

APPENDIX ONETHE FORMATION OF WATER HOLES  
IN THE EASTERN SELOUS GAME RESERVE, TANZANIA

## INTRODUCTION

The high carrying capacity of the eastern Selous Game Reserve is in part due to a network of permanent and seasonal water holes. This area supports a game biomass of up to 14,000 kg per km<sup>2</sup> on a habitat<sup>of</sup> scattered tree grassland with short annual and perennial grasses. The distribution and formation of these water holes have been examined as part of a long term ecological study at the Miombo Research Centre (38° 30'E 8° 30'S) in the Selous Game Reserve.

## GEOLOGY AND SOIL STRUCTURE

The basic geology of the area has been described by Spence (1957) and Haldemann (1962) and is summarised by Rodgers (1968). The salient features are mentioned here.

A schematic profile of the area is shown in Figure I. The Tundu Hills (680m) composed of Karoo sandstone formations (the Rufiji beds) with abundant siltstones, shales and mudstones, descend to a flat river terrace (150m) of Recent and Tertiary sand and clay deposits. The upland Karoo areas have free draining sandy red soils (pH 5-6) to a depth of over 10m which support a Brachystegia woodland community ("miombo"). Under the soil layer is a hard impermeable non-lateritic iron pan which covers the bed rock of white sandstones. These sandstones may be slightly alkaline with a variable calcium and sodium

content. Animal salt licks are common where this layer is exposed in erosion gullions.

The outwash plain has a top soil of a hard structureless clay sand overlying a nodular calcium carbonate concretionary layer at 30 to 60cm depth. The soil is highly alkaline (pH 9.5 to 10.0) with sodium forming up to 40% of the total exchangeable bases. At depth in the soil (2 to 6m) are thin strata (1-2cm in depth) of sand which carry a seasonal water flow.

It seems probable that past erosion and leaching of the Karoo rocks has led to the high concentrations of sodium and calcium in the outwash plain. The sodium concentrations have caused a replacement of calcium and deposition of calcium carbonate nodular concretions. High sodium levels have also added to the dispersion of clay particles causing impermeable drainage conditions (Black 1968).

Present rainfall averages 760mm per year in a six-month (November - April) season. This precipitation will descend through the deep sands to the iron pan and flow sub-surface to the outwash plain. At the geological boundary of the Karoo and Recent deposits a series of seepage springs occur. These springs can be seen the length of the Selous Reserve and are regional, not local phenomena.

#### WATER HOLE DISTRIBUTION AND DESCRIPTION

The outwash plain is essentially flat, descending less than 100m over 11km. There are few drainage lines or depressions. Water holes are scattered in a seemingly random pattern throughout the entire area. The holes are invariably

associated with termitaria and usually with large trees of Mimusops schleibeni and Tamarindus indica.

Several stages of pool development can be seen from small water-filled hollows at the basis of termitaria, to large mature pools, to senescent pools which are silted up and carry dense sedge or riverine vegetation.

Large pools are essentially circular and several have diameters of 40 to 50m and are up to 1.2m deep in the centre. Some pools have islands or peninsulas of termitaria. Many areas of this flat outwash plain have up to four such large pools per km<sup>2</sup> and many more smaller ones. The pools are easily seen on small scale (1:48,000) aerial photographs of the region.

As the pool grows, a characteristic edge thicket develops. Typical species are Markhamia acuminata, Heinsia crinita and Lamprothamnus zanguebaricus. Hippopotamus frequent the larger pools and their tracks often cause small erosion gullies leading to silting.

#### DISCUSSION

It is suggested that the deep rooting tree species associated with the water holes allow an up-welling of water by penetrating the hard-pan and tapping the water bearing sand strata. Animal diggings or mud wallows at the base of the termitaria, for minerals or water, will release the water and form a hollow for it to flow into, this process is shown in figure 2. Run off from surrounding areas assists in maintaining water levels. Such hollows hold water through the wet season but dry up rapidly

following the end of the rains. The hollows typically contain many sedges and moisture loving grasses, e.g. Echinochloa haploclada.

At the other end of the scale one can see the invasion of large pools by grasses, Echinochloa and Setaria species, and large sedges. Some pools show an invasion of woody species such as Aeschynomene species in open water and many Rubiaceae riverine species along the edge. Several sites of what must have been pools in the past have been examined; circular patches of dark silt clay with dense riverine thicket with anthills, associated trees and old hippopotamus trails are evident.

From these subjective observations it is postulated that pool or water hole formation is a dynamic process, new pools forming at the base of termitaria and old pools silting up and being invaded by sedges and riverine shrubs. Figure 3 illustrates pool growth through five stages of development.

The difficulty is to explain the succession from the early diggings to the mature pools. Several pools have local names, and the questioning of past residents of the area about specific pools reveals that their formation is a slow process, probably taking well over 100 years. Over the eight years of the authors experience of the area, change is evident in the early and late stages, but not in the middle stages. In the absence of alternative theories it is supposed that animal digging and wallowing (especially the activity of hippopotamus) will slowly increase the diameter and depth of the hole. As the pools widens, silting from trail erosion and surface wash will allow eventual plant invasion.

Weir (1965) discusses water hole formation from a different habitat in the Wankie National Park, Rhodesia. He notes the association between water holes (pans) and termitaria, especially in the pans earlier stages, and states the pan origin is attributable largely to zoogenous erosion by large mammals, and that their further evolution may be critically affected by these mammals. Weir suggests the initial digging by animals is in order to obtain accumulated soil chemicals from the termitaria. He attributes further growth of the pans to animal activity, mud removal and trampling causing air dispersion of dust particles.

In general the ideas of Weir and those expressed in this paper agree, and differences are attributed to differences in the physical environment.

Observation of pool water levels shows major annual changes. A pool which holds water throughout one dry season may be dry at the end of the rains in succeeding years. Two adjacent pools of similar size may show completely different water levels at any one time. It is thought that such variation is due to variable sub surface flow and that local rainfall and surface flow are not of primary importance in determining dry season water levels.

It is concluded that water holes in this area are not permanent structures and their formation is a function of topography and geology. Water holes are dependant on animal activity for their development. Water retention is governed not only by size and local rainfall and surface flow but by an annually variable sub surface water flow.

APPENDIX TWO.PAST WANGINDO SETTLEMENT IN THE EASTERN  
SELOUS GAME RESERVE.

(Copied from: Rodgers, W.A. 1976, Tanzania  
Notes and Records Vol. 77/78 21-26)

Introduction

A large portion of what is now the Eastern Selous Game Reserve in Rufiji, Kilwa and Nachingwea Districts was settled by the Wangindo people prior to their enforced emigration in 1945 due to a sleeping sickness epidemic. Their settlement has left considerable effect on the vegetation. The opportunity was taken in 1970 to question several old villagers who were born in this area.

Past History

The Wangindo are a Bantu people with probable Mozambique origins who in the past reached as far west as the Ulanga River where they intermingled with the Wapogoro, in the north almost up to the Rufiji River, to the Matumbi Hills in the east and to Liwale and along the Mbarangandu River in the south. A people of shifting cultivators, hunters and gatherers, dominated by their more warlike Wangoni neighbours, they were never very numerous and settlements were scattered over large areas of empty bush.

From spoken accounts it is evident that the Wangindo suffered from Arab and coastal slavers, even into the early part of this century. Stories were told of individual households stealing one another's children who were then bartered with the Arabs for goods such as salt, cloth and muzzle-loaders, shot and powder.

In the latter half of the last century the Ngoni wars occurred. The elders I spoke to now regard these wars as a joke, relating how the Wangindo fled into the thickets with no organized attempt at defence against the Wangoni raiding parties. The story is told of how the Wangindo were dependent on the Arabs for many necessities and lost many young people in the process; and then in turn were attacked by the Wangoni for these very necessities resulting in further loss of life. It is remarkable that though there was social intercourse between neighbouring Ngindo settlements such as marriage, movements, and social 'ngomas' there was no attempt at communal defence, often one settlement running away when their neighbours were attacked by Wangoni.

Eventually, with the establishment of German Colonial rule, the Wangoni wars died out and the more scattered settlements came together. However, with the Maji Maji War in 1905 and the stern retribution by the Germans, organized settlement temporarily disappeared.

These three factors: slaving, the Wangoni, and the German oppression following Maji Maji, all helped to keep the Wangindo population at a very low level, and it seems that their numbers must have been at their highest at the time of their moving in 1945.

The eastern Selous Game Reserve near Ngarambe village (38°35' 3E 8°30' 3S) which forms the study area for the Miombo Research Centre, was largely ignored by German development whose closest 'bomas' were at Utete and Liwale both over seventy miles away. A small German government cotton farm of about five acres was started on the Lukiliro River near Fundi Yaiya and a German settler started to build a house near this site. Neither were successful, although the low stone walls of the house still stand. The Germans pushed motor roads across the area, one from Liwale to Utete with a branch near Fundi Yaiya to Libungani, Kitope and Madaba settlements. These roads were straight, well-aligned and even banked, all built through forced labour in lieu of tax. The Germans introduced taxation which at first was payable in latex from the wild rubber trees (Landolphia spp.) the then principal form of commerce in the area, later the tax was fixed at one shilling per year.

The 1914-18 war passed through this area and relics still exist in the form of gun emplacements on the Rufiji, the occasional cartridge case, button or horse-shoe. A small length of signalling wire was recovered some years ago. It is probable that many Wangindo were conscripted as porters for the German Army. Ghost stories are numerous from this war period, the Wangindo being highly superstitious.

Next came the British occupation and the start of local government with the provision of a local 'baraza' at Muhinje, the occasional trading post, the appointment of headmen and regular visits from the District Officer and Game Warden. The area



was always underdeveloped and agriculture, such as it was, was basically at a subsistence level. Exports were wild rubber latex and later gum copal from the tree. Trachylobium verrucosum; beeswax was occasionally sold. As such the situation remained until 1945 when the whole population was removed due to the sleeping sickness epidemic. Most people were settled in hastily-built villages along the Matandu River near Njinjo. From there they gradually spread back again along the new boundaries of the Selous Reserve (designated in 1947) where Ngarambe village is the closest large settlement.

#### Social Organization and Culture.

As was mentioned above, the Wangindo were basically a people of limited shifting agriculture and hunters and gatherers. Living in an inhospitable environment with a seven-month drought, poor soils and unsteady water supplies, conditions were of necessity cruel and unkind. This fact was highlighted by the need to hide deep in forests to escape the world of the Wangindo and Achele. In such days millet, maize and ~~manihot~~ were the major crops. Millet was mainly used for brewing beer for ~~family~~ use. Also appeared very much later, as did oxen, were common, but only the odd headman or wealthier person had goats as <sup>a</sup> sign of prestige. These animals were feared by others and often killed. From way back in time, the Wangindo have suffered years of famine, as was often the case even recently. The choice of settlement is mainly dictated by good crops sites rather than

close access to permanent water. The Wangindo people have a considerable knowledge of natural vegetation and many fruits, leaves, roots, mushrooms and animals were utilised, even to the extent of gathering grass seeds for grinding into porridge (Crosse-Upcott, 1958).

Along with such knowledge of famine foods, went an enormous number of local medicines, often concocted from several different plants, which were used for various purposes all the way from curing stomach ache to reputedly ensuring the sex of unborn babies.

Honey was highly sought after and many different species of bees were known although little use was made of homestead hives. Whole families would spend long periods away from their settlement, collecting honey.

Hunting again provided a large part of their diet and Wangindo were proficient in the use of muzzle-loader guns as well as poisoned arrows. (Poison was extracted from the roots of a rather uncommon shrub, Acokanthera schimperi, and the knowledge of preparation was known by only a few). Each settlement had its group of 'fundis' or specialist hunters who would supply all with meat in return for other foods. Communal drives with nets were held for forest duiker, common duiker, suni and hares.

Prior to the spread of Islam, most game species, but not elephant, were eaten and in times of famine even rats and insects. Religion later prevented the eating of pig and hippo meat. But,

in addition to these, many of the Wangindo people in this area will not eat striped animals such as zebra, eland, kudu, or bushbuck as they believe they may catch leprosy.

Greatly to my surprise, all the elders that I questioned adamantly agreed that up till about the 1920s elephant in the area were virtually unknown, if present at all. The elders related stories of how the British colonial settlement in the Kilosa, Mahenge and Songea-Tunduru area drove the elephants down from the hills into this area. The advent of British rule is now firmly fixed in their minds with the coming of the elephant.

It is probable that the whole of the area from Kilwa inland almost to the Ulanga River used to carry a far lower elephant population than at present. The nearby coastal town of Kilwa was an important Arab trading post for centuries, and ivory being even more valuable than it was recently, must have resulted in considerable hunting in the hinterland.

Stories abound of how occasionally Ngindo hunters would follow a single elephant track for days in the hope of getting ivory. But reports of Sutherland (1912) shooting elephant from the Luwegu River and German control of elephant along the Rufiji River would tend to contradict this. Again this recent colonisation of new areas by elephant in East Africa has been recorded elsewhere (Lamprey, et al, 1967) and is usually due to intense cultivation of highland areas, e.g. Kenya highlands and the Serengeti, Mount Kenya and Ukambani.

In order to facilitate movement, honey collection and hunting, large areas of bush were burnt as early as possible each year, although care was taken in lowland areas to ensure that all neighbouring settlements' crops were harvested before burning.

At the time of the 1945 move or the 'kihamu', settlement was evenly scattered over what is now the whole of 1,200 square mile research block of the Selous Game Reserve. As far as is known the total population would have been about one thousand families. The largest settlement was all along the upper Lukuliro River from Mpapule through Mpanga panga, Nunga, Mpingo, Fundi Yaiya to Kiwanga. According to the colonial-appointed headman, tax payers numbered nearly three hundred in this one area. Other large settlements were at: Nangue, Macharya Likwaju, Iihangwa, Timbe, Balenje, Mwendu, Namatogoro and Namamba.

The last of the major forest settlements, a place called Libungani, was left in 1933 when the inhabitants moved to Mpingo and Lukuliro.

The pattern of cultivation differed from area to area, but the inherent fertility of a site appeared to be the most important factor in area selection. Many soil and vegetation types were recognized and many indicator species were used. In the past thickets were the first choice and here deep soil/sand ridges were chosen in preference to the upper slopes which were often rocky with white sands and characterized by a sparse Brachystegia microphylla canopy. On the chosen site, all the smaller trees and ground layers were cut and burnt, and for the first two years left fallow or planted with finger millet. After this came cassava and then other crops for four or five years

before moving on and felling another area. This shifting cultivation, therefore, left its mark over a wide area. Many large blocks of thicket were opened up to fire thus preventing regeneration. Such an open woodland left after clearing and burning is of distinctive formation akin to the Zambian 'Chipya' types. It is known locally as 'Chao'. Dominant trees are Pseudolachnostylis maprouneifolia, Combretum zeyheri, Strychnos innocua and Millettia stuhlmannii and Ptelelopsis myrtifolia, two thicket remnants. Shrubs and herbs are rare and there is a dense coarse grass cover characterised by Hyparrhenia and Andropogon species. Such a coarse grass cover burns fiercely even early in the season and the regeneration of fire-tender or semi-tolerant species of thicket and Brachystegia communities is prevented. It is now common to find on flat top ridges in the thicket massif of the central Selous the following pattern:

- (1) Steep-sided slopes of poor, eroded, rocky soils with a cover of Brachystegia microphylla over thicket, large erosion basins are common (a source of impure salt in past times).
- (2) On ridge tops, a peripheral cover of dense forest or thicket, often less than one hundred metres wide. These communities are very rich in species.
- (3) A central area of 'chipya' fierce fire woodland.

In areas where clearing has not been open to fire or recently closed, thicket pioneers rapidly depress the grass growth and true thicket is gradually reinstated. Common thicket pioneers

Here are species of Landolphia, Vernonia and Dichrostachys cinerea.

Exposed thicket blocks, away from steep slopes virtually always show a peripheral 'chipya' woodland, indicating either past fringe cultivation or the gradual inroads of fire.

Valley bottom settlement, which was usual in the later years of colonial rule, followed a different pattern. Broad, flat, alluvial clay valley bottoms were chosen. Here gardens could be left for several years as annual alluvium sediments were deposited. These areas supported large numbers of people and crops were basically maize, millet, rice and cassava. Coconuts, cashew nuts, pawpaw and bananas were also grown.

These areas were originally covered with a medium height woodland of clay or impeded drainage associated trees e.g. Trachystegia boehmii, Vitex doniana, Sclerocarya caffra, Abolobonocarpus andogensis etc., with occasional thicket patches. Now Terminalia sericea and many Combretum species dominate over a tall rank grass cover. Some areas have dense tangles of shrubby species the so called 'Mafundu' bush.

Organized crop protection (mainly from elephant) started in the 1930s with the provision of a Game Scout permanently stationed at Lukuliro, one Mohammed Nkanje. From what I could gather, he was probably killing around fifty elephants per year in the early 1940s. Further Game Scout postings and regular patrols by Game Warden Ionides took additional toll of elephant, buffalo and predators, as did poaching and licensed ivory hunting.

It can readily be imagined that a population of one thousand families depending on (and being proficient poachers of) game animals for their protein, would have had a large effect on game populations. If each family ate one kilogram of meat per week this is over five hundred animals per year.

All evidence shows that since 1945, and more particularly since 1956 when regular anti-poaching patrols were introduced, game populations have increased tremendously. This increase is still continuing and present estimates put the game population in the total 1,200 square mile area at just under 30,000 animals, including 1,000 elephant (Rodgers, 1969).

In this study area several well-watered drainage valleys were never cultivated (poor soils). These and many smaller valleys would have been left free for animal use, although frequently burnt and hunted. In other areas of high density of human settlement in the miombo habitat, e.g. Northern Zambia, the presence of settlement around all permanent waterholes and springs must have had an even more devastating effect on wildlife than continual hunting.

Analysis of settlement sites shows that in 1945 about ten percent of the total area was under settlement and I estimate that including past thicket cultivation about 25 percent of the study area has been under some form of settlement in the last 100 years.

It is seen therefore that the 1945 population of 1,000 tax payers or families would have exerted, over several generations, a large influence on both vegetation types and animal populations.

- Note: 1. Plate 10 shows a typical ridge thicket system with evidence of recent settlement.
2. Kjekshus (1977) argues that Ngindo land in the 19th century was well populated with abundant crops and homesteads and that de-development took place from 1880 to 1950.

APPENDIX THREEPLANT SPECIES CHECKLIST FOR BLOCKS II1 AND II2.  
EASTERN SELOUS GAME RESERVE.

## INTRODUCTION.

My original checklist of the flowering plants of the eastern Selous was based on collections up to late 1972, (Rodgers & Ludanga, 1973). Since that time there has been further collecting in the study area (following the appointment of Kaj Vollesen as Botanist in 1975) and considerable taxonomic revision of the East African flora (studies leading to the publication of the "Flora of Tropical East Africa"). This has meant my checklist is now out of date. As the M.R.C. herbarium has been curated by Vollesen since 1975 and the additions and corrections to the checklist have resulted from his work, it is not possible to include a full up to date list in this thesis. However, Vollesen has very kindly offered to update the list for two major families, the Gramineae and the Leguminosae. These revised lists are included in this appendix. The symbol + indicates a new collection, the symbol \* indicates a name change from my earlier list. My original list is attached to a few copies of this thesis, Vollesen is intending to publish the revised list in 1979.



GRAMINEAE (Monocot). FTEA part 1 (1970)

FTEA part 2 (1976)

D.M. Napper, Grasses of Tanganyika (1965)

*Alloteropsis cimicina* (L.) Stapf

+ *A. papillosa* Clayton

*A. semialata* (R. Br.) Hitchc.

\* *Andropogon gayanus* Kunth var. *polycladus* (Hack.) Clayton

*A. schirensis* A. Rich.

*Aristida adscensionis* L.

*A. barbicollis* Trin. & Rupr.

*A. funiculata* Trin. & Rupr.

*A. hordacea* Kunth

+ *A. keniensis* Hearne

*Bewsia biflora* (Hack.) Goosens

*Brachiaria brizantha* (A. Rich.) Stapf

*B. deflexa* (Schumach.) Robyns

+ *B. dictyoneura* (Fig. & De Not.) Stapf

*B. leucrantha* (K. Schum.) Stapf.

*B. pubifolia* Stapf

*B. serrata* (Spreng.) Stapf

+ *Cenchrus ciliaris* L.

*Chloris gayana* Kunth

*C. mossambicensis* K. Schum.

+ *C. pycnothrix* Trin.

- C. virgata* Swi.  
*Cleistachne sorghoides* Benth.  
*Coelorachis lepidura* Stapf  
 + *Cymbopogon exenratus* (Hochst.) Stapf  
*C. giganteus* (Hochst.) Chiov.  
*Cymbosetaria sagittifolia* (A. Rich.) Schweickt.  
*Cynodon dactylon* (L.) Pers.  
*C. nlemfuensis* Vanderyst var. *nlemfuensis*  
*Dactyloctenium aegyptium* (L.) Wild.  
*D. giganteum* Fischer & Schweickt.  
 + *Dicanthium annulatum* (Forsk.) Stapf var. *annulatum*  
 \* *D. bladhii* (Retz) Clayton (= *Bothriochloa glabra*).  
 + *D. cristatum* (Forsk.) Stapf.  
 \* *D. insculptum* (A. Rich) Clayton (= *Bothriochloa pertusa*)  
*D. papillosum* (A. Rich) De Wet & Harlan  
*Digitaria ciliaris* (Retz.) Koel. ssp. *ciliaris*  
 + *D. comifera* Pilg.  
*D. debilis* (Desf.) Willd.  
*D. gymnostachys* Pilg.  
*D. gayana* (Kunth.) Stapf.  
 + *D. longiflora* (Retz.) Pers.  
*D. milaniana* (Rendle) Stapf  
 \* *D. nuda* Schumach  
 + *D. perrottetii* (Kunth) Stapf  
*Echinochloa colona* (L.) Link  
*E. crus - pavonis* (H.B.K.) Schult.

- E. haploclada* (Stapf) Stapf  
*Eleusine indica* (L.) Gaertn. ssp *africana* Phillips  
 + *E. coracana* (L.) Gaertn.  
*Elymandra grallata* (Stapf) Clayton  
*Enteropogon macrostachyus* (A. Rich) Benth.  
*Eragrostiella bifaria* (Vahl) Bor  
*Eragrostis aethiopica* Chiov.  
*E. aspera* (Jacq.) Nees  
*E. atrovirens* (Desf.) Steud.  
*E. castellaneana* Busc. & Muschel.  
*E. ciliaris* (L.) R. Br.  
 + *E. gangetica* (Roxb) Steud.  
*E. lappula* Nees  
*E. namaquensis* Schrad. var ~~namaquensis~~  
*E. pilosa* (L.) Beauv.  
*E. racemosa* (Thumb.) Steud.  
*E. setulifera* Pilg.  
*E. superba* Peyr.  
 + *E. tenella* (L.) Roem. & Schult.  
*Eriochloa meyerana* (Nees) Pilg.  
*E. procera* (Retz.) C.E. Hubb.  
*E. parvisculpta* C.E. Hubb.  
*Eustachys paspaloides* (Vahl) Lanza & Mattei  
*Heteropogon contortus* (L.) Roem. & Schult.  
*H. melanocarpus* (Ell.) Benth.

- + *Hyparrhenia figariana* (Chiov.) Clayton
- H. filipendula* (Hochst.) Stapf var *filipendula*
- + *H. rufa* (Nees) Stapf
- Hyperthelia dissoluta* (Steud.) Clayton
- Imperata cylindrica* (L.) Beauv.
- Ischaemum afrum* (J.F. Gmel) Dandy
- Leptocarydion vulpiastrum* (De Not.) Stapf
- + *Leptochloa chinensis* (L.) Nees
- L. panicea* (Retz.) Ohwi
- L. squarrosa* Pilg.
- L. uniflora* A. Rich
- + *Lepturus radicans*. (Steud) A. Camus
- Loudetia arundinacea* (A. Rich.) Steud.
- L. flavida* (Stapf) C.E. Hubb.
- L. simplex* (Nees) C.E. Hubb.
- Megastachya mucronata* (Poir.) Beauv.
- Miscanthidium* sp.
- Oryza eichengeri* Peter
- O. longistaminata* Chev. & Roehr.
- O. punctata* Steud
- Oxytenanthera abyssinica* (A. Rich.) Munro
- Panicum aphanoneurum* Stapf
- P. deustum* Thumb.
- P. heterostachyum* Hack.
- P. infestum* Anderss.

- P. massaiense* Mez  
*P. maximum* Jacq.  
*P. meyeranum* Nees  
*P. subalbidum* Kunth.  
*P. trichocladum* K. Schum.
- + *Paspalum glumaceum* Clayton
- \* *P. scrobiculatum* L.
- Pennisetum polystachyon* (L.) Schult.
- Perotis hildebrandtii* Mez
- P. patens* Gand.
- + *Phragmites mauritianus* Kunth.
- Pogonarthria squarrosa* (Roem. & Schult.) Pilg.
- Polyneura squarrosa* Peter
- + *Rhytachne latifolia* Clayton
- Rottboelia exaltata* L.f.
- Sacciolepis curvata* (L.) Chase
- Schizachyrium brevifolium* (Sw.) Biise
- S. exile* (Hochst.) Pilg.
- S. sanguineum* (Retz) Alston
- Schoenefeldia transiens* (Pilg.) Chiov.
- Setaria incrassata* (Hochst.) Hack.
- + *S. pumila* (Poir.) Roem. & Schult.
- S. planifolia* Stapf
- S. sphacelata* Stapf & C.E. Hubb.
- \* *Sorghum arundinaceum* (Willd.) Stapf

- S. versicolor* Anderss.  
*Sporobolus festivus* A. Rich  
*S. fimbriatus* Nees  
*S. ioclados* (Trin.) Nees (= *S. marginatus*)  
*S. pyramidalis* Beauv.  
*S. stolzii* Mez  
*S. subglosus* A. Chev.  
*S. virginicus*. (L.) Kunth  
+ *Stenotaphrum micranthium* (Dlsv.) Hubb.  
+ *Tetrapogon tenellus* (Roxb.) Chiov.  
*Thelepogon elegans* Roem. & Schult.  
*Themeda triandra* Forsk.  
\* *Tragus heptaneuron* Clayton  
*Tristachya bequaertii* De Wild.  
*T. nodiglumis* K. Schum.  
++*Urochloa mossambicensis* (Hack.) Dandy  
*U. pullulans* Stapf  
+ *U. roptans* (L.) Stapf  
*U. trichopus* (Hochst.) Stapf  
*Vetiveria nigritana* (Benth.) Stapf  
+ *Vossia cuspidata* (Roxb) Griff.  
*Zonotroche inamoena* (K. Schum) Clayton

LEGUMINOSAE (sensu lato). Dicot.CAESALPINIACEAE FTEA (1967)

- Afzelia quanzensis* Welw.  
*Bauhinia tomentosa* L.  
*Brachystegia boehmii* Taub.  
*B. bussei* Harms  
*B. microphylla* Harms  
*B. spiciformis* Benth.  
*B. utilis* Hutch. & Burt Davy  
*Burkea africana* Hook.  
*Cassia abbreviata* Oliv.  
*C. auriculata* L.  
*C. absus* L.  
*C. burtii* Bak. f.  
*C. grantii* Oliv.  
*C. mimoscoides* L.  
*C. obtusifolia* L.  
*C. petersiana* Bolle  
*C. siamea* Lam.  
*C. singueana* Del.  
*C. sp.*  
*Cordyla africana* Lour.  
*Cryptosepalum maraviense* Oliv.  
*Dialium holtzii* Harms  
*Erythrophleum africanum* (Benth.) Harms

*Julbernardia globiflora* (Benth.) Troupin

*Tamarindus indica* L.

*Tessmannia densiflora* Harms

*Trachylobium verrucosum* (Gaertn.) Oliv.

*Tylosema fassoglensis* (Schweinf.) Torre and Hillcoat

MIMOSACEAE FTEA (1959)

*Acacia brevispica* Harms

*A. robusta* Burch. ssp. *usambarensis* (Taub.) Brenan

*A. hockii* De Wild.

*A. macrothyrsa* Harms

*A. nigrescens* Oliv.

*A. nilotica* (L.) Del. ssp. *kraussiana* (Benth.) Brenan

*A. senegal* (L.) Wild.

*A. sieberiana* DC. var. *sieberiana*

*A. zanzibarica* (S. Moore) Taub.

*Albizia amara* (Roxb.) Boiv.

*A. adianthifolia* (Schumach.) W.F. Wight

*A. anthelmintica* (A. Rich.) Brogn.

*A. harveyi* Fourn.

*A. petersiana* (Bolle) Oliv.

*A. versicolor* Oliv.

*A. zimmermannii* Harms

*Amblygonocarpus andongensis* (Oliv.) Exell & Torre



*Dichrostachys cinerea* (L.) Wight & Arn.

*Elephantorrhiza goetzii*

*Entada chrysostachys* (Benth.) Drake

*Mimosa busseana* Harms

*M. pigra* L.

*Neptunia oleracea* Lour.

PAPILLIONACEAE FTEA (1972)

*Abrus precatorius* L. ssp. *africanus* Verdc.

+ *A. pulchellus* Thw. ssp. *tenniflorus* (Benth.) Verdc.

*Aeschynomene cristata* Vatke var. *pubescens* J. Leonard

*A. indica* L.

\* *A. mossambicensis* Verdc. ssp. *longestipitata* Verdc.

+ *A. nyassana* Taub.

*A. uniflora* E. Mey.

*Alysicarpus glumaceus* (Vahl) DC. var. *glumaceus*

*A. ovalifolius* (Schumach. & Thomon.) J. Leonard

+ *Baphia kirikii* Bak.

*B. massaliensis* Taub.

*Clitoria ternatea* L.

*Crotalaria axillaris* Ait.

*C. barkae* Schweinf. f. ssp. *zimmermannii* (Bak.)

*C. cephalotes* A. Rich

- C. goodiiformis* Vatke  
*C. hyssopifolia* Klotzsch  
\* *C. kirkii* Bak.  
+ *C. laburnifolia* L. ssp. *laburnifolia*  
+ *C. laburnoides* Klotzsch var. *laburnoides*  
+ *C. lanceolata* E. Mey. ssp. *lanceolata*  
+ *C. microcarpa* Benth.  
*C. pterocalyx* Harms  
*C. reptans* Taub.  
+ *C. steudneri* Schweinf.  
*C. vasculosa* Benth.  
*C. virgalata* Klotzsch  
+ *Cuclocarpa stellaris* Bak.  
*Dalbergia arbutifolia* Bak. ssp. *arbutifolia*  
*D. armata* E. Mey.  
*D. boehmii* Taub. ssp. *boehmii*  
*D. melanoxydon* Guill. & Perr.  
+ *D. obovata* E. Mey.  
*Desmodium barbatum* (L.) Benth. var. *procumbens*  
*D. triflorum* (L.) DC.  
*Droogmansia pteropus* (Bak.) De Wild.  
*Eriosema burkei* Harv.  
+ *Indigofera colutea* (Burn. f.) Merr.  
*I. cuneata* Bak.  
\* *I. dyeri* Britton. var. *major*

- I *I. erythrogamma* Bak.
- I. excellii* Torre
- I. garkeana* Vatke
- I. hirsuta* L.
- I. lobata* Gillett
- I. malongensis* Cronq.
- + *I. microcarpa* Desv.
- + *I. nummularifolia* (L.) Alston
- + *I. ormocarpoides* Bak.
- I. praticola* Bak. f.
- I. rhynchocarpa* Bak. var. *rhynchocarpa*
- I. schimperi* Jaub. & Spach. var. *schimperi*
- + *I. secundiflora* Poiv. var. *rubripilosa* De Wild.
- I. subcorymbosa* Bak.
- I. tinctoria* L.
- \* *I. trita* L.f. var. *scarbra* (Roth.) Ali
- + *I. trita* L.f. var. *subulata* (Poiv.) Ali
- I. viscidissima* Bak. ssp. *orientalis* Gillett
- Lonchocarpus bussei* Harms
- L. capassa* Rolfe
- Macrotyloma maranguense* (Taub.) Ver. & S.
- + *Millettia bussei* Harms.
- M. eetveldeana* (Micheli) Hauman
- M. micans* Taub.
- M. stuhlmannii* Taub.

- Mundulea sericea (Willd.) A. Chev.  
 Neoratanenia mitis (A. Rich.) Verdc.  
 + Ormocarpum kirkii S. Moore  
 O. sp. nov.  
 Pericopsis angolensis (Welw.) Van Meeuwen  
 Pseudarthria hookeri Wight & Arn  
 Pterocarpus angolensis DC  
 P. tinctorius Welw. var. megalocarpus  
 P. rotundifolius (Sond.) Druce  
 + Rhynchosia albissima Gand.  
 + R. densiflora (Roth.) DC.  
 + R. ~~microantha~~ Harms  
 R. minima (L.) DC. var. minima  
 + R. sublobata (Schimach. & Thonn.) Meikle  
 + R. viscosa (Roth) DC.  
 + Rothia hirsuta (Guill. & Perr.) Bak.  
 + Sesbania greenwayi Gillett  
 S. hirtistyla Gillett var hirtistyla  
 Sphenostylis manginata E. Mey ssp. erecta (Bak. f.) Verdc.  
 Stylosanthes fruticosa (Retz) Alston  
 + Tephrosia noctiflora Bak.  
 + T. pentaphylla (Roxb.) G. Don  
 T. pumila (Lam.) Pers.  
 + T. purpurea (L.) Pers. ssp. leptostachya (DC.) Brummitt  
 + T. purpurea (L.) Pers. ssp. leptostachya var. pubescens Bak.

- + *T. stormsii* De Wild. var. *stormsii*
- + *T. villosa* (L.) pers. ssp. *ehrenbergiana* (Schweinf.) Brummitt
- + *Teramnus labialis* (L.f.) Spreng ssp. *arabicus* Werdw.
- + *Vigna friesiorum* Harms
- + *V. kirkii* (Bak.) Gillett
- + *V. macrorrhyncha* (Harms) Milne Redh.
  - V. pubescens* Wilczek
- + *V. reticulata* Hook.f.
  - V. vexillata* (L.) A. Rich var. *angustifolia*
- Xeroderris stuhlmanii* (Taub.) Mendonca & E.P. Sousa
- \* *Zornia glochidiata* DC.

## APPENDIX FOUR.

THE CLASSIFICATION AND ORDINATION OF PLANT  
COMMUNITIES

## A4.1 Introduction.

Multivariate analysis of vegetation communities is being increasingly used in plant ecology, although few studies have been conducted in the African woodlands; (Boaler, 1966; Kershaw, 1968; Ramsey & Leeuw, 1964; and Lawton, pers. comm.). The methods of analysis themselves are objective (and quantitative in the case of ordination) but the interpretation of their results does require subjective knowledge of field conditions. Furthermore the methods of data collection are often subjective as regards quadrat size, site selection, sampling intensity etc, and may all affect the analysis. However with these limitations in mind the methods do allow the objective confirmation of field impressions and can produce data on species or site associations or similarities which may not be immediately apparent in the field. Furthermore the technique of Principal Component Analysis can allow the correlation of quantitative environmental parameters (eg. pH, altitude, clay content etc.) with objective

gradients of species or site variation. These correlation techniques were not considered in this study.

#### A4.2. Classification or Ordination?

Classification treats the vegetation as being composed of discrete entities or associations which are classified on the basis of the presence or absence of one character, i.e. they are divisive and monothetic. Classification analyses are relatively simple in method and hence simple to interpret. They have disadvantages in that they can only use qualitative data, eg. presence-absence, and the analysis gives no idea of the interrelationships of groups of sites or species. Further the splitting on the basis of one character destroys any nature of a continuum of vegetation communities.

Ordination methods were designed to deal with a vegetation continuum, the analysis can use quantitative data and can show the relationships between species and sites groupings. Analysis is complex and the interpretation of results is difficult and often controversial, Pielou (1969).

For this study I decided to use classification techniques followed by ordination as I had both qualitative

and quantitative data. It was hoped that both methods would give results of ecological value.

#### A4.3 Classification.

Several methods of classification were available as "packaged" computer programmes, these were:

- a) Williams and Lambert Association Analysis  
(Normal and Inverse).
- b) Information analysis (Normal and Inverse).
- c) Cluster analysis.

Information analysis (which uses a semi agglomerative technique) was attempted but results tended to show a large number of small associations of little apparent meaning and so the method was discarded.

Association analysis (Williams and Lambert, 1959 and 1961) is an objective hierarchical technique which considers the chi square association levels between all species in a two way data matrix; removing the species with the highest chi square and re-analysing the resultant matrix and so on until a preset low level of chi square is reached.



The reverse matrix is used in the inverse analysis. Standard practice sets the analysis parameters of 'SIGCHI', the lowest level of chi square to be used at  $NQ$  where  $NQ$  is quadrat number; of MINNO, the minimum number of species occurrences in the data set, at  $\frac{N}{50}$  where  $N$  is species number; and  $Z$ , the maximum number of associations or groups to be produced at 12 or 15. The analysis used species total chi square values for choosing division levels and not maximum chi square for any species pair. Such total levels are shown on the vertical axis of the dendrograms in chapter 3.2.

Cluster analysis followed the technique of Legendre and Rogers (1972). The concept of the density of species linkage 'd' is used in figure 3.5, and saves the drawing of detailed constellations as in figure 3.10 or as in Welch (1960).

#### A 4.4. Ordination.

Several methods of ordination were available, but Principal Components Analysis (PCA) was used as it offered a larger data matrix and allowed a more rigorous analysis producing axes with a known variation content. PCA is a

method of multivariate analysis which can interpret data where several quantitative observations are made on several variates. PCA changes the variates which are correlated between each other into an equal number of uncorrelated components. This transformation gives two results, a set of eigen values, which are the variances of the new components, and a set of eigenvectors which are the weighting or loadings of each original variate on the new components.

Usually the first few eigen values will account for up to 95% of the total variance. The size of the variance content of each eigen value is an indication of its importance in ordering the data. These first few eigen values are referred to as Principal Components and data observations can be placed graphically on the component axes. Examination of the eigen vectors shows which variates are heavily loaded on each component. These variates become of prime importance in assessing the field population and the environmental factors affecting it.

#### A 4.5. The Computer Programmes.

The Department of Botany and Microbiology of the University College of Wales, Aberystwyth offered a completely

prepackaged set of computer programmes for vegetation analysis and ordination. Each analysis technique had a computer stored programme module and so data processing could take place serially. All analyses were performed on an ICL 4130 computer.

Field data was contained in a master data set containing species names, site grid, presence and absence and % frequency data. From this master file further data files were prepared for classification in both the inverse and normal modes and for PCA ordination in the inverse and normal modes.

Figure A 4.1 shows a flow diagram of analysis procedures.

#### A 4.6. Discussion.

Inverse association analysis had a tendency to produce "chaining" or the splitting off of small divisions without a dichotomous branching. This process can produce small groups of little ecological meaning. Mean number of species per quadrat and hence quadrat size will affect chaining, low values increasing chaining and vice versa. At the extreme case a point quadrat of 1 species per site would produce as many associations as species.

Despite the tendency to 'chain', inverse analysis results appear meaningful, more so if adjacent groups or groups split at low levels of chi square are lumped.

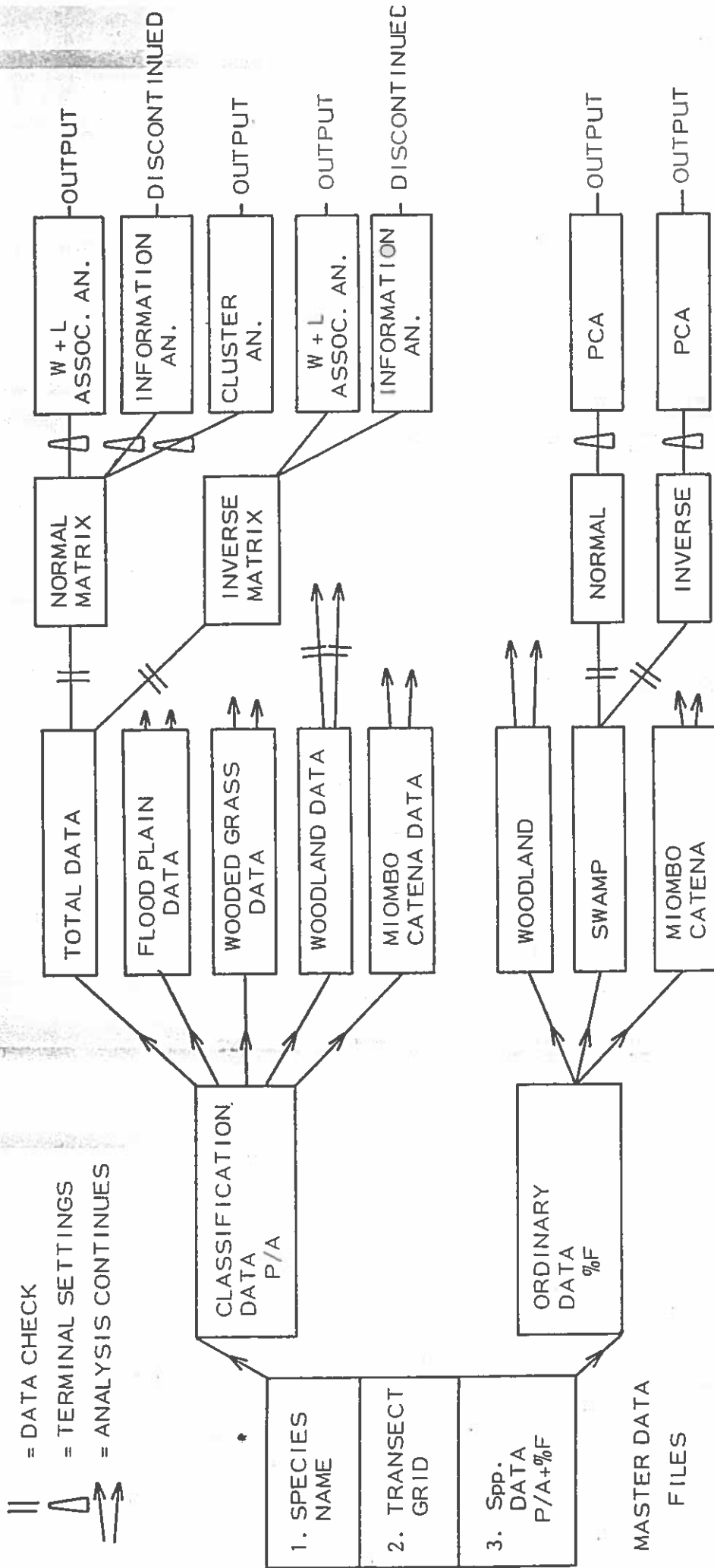
Conversely the large quadrat size used in this study, effectively  $6.25\text{m}^2$  (100 x 25cm square quadrats per site), but spread over an area of some 1 to 2 hectares at each site may have adversely affected association analysis. The large size and spread of quadrats meant many species were included in the presence/absence data matrix with a low frequency and could be atypical or a random inclusion for a particular community. The use of 'MINNO' terminators and the field exclusion of apparently "different" quadrat sites, (wallows, holes etc etc) may have prevented much noise but further manipulation of terminator levels could perhaps have given more meaningful results.

Constellation analysis of the small data sets were masked by edge species. In this case the few quadrats peripheral to the main community under analysis would typically contain the same species and hence produce the highest chi square values. Species with a high frequency tended to produce many negative associations, especially with peripheral species.

However it is believed that the knowledge of the ecotonal and transitional species gained from the inclusion of peripheral sites outweighs the disadvantages of reduced numbers of positive linkages within the main community.

As was mentioned in chapter 3.2., PCA inverse ordination of % frequency data was dominated by species of high frequency, both in the number of sites per data set and average frequency for all sites. However this dominance by the tall grasses is a real phenomenon ecologically as well as on the PCA print out. Forbs and small grasses within a relatively homogenous association are perhaps distributed by chance, eg. small open spaces, in shade patches etc and may not reflect environmental gradients to any great degree. Briefly they are species of little ecological information as regards this method of analysis.

FIG. A4.1 FLOW DIAGRAM OF COMPUTER ANALYSIS OF VEGETATION COMMUNITIES



APPENDIX FIVE

MINERAL CONTENT OF SOME SOILS, RANGE GRASSES  
AND WILD ANIMALS FROM SOUTHERN TANZANIA  
(from E. Afr. Agr. For. J. 1976.)

## INTRODUCTION

During the course of ecological studies in the Selous Game Reserve, south east Tanzania, the opportunity was taken to use the facilities afforded by the Mionbo Research Centre (38° 30'E, 8° 30'S) and the Central Veterinary Laboratories in Dar es Salaam to analyse soil, grass and wild animals' blood serum and liver for mineral content. Results are presented here for calcium, phosphorus, magnesium, copper and, in very few cases, cobalt.

Two distinct soil and vegetation types are represented in the study <sup>area</sup> surrounding the research centre. One, a short-grass scattered tree grassland on poorly drained alkaline clay sands and the other, a tall-grass woodland on free draining acid red sandy earths (the "miombo", Brachystegia woodlands, habitat of eastern and central Africa).

The short grass area is dominated by a mixture of annual and perennial species of Digitaria, Urochloa, Eragrostis, Sporobolus, Chloris and Brachiaria. Soils are grey sands with a variable clay content and a calcareous nodular pan at 30 to 60 cms depth. Both calcium and sodium content are high, as such pH is 9.5 or above.

The long grass area is dominated by tall, coarse, tussock perennial species of Loudetia, Andropogon, Themeda and Hyparrhenia. These species exhibit a rapid flush of green growth after burning in the dry season. Soils are old, free draining, acid, low NPK status, red, sandy earths with a nonlateritic hardpan at depth.

#### METHODS

Soil samples were taken from a series of soil pits throughout both habitats. Air dried samples were analysed at the Ilonga Agricultural Research Station, Kilosa, Tanzania using standard techniques.

Data on grass mineral content were taken from the results of a larger investigation of productivity and nutrient content, undertaken in 1969 to 1972. Grass samples were clipped to ground level from permanent grazing enclosures and other randomly selected sites within swards of differing species composition. Clipped samples were separated into green leaf, dry leaf and stem fractions, air dried and analysed for chemical content at the Central Veterinary Laboratories, Dar es Salaam using standard analytical techniques.

Data on mineral composition of animal tissue was taken from the results of a series of post mortem examinations of wild animals from 1969 to 1972. Animals were shot in early to mid morning and samples collected within an hour of death. Blood serum was obtained by centrifuging. Frozen whole blood and serum, and sections of liver preserved in 70% ethyl alcohol were sent to the Central Veterinary Laboratories for routine mineral analysis.



## RESULTS

Mineral analyses of soil samples are shown in Table I. Data are shown as a mean of several sites within each habitat. (Valley sites, thicket and rocky sites etc. are excluded). These results are compatible with data from a more detailed soil survey of the eastern Selous Game Reserve, Rodgers (unpublished data).

Grass sample analyses for 7 species from different times of the year are shown in Table II. Mean values for 58 separate analyses are shown at the foot of the table.

Animal tissue data are shown in Table III for 6 species: Nyassa wildebeest, impala, sable, Lichtensteins hartebeest, hippopotamus, buffalo and lion.

Wildebeest and impala data showed no correlation between mineral content and season or sex.

## DISCUSSION

The soils of the area are extremely low in nutrients, the high sodium levels of the alkaline soil also affecting phosphorus uptake by plants, Russell (1961).

The grass analysis shows exceptionally low levels of phosphorus, Andrew and Robbins (1971); although levels of calcium, magnesium and copper fall within requirement levels for grazing animals as detailed by Maynard and Loosli (1971) and Davis and Skidmore (1966).

The mean grass phosphorus content as determined in this study is 0.127%. Recommended levels for domestic livestock range from 0.25% (Davis and Skidmore 1966), 0.35% (Stent 1933), and 0.30% to 0.15% (Worden, Sellers and Tribe 1963). Levels below 0.15% can produce phosphorus deficient diseases. The mean calcium/phosphorus ratio 2.5:1 agrees well with recommended levels (Worden, Sellers and Tribe 1963), although there are wide seasonal variations.

Table II clearly shows the rapid decrease in phosphorus levels and a corresponding increase in calcium as the plant matures. At the height of the dry season with no burning this results in the very low phosphorus level of 0.05% or less and a detrimental Ca/P ratio of up to 12:1. However, widespread fires causing a flush of regenerating nutritious grass, and a high degree of grazing selection by indigenous animals will alleviate such nutrient deficiencies.

Animal tissue levels are high or normal for similar tissue in domestic livestock, e.g., about 10 mgm/100 ml for calcium, 2-3 mgm for magnesium, 0.07 to 0.17 mgm for blood copper and 10-50 ppm for liver copper. (Maynard and Loosli 1971; Worden, Sellers and Tribe 1963).

The high level of liver copper values is of interest as compared with domestic stock, but these values agree with those of Howard (1964) in a survey of 19 species of East African mammals. As in Howard's survey, hippopotamus showed the highest copper levels. The high level of blood calcium in lion reflects the dietary intake of this animal as considerable amounts of bone are ingested.

Phosphorus whole blood levels are very low compared with an accepted normal range for cattle of 35 to 45 mgm. The levels of 6-15 found in this study are low enough to cause

impaired fertility in cattle (Moustgard 1959). This however is not the case as pregnancy rates for mature wildebeest and impala approach 100% as determined by post mortem examination.

From these results it is suggested that indigenous wild animals are adapted to forage which is low in phosphorus content and that they can exist at high reproductive rates on phosphorus levels low enough to cause phosphorus deficient diseases and impaired reproduction in domestic animals. Such tentative conclusions emphasise the growing need for experimental research using tame or captive animals.

#### SUMMARY

During ecological studies at the Mionbo Research Centre, Selous Game Reserve, south east Tanzania, the opportunity was taken to analyse and compare mineral content of soil, grass and animal tissue. Soils and grass samples are low in phosphorus content, which is reflected in low levels of animal whole blood. Values for calcium, magnesium and copper compare with values given for domestic livestock. Phosphorus values are low enough to cause disease and impaired reproduction in livestock. As animals were healthy and showed a virtual 100% pregnancy rate it is suggested that indigenous wild animals are adapted to a range which is low in phosphorus content.

TABLE I  
MINERAL COMPOSITION OF SOIL SAMPLES

<u>Soil Type</u>	<u>Depth</u> <u>cms</u>	<u>pH</u>	<u>%</u> <u>CaCO<sub>3</sub></u>	<u>Mineral Composition</u>				
				<u>Ca</u>	<u>Mg</u>	<u>Na</u>	<u>K</u>	<u>P</u>
Alkaline grey sands  (Mean of 3 Sites)	0-10	8.0	1.5	2.8	0.1	0.5	0.15	1.6
	10-75	9.9	6.8	14.4	2.0	5.1	0.12	6.0
	75-100	10.0	5.6	22.2	3.0	7.0	0.15	3.5
Acid red sands  (Mean of 4 Sites)	0-10	6.1	1.5	4.8	1.0	0.25	0.12	1.1
	10-20	5.8	2.0	4.6	0.9	0.23	0.10	0.6
	20-150	5.7	1.5	4.2	0.7	0.20	0.08	0.3

A5-6

NOTE: pH analysis used a 1:2.5 H<sub>2</sub>O solution  
% CaCO<sub>3</sub> is free CaCO<sub>3</sub> in the soil  
Ca, Mg, Na, K are expressed as Millieq./100gr  
Phosphorus is expressed as ppm of available phosphorus (HCl extraction method)

TABLE II  
MINERAL COMPOSITION OF RANGE GRASSES

Species	Date Collected	Growth Stage	Total					Cu in ppm	Ca:P Ratio	
			Ash in %	Ca in %	P in %	Mg in %				
<u>Loudetia</u> sp.	1. 8.69	Dry leaf	6.8	0.38	0.05	0.21	2.7	7.6:1	} Tall grass habitat	
"	1. 8.69	Dry leaf	6.1	0.45	0.04	0.15	3.0	11.3:1		
"	8.10.69	Dry leaf	6.6	0.44	0.04	0.20	6.2	11.0:1		
"	20.10.69	Regen. green leaf	9.5	0.27	0.25	0.15	8.1	1.2:1	} Tall	
"	30.11.69	Regen. green leaf	8.6	0.35	0.19	0.15	11.6	1.7:1		
"	30.11.69	Regen. green leaf	10.3	0.35	0.25	0.14	8.3	1.3:1		
<u>Andropogon schirensis</u>	3. 2.69	Dry leaf	6.8	0.31	0.05	0.11	3.3	6.2:1	} Short grass habitat	
"	4. 2.69	Regen. green leaf	-	0.26	0.08	0.10	2.8	3.3:1		
"	4. 2.69	Green leaf (not burnt)	-	0.30	0.10	0.12	3.5	3.1		
"	7.10.69	Regen. green leaf	10.6	0.17	0.15	0.17	8.2	1.1:1	} 2:1	
"	6. 2.70	Regen. green leaf	-	0.18	0.09	-	-	2.8:1		
<u>Panicum infestum</u>	6. 2.70	Green leaf	-	0.22	0.08	-	-	2.8:1		
"	6. 2.70	Green leaf	-	0.16	0.10	-	-	1.6:1	} 8.2:1	
<u>Digitaria milaniana</u>	1. 8.69	Dry whole plant	7.1	0.41	0.05	0.19	6.2	8.2:1		
"	15. 3.70	Green leaf	10.6	0.40	0.21	0.06	5.5	1.9:1		
<u>Urochloa trichopus</u>	15. 4.70	Green leaf	9.7	0.59	0.06	0.11	5.9	3.8:1	} grass habitat	
"	15. 2.70	Green leaf	9.1	0.35	0.12	-	-	2.9:1		
<u>Brachiaria leucantha</u>	15. 3.70	Green leaf	19.2	0.38	0.08	0.04	2.1	4.8:1	} 11:1	
<u>Dactyloctenium</u> sp.	15. 3.70	Green leaf	9.2	0.44	0.04	0.09	2.1	11:1		
Mean of 58 analyses			6.9	0.32	0.127	0.14	8.8	2.46:1		

TABLE III  
MINERAL COMPOSITION OF ANIMAL TISSUES

<u>Species</u>	<u>No. of animals killed</u>	<u>Ca</u>	<u>P</u>	<u>Mg</u>	<u>Co</u>	<u>Blood Cu</u>	<u>Liver Cu</u>
		<u>PPM/100ml</u>	<u>PPM/100ml</u>	<u>PPM/100ml</u>	<u>PPM</u>	<u>PPM/100ml</u>	<u>PPM</u>
Impala	12	14.2	15.35	2.40	1.02	0.75	91.2
Wildbeest	22	14.8	10.66	2.11	0.65	0.71	42.8
Harthebeest	3	13.8	6.85	2.09	-	0.67	92.0
Sable	6	14.3	15.4	2.33	-	0.77	108.0
Hippopotamus	2	16.9	-	2.53	-	0.39	571.0
Buffalo	2	15.6	-	2.53	-	0.9	136.0
Lion	5	31.8	10.2	2.01	-	0.68	36.0

NOTE: Phosphorus levels are for whole blood, others for blood serum.

APPENDIX SIXTHE LION (PANTHERA LEO, LINN) POPULATION  
OF THE EASTERN SELOUS GAME RESERVE

(from E. Afr. Wildl. J., 1974,  
Volume 12, pages 313-317.)

## INTRODUCTION

The Selous Game Reserve, of approximately 50,000km<sup>2</sup> of uninhabited country in southeast Tanzania has been utilised by tourist hunting safaris since 1964. As these safaris operate on a block and quota basis (present policy allows 138 lions per year from a total of forty-five blocks) there is a need for information on the size and composition of the lion population to set adequate quotas.

Despite the tremendous interest and sentiment attached to all large carnivora, there is a lack of detailed knowledge on lion density and sex and age composition in the literature. Since the inception of the Mionbo Research Centre (38°30'E, 8°30'S) on the eastern boundary of the Selous in 1968, research staff have kept detailed records of all lion sightings and this data has been filed on 5 x 3 reference cards. This short paper summarises the available data from 1967 to 1972 as an attempt to set a biologically adequate hunting quota for lion.

The research area covers two hunting blocks totalling 1,900 km<sup>2</sup> in the eastern Selous. The topography is slight, varying from 100 m to 750 m. Annual rainfall averages 760 mm in a single 5-month season. Two major habitat types occur, a scattered tree short grassland on alkaline soils and a tall grass 'mionbo', Brachystegia, woodland on red acid soils. There is a resident game population of some 40,000 animals, Rodgers (1969). Major species are shown in Table 3.

## RESULTS

(1) POPULATION ESTIMATE. Accurate census of extensive lion populations is difficult without recourse to long term studies involving marking or photographic recognition, Pennycuick & Rudnai (1970). However, for a management exercise designed to show if a hunting quota increase from three to five lions per year is possible then a minimum figure for population size can suffice. Three rough census methods have been used and though none was satisfactory in that an accurate population estimate was not obtained, the three methods together do serve to show the general order of population size.

In 1968, twenty-three consecutive nights were spent on a walking coverage of the study area, each camp being at least 13 km away from the previous camp. A note was made on the number of nights lions were heard roaring. The following assumptions were made, none of which affect a minimum population estimate. One, that lions heard roaring were within a circle of 4-km radius, this figure is high for woodland country with continuous wind, Stevenson-Hamilton (1947). Two, that on each roaring night a single lion group was approximately equal to the mean group size seen over the year. Note that lions present but not roaring and two or more prides present do not affect a minimum estimate.

A minimum estimate of population size was determined as follows:

Mean group size (1967 and 1968)	3.2 (n = 36)
Total census area	1900 km <sup>2</sup>
Roaring circle area (4 km radius)	50.2 km <sup>2</sup>
Total number of nights	23
Nights heard roaring	18

$$\text{Minimum population estimate} = \frac{18 \times 1900 \times 3.2}{23 \times 50.2} = 97$$



In 1970, 1971 and 1972 it was possible to identify several groups and single lions which were frequently sighted on the basis of group composition, area, and individual characteristics, e.g. mane, colour and scars. In 1970, sixty-nine animals; 1971, eighty-one animals; and in 1972, seventy-seven animals were so identified. The home ranges of these groups, based on rather scanty evidence, appear to cover less than half the research area. Slightly over half of the lion sightings were assigned to these known groups each year. Total population size would therefore be about 150.

In June, 1970, it was decided to selectively shoot a number of maneless male lions in a small portion of the research area and from the resulting change in sex ratios determine the total population size using the methods outlined by Hanson (1963), Rupp (1966) and Paulick & Robson (1969). Adult sex ratio data were determined within the shooting area for the 6-month period prior to and after the removal exercise. An estimate of variance for these ratios was determined from a technique described by Cochran (1963).

Given the high variance for sex ratio data and possible total lion population of fifty in the reduction area of 650 km<sup>2</sup>, then eight adult male lions removed would have been an adequate sample (Paulick & Robson, 1969). Unfortunately, only five males were shot in the 10-day reduction period.

Sex ratio data with standard error was:

January-June 1970	55.1 ± 20.6% males (n = 23)
June-November 1970	51.9 ± 15.3% males (n = 21).

Population size was calculated by the formula

$$N = \frac{M - p_2 M}{p_2 - p_1}$$

where N is the total population of both categories, M the effective change of one category (negative for removals) and  $p_1$  and  $p_2$  the initial and changed ratios.  $N = 83$  adults for the reduction area. Paulick & Robson (1969) give a formula for the variance of this estimate, but its use is invalidated by the low sample. As such, use of this estimate alone is scarcely valid.

However, using estimates from all three census techniques a working figure of 150 lions is assumed.

(2) GROUP COMPOSITION. Data on average group size, sex ratio and number of cubs for 1967 to 1972 are given in Table 1.

Groups specifically followed up, groups seen twice on one day and groups only partially differentiated have not been included in the analysis. Cubs as used here include those not fully grown as regards body size, not weight, i.e. up to about 30 months old.

TABLE 1. Lion group composition and size from the Eastern Selous Game Reserve from July, 1967 to December, 1972

Year	Group sightings	Total animals seen	Mean group size	Adult sex ratio % male	Immatures (% of total)
1967	16	53	3.3	41.7	23
1968	20	62	3.1	49.1	23
1969	47	150	3.2	43.5	29
1970	73	317	4.3	50.2	21
1971	86	271	3.2	43.9	15
1972	56	174	3.1	45.7	16
Overall Total	298	1027	3.4	46.2	21

TABLE 2. Frequency of group size observations, 1967-1972

Group size	No. of observations	% frequency
1	70	23.5
2	83	27.9
3	50	16.8
4	41	13.8
5	13	4.4
6	11	3.7
7	7	2.3
8	6	2.0
9	3	1.0
10 +		4.6

TABLE 3. Numbers of females with cubs of different litter size and without cubs

Litter size	No. of observations	% total
0	286	87.8
1	12	3.4
2	31	8.7
3	22	6.3
4	3	0.9

TABLE 4. Lion prey species recorded from actual kills with estimate of prey population size (Rodgers, 1969, 1970) and prey preference ratings (Pienaar, 1969)

Species	No. of kills	% of total kills	Population size	% total population	Preference rating
Wildebeest, <u>Connochaetes taurinus</u> <u>johnstoni</u> Schäfer	26	33.7	10,000	25.6	1.3
Warthog, <u>Phacochoerus aethiopicus</u> Pallas	19	24.6	3,000	7.7	3.2
Buffalo, <u>Syncerus caffer</u> Sparrman	17	22.0	2,500	6.4	3.4
Zebra, <u>Equus burchelli</u> Gray	5	6.4	3,500	9.0	0.7
Eland, <u>Taurotragus oryx</u> Pallas	4	5.1	1,000	2.6	1.9
Hartebeest, <u>Alcelaphus lichtensteini</u> Peters	3	7.7	4,000	10.3	-
Sable, <u>Hippotragus niger</u> Harris	1		600	1.5	-
Reedbuck, <u>Redunca arundinum</u> Erxleben	1		500	1.4	-
Impala, <u>Aepyceros nélanus</u> Lichtenstein	1		14,000	35.8	-
Total	77	99.3	39,100	100.3	-

Increasing number of sightings per year is due to an increased coverage of the area by more observers. Frequency of group size observations are given in Table 2. Data on the numbers of females seen with and without cubs is shown in Table 3, the high percentage apparently without cubs is partly biased as some females will have young cubs on their own or with another female.

(3) PREY SELECTION. Only sightings of lions actually on a kill are included, to date seventy-seven kills have been recorded. Data are shown in Table 4 with estimates of prey species population size (Rodgers, 1969, 1970).

#### DISCUSSION

Assuming an estimate of 150 for the lion population gives a density of close to 0.08 lion per km<sup>2</sup>, a figure which is low in comparison with published data from intensive studies of small areas, but comparable with density estimates from large areas. Table 5 gives density data from other studies for comparison. Sex ratio data for this area is unusual in the high proportion of adult male lions, a sex ratio of close to unity being scarcely altered after the removal of twenty-four males in the last 6 years. Data on mean group size, sex ratios and the proportion of immatures from other areas are shown in Table 5.

Approximately 21% immatures in this area means an adult female-immature ratio of 1:0.55 very much lower than the potential reproductive rate. Whether this is due to low natality or high mortality is not known.

With an estimate of 150 lions of which approximately fifty are adult males it is biologically feasible to considerably increase the quota from the six allowed at present. A check on the possibility of over-hunting can be made by annual assessment of the adult sex ratio which could drop to 1 : 3 without risk to breeding success.

TABLE 5. Lion densities and population composition from this and other published studies.

Area	Density	Adult sex ratio % males	% immatures	Notes
Ngorongoro Crater	0.2 km <sup>2</sup>	-	-	
Nairobi National Park	0.23-0.24 km <sup>2</sup>	14.3	57-60	Based on known animals in a small area
Manyara National Park	0.38 km <sup>2</sup>	33.3	20-25	
Kafue Park Zambia	0.12 km <sup>2</sup>	37.0	-	
Serengeti National Park	0.07 km <sup>2</sup>	25.6	40-52*	Estimates or minimal counts over a large area
North-East Selous	-	38.5	27	
Kruger National Park	0.05 km <sup>2</sup>	-	-	
East Selous	0.08 km <sup>2</sup>	45.8	21	

\* 1st figure refers to 0-2-year olds; 2nd figure to 0 - 3-year olds.

Four main habitats occur, a tall grass *Brachystegia/Combretum* woodland on deep, red, acidic, sandy soils; a short grass scattered tree/shrub grassland on alkaline hard pan clay sands; a dense thicket on sandy ridges and a tall grass, seasonally flooded swamp grassland. The vegetation is described in detail in Rodgers & Ludanga (1973). Of the four habitat types, the latter two are only very rarely frequented by mammal species considered in this paper.

The area contains a large game population. Numerically dominant species are: wildebeest (10 000); impala (12 000); zebra (4000); hartebeest (3000), which are virtually confined to the tall grass woodlands; and warthog (approximately 5000). Rainy season concentrations on the short grass can produce densities of up to sixty animals per km<sup>2</sup> (Rodgers, unpublished data).

#### Methods

The study area is crossed by over 250 km of permanent transects, used for game census and vegetation analysis. From November 1967 until May 1972 this network was covered several times per month, usually by vehicle, occasionally on foot. Along each transect all animal groups seen were noted, counted and, for small groups, sex and age composition noted.

All species, except for zebra, occurred in discrete groups varying from 1 to a maximum of 150 at all times of year. Zebra family units, in the rains, tended to associate into loose aggregations, and it was frequently impossible to determine accurately the size or extent of any one group.

Group size data from all transects were collected and tabulated for each species for each month, and monthly mean group size and standard error were calculated using an Olivetti Programma 101.

This data and field observations showed that over 95% of wildebeest groups of size ten and under were all male, and that virtually all single impala were males. For this study it is assumed that wildebeest groups of ten or less, and single impala, are in fact male. Similarly, wildebeest groups of over ten were nearly always breeding herds comprising females, immatures and herd males (Stobart, 1970). For this study wildebeest groups of over ten are assumed to be breeding herds.

From the monthly data, large tables were prepared showing for the whole study period, the number of groups in each size class from 1 to 10 singly; from 11 to 100 in fives (i.e. 11-15, 16-20); and from 101 upwards in tens (i.e. 101-110). The number of groups in each size class was then shown as a percentage of the total.

Data extracted from these tables for this paper included the percentage of single males for impala and wildebeest, the percentage of small male groups (size 1-10) for wildebeest, and mean group size for wildebeest breeding herds.

Data were further broken down into dry (August to December) and rainy (January to July) seasons to compare the overall change in percentage frequency of group size for impala and wildebeest.

From July 1970 until May 1972, field observations included information on the number of calves (animals of 0-12 months, wildebeest having a restricted calving season from late November to late December) per wildebeest breeding herd. This information was determined as percentage calves per breeding herd. Monthly rainfall totals from late 1967 through 1972 were available from the Miombo Research Centre within the study area.



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## Seasonal change in group size amongst wild herbivore species

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### Summary

Group size, a parameter increasingly used in mammal census work is discussed in the light of 47 months' data for five gregarious species. It is shown that group size parameters fluctuate seasonally, can be correlated with social and reproductive behaviour and are basically predictable. Species with a closed family unit structure have a constant group size whilst those with an open structure exhibit large seasonal fluctuations.

Group density and group size for two finite animal populations are compared and independent variables are found to be significantly correlated.

### Introduction

The theory underlying large mammal census techniques includes the assumption that the population to be censused is distributed at random through the sample area. In the case of gregarious animals this is clearly not so, and it is the animal groups or clumps which approach a random distribution. Yapp (1956) proposed the use of group size parameters in census studies of bird populations using line transect techniques. Similar techniques are being used in mammal census in woodland habitats in Tanzania (Hemingway (1971) and Rodgers (1969)).

This paper utilizes data on group size for five herbivore species from 1967 to 1972 to investigate the nature of group size parameters and shows that such parameters are not constant but fluctuate seasonally and can be correlated with changes in social and reproductive behaviour.

Data are presented in detail for the Nyassa wildebeest, (*Connochaetes taurinus* Lichtenstein); Southern impala (*Aepyceros melampus melampus*, Lichtenstein) and in detail for zebra (*Equus burchelli*, Gray); hartebeest (*Alcelaphus lichtensteini*, Lichtenstein); and warthog (*Phacocoerus aethiopicus*, Pallas).

### Study area

The study was confined to the 2000 km<sup>2</sup> research area of the Miombo Research Centre (3°E, 8°30'S) in the Eastern Selous Game Reserve. The altitude varies from 120 m to 1000 m a.s.l and receives a mean 760 mm annual precipitation in a single, late September to early May, rainy season.

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Table 1. Monthly mean group size ('S') for wildebeest from November 1967 to May 1972 (with number of observations 'n' and standard error 'S.E.')

Month	1967			1968			1969			1970			1971			1972			Overall monthly means		
	n	S	S.E.	n	S	S.E.	n	S	S.E.	n	S	S.E.	n	S	S.E.	n	S	S.E.			
Jan.	54	15.1	3.0	—	—	—	39	18.7	3.5	174	19.0	2.4	164	12.6	1.8	161	19.6	1.8	17.0		
Feb.	—	—	—	—	—	—	45	20.6	2.9	158	16.9	2.1	322	19.3	1.4	158	24.6	1.9	20.4		
March	—	—	—	—	—	—	53	21.9	4.1	120	10.6	1.9	268	13.8	1.6	153	22.3	2.3	17.2		
April	79	17.8	2.8	—	—	—	—	—	—	239	15.3	1.6	212	10.8	1.5	163	21.5	2.1	16.4		
May	56	14.0	2.4	—	—	—	55	14.5	3.1	202	17.4	1.9	140	13.9	1.7	65	21.9	2.4	16.3		
June	—	—	—	—	—	—	74	16.0	2.5	195	15.2	1.7	211	16.6	1.8	—	—	—	15.9		
July	41	14.9	2.6	—	—	—	116	15.6	2.1	204	16.4	1.6	202	14.4	1.6	—	—	—	15.3		
Aug.	72	12.6	2.1	—	—	—	119	13.4	2.1	107	12.7	1.7	51	14.0	2.2	—	—	—	13.2		
Sept.	74	8.5	3.4	—	—	—	115	10.8	1.4	112	9.3	1.8	141	12.3	1.9	—	—	—	10.2		
Oct.	41	9.0	2.8	—	—	—	81	8.1	1.4	96	6.8	1.5	117	13.4	1.9	—	—	—	9.4		
Nov.	—	—	—	—	—	—	139	10.8	1.7	42	4.2	1.9	95	8.8	2.1	—	—	—	8.7		
Dec.	—	—	—	—	—	—	175	21.2	2.3	240	12.6	1.7	104	17.6	2.0	—	—	—	17.1		
Annual mean	8	12.3	1.2	11	15.6	1.39	12	13.0	1.31	12	14.0	0.83	12	14.0	0.83	12	14.7	1.03	12	14.7	1.03

Data from different group size parameters were examined for correlation by determining correlation coefficients ( $r$ ) and significance values of such coefficients were obtained from standard tables. Where necessary, annual means and percentages were compared by the appropriate tests as given in Bailey (1959). All calculations were performed with an Olivetti Programma.

### Results

Tables 1, 2 and 3 show monthly mean group size with standard error and number of groups examined per month from 1967 to 1972 for wildebeest, impala, zebra, hartebeest and warthog respectively. The final column in each table gives an overall mean for each month over the 5 years of the study. Annual means for 1968 to 1971 are also shown in the table. Fig. 1 compares the overall monthly means of all species and Fig. 2 compares annual monthly means for wildebeest.

Table 4 shows data on percentage frequency of single male groups and small male groups and mean breeding herd size for all months for wildebeest. The final column shows an overall monthly mean for each parameter and separate annual means are also shown. Overall means for these three parameters are compared with mean group size in Fig. 3. Table 5 shows data on percentage single male groups for impala. These are compared with overall mean group size in Fig. 4.

Various parameters of wildebeest and impala group size were tested for correlation. Results are shown in Table 6, with significance levels of the calculated correlation coefficient.

Table 7 compares differences between dry and rainy season group size frequency for wildebeest and impala.

Table 8 shows the mean monthly calf content (%) of wildebeest breeding herds from May 1970 to May 1972. Numbers of herds counted per month are shown in the Table.

Rainfall figures for the study period are shown in Table 9. Monthly rainfall data and wildebeest and impala group size data were examined for any possible correlation from year to year. Following Jarman & Jarman (1974) a correlation was found with mean monthly group size and the sum of the preceding 2 months' rainfall. (Impala,  $r = 0.88$ ,  $n = 12$ , Sig. 0.1% level; wildebeest,  $r = 0.767$ ,  $n = 12$ , Sig. 0.1% level.)

Examination of Fig. 2 shows that whilst rainy season monthly values of wildebeest differ from year to year, the shapes of the curves are very similar. Adjustment of the curves for the 3 full years data 1969 to 1971 showed that if 1971 data are taken as a base line, and the 1969 data retarded by 1 month and the 1970 data advanced by 1 month, then the 3 years' curves show very close agreement. Similarly, 1972 stays the same and 1968 is retarded. This is shown in the insert of Fig. 2.

### Discussion

#### (1) Group size data and social behaviour

The results of field observations as detailed above would appear to agree with published accounts of the animal species' behaviour. There is an obvious difference between species with an open membership social structure, which show a marked seasonal change in group size pattern, i.e. wildebeest and impala, and those with a more simple constant family unit or fixed membership social structure, which maintain a similar group size pattern throughout the year. Zebra data are obscured in the rains by inaccurate herd discrimination.

Table 3. Monthly mean group size for Lichenstein's hartebeest, zebra and warthog from November 1967 to May 1972

Month	1967			1968			1969			1970			1971			1972			Monthly means		
	LH	Z	Wh	LH	Z	Wh	LH	Z	Wh	LH	Z	Wh	LH	Z	Wh	LH	Z	Wh	LH	Z	Wh
Jan.	4.6	14.5	3.2	5.1	15.4	—	6.0	7.2	2.9	5.8	7.9	3.2	5.4	12.5	3.6	5.4	11.5	3.2	5.4	11.5	3.2
Feb.	—	—	—	5.5	10.3	3.8	5.8	11.1	3.2	5.7	12.4	3.0	6.9	13.1	3.4	5.9	11.8	3.3	6.9	13.1	3.4
March	—	—	—	5.4	17.2	3.2	6.3	17.0	3.0	4.9	9.3	3.6	6.8	7.6	3.5	5.6	12.8	3.3	6.8	7.6	3.5
April	4.3	11.1	3.3	—	14.5	—	5.8	18.9	3.0	5.4	12.3	3.6	6.6	13.8	3.8	5.5	14.1	3.5	6.6	13.8	3.8
May	4.4	6.8	3.1	—	6.5	3.7	4.9	13.3	2.7	4.7	7.6	2.9	5.3	9.6	3.7	4.9	8.8	3.2	5.3	9.6	3.7
June	—	—	—	5.2	—	3.6	5.8	8.3	3.2	5.5	7.6	2.9	5.3	8.0	3.2	5.3	8.0	3.2	5.3	8.0	3.2
July	—	9.6	2.9	5.4	6.5	3.4	5.7	7.0	3.4	5.4	12.5	3.9	4.8	8.5	3.1	4.8	8.5	3.1	4.8	8.5	3.1
Aug.	4.2	10.5	3.2	4.8	8.5	2.9	5.2	8.5	3.4	4.9	6.7	2.8	4.8	8.5	3.1	4.8	8.5	3.1	4.8	8.5	3.1
Sept.	5.2	6.8	3.7	5.2	7.3	3.0	4.7	9.0	3.8	4.1	5.9	3.5	4.8	7.8	3.5	4.8	7.8	3.5	4.8	7.8	3.5
Oct.	5.6	6.1	3.6	5.3	9.3	3.5	4.4	8.0	3.5	5.9	7.6	3.5	5.3	7.8	3.6	5.3	7.8	3.6	5.3	7.8	3.6
Nov.	5.3	10.4	3.2	5.4	7.6	4.1	4.5	8.2	4.5	4.4	9.1	4.4	5.3	8.9	4.2	5.3	8.9	4.2	5.3	8.9	4.2
Dec.	—	—	—	6.2	12.5	3.4	—	10.1	3.4	4.9	7.9	4.4	5.4	10.2	3.7	5.4	10.2	3.7	5.4	10.2	3.7
Annual mean	5.0	9.3	3.3	5.4	10.5	3.4	5.4	10.6	3.3	5.2	8.9	3.5	5.4	10.6	3.3	5.2	8.9	3.5	5.4	10.6	3.3

Table 2. Monthly mean group size ('S') for impala from November 1967 to May 1972 (with number of observations 'n' and standard error 'S.E').

Month	1967		1968		1969		1970		1971		1972		Monthly mean for means groups of 2 or over				
	n	S	n	S	n	S	n	S	n	S	n	S					
Jan.	42	12.3	2.2	—	—	—	220	9.0	1.1	324	8.8	0.8	244	9.6	1.2	9.9	12.4
Feb.	—	—	—	58	16.7	3.2	260	9.9	1.0	532	10.8	0.7	316	12.8	0.9	12.5	17.2
March	—	—	—	49	17.1	3.1	170	10.1	1.3	364	9.9	0.5	264	10.8	1.0	12.0	16.1
April	49	12.8	2.0	—	—	—	186	12.2	1.4	208	11.3	0.9	145	15.7	1.3	13.1	16.7
May	47	11.9	1.6	60	16.6	2.0	163	15.3	1.5	219	12.4	1.1	116	13.7	1.6	14.0	16.1
June	—	—	—	77	15.0	1.9	279	11.6	0.8	315	16.8	0.7	—	—	—	14.5	15.8
July	51	11.7	1.6	127	15.9	1.2	336	11.2	0.6	333	11.2	0.5	—	—	—	12.5	13.1
Aug.	73	11.1	1.1	185	11.6	0.8	210	11.0	0.8	650	8.4	0.6	—	—	—	10.5	11.1
Sept.	122	6.8	0.5	264	7.6	0.4	250	7.2	0.8	269	5.1	0.7	—	—	—	6.7	7.5
Oct.	54	7.2	1.2	218	5.6	0.4	296	7.6	0.7	167	6.7	1.2	—	—	—	6.8	7.9
Nov.	128	12.6	1.6	102	10.7	1.3	304	8.9	1.1	420	5.2	0.9	—	—	—	9.2	11.0
Dec.	—	—	—	164	11.3	1.4	429	10.2	0.6	210	7.9	1.0	—	—	—	9.8	11.8
Annual mean	8	10.6	2.3	10	12.8	1.5	12	10.3	2.2	12	9.5	1.0	—	—	—	—	—





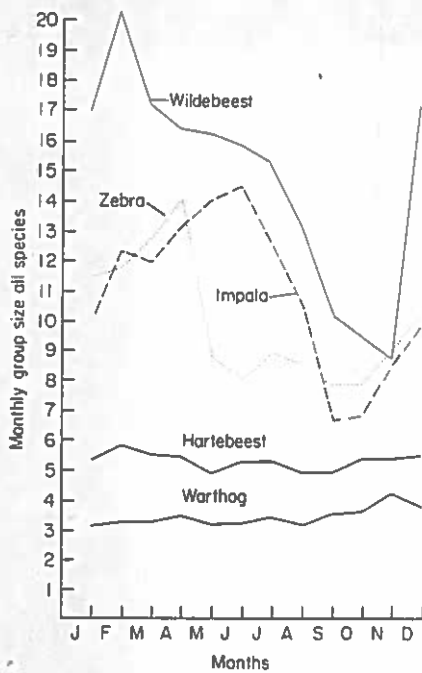


Fig. 1

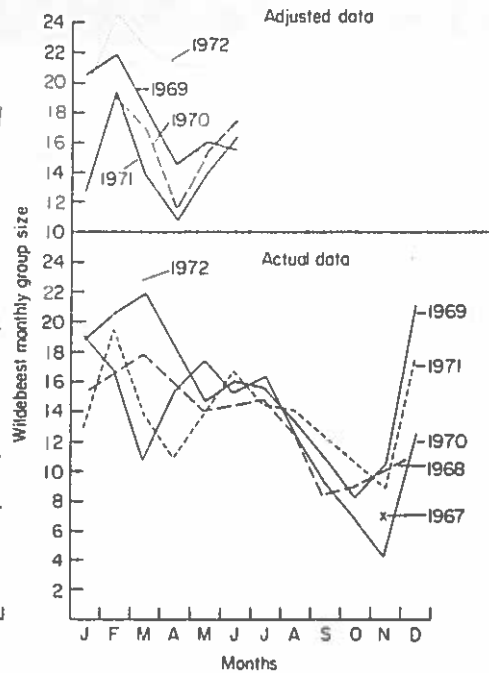


Fig. 2

Fig. 1. Seasonal change in monthly mean group size for wildebeest, zebra and impala, open group social structure; and hartebeest and warthog, closed group social structure.

Fig. 2. Monthly change in wildebeest mean group size for five years. Insert shows adjusted data where monthly means are advanced or retarded by 1 month.

Warthog are normally found in small family groups with additional males making up bachelor groups of 1-5 animals, Child, Roth & Kerr (1968). This social grouping is constant throughout the year. From this study, results for warthog show a mean group size of 3.4 for all months and a maximum monthly range of  $\pm 1.0$  from this mean. Data for all 5 years are similar, and all years show a slight increase in group size during the farrowing period starting in September, through to November.

Lichtenstein's hartebeest show a similar family group social structure, consisting of a herd male, females and immatures, Dowsett (1966), Wilson (1966) and Mitchell (n.d.). Small bachelor groups are frequent, but single males only rarely seen. The field observations shown here support these conclusions, mean group size showing little variation during or between years.

Zebra data collection posed problems during the rains and for this period the results are virtually meaningless. During the dry season, however, results from all years are very similar, zebra occurring in small family units, nearly all of them in the woodland habitats. Family units begin to aggregate again at the start of the rains.

The impala under a single rainy season regime calve once a year, normally in September-October. Unlike the Nairobi National Park situation as described by Schenkel (1966), in this area the rigid social structure of herd male with a large harem and separate bachelor male groups, breaks down after the rut. From mid-April onwards, male and female groups intermingle; single males are no more a feature of the population (see Fig. 4). During the calving period the female breeding herds break

Table 6. Correlation coefficients (*r*) of wildebeest and impala group size parameters

Parameter	Correlation coefficient ' <i>r</i> '	Significance level
Wildebeest group size and Wildebeest breeding herd size	0.757	<1%
Wildebeest group size and Wildebeest single male %	0.246	N.S.
Wildebeest group size and Wildebeest male group %	-0.773	<1%
Wildebeest group size and Impala group size: (All data)	0.720	<1%
Wildebeest group size and Impala group size (1969 only)	0.923	<0.1%
Wildebeest breeding herd size and herd calf content %		
1970-71-72 only (a) all data	0.863	<0.1%
(b) monthly means	0.598	≤1%
Impala single male % and Impala group size	0.03	N.S.

Table 7. Dry and rainy season group size frequency for wildebeest and impala, showing '*d*' the level of difference and the significance level

Group size	Wildebeest				Impala			
	Dry	Rains	' <i>d</i> '	Sig. level	Dry	Rains	' <i>d</i> '	Sig. level
1	40.3	47.8	5.702	<0.1%	17.4	23.2	8.472	<0.1%
2-9	27.9	20.3	7.068	<0.1%	57.7	42.5	18.957	≤0.1%
1-10 (combined)	68.2	68.1	0.081	N.S.				
10-39	19.8	16.5	3.376	<0.1%	21.4	27.1	7.907	<0.1%
40-69	8.5	11.6	3.676	<0.1%	} 2.9	6.9	5.323	<0.1%
70+	3.2	4.7	2.691	<1%				
No. of groups	1442	3338			3801	4440		

down into small groups. Following calving, the breeding herds slowly reform single males and male territoriality and antagonistic behaviour become more common.

Wildebeest in the Selous occur in discrete groups which are normally well separated from neighbouring groups. No seasonal aggregations or uniform spacing of individuals and small groups occurs, which contrasts with the Northern Territory wildebeest as described by Estes (1966). Males are territorial for a large part of the year, although the number of single males does increase slightly during the April rut (see Fig. 4). There appears to be no parallel to the situation in impala where the breeding herd breaks up into very small units during the calving period, although group size is smaller at this time.



Table 5. Monthly percentage of single males for impala from November 1967 to May 1972

Month	1967	1968	1969	1970	1971	1972	Monthly means
Jan.		28.5	—	31.8	26.4	26.4	21.7
Feb.		—	18.9	31.8	34.3	29.3	28.6
March		19.4	22.4	31.9	34.9	27.4	27.2
April			—	25.9	28.8	15.2	23.3
May		12.0	13.3	19.6	21.9	4.8	14.3
June		—	11.7	1.1	14.0		8.9
July		2.1	5.5	4.8	7.8		5.1
Aug.		4.2	6.5	1.9	9.7		5.6
Sept.		8.2	14.4	11.7	15.6		12.4
Oct.		10.0	15.1	19.2	20.9		16.3
Nov.	16.4	20.0	23.4	12.0	19.3		18.2
Dec.	—	—	25.0	15.7	15.9		18.9
Annual means		13.4	15.6	17.2	19.1		

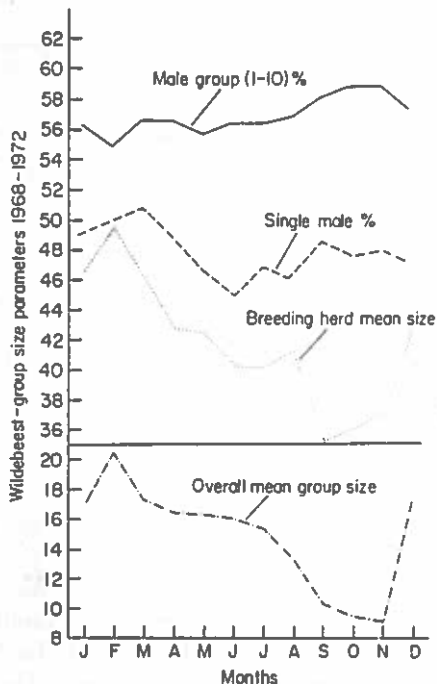


Fig. 3

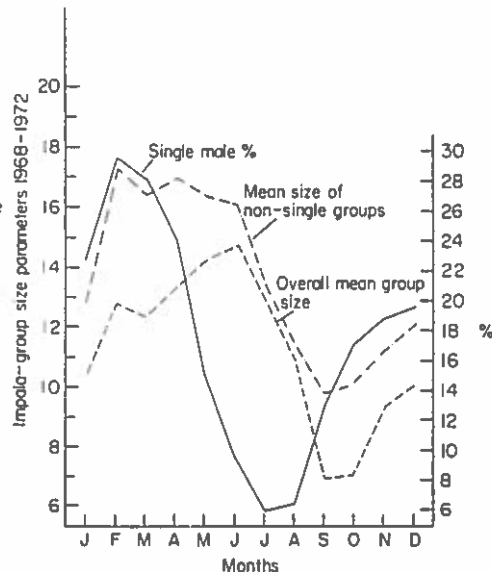


Fig. 4

Fig. 3. Wildebeest group size parameters over five years. —, Male group (1-10)%; ---, single male %; . . . ., breeding herd; - · - ·, overall mean group size.

Fig. 4. Impala group size parameters over 5 years. —, Single male %; ---, mean size of non-single groups; - · - ·, overall mean group size.

Table 9. Rainfall data. Miombo Research Centre, Kingupira (Rainfall in millimetres)

Month	1967		1968		1969		1970		1971		1972		1973	
	Total	Days Rain	Total	Days Rain	Total	Days Rain	Total	Days Rain	Total	Days Rain	Total	Days Rain	Total	Days Rain
Jan.			88	10	171	3	125	18	157	11	73	10	279	17
Feb.			48	6	105	6	313	17	19	4	95	14	115	9
March			196	?	120	12	89	10	109	15	168	16	206	13
April			203	?	61	11	98	9	137	23	127	20	94	18
May			4	3	70	5	6	4	6	4	51	15	38	4
June			0	0	0	0	1	1	2	1	0	0	1	1
July			0	0	0	0	8	3	7	4	0	0	0	0
Aug.			0	0	1	1	0	0	0	0	0	0	0	0
Sept.			3	1	2	3	47	8	1	2	4	1	1	1
Oct.			4	2	27	4	5	2	19	6	65	10	7	3
Nov.			121	15	131	15	13	2	7	4	72	10	32	10
Dec.	206	16	104	9	26	5	156	14	125	16	105	16	69	13
Totals			765		714	65	861	88	589	90	759	112	842	89
Total in inches			30.45		28.58		34.43		23.56		30.36		33.69	

Table 8. Wildebeest breeding herd calf content as a percentage

Month	1970		1971		1972		Mean
	%	Sample size	%	Sample size	%	Sample size	
Jan.			32.8	24	35.8	84	34.1
Feb.			31.7	21	32.8	53	32.2
March			31.3	36	32.9	44	32.1
April			30.8	40	32.3	39	31.5
May	29.8	57	29.5	38	29.6	51	29.6
June	—	—	29.0	29			29.0
July	28.9	42	31.1	24			30.0
Aug.	28.7	38	25.7	41			27.2
Sept.	—	—					
Oct.	22.7	47	21.2	32			21.9
Nov.	24.1	29	25.3	62			24.7
Dec.	26.4	50	28.0	47			27.2

Monthly standard deviations average 24% of the means, and the range of observations of January–March individual herds varies from 19.2% to 43.9% calf content.

### (2) Male groups

Male groups (size 1–10) formed about two thirds of the total wildebeest groups observed during this study, although in numerical terms they form less than 10% of the total population. These male groups form a remarkably constant feature of the population, fluctuating only slightly from month to month and year to year (monthly range of 62.2 to 72.0% and an annual range of 65.3 to 71.2%). This fraction does contain the more variable element of single territorial males. The single males vary from 36.9 to 51.7% of the groups observed from month to month, peaking during the months of the rut (March, April). Annual variation in proportion of single male groups is slight, from 42.3 to 49.7%.

Despite their being the largest proportion of the groups observed, the single males show no significant correlation with total group size, though the very number of observations of single males is so high that any variation in monthly or annual percentage single males must be reflected in overall group size figures. The all-male groups percentages, however, do show a significant inverse correlation with total group size (Table 6) due largely to an increase in male groups during the months of September and October.

Impala single males show a striking seasonal change. Averaging up to 30% of all groups observed during the rut, single male groups then drop to a low point of 5% before calving, and then slowly rise again. Percentage of single males in all groups observed shows no significant correlation with mean group size. It is of interest that Schenkel (1966) makes no mention of single males whilst Dasman and Mossman in Central Africa (1962) state that single males form 43% of all groups observed during the rut (compared with 28% here) and less than 10% of all groups just after calving (12% from this study). Leuthold (1970), however, shows between 19 and 27% single males for the Nairobi National Park during a December to August study.

Data from this study show single hartebeest (unsexed) formed less than 5% of all observations. Stobart (1970) observed single yearling males on a number of occasions in this area. Dowsett (1966) and Mitchell (n.d.) remark on immature males being expelled from breeding herds at about 10–12 months of age. Mitchell quotes 5.9 as

Table 10. Comparison of group size and group density for wildebeest and impala for rainy season and short grass habitat only

Month	Transact					Wildebeest					Impala					
	miles	No. of animals	No. of herds	Mean group size 'x'	Groups per mile 'y'	Animals per mile	Groups per mile 'y'	Mean group size 'x'	No. of animals	No. of herds	Animals per mile	Groups per mile 'y'	Mean group size 'x'	No. of animals	No. of herds	Animals per mile
Nov. 1967	132								2066	119			17.4			15.7
Jan. 1968	42	622	29	21.4	0.97	14.8	0.97	21.4	483	34	14.8	17.4	0.90			15.7
April/May 1968	78	1092	87	12.5	1.21	14.0	1.21	12.5	1004	46	14.0	14.2	1.06			11.5
Jan./Feb. 1969	83	1193	68	17.5	0.92	16.1	0.92	17.5	1397	85	16.1	21.7	0.60			12.9
March 1969	89	1196	54	22.1	0.68	15.0	0.68	22.1	1174	74	15.0	16.6	1.02			17.0
May 1969	80	954	56	17.0	0.89	13.8	0.89	17.0	1172	73	13.8	15.8	0.84			13.2
Dec. 1969	183	3177	136	23.4	0.73	17.4	0.73	23.4			17.4	16.0	0.91			14.7
Jan. 1970	155	3325	172	19.3	1.11	21.4	1.11	19.3	2104	212	21.4	10.0	1.43			13.6
Feb. 1970	129	2181	134	16.2	1.03	16.9	1.03	16.2	1947	206	16.9	9.4	1.6			15.1
March 1970	112															
April 1970	170	3917	242	16.2	1.32	23.0	1.32	16.2			23.0					
May 1970	140	3661	205	17.8	1.4	26.1	1.4	17.8	1418	163	26.1	8.7	1.46			12.7
Jan. 1971	130	2048	169	12.1	1.68	15.8	1.68	12.1	2416	200	15.8	12.2	1.17			14.3
Feb. 1971	253	5911	318	18.6	1.20	23.3	1.20	18.6	2579	173	23.3	14.9	1.21			18.4
March 1971	181	3291	203	16.2	1.12	18.2	1.12	16.2			18.2					
April 1971	91	2077	177	11.7	1.94	22.8	1.94	11.7			22.8					
May 1971	129	2105	158	13.3	1.22	16.3	1.22	13.3			16.3					

Coefficients of regression and correlation ( $y = a + bx$ )

Wildebeest Mean group size/group density  $a = 2.33$ ,  $b = -0.07$   
 $r = -0.845$  13 d. of f. significant at 0.10% level  
 Impala Mean group size/group density  $a = 1.96$ ,  $b = -0.06$   
 $r = -0.872$  9 d. of f. significant at 0.10% level.

mean group size for breeding herds and 3.8 for bachelor herds; Dowsett quotes 8.2 overall; this study shows a mean figure of 5.4. Wilson (1966) quotes a 2.9 group size and up to 35% singleton groups from an intensively hunted area, but Dowsett believes this to be atypical.

From the data it is concluded that male groups, whilst undergoing regular seasonal changes, associated with the annual rut, arithmetically play a relatively insignificant role in influencing monthly overall group size.

### (3) *The female groups*

The breeding herds in wildebeest and impala account for over 90% of all individuals in the population. Data for both species show similar characteristics, a rise in herd size during the rut and then a gradual decrease during the dry season, rising again in December at the start of the rains.

The peak in herd size during the rut is most probably due to the activities of the territorial males in the case of impala; and for wildebeest partly due to male herding activity, but also to the increase in herd size due to the addition of calves in December. Wildebeest herd size rises from thirty-six to forty-six from November to December, a time when herds contain some 30% of new calves. Wildebeest breeding herd size and calf content are significantly correlated variables (Table 6). Calf increments to the impala population occur in September to October, when herd sizes are lowest.

Wildebeest breeding herd size falls steeply from the peak values during the rut, to a steady level from May to August, and then another steep decline in August to September. The second decline is mirrored by a sharp rise in male groups, leading to the assumption that yearling males are expelled from the breeding herds at this time, 2 months or so before calving occurs. Table 7 shows the seasonal changes in group size composition. It is seen that with the exception of all-male groups in wildebeest, all other size classes show significant changes, herd size generally decreasing during the dry season. These changes are even more noticeable when the adjacent months of March, April, May and again August and September are compared.

Wildebeest mean group size and breeding herd size are significantly correlated variables, and it is concluded that it is the breeding herd size that largely influences the parameter of mean monthly group size.

### (4) *Group density*

This study deals with finite populations of animals. Individuals are virtually restricted to the immediate study area for at least 7 months of the year. As such the two parameters of herd size and herd density are totally dependent variables for a numerically stationary population. As a check on the concepts of group size expressed in this study, an index of group density is compared with data on group size for wildebeest and impala during the months of December to June from the short grassland habitats. The index of group density is simply the number of groups observed each month divided by the transect distance covered each month. Restriction of data to time and area allows homogeneous data to be used, which are not affected by differential visibility caused by fire and habitat differences etc. Mean group size and the index of group density for wildebeest and impala are shown in Table 10, with their correlation and regression coefficients.

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### (5) Annual change

Annual changes in all parameters are slight, and in no case did successive years' annual means vary significantly. Wildebeest group size varies from 12.3 to 15.6; impala from 9.5 to 12.8; hartebeest 5.0 to 5.4; warthog from 3.3 to 3.5; and zebra from 8.9 to 10.6. Single males percentage in wildebeest varied from 42.3 to 49.7 and for impala from 13.4 to 19.1. All-male group percentages for wildebeest varied from 65.3 to 71.2 and mean breeding herd size from 39.7 to 42.6.

Such non-significant and non-directional annual changes are a further indication that group size is a meaningful and seasonally predictable parameter. Leuthold & Leuthold (1975), in a study of ungulate group size in Tsavo National Park, Kenya, believe that such size parameters may be useful in providing a preliminary assessment of a species' social organization. Further they state that group size varies in relation to different external conditions, e.g. vegetation and that base line data on group size parameters may assist evaluation of future ecological developments.

### Conclusions

This paper has shown that the concept of group size is meaningful and, within certain limits, predictable. Animal species with a closed family unit social structure exhibit small fluctuations in group size, whilst those with open structures exhibit large seasonal changes which can be correlated with the animals' reproductive behaviour. The data reinforce accepted ideas of social behaviour in impala and hartebeest in the woodland habitat, and in no case do the data conflict with such theories. The data have possible value in acting as a base line to compare possible future ecological changes.

### Acknowledgments

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## Notes and Records

### Seasonal diet preferences of impala from South East Tanzania

Several authors have recently published data on seasonal changes in diet preferences of impala (*Aepyceros melampus* Lichtenstein), e.g. Stewart (1971), Azavedo & Agnew (1968), Lamprey (1963) and Talbot (1962). These published data show wide differences in diet browse content from different areas of Africa.

This note summarizes data collected from field observations and post mortem examination over a 7-year period in the eastern Selous Game Reserve, South East Tanzania (38° 30'E, 8° 30'S). Rodgers (1973) describes the study area. Two main habitats occur, scattered-tree short grassland on alkaline soils (favoured by impala) and the more typical tall grass *Brachystegia* species 'miombo' woodland. Rainfall averages 760 mm p.a. in a 6-month, November to April, period which is followed by a 6-month drought. The largely annual grass cover of the preferred habitat coupled with widespread early burning means little dry season grazing is available for an impala population averaging 25 animals per km<sup>2</sup> throughout the 420 km<sup>2</sup> area (density determined by foot and vehicle transect counts from 1968 to 1974).

Impala browse species were determined from field observation and, where possible, by identifying macroscopic fragments from rumen contents. Results, with a subjective estimate of frequency of selection are given in Table 1. Frequency estimates are based on amount of the plant species in the rumen and the number of rumens containing that plant species. Monocotyledon (grass and sedge) species preferences were not examined.

Rumen contents from twenty-nine shot mature animals were examined in greater detail for dicotyledon (browse) content. The technique used is a simplified version of that of Stewart (1971). Rumen contents were removed, mixed thoroughly and five handfuls from different parts of the contents were placed in a polythene bag, saturated with 4% formalin and stored.

On examination the content samples were again mixed and divided into five parts. A Petri dish was marked with a grid of lines 1 cm apart to facilitate counting. A portion small enough to prevent overlapping of particles was placed in water in the dish and, using a low power microscope, thirty-three particles over 2 mm in size were examined per dish. Particles were assigned to either dicotyledon or monocotyledon classes (or occasionally to an 'unknown' class). Five dishes per subsample or twenty-five per animal were so examined. Results for all twenty-nine animals for percentage dicotyledon and month of collection are shown in a simple bargraph in Fig. 1. Mean monthly rainfall totals are also shown in the Fig. As percentages were assessed for twenty-five sub-samples for each animal examined, standard errors of the estimated dicotyledon percentage count were determined, these ranged from 3 to 24% of the mean estimate. Errors were considerably lower for animals with higher dicotyledon contents.



Table 1. Impala browse species as determined by field observations and rumen contents examination

Plant Species	Family	Part Eaten	Notes (see below)
<i>Acacia nilotica</i> (L.) Del.	Leguminosae	Leaf (Fruit)*	o
<i>Acacia robusta</i> Burch.	Leguminosae	Leaf (Fruit)	o
<i>Acacia senegal</i> (L.) Wild.	Leguminosae	Leaf & Fruit	c
<i>Acacia zanzibarica</i> (S. Moore) Taub	Leguminosae	Leaf (Fruit)	o
<i>Azelia quanzensis</i> Welw.	Leguminosae	Flower	f Aug. to Oct.
<i>Albizia anthelmintica</i> (A. Rich.) Brogn.	Leguminosae	Leaf (Fruit)	o
<i>Barleria</i> sp.	Acanthaceae	Leaf & Stem	o
<i>Boscia corymbosa</i> Gilg.	Capparaceae	Leaf	o
<i>Combretum</i> spp.	Combretaceae	Leaf*	o
<i>Corchorus olitorius</i> L.	Tiliaceae	Leaf	o
<i>Diplorhynchus condylocarpon</i> (Muell-arg.) Pichon	Apocynaceae	Leaf	o
<i>Dobera loranthifolia</i> (Warb.) Harms	Salvadoraceae	Leaf & Fruit	c
<i>Harisonia abyssinica</i> Oliv.	Simaroubaceae	Leaf	o
<i>Hugonia busseana</i> Engl.	Linaceae	Leaf & Fruit	o
<i>Jasminum fluminense</i> Vell.	Oleaceae	Leaf	f all dry season
<i>Kigelia aethiopum</i> (Fenzl) Dandy	Bignoniaceae	Flower*	o
<i>Salvadora persica</i> L.	Salvadoraceae	Leaf	f all dry season
<i>Spirostachys africana</i> Sond.	Euphorbiaceae	Leaf	f all dry season
<i>Suregada zanzibarensis</i> (Baill.) Meull arg	Euphorbiaceae	Leaf*	c
<i>Tamarindus indica</i> L.	Leguminosae	Leaf & Fruit*	o
<i>Turraea nilotica</i> Kotschy and Peyr	Meliaceae	Leaf & Fruit	f all dry season

o=occasional observations; c=common; f=frequent; both in numbers of animals with the species in the rumen contents and the quantity in the rumen.

Those species marked with an asterisk are recorded from field observation only.

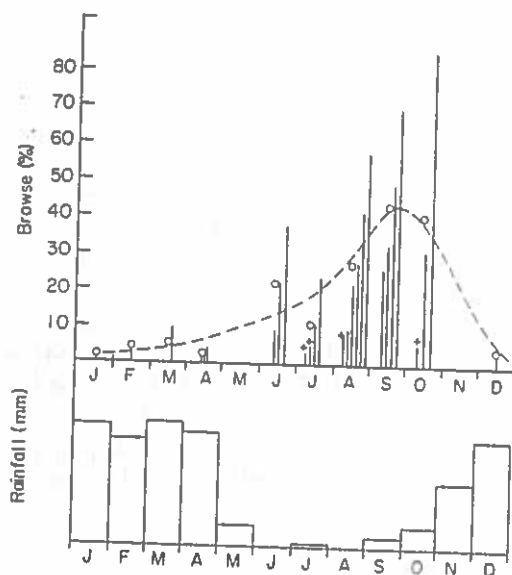


Fig. 1. Seasonal variation in browse content from impala rumen contents. o, monthly mean; +, animals from fire-induced fresh graze.

*Discussion*

The results in Fig. 1 clearly show an increasing use of browse as the dry season progresses (July to December). High peaks in September and October are due almost entirely to large amounts of *Azelia* flowers in the rumen. Low figures for the dry season are all from animals shot within the 'miombo' habitat where dry season burning produces a nutritious green grass flush. At such times use of browse is severely reduced. It seems clear that the locality of the animal in relation to immediate burning regime and plant species availability will affect the proportion of browse in the diet.

As surface water is not limiting in the research area, diet selection is almost certainly for higher nutritional content (protein) than the coarse grass growth can provide. Rees (1973) states the high level of protein in dry season browse and shows how cattle, predominantly grazing species, readily turn to browse when the availability of adequate grazing is low. Previous work, Anon. (1960), Lamprey (1963), Talbot (1962) and Azavedo & Agnew (1968) would indicate an increasing dependence on browse as dry seasons become more prolonged through southern Tanzania to Central and South Africa.

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APPENDIX NINETECHNIQUES FOR SAMPLE STRIP WIDTH ESTIMATION IN WILDLIFE CENSUS

Chapter five of this thesis made mention of the literature dealing with the problem of strip width estimation in wildlife census. I used for this thesis a stripwidth estimator of:

$$SW = 4\bar{y} \text{ where } \bar{y} \text{ is mean perpendicular sight}$$

distance. This appendix discusses the rationale for this choice.

## 5.413. Strip width estimation.

## (a) Early estimators.

The original King census method (Leopold, 1933), proposed a strip width estimator of:

$$S.W. = 2\bar{r}$$

where  $\bar{r}$  is the mean of all angular sighting distances (the distance from the animal to the observer at the point of first sighting, see figure 5.1).

Hayne (1949) suggested the use of the harmonic mean ( $\bar{H}$ ) of angular sighting distance was less biased and proposed:

$$SW = 2\bar{H}$$

Note that the figure 2 is to cover both sides of the transect line.

Webb (1942) appears to be the first to use a perpendicular sighting distance ( $y$ ) model (whilst censusing N. American hares) and he proposed a strip width model of:-

$$SW = 2\bar{r} \sin \bar{\alpha}$$

where  $\bar{\alpha}$  is the mean sighting angle (see figure 5.1). Hayne showed theoretically that  $\bar{\alpha}$  should equal  $32.704^\circ$ , Gates (1969) by computer simulation said  $\bar{\alpha}$  should be  $32.69^\circ$  and Robinette et al (1974) by field trials showed  $\bar{\alpha}$  for small and medium sized animals to be  $33.5^\circ$ . Webb's expression becomes  $SW = 2\bar{y}$  by trigonometry.

Dasmann and Hossman (1962) used this estimator whilst counting ungulates of known number in a one square mile reserve in Rhodesia, the first African ground sample census I know of.

Gates et al (1968) Model 1 also proposes the use of  $SW = 2\bar{y}$  although his density estimator is  $D = \frac{n - 1}{2y \times L}$  instead of the more usual  $D = \frac{n}{2y \times L}$

Gates (1969) proposed two further estimates based on angular sighting distances where:

Gates II  $SW = 2\bar{r}$  and a density estimator of

$$D = \frac{2n - 1}{2L \bar{r}}$$

Gates III  $SW = 2\bar{G}$  and a density estimator  $D = \frac{n}{2L\bar{G}}$

where  $\bar{G}$  is the geometric mean of angular sighting distances.

Assuming the mean sighting angle ' $\bar{\alpha}$ ' does approximate  $32.704^\circ$  then there appears to be a dichotomy of estimation methods as

$$\bar{G} = 1.85\bar{y} \quad (\text{when } \bar{\alpha} = 32.704).$$

Expressing all estimators in terms of  $\bar{y}$  we have 2 distinct types of estimator, viz:-

Those using single $\bar{y}$	Those using almost double $\bar{y}$
Webb, $SW = 2y$	Ming $SW = 2 \times 1.85y$
Dasmann & Hossman, $SW = 2y$	Hayne $SW = 2 \times 1.85 (\bar{y}_{II})$
Gates I, $SW = 2y$	Gates II $SW = 2 \times 1.85\bar{y}$
	Gates III $SW = 2 \times 1.85(\bar{y}_{II})$
	and
	Rodgers (this study)
	$SW = 2 \times 2\bar{y}$

Robinette et al. (1956, 1974) and Gates (1969) have investigated the efficiency of these estimators by field trials with objects of known density and by computer simulation. Definite patterns emerge from such investigations, which are a

function of the distribution of sighting distance frequencies. Such frequency distributions are related to characteristics of the animals behaviour and vegetation cover. Figure 5.3a, and 5.3b show two such possible distributions; 5.3a, shows a negative exponential model and 5.3a\* positive half normal model. The negative exponential model fits field data when small animals are flushed from dense cover; the animal flushing and hence its sightability depending on close observer proximity. The positive half normal model would appear to be the case where larger animals are sighted in areas of some restriction to visibility, e.g. African ungulates in woodland habitats. In this case all animals are likely to be seen for some distance from the transect with a subsequent fall off as vegetation obscures visibility, and a final tail will result as a few animals will be seen at greater distances through gaps in the vegetation. This model could be called a plateau - slope - tail model, (Rodgers, 1971).

Robinette and Gates have shown different efficiencies for several estimators for these two models. These efficiencies can be stated as positive or negative bias (over or under-estimation). Their results may be stated as follows, (as density bias not  $S^2$  bias, note difference for Gates II model where density involves the use of  $(2n-1)$ ).

<u>Half normal model</u>	King estimator	Slight -ve bias	1.8%
(Robinette)	Hayne	+ve "	41%
	Webb	+ve "	35%
	Gates I	+ve "	48%
	Gates II	+ve "	90%
	Gates III	Slight +ve "	12%
(Gates)	King	Slight -ve bias	9.7%
	Hayne	+ve "	25.1%
	Webb	+ve "	55.3%
	Gates I	+ve "	57%
	Gates II	+ve "	53%
	Gates III	Slight -ve "	5.0%
<u>Negative exponential model</u>	King	-ve bias	76.4%
(Gates)	Webb	Slight +ve "	2.8%
	Gates I	Slight +ve "	0.3%
	Gates II	Slight -ve "	0.4%
	Gates III	-ve "	53.8%

One can conclude from these results that for the negative exponential model, Gates I and Webb estimators provide the best result, i.e. using  $SW = 2y$ . King and Gates III underestimate by 76 and 54%, or the strip width component is too large, i.e.  $SW = 3.7y$ . For the positive half normal model King and Gates III provide the best results whereas Gates I and Webb overestimate

densities by 35 to 55% as the strip width component is too small.

Dasmann and Mossman, using Webb's estimator obtained "very variable results which seemed generally to considerably overestimate the true population", Hirst (1969).

Gates et al (1968) shows that the negative exponential curve fits the data from flushing distances very closely, the chi square test for goodness of fit giving a value of 2.295 with 5 d.f. Kovner, Hemingway and Patil (1977) show a close approximation of the positive half normal distribution to data from sighting distances for African ungulates.

Assuming the positive half normal model to fit in the African case then estimators close to Kings (where  $SW = 3.7y$ ) will give the best results. My estimator of  $SW = 4y$  is relatively close to King's but will underestimate density by some 7%. Where census data are to be used for exploitation such an underestimate is preferable to possible overestimation.

(b) The choice of angular or perpendicular strip width estimators.

From a field viewpoint perpendicular distances are easier to deal with on vehicle counts as a vehicle may have moved



## A 9.7

some distance from a point of first sighting before an observer can instruct the driver to stop. Reversing to the approximate point of first sighting is not practical. On foot counts however it is frequently not possible to find the transect point where the animal is perpendicular to the transect. Further, additional sightings between the point of first sighting and the perpendicular point would be difficult to cope with. As a general rule therefore, perpendicular distances are preferable for vehicle counts and angular distances are preferable for foot counts.

On theoretical grounds Gates (1969) states that where there is some question of  $\bar{\alpha}$  not being close to  $32.704^\circ$  ( $0.577 - 1$  radians) then the use of perpendicular distances is to be preferred. Robinette et al (1974) show that for some counts of larger mammals eg. elephant and eland,  $\bar{\alpha}$  is significantly larger than  $32.7^\circ$ .

- (c) The use of empirical or non parametric methods to estimate strip width.

Some authors have attempted to use graphical methods to estimate strip width from actual frequency distributions of field distance data, eg. Emlen (1971), Anderson and Pospkala (1970) and Rodgers (1971). These basically non mathematical

estimates have been discussed more objectively by Burnham and Anderson (1976).

The methods are based on the argument that for the positive half normal model the actual density observed over the first and highest frequency distance classes (ie. the plateau) is equivalent to the real density. Observed density in more distant classes is lower due to vegetation obstruction. If this is so then density can be estimated from the first distance class and other results ignored. This does in fact waste much data and also increases the variance estimate which is dependent on the number of observations (Eberhardt 1968, Caughley 1977). The Kelker Belt transect utilises this argument to select an appropriate strip width for use as a fixed width transect model (Hirst, 1969). Figure 5.3c illustrates this, where line A-B is maximum density and a perpendicular is dropped at the point where the curve slopes downwards; the intercept of this line on the distance axis is the effective strip width. Rodgers (1971) suggested that in order to avoid wastage of data the line A-B could be extended and another perpendicular dropped (line CD) so that the animals missed before CD are equalled by the animals seen after CD, (areas x and y in figure 5.3d). In this case the intercept of line CD on the distance axis gives the actual strip width (per side of transect) utilising all data. In some cases Rodgers (1971), and Hirst (discussed by Robinette et al 1974), there is an

initial dip in the distribution curve, (see figure 5.3e). This can be explained by observer-animal interaction when moving along the transect line. The observer scares animals away from the transect thus raising numbers in later distance classes. It is possible that animals are inhibited from using space close to the transect tracks by dust or odour on trackside vegetation. This is not thought likely in this study. Schultz et al (1957) believes that observer efficiency is increased by using pre-cut tracks. Rodgers (1971) proposed lowering the line AB to compensate for the dip in initial frequency, figure 5.3e.

My estimates of strip width from such graph plots were compared with estimates from the expression  $SW = 4\bar{y}$  for 5 species in 1969/1970. Results are as follows:

<u>Species</u>	<u><math>SW_1</math> (by <math>SW = 4\bar{y}</math>)</u>	<u><math>SW_2</math> from graph plot</u>	<u><math>SW_1/SW_2</math></u>
Wildebeest	552m	558	0.99
Zebra	492	476	1.03
Warthog	508	286	1.08
Impala	392	388	1.01
Hartebeest	424	424	1.00
	Mean Value		<u>1.02</u>

These results show very close agreement and vindicate the use of  $SW = 4\bar{y}$  as a strip width estimator.

## (d) Recent strip width estimators.

Earlier studies showed that frequency distributions approached two general forms: the negative exponential and the positive half normal. Other forms could be a decreasing straight line . Gates (1969), or a case typical of open plains, a continuous horizontal line to the limits of human visibility. If these forms do hold for field data then the mathematical characteristics of the curves can be used to estimate strip width viz:

Negative exponential	$f(y) = e^{-y}$
Positive half normal	$f(y) = \frac{2}{\sqrt{2\pi}} e^{-y^2/2}$

It may be that actual frequency distributions are not exactly one or the other of these forms but somewhere in between. Hemingway (1975) and Kovner et al (1977) suggested objective methods to determine choice of model and hence the most suitable estimator of strip width. Burnham and Anderson (1976) suggested fitting polynomials to frequency distributions from very large sets to reduce dependence on parametric models. Hemingway (1975) proposed using the expression:

$$E = \frac{\bar{y}^2}{\text{var } y} \quad \text{where } E \text{ is an objective determinant of strip width model.}$$

When  $E > 2.3$  a continuous straight line model is indicated

$E < 2.2.3, > 1.3$  a positive half normal model is indicated

$E < 1.3$  a negative exponential model is indicated.

Values of  $E$  were computed for all density calculations in this study.

Mean results for each species are as follows:-

Wildebeest	$E = 2.39$	Range 1.94 - 2.97
Zebra	$E = 2.26$	Range 1.74 - 3.10
Impala	$E = 1.99$	Range 1.47 - 2.48
Warthog	$E = 1.83$	Range 1.43 - 2.58.

The range of 'E' straddles the predictive value of 2.3. Note also that  $E$  tends to decrease with decreasing  $\bar{y}$ . However, the value of  $E$  is closely dependent on the value of  $\text{var } y$  which itself is governed by the distribution of  $y$ . In cases of a long tail, i.e. observations (even very few) at large distances, then  $\text{var } y$  is very large compared to  $\bar{y}$  and  $E$  is accordingly small. A case for impala showed that 9 sightings at 350m and over out of more than 500 sightings contributed over 40% of the variance value.

Hemingway proposes 3 distinct estimators of SW depending on the value of  $E$ . These are

Negative exponential ( $E < 1.3$ )  $SW = 2\bar{y}$  (i.e. same as Webb)

Positive half normal ( $E < 1.3 - 2.3$ )  $SW = \sqrt{2 \text{MSy}}$  (MSy = Mean square  $y$ )

Continuous straight line ( $E > 2.3$ )  $SW = 4\bar{y}$  (i.e. same as Rodgers)

Choice of strip width estimator therefore is difficult. We have seen that the King census estimator of  $SW = 2\bar{r} = 3.7\bar{y}$  is relatively unbiased for the half normal model. Rodgers estimator of  $4\bar{y}$  approximates that of King but has a slight negative bias. Empirical methods show close agreement with  $4\bar{y}$ . But if one accepts the half normal model as representative of this situation then mathematical theory dictates the use of  $SW = (2\bar{x}MSy)^{\frac{1}{2}}$ . Hemingway's prediction value E varies for my data between indicating  $4\bar{y}$  and  $(2\bar{x}MSy)^{\frac{1}{2}}$ . Choice then is really between these two models.

How are these related for my data? Values for different species are as follows:

Species	Time	A( $4\bar{y}$ model)	B( $(2\bar{x}MSy)^{\frac{1}{2}}$ )	A/B	
Wildebeest	1976	529.84	398.02	1.33)	} 1.36
	1971	483.87	351.14	1.38)	
	1972	465.0	337.0	1.38)	
Zebra	1976	510.49	386.93	1.32)	} 1.35
	1971	441.46	330.86	1.33)	
	1972	424.74	306.00	1.39)	
Impala	1976	376.85	295.29	1.28)	} 1.30
	1971	346.54	269.10	1.29)	
	1972	362.16	271.08	1.34)	
Warthog	1976	300.28	247.54	1.21)	} 1.29
	1971	333.92	257.21	1.30)	
	1972	340.94	251.62	1.35)	

MEAN VALUE 1.33

Therefore, on average, the use of  $(2\pi MSy)^{\frac{1}{2}}$  gives a strip width some 33% less than  $4\bar{y}$ , and so gives a density estimate 33% higher than  $4\bar{y}$ . Which is the more likely to be correct? In some ways it does not matter a great deal, for as Margalef (1968) has said, the main purpose of gathering information by sampling is to detect change efficiently rather than to estimate condition accurately at any particular time. The question of which estimator to use is **decided in chapter 5.**

#### 5.45. Variance Estimation.

No variance estimators for density or population size were available for early census models. Gates et al (1968) and Gates (1969) produced the first mathematical treatment of variance estimators. Previous workers, e.g. Eberhardt (1963) had advocated the use of repeated transects and thus finding a mean density and a variance estimate for the mean. Burnham and Anderson (1975) still advocate this method and put forward the variance estimator for sample density as

$$V(\bar{D}) = \frac{\sum L (D - \hat{D})^2}{(\sum L) (r - 1)} \quad \text{for replicate transects}$$

where  $r$  is transect number and  $L$  transect length. This expression is simply the normal expression for variance of a sample, weighted for transect length.

This estimator produces very much lower confidence limits for the estimated density than the estimator of Heningway used in this study, when all transects are considered. But when mean densities for each transect (from all replicates of that transect) are used for the 6 major transects then confidence limits are close to those of Heningways estimator, viz:-

Species & Time	Heningway	Burnham & Anderson
Wildebeest (total) 1976	27.16 $\pm$ 13.6%	27.16 $\pm$ 11.8%
Zebra (total) 1976	16.17 $\pm$ 17.9%	16.17 $\pm$ 17.4%

Burnham and Anderson (1976) state that they prefer the approach of Eberhardt (1968) in estimating variability from replicated field sampling instead of theoretical variances based on parametric models. Heningway's (1975) estimator for coefficient of variance is based on parametric models, but does appear to consider other sources of inherent variability than only that of between transect variance.

The use of group density rather than animal density is an additional source of variation and Heningway's estimator also relates to the population density rather than to the sample density as the expression  $(1-P)$ , where P is the sampling fraction, is built in to the estimator.



Hemingways estimator for the coefficient of variation for estimated population density of:-

$$C = \frac{\frac{dA}{A} \times \bar{g}^2 (1-p) + n \left( \frac{3Z + \bar{g}^2}{n} + Z \right)}{dA_g}$$

is preferred for use in this study despite its more complex computation. The upper portion is made up of two components, one dealing with variance of density due to sampling intensity (P), and the other due to group size variance.

Strictly speaking, mean density of animals is derived from mean group density and mean group size, each with its own variance, e.g.:

$$\bar{D}_A \pm V_{DA} = (\bar{D}_G \pm V_{DG}) \times (\bar{g} \pm V_g)$$

For the case of a finite population of animals, which I assume to be the case here, group density and group size are linearly related (discussed in Rodgers 1977, see appendix). As such they are dependent variables with a negative correlation ( $r = -0.85$  for wildebeest,  $n = 12$ ). Goodman (1960) shows that the variance estimator can be broken down to:-

$$\text{Var (product)} = \text{Var of A} + \text{Var of B} + \text{Co var AB}$$

in the case of dependent variables.

In this case covariance AB is negative so the total variance is reduced for negatively correlated dependent variables.

Hemingway (1975) and Kovner et al (1977) consider that D and  $\bar{g}$  are not dependent so covariance AB = 0 and their variance estimators are thus positively biased.

However, preferring to err on the side of caution and as this thesis is not a mathematical investigation of census theory Hemingways 1975 estimator is used as it is.

Note that the variance estimator is the same expression for the 4y model and the  $(2 \text{ II MSy})^{\frac{1}{2}}$  model. As strip width is smaller in the latter case, sample area is smaller, sampling fraction, P, is smaller, and so the variance is slightly larger. Examples are as follows:-

Species	$SW_A = 4y.$	$SW_B = (2 \text{ II MSy})^{\frac{1}{2}}$
	D $\pm$ CI%	D $\pm$ CI%
Wildebeest 1976	27.15 $\pm$ 13.6	36.15 $\pm$ 15.0
Zebra 1976	16.17 $\pm$ 17.9	21.33 $\pm$ 19.7
Impala 1976	28.70 $\pm$ 12.7	36.62 $\pm$ 13.3
Warthog 1976	9.43 $\pm$ 12.9	11.43 $\pm$ 13.2

APPENDIX TENTHE ESTIMATION OF FEEDING AND NUTRITIONAL PARAMETERS

## General.

Chapter seven of this thesis described the need to derive feeding and nutritional parameters from published studies, and noted that these studies frequently refer to domestic livestock or wildlife from different habitats to those of the Selous. In some instances, published predictive equations differ considerably, necessitating careful choice of the estimator to be used. This appendix discusses some of these estimators and gives reason for the choice made in this thesis.

1. Estimation of dietary crude protein from faecal nitrogen values (Thesis chapter 7.133).

Two predictive regression equations were mentioned:

- 1)  $CPd = 1.677 CPf - 693$  ( $r = 0.958$ ,  $p < 0.01$ ) (Bredon et al. 1963)
- 2)  $CPd = 1.06 CPf$  dry season, and  $CPd = 1.15 CPf$  wet season, (Arman, Western, pers. comm.)

Bredon's equation is an interspecies mean value, and was used by Duncan (1975) in his topi study. Arman's equations were derived for wildebeest in Amboseli in South Kenya.

Two other equations are available, viz:

- 3)  $CPd = 12.8 Nf - 95$  (Arman & Hopcraft 1975)
- 4)  $CPd = 15.0 Nf - 84$  (Arman & Hopcraft 1975)

where CPd is in gm per kg of forage and Nf is faecal nitrogen in gm per kg of faecal matter. Equation 3 is for studies based

on sheep, goats, hartebeest, gazelle and duiker, and equation 4 is for studies based on lagomorphs, warthog, hippopotamus, eland and wildebeest.

These four equations give very varied results, viz:

Season	CP(faeces)	N.(faeces.)	Equation (CPd)			
			1	2	3	4
Wet	11.5%	1.84%	12.36%	13.23%	14.5%	19.2%
Dry	6.5%	1.04%	3.97%	6.89%	3.81%	7.2%

Arman and Hopcraft (1975) state that with a total graze diet good approximation can be obtained from both equations 3 & 4, but with a mixed browse/graze diet, regressions have much wider confidence limits. Their equation 3 is for ruminants and equation 4 is for non ruminants plus eland & wildebeest (the major study species for this thesis) on all grass diets. Both their equations have points to recommend them for this study, but as they give very different results and it is not possible to make a rational choice, they are not considered further in this study.

Bredon's & Arman's Equations (1 & 2) are considered further and section 7.223 examines the results of using both equations for data for four species from this study.

## 2. Estimation of crude protein digestibility coefficients.

(Chapter 7.134)

Four equations predicting digestible protein (DP) or the digestibility coefficient of crude protein (DC) from crude protein (CP) values have been considered. Whilst

they differ markedly in format, they produce similar results, viz:

Author	Equation	Calculated Digestible Protein from two Different Values of Crude protein.	
		CP = 5%	CP = 15%
Milford & Minson (1964)	DP=0.899CP-3.25	1.25%	10.25%
Bredon & Marshall(1962)	DC = 9.59+4.28CP	1.55	11.07
Glover & French (1957)	DC=70logCP-15	1.70	10.10
Bredon et al. (1963)	DC=100.89logCP-44.45	1.30	11.13

The equation of Bredon et al (1963) is derived from tropical range grasses and as other estimators of Bredon et al. are used in thesis, I have chosen the particular estimator as well.

3) The determination of grazing offtake by exposure experiments.

(Chapter 7.142).

The grazing exposures in the typical Terminalia habitat and heavily grazed area of Lihangwa (both short grass scattered tree grassland communities) which were described in chapter four were used to determine grazing offtake. Methods followed those outlined in Milner & Hughes (1968).

Sample plots were clipped outside the enclosure (open to grazing and trampling) and within the enclosure (closed to ungulate and African hare use but open to small mammal, bird and insect use). The expression

$$GO = a - b \times \frac{(\log C - \log b)}{(\log a - \log b)}$$

was used to determine grazing offtake (G.O.) where

- a = Biomass outside enclosure at the first clipping
- b = Biomass outside enclosure at the second clipping,
- c = Biomass inside enclosure at the second clipping.

Data are for grass (excluding dicots and sedge) dry matter as  $\text{gm/m}^2$ . Milner & Hughes (1968) state this technique is satisfactory over long periods of heavy grazing. Three periods were used:-

- 1) Terminalia enclosure, 90 day period, rains, 16/3/71 to 14/6/71
- 2) Lihangwa enclosure, 169 day period, rains, 8/2/71 to 11/7/71.
- 3) Lihangwa enclosure, 123 day period, dry season, 11/7/71 to 11/11/71.

Clipping figures used were based on the mean of 2 randomly chosen  $1\text{m}^2$  quadrats within the enclosure and 4 randomly chosen  $1\text{m}^2$  quadrats outside the enclosure at each clipping date.

Information on animal use of the enclosure area came from census data described in chapter 5 and 6. Densities for the mile segment of transect including the enclosures were computed for the clipping period, and expressed as densities per hectare. Figures for wildebeest, zebra, impala, buffalo and warthog were so obtained. Areas within and outside the plot were open to grazing by small mammals, birds and invertebrates.

Results for total offtake for each grazing period are given in table 7.8. Five grazing species are documented:

wildebeest, impala, buffalo, warthog and zebra, their total density can reach as high as 1.5 animals per hectare in the rainy season.

Values in table 7.8 show a mean offtake of 3.83 kg/ha/day by a mean density of 1.06 grazers/ha/day or some 3.63 kg by an "average" grazing animal. If one "lumps" the less frequent species, buffalo, warthog and zebra into an "other species class" then with three offtake equations and three unknowns (wildebeest, impala and other species) it is possible to solve for each unknown using simultaneous equations.

Results are as follows, as grazing offtake per day.

Wildebeest = 4.18 kg.

Impala = 4.04 kg.

"other" = 2.40 kg.

Little importance should be attached to these figures as the experimental techniques suffer from several disadvantages and the lumping of species gives rise to mathematical inaccuracies as well as depending on several doubtful assumptions. However, the results could show the general order of magnitude for offtake and lend credence to figures determined in other ways (see below).

4) Dry matter intake rate as a function of food quality.

(chapter 7.143)

Working with wild and 'tamé' Coke's hartebeest in Kenya rangelands Stanley-Price (1974) was able to determine a number of regression equations linking variables relevant to the

the rate of dry matter food intake (DMI). Those of potential relevance to this study are discussed here.

a) Faecal Nitrogen.  $DMI = 109.46 Nf - 61.89$  ( $r=0.681$ )

where  $Nf$  is faecal nitrogen and DMI is  $gm/kgW^{0.73}$  per day.

b) Grass Moisture.  $DMI = 2.733GM - 10.91$  ( $r=0.892$ )

where  $GM$  is grass moisture percentage.

c) Particle Retention Time (RT) and Rumen Dry Matter Content

(RDM) where  $DMI = \frac{RDM}{RT} \times 24$  with RDM in kg, RT in hours

and DMI in kg/day.

Stanley-Price showed mean retention times of 20 and 50 hours for wet and dry season forages for hartebeest on Themeda range in Kenya Masailand. An average annual figure of 55 hours is therefore close to Annison & Lewis's (1959) mean value of 48 hours. Stanley-Price also suggested correlation between % crude protein and forage specific gravity and therefore between specific gravity and retention time. By combining the relationships between these variables one can construct a predictive relationship for retention time from forage crude protein content, and hence estimate DMI eg.

Crude Protein	Retention Time	DMI/Day
3%	90 hours	24/90 RDM
9%	20 hours	24/20 x RDM

Data from Stanley-Price's correlation plots have been combined into a new plot of CP versus RT. This is shown in figure 7.6a. Note that a retention time of 15 hours is



taken as the maximum rate of throughput; this rate is achieved with a diet of 11% CP content.

Grass moisture data is not readily available for this study, leaving a choice between estimates based on faecal nitrogen content and forage crude protein content. These two methods give considerably different results. For example a 273 kg male wildebeest with a 4.2 kg rumen contents weight would show the following dry matter intake values.

Method	Season	CPD/Pd/FN	DMI
Annison & Lewis	Year average	Immaterial	2.10 kg/day
Hopcraft & Arman	Year average	Immaterial	3.81
S-Price(FN)	Dry	FN = 1.3	5.40
S-Price(FN)	Rains	FN = 1.6	7.60
S-Price(CP)	Dry	CPd = 6.0	2.14
S-Price(CP)	Rains	CPd = 2.5	6.56

I presume that the structural relationship of crude protein to specific gravity to rumen retention time may be a more realistic interspecies relationship, than extrapolating from the physiological basis of relating faecal nitrogen to intake for hartebeest on Themeda range in Kenya. As there are distinct differences in rumen contents weight and through put times for different seasons the predictive equations of Annison and Lewis and Hopcraft and Arman are of little value. For this study I have used a relationship between crude protein and dry matter intake rate, adapted from Stanley-Price (1974).

## 5) Estimation of Nutrient Intake

(chapter 7.15)

Butterworth & Diaz (1970) suggested that for tropical grasses, total digestible nutrient (TDN) content could be estimated from the following expression:

$$\text{TDN} = 51.2 + 4.26 \log \text{CP} - 0.25 \text{CF} + 5.12 \log \text{EE}$$

where CF is crude fibre and EE is ether extract or fat.

Full proximate analysis of forage grasses was carried out infrequently in this study. Values relevant to the wooded grassland habitat are as follows: where NFE is carbohydrate or nitrogen free extract.

MONTH	CP	CF	EE	NFE	Ash
Nov	14.8%	25.8%	1.6%	47.1%	10.3%
Feb	11.3	28.8	2.0	47.3	10.6
May	5.2	35.4	1.1	51.8	6.1
Aug	2.9	31.8	1.0	52.2	7.1

Estimates for TDN were calculated for each of these four months and plotted against crude protein content. As the graph was curvilinear, regression values were not determined, but values of TDN read off from the graph. The graph plot is shown in fig. 7.6c.

## 6) Estimation of theoretical nutritional requirements.

(chapter 7.16)

Chapter seven mentioned that recent studies into metabolic activity rates of ruminants have shown considerable variation from the initial interspecific

mean value of  $W^{0.73}$  (Brody 1945). Cattle, for example, usually give results some 15% above, and sheep some 15% below Brody's value. Moen (1973) discusses the sources of intra and interspecific variation in the measurement of basal metabolism, and Stanley-Price (1974) discusses these differences with respect to East African conditions. He concludes that physiological adaptations to environmental stress can bring about significant deviations from the interspecies mean, for example he quotes the Dicotyle (ant) as having a metabolic rate coefficient of  $49.0W^{0.73}$ , showing a reduced metabolic rate to counteract Saharan heat stress.

Until recently, published studies dealt only with domestic stock in temperate regions, however a number of studies now deal with domestic and wild animals in the tropics. Their results show a wide range of metabolic coefficients, but as yet no overall pattern to allow the rational choice of a predictive expression has emerged. Some of the variation is undoubtedly due to different experimental methods and conditions, but much is due to real differences between species. Many studies show BM rates for African ungulates to be higher than Brody's values (e.g. Rogerson 1970 for wildebeest and eland) but Stanley-Price (1974) argues convincingly for a lower hartebeest. The following table shows the scale of variation from various predictive expressions,

<u>Source</u>	<u>Expression</u>	<u>Experimental Species</u>
Brody (1945)	$70 W^{0.73}$	Wide range of mammals
Maynard & Loosli (1962)	$70 W^{0.75}$	Domestic stock
Hopcraft & Arman (1970)	$70 W^{0.85}$	E. African wild & domestic stock
Rogerson (1970)	$104 W^{0.73}$	Wildebeest
Rogerson (1970)	$111.2 W^{0.73}$	Eland
Blaxter (in S-Price)	$52.4 W^{0.73}$	Sheep
S-Price (1974)	$51.5 W^{0.73}$	Hartebeest
Rogerson (1970)	$80.4 W^{0.73}$	Cattle (S. Africa)
S-Price (1974)	$49.0 W^{0.73}$	Bedouin Goat

In the absence of specific experimentation to determine basal metabolic rate for the species and area in question (as in this study) it is necessary to choose the most appropriate estimator from published studies. Choice is important as energy requirements (MER) are determined directly from BM and requirements for digestible protein (DPR) and total digestible nutrients (TDNR) are determined indirectly.

Three coefficients have been chosen for the prediction of basal metabolic rate, this choice covers most of the range of published values. As data are being used to show comparisons between species and seasons and not being used to formulate diets for example (i.e. in a relative not an absolute sense).

Coefficients chosen are those of Brody, Rogerson (wildebeest), and Hopcraft & Arman.

Studies on digestible protein requirements (DPR) and total digestible nutrient requirements (TDNR) show similar relevance to large African ungulates, all three are used in this thesis. Three values are chosen as follows:

Source	Expression (gm/day)		Experimental Species
	DPR	TDNR	
Brody (1945)	$3.65 \times W^{0.73}$	$35.2 \times W^{0.73}$	Wilderange Mammals
Elliot & Topps (in S-Price 1974)	$1.30 \times W^{0.73}$	$22.0 \times W^{0.73}$	Tropical Livestock
Maynard & Loosli (1962)	$2.78 \times W^{0.75}$		Temperate Livestock
Crampton & Harris (1969)		$31.8 \times W^{0.73}$	Temperate Cattle