lower tsetse and trypanosome challenge in order to utilize the relatively abundant forage and water resources.

However, it would appear that this traditional view is no longer generally valid. Fricke (1979) and Putt et al (1980), in independent analyses of jangali tax returns, have both demonstrated that since the 1950s the overall numbers of tax returns have declined in the north, but risen in the south. Thus there appears to have been a marked southward drift in the distribution of Nigeria's cattle population. A substantial body of circumstantial and anecdotal evidence supports this conclusion, and it seems likely that this trend has been further encouraged by the Sahel drought of the late 1960s and early 1970s.

Such a phenomenon is clearly of great importance to Nigeria, which has a combined policy of relocating the national herd in more southerly latitudes, and settling pastoral communities (David-West, 1980). It is therefore desirable to establish by more direct methods whether there is indeed a substantial and comparatively static population of cattle in the subhumid zone. Until recently, such estimates of cattle numbers and distributions have not been available. Answers to the fundamental questions: How many cattle are there? and where are they to be found? have remained largely a matter of conjecture and speculation.

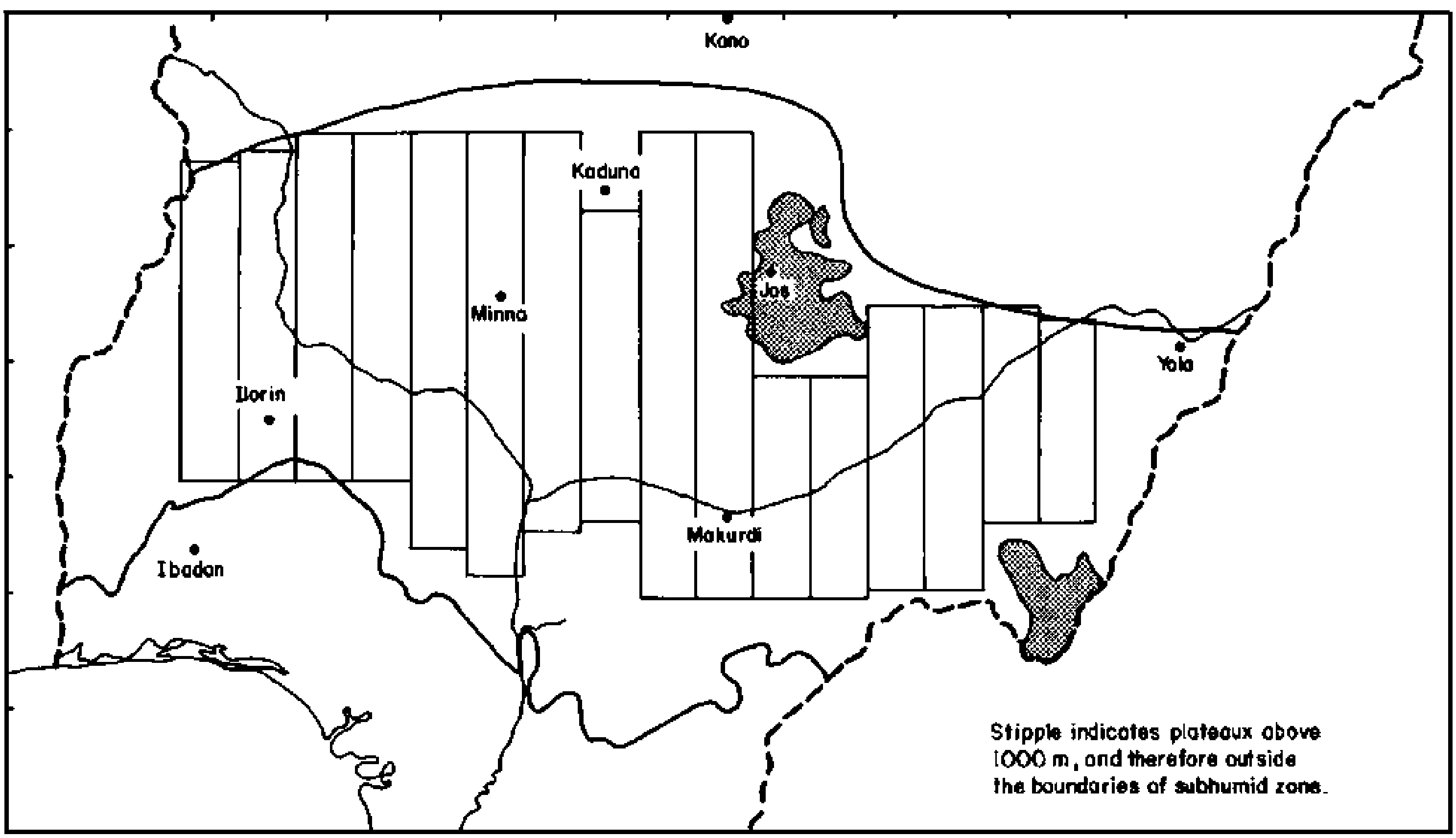
Low-level aerial survey

In order to obtain more objective measures of cattle distribution and abundance in the Nigerian subhumid zone than had previously been undertaken, ILCA adapted and extended an existing technique of wildlife population assessment, based on low-level aerial survey, or systematic reconnaissance flights (Norton-Griffiths, 1978; Milligan et al, 1979; Milligan and de Leeuw, 1983).

Time, manpower and financial constraints limited high sampling intensity aerial surveys to specific case study areas, but nevertheless low-intensity surveys over some 356 510 km^2 of the subhumid zone were carried out during March and July 1983 (dry and wet seasons, respectively). The primary objectives were to put the ILCA case study areas into zonal perspective; to assess overall cattle distribution gradients; and to determine seasonal changes in cattle density and herd size. With the necessarily low sample intensity, estimation of total cattle numbers was considered to be of secondary importance, and the figures obtained should be treated as a first approximation, and as a basis for further study. Nevertheless, the results were of considerable general interest, as they provided the first objective measure of the size of the Nigerian subhumid zone's cattle population. They have therefore been used in this paper to examine the zonal cattle populations in the light of the changes described in the proceeding pages.

Essentially the ILCA aircraft, a high-winged, twin-engined Partenavia P68B, flew a series of 16 north-south parallel flight lines of varying length, across the subhumid zone, at intervals of half a degree of longitude (56 km), as indicated in Figure 2. At the selected flying altitude of 1000 feet above ground level, back-seat observers, to the left and right of the aircraft, monitored two strips of ground, each 400 m wide, giving a sampling intensity of 1.4%. The size of all cattle herds seen within these strips was estimated by eye, and wherever possible a 35-mm photograph was also taken, using cameras fitted with zoom lenses. Subsequently, herd size was accurately counted from these photographs; observer biases were determined; and corrections were made to observer estimates. These corrected figures were then used to calculate cattle density and estimate population size by the ratio method (Jolly, 1969).

Figure 2. Longitudinal blocks sampled during low-altitude, low-intensity aerial survey of the Nigerian subhumid zone.



Estimates of cattle and herd numbers

There was no significant difference between overall seasonal cattle population estimates (Table 1). For the area surveyed they ranged from 3.4 million head in the wet season to 3.7 million head in the dry season, equivalent to a total of between 4.3 and 4.7 million head for the Nigerian subhumid zone as a whole. The dry-season estimate of 10.3 animals per km^2 was only 8% higher than the wet-season value of 9.4 animals per km^2. Thus, no major dry-season net influx of cattle was detected. This would indicate that either seasonal immigration was more or less equal to emigration; or, as seems more likely in view of the probable increase in sedentarization of the Fulani, most seasonal cattle movements occurred only on a relatively modest scale and took place largely within the subhumid zone.

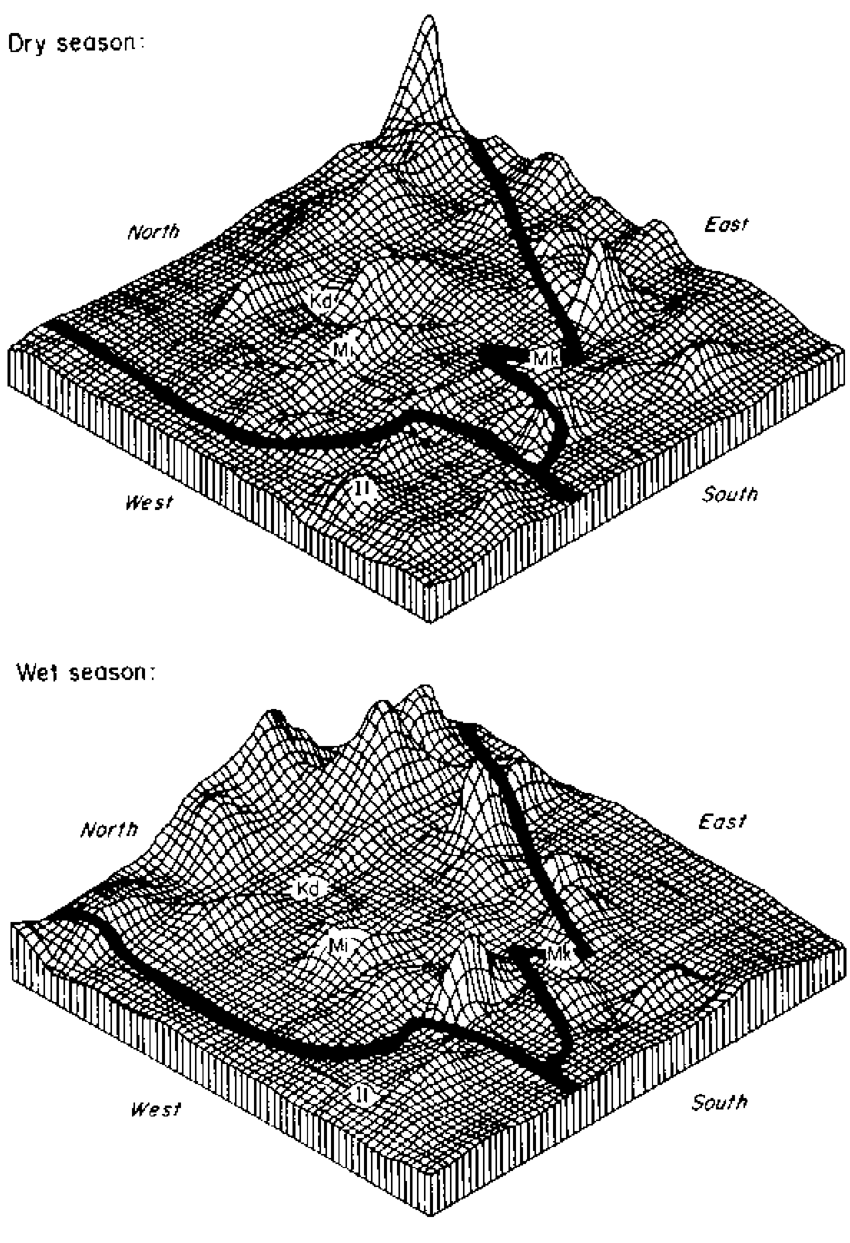
Although only minor seasonal differences were found in the estimated size and density of the subhumid zone's cattle population, a substantial 25% difference in mean herd size was detected (Table 1)[1/]. Mean herd size in the dry season was 55, whilst in the wet season it increased to 68 animals per herd. This resulted in a marked fall in the estimated number of herds in the surveyed area from 66 000 in the dry season to 49 000 in the wet season, or 85 000 and 63 000 respectively for the subhumid zone as a whole. In terms of overall herd density this amounted to a decline from 18 to 14 herds per 100 km^2. Such seasonal changes in mean herd size have been detected in other aerial surveys within the subhumid zone (Milligan et al, 1979) and are largely due to the Fulani management practice of herd splitting during the dry season (Okali and Milligan, 1980).

[[1/] Throughout this paper the term 'herd' is used to mean 'grazing unit', i.e. the groupings of cattle that are observed from the air.]

Distribution of cattle

The contrasting patterns of wet- and dry-season cattle distribution over the subhumid zone are represented by the three-dimensional surfaces shown in Figure 3, in which cattle density is indicated by apparent height.

Figure 3. Dry-season cattle distribution in the Nigerian subhumid zone.



Caution is required in the interpretation of these surfaces, as the coordinates of the subhumid zone have been transformed in order to make the information amenable to three-dimensional computer analysis. Effectively the east-west dimension has been foreshortened, and the north-south dimension has been equilibrated, so that the whole of the Nigerian subhumid zone is represented by a square. However, as an aid to orientation and better understanding, the course of the Benue and Niger rivers, and the location of major towns have been indicated.

Comparison of the two surfaces illustrates clear changes in seasonal cattle distributions. Although cattle were found throughout the zone in both seasons, their overall distribution was far from uniform and shows a generally clumped pattern which was most pronounced during the wet season. In the dry season the cattle were more evenly distributed, with higher densities occurring to the east and northeast, and lower densities to the southeast and along the southern, western and most of the northern boundaries.

In contrast, wet-season cattle distribution appeared to be generally more restricted and concentrated within a broad central region to the north of the Niger and Benue rivers. The highest densities occurred on the northern boundary of the subhumid zone, with a progressive decrease in density further south, particularly to the southwest and the southeast. In more southerly latitudes dry-season cattle density exceeded that found in the wet season, whilst in more northerly parts of the zone the reverse was the case. Only in the extreme east and north of the region was there any indication of substantial cattle movements between seasons, and there were significant numbers of livestock in the southern half of the study area during both surveys.

Table 1. Cattle and herd estimates for the Nigerian subhumid zone, derived from low-intensity, low-level aerial surveys.

	Dry season	**Wet season**
Area of subhumid zone (km^2)	455,500	455,500
Area surveyed (km^2)	356 510	356,510
Area sampled (km^2)	4 959	4,536
Sample intensity (%)	1.4	1.3
Date of survey	March 1982	July 1982
Mean cattle density/km^2	10.25	9.44
Mean cattle stocking rate/ha	9.8	10.6
Estimated number of cattle		
In area surveyed	3 654 200	3 365 500
In subhumid zone	4 668 900	4 299 900
Mean herd density/100 km^2	18	14
Mean herd size	55	68
Estimated number of herds		
In area surveyed	66 440	49 490
In subhumid zone	84 890	63 230

Cattle density and vegetation type

Table 2 gives the seasonal mean cattle densities and mean herd sizes in each of the predominant vegetation types within the surveyed area of the subhumid zone, based on Side Looking Airborne Radar Vegetation and Land Use Maps (FDF, 1978). The estimated area of the major vegetation and land use types is also shown, as is the proportion estimated to be under cultivation within each.

The highest cattle densities were found during the dry season in regions where aquatic grassland and riparian vegetation predominated. Mean densities of more than 30 head per km^2 were encountered and reflected a concentration of cattle in riverine floodplains and in proximity to perennial water sources, as represented by riparian forest. However, because these vegetation types amounted to only 3% of the surveyed area, the proportion of the total cattle population they contained was relatively small around 10% in the dry season and 3% in the wet season.

Little seasonal change was evident in the cattle density within transitional woodland. This was much the largest vegetation and land-use category, amounting to some 40% of the surveyed area, but at 6-7 head per km^2, was one of the least well stocked. As a consequence, this category contained only 24% of the estimated overall cattle population in the dry season, and 30% in the wet season.

Cattle density in woodland vegetation was somewhat higher than in transitional woodland, but showed little seasonal change and remained constant at about 10 animals per km^2. However, as this vegetation type only occupied some 7% of the surveyed area it contained a relatively small proportion of the overall cattle population.

The four remaining vegetation and land-use types, occupying some 46% of the surveyed area, contained approximately 60% of the estimated overall cattle population in both the wet and dry seasons. A feature common to each of these vegetation and land-use categories was that more than 20% of their land area was under cultivation. In the two farmland categories cattle density increased from around 11-12 animals per km^2 during the dry season to 16-17 per km^2 during the wet season. The other two categories, wooded-shrub-grassland and farmland/woodland mosaic, showed the opposite trend in cattle density, with a decline from about 13 animals per km^2 in the dry season, to between 8 and 11 in the wet season.

Cattle density and land-use intensity

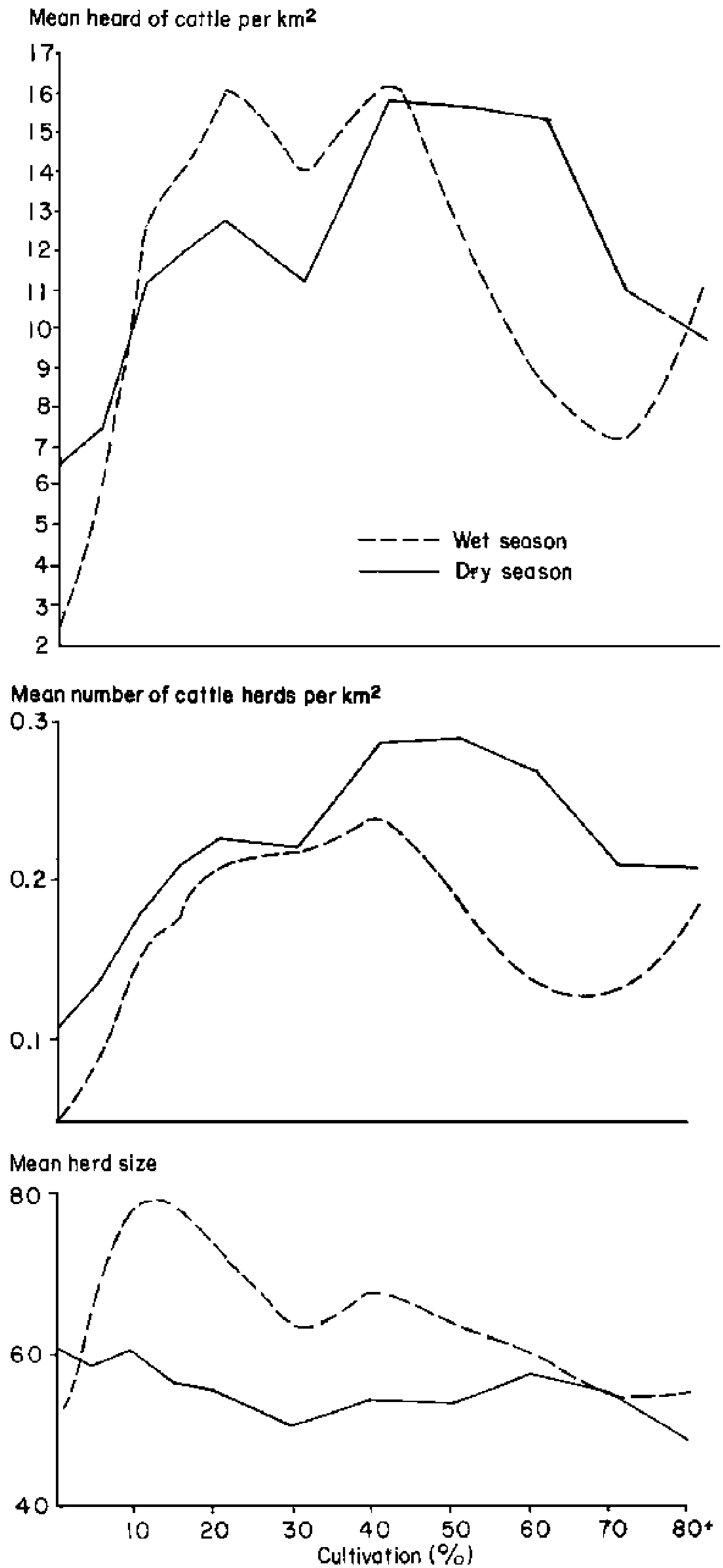
The distribution of cattle in relation to cultivation levels was also examined in more detail than was possible from the SLAR maps, using estimates of cultivation made from the air. These do not include fallow land. Figure 4 shows the variations in mean cattle density, mean herd density and mean herd size that were found at different levels of land-use intensity. Very few cattle were found in areas where cultivation was absent, particularly in the wet season. In both seasons mean cattle density rose progressively to reach a peak of approximately 16 animals per km^2 at between 20 and 40% cultivation. At higher cultivation levels, cattle density decreased in both seasons, but more so in the wet season.

Table 2. Seasonal cattle density and mean herd size in the predominant vegetation and land-use types of the Nigerian subhumid zone.

Vegetation and land-use types	% Area	% Cultivation[a/]	Cattle density[b/]		% Total cattle		Mean herd size	
			Dry	Wet	Dry	Wet	Dry	Wet
Woodland	7	10	9.77 (31%)	9.97 (86%)	7	7	65	111
Transition[c/]	40	12	5.94 (18%)	7.20 (25%)	30	23	50	63
Wooded-shrub-grassland	6	21	13.44 (30%)	8.37 (18%)	5	8	46	52
Mosaic[d/]	24	30	12.95 (16%)	10.76 (19%)	27	31	62	77
Farmland 30 - 60%	8	26	11.89 (15%)	17.23 (25%)	14	10	50	64
Farmland > 60%	8	50	11.17 (46%)	15.98 (26%)	14	9	49	61
Aquatic grassland	2	7	31.22 (21%)	4.08 (64%)	1	6	78	51
Riparian	1	12	30.02 (39%)	12.92 (89%)	2	4	83	92
Minor Types	4	8	-	-	-	2	-	-
Total/Mean	100	20	10.25 (11%)	9.44 (16%)	100	100	55	68

[a/] Figures in parenthesis are percentage standard errors.
[b/] Visually estimated during aerial survey.
[c/]Transitional between woodland and wooded-shrub-grassland
[d/] Mosaic of wooded-shrub-grassland and farmland, with 30 - 60% cultivation.

Figure 4. Variation in cattle density, herd density and herd size with land-use intensity in the Nigerian subhumid zone



Mean herd density followed a similar pattern to that of cattle density, but it was evident that dry-season herd densities were consistently higher than in the wet season.

A maximum mean herd size of some 80 animals was found during the wet season at land-use intensities of between 10 and 20%. At higher levels of cultivation mean herd size progressively declined. In contrast, during the dry season mean herd size appeared to be relatively stable, fluctuating between 50 and 60 animals per herd, aver a wide range of land-use intensity.

Discussion and conclusions

Referring to the typical seasonal movement of cattle in Nigeria, Glover (1960) commented that: "The annual migration of Fulani takes two forms in the dry season. In one the movement is local; the herds only go short distances into neighbouring river valleys which are often infested by tsetse flies where grass and water can be found. This form of local migration also includes the movement of cattle from high ground, like the Jos Plateau, into the surrounding foothills. The other form, which applies to most of the Fulani cattle, consists of a journey southwards, covering hundreds of miles in search of food and water. The herds often traverse large fly belts an the way and may well spend the whole dry season in tsetse infested country."

Nearly a quarter of century has elapsed since that description was written, and during that time the Nigerian environment has been modified substantially; the pattern and extent of seasonal cattle movement has altered significantly; and the proportion of nomadic cattle owners has declined (Oxby, 1982). Van Raay (1975) considered that only 12% of Nigerian Fulani were fully nomadic, while he regarded 38% to be semi-settled, and the remaining 50% to be fully settled.

For many years, the primary cause of the profound and widespread changes in the Nigerian environment has been the rapid increase in human population, which has led to an ever increasing demand for food and land. This demand has been further exacerbated by the immigration of pastoralists from the Sahel in response to the frequent droughts. As a result there has been greater competition for land in areas of high human population density, and consequently a progressive expansion of agriculture into areas of lower human population density. The latter process has been both encouraged and channelled by the expansion of Nigeria's major road network, particularly into the moderately high rainfall areas of the subhumid zone.

In the past, both the northern and southern regions of Nigeria were recognized as areas of high human population density, with the central 'Middle Belt' being characterized by relatively low human population levels and little cultivation (Buchannan and Pugh, 1955). However, as reflected in the SLAR vegetation and land-use maps, circumstances have changed and these characteristics can no longer be considered valid for the zone as a whole. Not only are local populations increasing in size, but also, because of increased land pressure, both to the north and to the south, people are leaving their traditional areas and are moving into and settling within the subhumid zone.

It is apparent that the main thrust of this agricultural expansion within the subhumid zone has been experienced in a central bridging band, from Kano State in the north, southwards to the west of and including the Jos Plateau, through Abuja, across the Niger and Benue fork, towards Benin city and Enugu. There has been a consequent expansion of markets and trade routes into areas of previously high tsetse and trypanosomiasis challenge.

The increasing extent and intensity of both farming and hunting within this central bridging belt has greatly changed the pattern of vegetation and land use, and inevitably led to an overall reduction in wildlife species, and in many places brought about their local extinction. Thus both natural habitats and hosts of tsetse, the vectors of trypanosomiases, have declined, which in turn has brought about a widespread reduction in the flies' distribution. The two savanna species, G. morsitans and G. longipalpis, which typically have high trypanosome infection rates, have been most severely affected by the changes taking place within the subhumid zone, and their overall distribution has contracted. This, together with the general decline in the wildlife reservoir of trypanosomiasis has resulted in a marked reduction in the silvatic cycle of disease transmission.

In contrast, the riverine species of tsetse G. palpalis and G. tachinoides, which have comparatively low infection rates, have tended to persist despite widespread environmental changes brought about by agricultural expansion. In part their continued survival has depended on their close association with riverine forest and thicket vegetation, and the greater human effort required to convert this type of vegetation into farmland. The continued survival of riverine species of tsetse has also depended on their more catholic feeding habits; in particular, their ability to adapt to the alternative hosts provided by the frequent, regular passage of cattle and people at forest crossing and watering points.

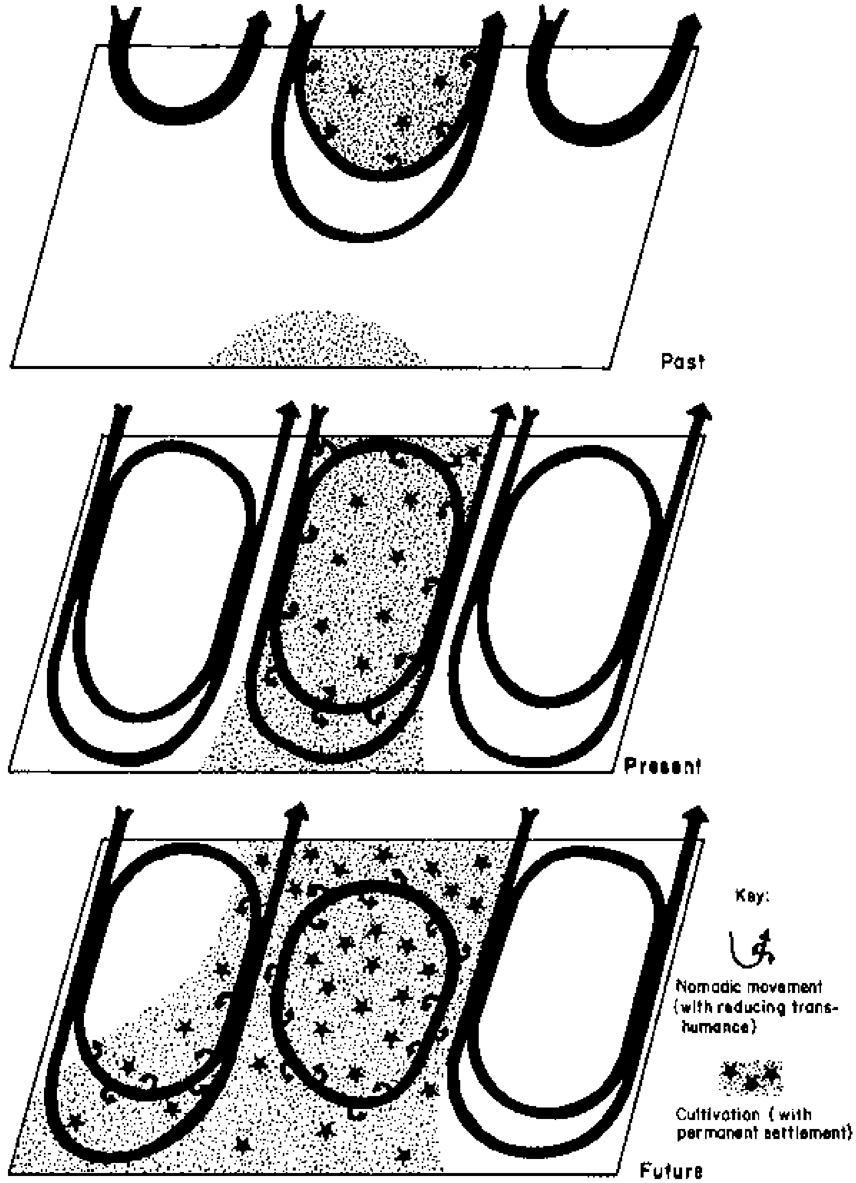
Nevertheless, because of the very restricted distribution of riverine tsetse, their relatively limited abundance, and their low infection rates, typically with trypanosomes of non-silvatic origin, the trypanosomiasis challenge they represent is likely to be relatively low.

The distribution of cattle within the subhumid zone and the seasonal changes described in this paper are considered to represent a transitional stage in a continuing southward spread of Fulani cattle owners and their zebu stock. This southward drift is inextricably bound up with three interrelated factors. A long-term process of agricultural expansion, resulting from human population increase and greater competition for land resources, is generally opening up and changing the environment of the subhumid zone, and at the same time leading to a proliferation of local markets for the sale of dairy and meat products. This has led to a decline in the incidence of trypanosomiasis during the wet season, and a rise in levels of cultivation. Both these processes have encouraged an influx of pastoralists and their cattle. Many of these settle permanently, either because they were sedentary before they migrated, or because they were nomads but have abandoned their traditional way of life in response to the falling value of milk products relative to grain (RIM, 1984).

A schematic model of cattle distribution dynamics

A conceptual view of the possible overall dynamics of cattle distribution within the Nigerian subhumid zone is illustrated in the form of a three-phase model shown in Figure 5, in which past, present and future conditions within the zone are represented.

Figure 5. Schematic model of the dynamics of cattle distribution in the Nigerian subhumid zone.



In the past, zebu distribution was transient and limited largely to a dry-season influx of nomadic cattle from the north, indicated by the broad pathways entering and exiting the zone. Cultivation, represented by stipple, is shown encroaching the zone centrally from both the north and the south.

Associated with the expansion of agriculture into the subhumid zone, there has been an increasing degree of sedenterization amongst Fulani cattle owners. This has involved both a reduction in the range of their seasonal transhumance, represented in Figure 5 by the 'eddies' spiralling off the schematic pathways of cattle movement; and an increased proportion of permanent settlement, symbolized by stars.

As time passed and population increased, agricultural expansion was focussed an the central bridging band across the subhumid zone, but because of generally increased competition for limited land resources to the north, seasonal cattle movements extended progressively further south into the subhumid zone. This southward dispersal of cattle, which has occurred across the entire zone, has been encouraged by a trend of increasing aridity further north, and by a general decline in the distribution and abundance of tsetse and a consequent reduction in the significance of trypanosomiasis.

This situation is illustrated in the central model of Figure 5, representing conditions at present, in which substantially reduced seasonal transhumance and increased settlement of Fulani and their cattle is indicated within the central bridging band of cultivation stretching across the subhumid zone. To the east and the west a southward dispersal of cattle has also taken place, to such an extent that much of the seasonal movement of cattle, even of long-distance transhumance (represented by the large oval pathways), is now believed to take place within the subhumid zone itself. The proportion of nomadic immigrants from further north is now considered to be low in comparison with permanent residents of the subhumid zone.

In the future, as land pressure in the central bridging zone, as well as to the north and south, continues to increase, as it must while the rural human population increases, it seems inevitable that agricultural expansion will increasingly be directed outwards to the west and east.

However, because of the siting of the new Federal Capital at Abuja and the major commercial/communication axis linking Lagos, Ibadan, Abuja, Kaduna and Kano, preferential agricultural expansion and land development are likely to take place to the south and west. Thus, as indicated in the future model of the subhumid zone, southwestward spread of arable agriculture and rural populations can be anticipated, along with a closely associated dispersal of cattle and Fulani who can be expected to settle and gradually establish a system of mixed farming.

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