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A CENSUS OF THE LARGE MAMMALS OF LOLIONDO CONTROLLED AREA, NORTHERN TANZANIA

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SUMMARY

1. A general description is given of Loliondo Controlled Area which sets out the reasons for this census and the conditions that determined the manner in which it was conducted. The major features of the vegetation and fauna are outlined.

2. The census was primarily a stratified sample count, and the types of stratification and sampling are described.

3. Some areas were total-counted using a series of adjacent counting blocks.

4. In a few instances large groups of animals were estimated rather than counted, but aerial photographs were taken to allow an estimate of bias to be made.

5. A number of practical considerations did not allow the census to follow the original plan in every detail.

6. The results are set out in Tables 3 and 4, and Figure 4. They show considerable, and rather variable, bias in estimations of numbers in large groups of animals. The estimates of numbers from sample counts for most species show wide confidence limits, but agree satisfactorily in such cases where a comparison can be made with the estimates from total counts. It is thought that a more efficient stratification, and a larger number of samples, will reduce the standard error of such estimates, to give more acceptable fiducial limits.

7. The census of 6,734 km^2 occupied a pilot and observer for 10 d during which 41 h were flown in a Cessna 185 aircraft. The total cost was E.A.Sh.13,400.

8. The method is discussed, and proposals put forward for increasing the accuracy of sample counts.

9. The implications of the census results in the construction of sustained yield equations are considered.

10. Some ecological points emerging from the results are discussed.

INTRODUCTION

In 1966 the Principal Game Warden for Arusha, D. Anstey, set down a number of land-use plans for areas under his general jurisdiction. These were remarkable in that they were one of the first attempts in East Africa by an administrative body to rationalise land-use through the establishment of multiple and integrated systems of exploitation. One area which came into consideration was the Loliondo Controlled Area of northern Tanzania, lying between latitudes 1°40′S. and 2°50′S. and longitudes 35°10′E. and 35°55′E. Part of Anstey's proposal was to exploit the wild herbivore populations of this area through sustained-yield cropping. Accordingly the Tanzania Government requested Wildlife Services Limited, an East African company with experience in the fields of ecological survey and game management (Graham 1966, 1968; Laws, Parker and Archer 1967; Laws and Parker 1968), to carry out a survey and pilot cropping scheme. This paper describes the results of a census of the large mammals of Loliondo Controlled Area carried out by personnel of Wildlife Services Limited (A. D. Graham and I. S. C. Parker) using a sampling method first proposed by G. Jolly (pers. comm.) which has been adapted for this area. The data have been analyzed by the other author (R. M. Watson.)

LOLIONDO CONTROLLED AREA

1. Local geography and topography

Loliondo Controlled Area lies in Tanzania Masailand covering some 6,734 km^2 (2,600 square miles) immediately to the west of the

Gregory rift valley. Its northern, western and southern boundaries have no ecological meaning, merely marking the division between Loliondo Controlled Area and Narok District of Kenya Masailand, the Serengeti National Park, and Ngorongoro Conservation Area respectively. The eastern boundary follows the top of the western escarpment of the Gregory rift valley.

The dominant topographical element of the Controlled Area is the basement complex hills representing the southern part of the Loita massif, which extend 32 km southwards from the Kenya border down the middle of the region. More isolated basement hills are found to the west and south of the massif. The north-eastern part of the Controlled Area falls away steeply from the Loita hills to the major western escarpment of the Gregory rift valley. In the south-eastern corner of the area a plateau above the major escarpment, the Sale plains, gives way as one travels westwards to low and broken hills, which gradually ascend to the great Serengeti plain, whose north-eastern part extends into Loliondo Controlled Area. The altitude varies from more than 2,440 m (8,000 ft) on the summits of the Loita hills, to 915 m (3,000 ft) on the Sale plains. A watershed running in a north/south direction crosses the area; the Grumeti, Bololedi and Bolonaibor rivers drain westwards into Lake Victoria, and the Lelessuta and Arash rivers drain eastwards into the internal drainage basin of Lake Natron. The features are shown in Figure 1.

2. Vegetation

The major physiognomic divisions of the vegetation are shown in Figure 2. The influence of intensive stock grazing by the Masai and frequent fires set by these pastoralists must be considerable. Also important is the distribution of rainfall, which according to Watson (1967) shows a gradient running approximately north to south from 114 cm to 38 cm per year. These factors, together with differences in altitude, soils and drainage situations, create an extremely diverse vegetation. The Loita hills above 2,135 m (7,000 ft) support highland rain-forest with trees of cedar (*Juniperus procera* Hochst. ex Endl.) and podo (*Podocarpus gracilior* Pilger), interspersed with open grassland which is kept short by continuous grazing of domestic animals (Type I of Figure 2). The forest areas are receding as the result of fire damage at their edges. Below 2,135 m (7,000 ft) on the small but numerous southern Siana plains a *Themeda/Pennisetum* grassland predominates, characteristically located on the gently sloping valley sides and valley floors. These plains are surrounded by a broad-leaved type of woodland with *Terminalia, Combretum* and *Erythrina* spp., and a few *Acacia* and *Commiphora* spp. There are thickets in this region on the steeper slopes and hilltops, and stands of *Acacia drepanolobium* Harms ex Sjöstedt on more poorly drained soils (Type II of Figure 2).

To the south-west, in areas of lower rainfall, the woodlands/plains complex changes. The grassland areas become more extensive, becoming in the extreme south continuous as the north-eastern part of the vast Serengeti plains. The growth form of these grasslands is much shorter than the *Themeda/Pennisetum* grasslands and the dominant species are *Sporobolus* spp. and *Cynodon dactylon* (L.) Pers., with a large proportion of *Cyperus* spp. (Type III of Figure 2). The surrounding woodlands are much less extensive, and of the typical *Acacia/Commiphora* fine-leaved type. Stands of *Acacia drepanolobium* are equally numerous (Type IV of Figure 2).

The broken hills above the Sale plains are largely covered with *Acacia/Commiphora* woodland, but with higher proportions of *Commiphora* spp. than are found further west. These woodlands are showing signs of deterioration through over-grazing by cattle and other domestic stock (Type V of Figure 2).

The Sale plains are a saline grassland on unstable volcanic dust soils in which the dominant species are *Eustachys paspaloides* (Vahl) Lanza and Mattei, *Aristida* spp. and *Chloris* spp. In general they are kept short by the grazing pressures of domestic stock (Type VI of Figure 2). The northern parts of the Sale plains are covered by a dense *Commiphora* woodland. The steep eastern slopes of the Loita hills are thickly wooded with *Acacia* and *Commiphora* spp. (Type VII of Figure 2).

3. Large Mammals

The considerable variety of habitats presented by this wide range of vegetation types and altitudes supports an equal variety of large mammals, which are listed in Table 1 in order of abundance. The biomasses of large mammals calculated from weights determined during investigations into rinderpest in the area (Taylor and Watson, 1967), and from the population figures as derived from the census described in this paper, are set out in Table 2. These data should be treated with some caution since movements of large mammals across the boundaries of the Loliondo Controlled Area occur freely. However there emerge a number of interesting comparisons with the equivalent values for the Serengeti ecosystem (Watson, 1967 p. 130); these are included in Table 2. The

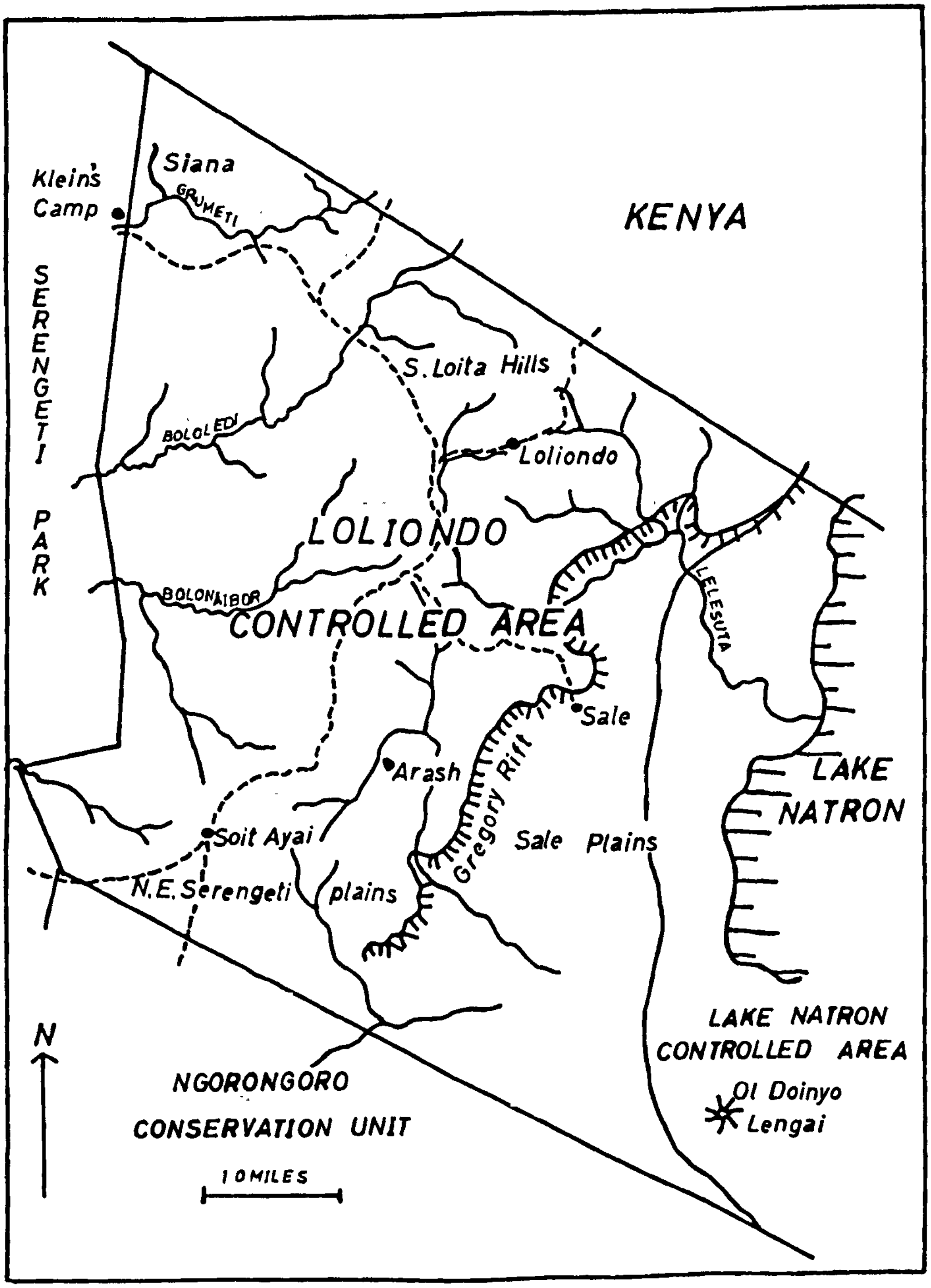

Figure 1
Loliondo Controlled Area—General geography.

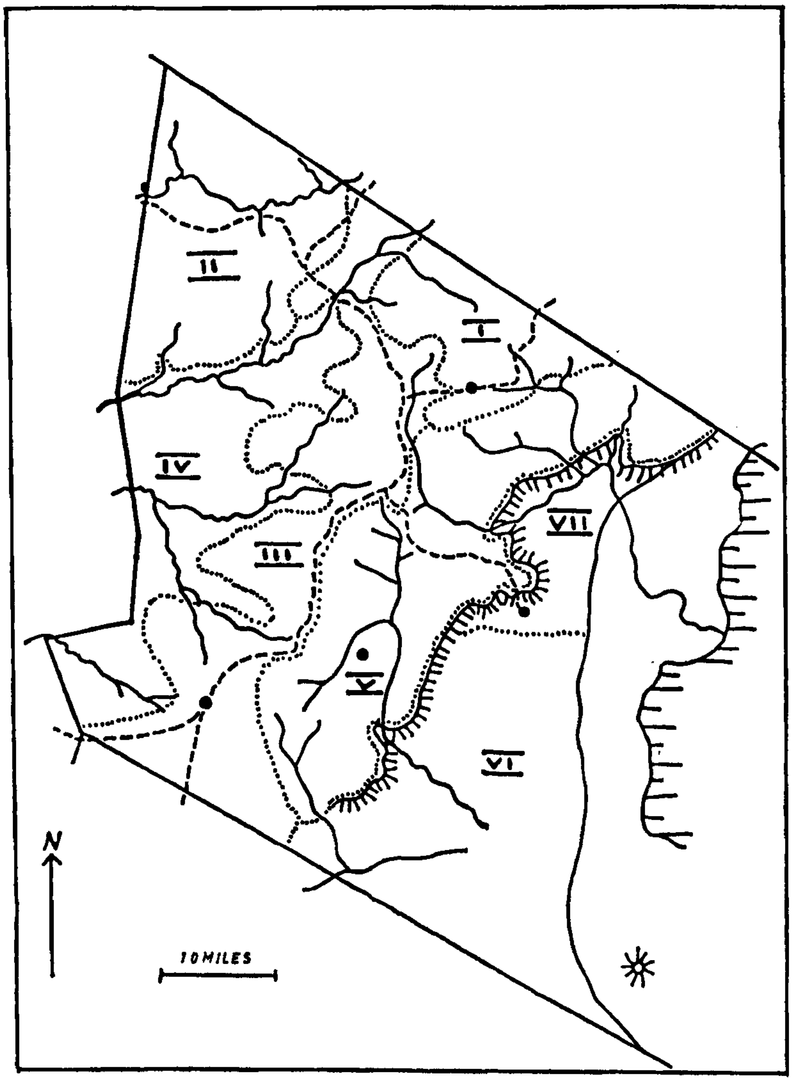

Figure 2

Loliondo Controlled Area—Vegetation zones.

Vegetation Type I : Highland rainforest and high grasslands
Type II : Broad-leaved woodlands and small areas of long grasslands
Type III : Short grasslands
Type IV : Acacia/Commiphora *fine-leaved woodlands*
Type V : Deteriorating Acacia/Commiphora *woodlands*
Type VI : Short saline grasslands
Type VII : Dense Commiphora *woodland*

biomass densities for the three major exploitation groups are of comparable order, although different species make very different relative contributions in the two areas. The high biomass density attributable to cattle in Loliondo Controlled Area should strictly speaking be included in the total for mixed feeders and browsers (exploitation group 3), and this will considerably disturb the comparison between Loliondo Controlled Area and the Serengeti ecosystem. The total biomass densities are, however, comparable if the cattle are included in group 3, and suggest that the presence of high densities of cattle is reducing the carrying capacity for wild animals. This question is considered in more detail in the discussion at the end of this paper.

The distribution and movement of the large mammals in the area in general follows

TABLE 1

Large mammals in Loliondo Controlled Area

Order of Abundance	Description	Name	This census
0	Extremely rare	Striped hyaena: *Hyaena hyaena dubbah* Meyer	—
		Mountain reedbuck: *Redunca fulvorufula chanleri* (Rothschild)	—
1	Rare	Steinbuck: *Raphicerus campestris neumanni* (Matschie)	—
		Klipspringer: *Oreotragus oreotragus shillingsi* Neumann	—
2	Occasional	Cheetah: *Acinonyx jubatus velox* Heller	—
		Oryx: *Oryx beisa callotis* Thomas	233
		Elephant: *Loxodonta africana africana* (Blumenbach)	123
		Bushbuck: *Tragelaphus scriptus dama* Neumann	—
		Rhinoceros: *Diceros bicornis bicornis* (Linnaeus)	—
3	Common	Topi: *Damaliscus korrigum jimela* (Matschie)	—
		Leopard: *Panthera pardus pardus* (Linnaeus)	—
		Lion: *Panthera leo massaica* (Neumann)	—
		Spotted hyaena: *Crocuta crocuta germinans* (Matschie)	—
		Golden jackal: *Canis aureus bea* (Heller)	—
		Silver-backed jackal: *Canis mesomelas mcmillani* (Heller)	—
		Reedbuck: *Redunca redunca wardi* (Thomas)	—
4	Frequent	Kongoni: *Alcelaphus buselaphus cokii* Günther	2,849
		Giraffe: *Giraffa camelopardalis tippelskirchi* Matschic	2,220
		Dik-dik: *Rhynchotragus kirkii thomasi* Neumann	—
5	Very frequent	Wildebeest: *Connochaetes taurinus albojubatus* Thomas	5,863
		Eland: *Taurotragus oryx pattersonianus* Lydekker	3,091
		Buffalo: *Syncerus caffer caffer* (Sparrman)	4,600
6	Abundant	Zebra: *Equus burchellii böhmi* Matschie	31,051
		Gazelle: *Gazella thomsonii ruwanae* (Knottnerus-Meyer) and *G. granti robertsi* Thomas	37,729
		Impala: *Aepyceros melampus suara* (Matschie)	14,776
7	Dominant	Cattle	92,610
		Sheep	—
		Goats	—

TABLE 2

Biomass and biomass densities in Loliondo Controlled Area and the Serengeti ecosystem

	Secondary producers	Total lb	Biomass kg	Biomass kg live wt per km^2	Biomass density for the Serengeti ecosystem in kg/km^2
Exploitation Group 1 Short grass feeders	Wildebeest	16.1×10^5	7.3×10^5	128	
	Zebra	93.0×10^5	42.2×10^5	739	
	Gazelle (both species)	26.4×10^5	11.9×10^5	210	
	Eland	18.5×10^5	8.4×10^5	147	
	Oryx	0.5×10^5	$.23\times10^5$	4	
	Total	154.4×10^5	69.9×10^5	1,228	2,907
Exploitation Group 2 Long grass feeders	Kongoni	6.1×10^5	2.8×10^5	48	
	Buffalo	46.0×10^5	20.9×10^5	365	
	Topi	2.3×10^5	1.0×10^5	34	
	Total	54.4×10^5	24.7×10^5	447	525
Exploitation Group 3 Mixed feeders and browsers	Elephant	5.0×10^5	2.3×10^5	40	
	Giraffe	33.3×10^5	15.1×10^5	264	
	Impala	11.8×10^5	5.4×10^5	94	
	Total	50.1×10^5	22.8×10^5	398	368
	Cattle	231.0×10^5	104.8×10^5	1,834	
Total for secondary producers		489.9×10^5	222.2×10^5	3,907	4,027

their known habitat preferences. The open grassland areas (Figure 2) comprising the north-eastern Serengeti plains, the smaller southern Siana plains, the grassland areas on the summits of the Loita hills, and the Sale plains are used by zebra, wildebeest, Thomson's gazelle, Robert's gazelle, eland, hartebeest and topi. The southernmost of these plains are for the most part too dry in the dry season and the plains game occupying them move northwards at the end of May onto the Loita hills and the better-watered Siana plains. The plains game exploit the woodlands fringing these small plains as the dry season progresses, returning to the southern plains as soon as the rains commence in late November. This movement is in close parallel with the greater migratory movements of the larger populations of plains game of the Serengeti, described by Watson (1967). In fact the migratory plains game make use of the north-eastern corner of the Serengeti plains for short periods in the wet season, and it has been calculated that those areas in Loliondo Controlled Area supply 2–3% of the resources for the Serengeti migratory wildebeest, and 2.5–3.5 % of the resources for the Serengeti zebra (Watson, 1967).

The various *Acacia/Commiphora* woodlands support more or less resident zebra, hartebeest, eland and a few topi, together with impala, elephant, rhinoceros, giraffe warthog, dikdik and steinbuck.

Buffalo are confined to the long grass plains of the north-west and the grassland areas of the Loita hills. Oryx occur on the Sale plains. Man and his domestic stock are notably the most ubiquitous of the large mammals.

This lengthy description of Loliondo Controlled Area has been necessary because of the influence of the factors described on the methods used in this census, and on the interpretation of the results.

METHODS

The dimensions of the area under consideration and the need to have an almost simultaneous census made it necessary to use an aerial sampling method of counting. Such a method has been described for a zebra census in the Serengeti ecosystem (Watson, 1967). For Loliondo Controlled Area the following procedure was adopted.

1. Stratification

Stratification is necessary because the area is not homogeneous either in terms of terrain and vegetation or distribution of animals. The objects of the stratification used in this count are threefold:

(i) to enable greater effort to be devoted to areas having the highest density of large animals;

(ii) to separate the total area into regions of more or less homogeneous density, thereby reducing the variance and fiducial limits of the count;

(iii) to separate the total area into regions presenting common problems of counting, thereby facilitating the application of adjustments for bias in counting, and the use of different counting methods in each stratum if necessary (for example the use of strip samples of different widths).

Using these criteria the stratification was made, and is shown in Figure 3. These strata may be described thus:

Stratum 1. Kuka—805 km^2. This stratum is hilly with steep-sided basement complex hills (representing weathered remnants of the south-eastern Loita massif) sheltering the valleys of the Grumeti and Bololedi headwater streams. The vegetation is predominantly woodland, with thickets on the hilltops and hillsides. The small plains areas (southern Siana plains) are found on the gently sloping valley floors. This stratum was judged to be one of the most difficult to count by strip sampling.

Stratum 2. Bololedi—689 km^2. The area is much less hilly and the areas of woodland and plains less intermixed than in stratum 1. The south-eastern part of the stratum is for the most part open grassland; the rest of the area is uniformly covered by *Acacia/Commiphora* woodland.

Stratum 3. North-eastern Serengeti plains—989 km^2. The Serengeti plains extend into Loliondo Controlled Area and cover the watershed of the southern section of the Area. Tongues of *Acacia/Commiphora* woodland extend eastwards from the Serengeti National Park boundary into this open grassland.

Stratum 4. Arash—940 km^2. The broken hills representing the weathered eastern edge of the Loita hills and the eroded edge of the north-eastern Serengeti plain watershed

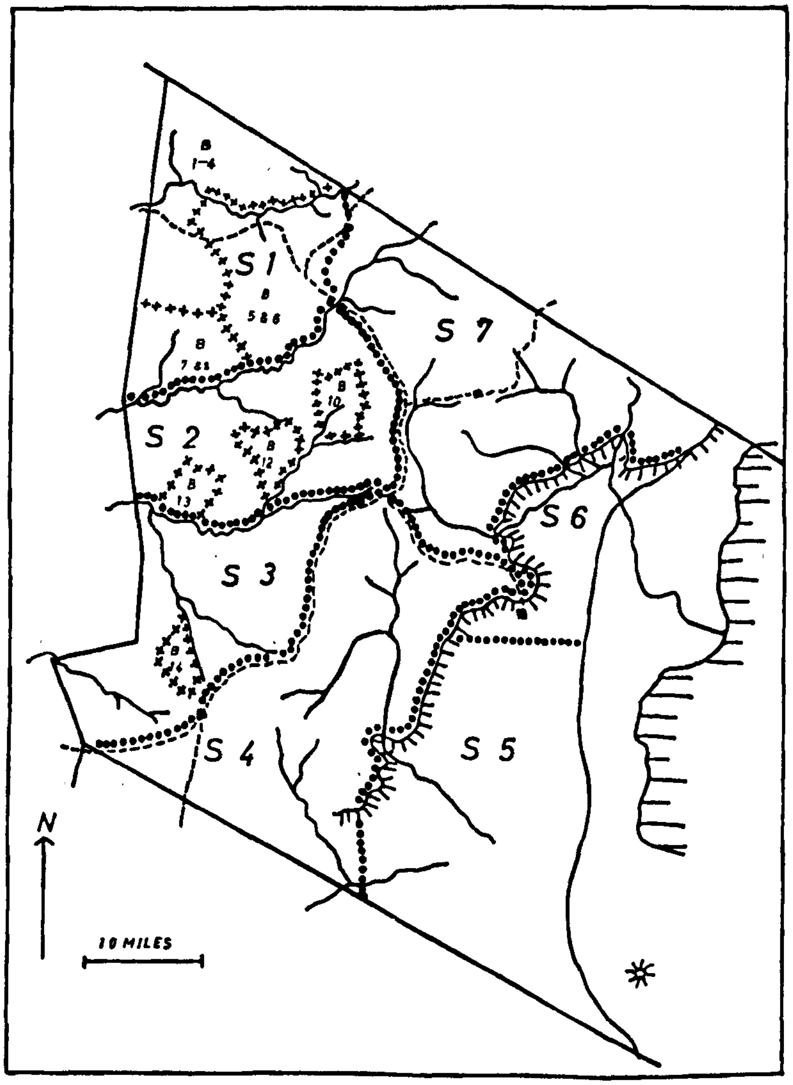

Figure 3
Loliondo Controlled Area showing strata and counting blocks.

comprise this stratum. The vegetation is dense *Acacia/Commiphora* woodland.

Stratum 5. Southern Sale plains—1,658 km². These are flat open grasslands showing no significant changes in altitude.

Stratum 6. Northern Sale plains—365 km². This stratum is covered by dense *Commiphora* woodland, and shows no significant changes in altitude.

Stratum 7. Southern Loita hills—1,278 km². The major highland area in Loliondo region makes up this stratum. The altitude varies from just over 1,830 m (6,000 ft) to over 2,440 m (8,000 ft). The vegetation of stratum 7 consists of closed canopy highland forest and dense thickets set among open grassland. This stratum presented the most difficulties as far as counting was concerned.

2. Sampling

The sampling procedure used within each stratum is strongly influenced by the need to employ 'strip-samples', this being, perhaps, the only feasible way to operate an aircraft economically in the counting of animals. Strip-samples were all orientated in a north-south direction, since this allows the observer to maintain uniform conditions of illumination by counting out of either side of the aircraft. No other considerations appeared to invalidate the use of strip-samples of constant north-south orientation.

The width of the strip counted was determined by two streamers attached to the wing-strut, which were calibrated to give a strip of appropriate width when the aircraft was flying at a height judged to be suitable for counting in the stratum under consideration. Both sample width, and the altitude for counting, may be varied according to conditions in each stratum. All large herbivores above the size of Thomson's gazelle were counted as they passed under the wing-strut between the two streamers. The observer was constrained by this method to keep his eyes in about the same position in the aircraft, and the pilot had to fly as far as possible at a constant height above the ground.

Strip samples were chosen in each stratum randomly, but with probabilities of selection proportional to size (as proposed by G. Jolly, pers. comm.). This effectively prevents the non-uniform size of samples from interfering with the subsequent analysis of results, and enables a valid estimate with confidence limits to be arrived at. The number of strip-samples chosen in each stratum was determined largely by the economics of the operation, but was generally such as to cover 5–20% of the stratum, the greater effort being devoted to strata with the higher densities of animals.

3. Counting errors

For a few species, large herds could not be accurately counted. These were estimated by the observer, and at the same time randomly selected herds were photographed with a 35 mm camera using a 50 mm lens from 244 m for subsequent more accurate counting. From the two sets of figures for estimated and counted numbers an adjustment factor was computed to enable the remaining estimated groups to be corrected. No attempt was made to estimate the bias in actual counting, but since the sample-strips were very narrow (300 m to 600 m) the observer did not have to count at high rates, and the animals to be counted were situated in conditions of optimal visibility. Therefore it is believed that these errors have been minimised, and will certainly be negligible when compared with the sampling errors.

4. Comparison of sample and total counts

The whole of stratum 1 was counted by a block system of total counting so that the results of the two methods of counting might be compared. Within each block (the blocks being chosen because of the ease of location of their boundaries), counting was carried out by dividing the terrain into small areas defined by drainage and then searching each area thoroughly. If the observer experienced difficulty in counting any animals they were either photographed, or circled until a satisfactory count was made. This method reduces the pressure on the observer to count everything in one pass since the aircraft remains in the area until the observer is satisfied that all the ground has come under observation and all animals seen have been reliably counted.

In strata 2 and 3 four blocks were counted in the same way, the blocks having again been chosen for ease of location of their boundaries both in the field and on a map. The results of this count have been treated as an alternative type of sampling, although the conditions of randomization for the positions of each block have not been fulfilled.

5. Departures from these methods imposed by practical problems

The following departures from the methods described were made necessary by practical problems encountered in the field.

(i) Time did not allow the counting by strip-samples of the whole of stratum 1. Instead blocks 7 and 8 (as demarcated for the total count of this stratum) were fully sampled.

(ii) The south-eastern 272 km^2 of stratum 3 were not sampled for two reasons. Firstly this area consists of appreciably higher land than the rest of the stratum and requires a separate treatment in flying which time did not permit. Secondly much of this area was occupied by several thousands of the Serengeti migratory wildebeest, which would have given a false impression of the abundance of this species in the area. Although this undoubtedly means that a significant number of resident wildebeest have not been counted, it is thought safer at this stage to err in this direction (see discussion at the end of this paper).

(iii) The total counting of stratum 1 was not completed, and blocks 5 and 6 comprising 274 km² were not counted.

(iv) The terrain of stratum 7 made the counting of this area all but impossible in the time available. An area of 186 km² of the stratum—part of a larger area of 262 km² which reconnaissance flying showed to hold large numbers of herbivores—was counted. The rest of the highlands, some 913 km², showed few large animals on preliminary reconnaissance and was not counted in this census.

(v) A 241 km² section of stratum 4 was sampled. Time did not allow the remaining 699 km² to be counted.

(vi) In stratum 5, 319 km² were not counted because of the difficulty of locating the exact boundary between the Ngorongoro Conservation Unit and the Loliondo Controlled Area; the remaining 1,339 km² were sampled.

Results

1. Estimates of bias

Bias in the numbers of animals estimated rather than counted was determined by a regression method. The plot of estimated numbers against numbers counted from

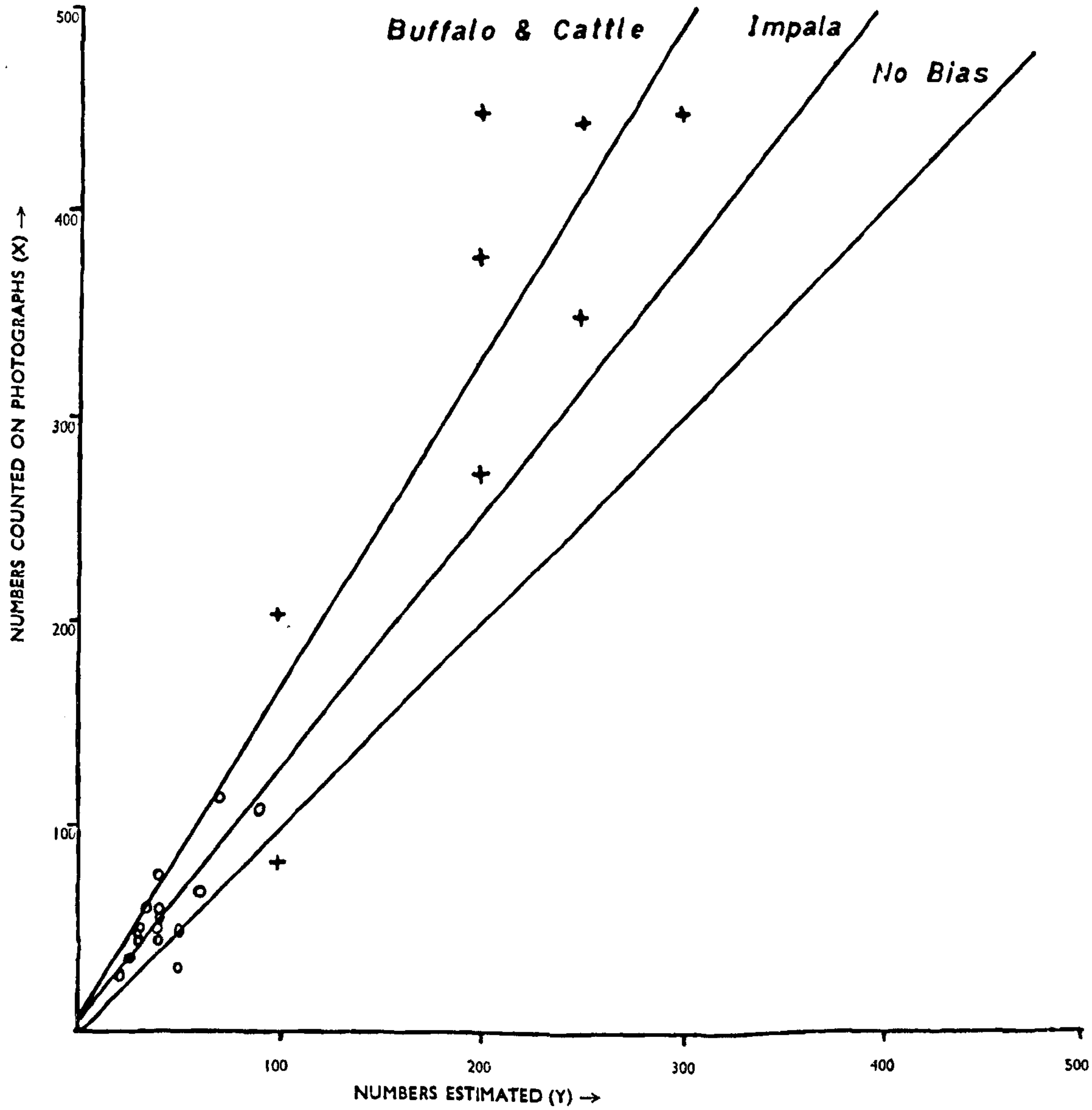

Figure 4

Plot of estimated numbers against numbers counted from aerial photographs. Buffalo and domestic stock are shown by a cross and impala by open circles. The two regression lines have been drawn in.

TABLE 3

Total count of large mammals

Block	Area in km²	Zebra N	Zebra D	Kongoni N	Kongoni D	Impala N	Impala D	Wildebeest N	Wildebeest D	Cattle N
part of stratum 1—small plains in *Acacia/Commiphora* woodland)										
7	62	29	0.47	55	0.89	1,340	21.61	0	—	3,844 (3,074–4,614)
8	93	0	—	103	1.11	847	9.11	2	0.02	281 (204–358)
	155	29	0.19	158	1.02	2,187	14.11	2	0.01	4,125
1	75	3	0.04	152	2.03	675 (550–800)	9.00	0	—	794 (563–1,025)
2	78	0	—	92	1.18	382 (257–507)	4.90	0	—	2,627 (2,165–3,089)
3	113	0	—	175	1.55	304 (287–322)	2.69	0	—	1,054 (746–1,362)
4	110	0	—	249	2.26	1,058 (986–1,130)	9.62	1	0.01	1,854 (1,623–2,085)
	376	3	0.01	568	1.51	2,419	6.43	1	0.01	6,329
	531	32	0.06	726	1.36	4,606	8.66	3	0.01	10,454
(part of strata 2 & 3—open grassland)										
10	52	524	10.06	0	—	91 (74–108)	1.75	95	1.82	281
12	41	775	18.91	54	1.32	14	0.34	98	2.39	135
14	34	2,017 (1,983–2,051)	59.30	1	0.03	0	—	67	1.97	0
	127	3,306	26.02	55	0.43	105	0.83	260	2.05	416
(part of stratum 2—*Acacia/Commiphora* woodland)										
13	41	195 (178–212)	4.76	37	0.90	389	9.49	0	—	216
	168	3,501	20.83	92	0.55	494	2.94	260	1.55	632
(part of stratum 7—grassland above 2000 m)										
15	186	669	3.59	8	0.04	277	1.49	137	0.74	2,734

N = number of animals (the figures in brackets are the 5% confidence interval)
D = density per km²

aerial photographs is shown in Figure 4. Impala are plotted separately from buffalo and cattle (these being the three species for which estimates were made) and the two regressions are $y=0.6489x+5.79$ and $y=0.5916x+25.21$ for impala and buffalo/cattle respectively, where y is the estimated number, and x the number counted from photographs of the same group. The variance of the first regression is 62.86 with a standard deviation of 7.93; for the second regression a variance of 1,585.7 with a standard deviation of 39.82 has been calculated. A small number of zebra, gazelle and eland were estimated, and to these estimates the impala regression has been applied (Table 3). This demonstrates the inaccuracy of estimating the number of animals in groups, even when only one observer is operating, and strongly supports the idea that large groups which cannot be accurately counted should be photographed. The corrections for all estimated groups have been made, with confidence limits set by the standard errors calculated above. These corrections have only been made to the total counts since no animals were estimated on the sample counts.

2. Total counts

The results of the total counts appropriately corrected as above are set out in Table 3 together with the densities for each species in the counting block. Of the large mammals

TABLE 3

Cattle	Gazelle		Buffalo		Elephant		Giraffe		Eland	
D	N	D	N	D	N	D	N	D	N	D
62.00	70	1.13	99	1.59	0	—	131	2.11	0	—
3.02	55	0.59	355	3.82	0	—	150	1.61	0	—
26.61	125	0.81	454	2.93	0	—	281	1.81	0	—
10.58	0	—	1,957 (1,803–2,111)	26.09	0	—	182	2.43	0	—
33.68	200	2.56	69	0.88	0	—	7	0.09	0	—
9.33	120	1.06	10	0.09	0	—	74	0.65	108	0.96
16.85	13	0.12	541	4.92	123	1.12	126	1.15	0	—
16.84	333	0.89	2,577	6.83	123	0.33	389	1.03	108	0.29
19.65	458	0.86	3,031	5.70	123	0.23	660	1.24	108	0.20
5.40	54	1.04	0	—	0	—	0	—	23	0.44
3.29	481	11.74	0	—	0	—	0	—	89	2.17
—	478 (444–512)	14.05	0	—	0	—	0	—	381 (359–403)	11.20
3.27	1,013	7.97	0	—	0	—	0	—	493	3.88
5.27	72	1.76	0	—	0	—	7	0.17	4	0.10
3.76	1,085	6.46	0	—	0	—	7	0.04	497	2.96
14.68	222	1.19	0	—	0	—	1	0.01	0	—

seen it was considered that zebra, cattle, both gazelle species, kongoni, impala, wildebeest, buffalo, giraffe, elephant and eland, by virtue of their visibility and/or normal social groupings, were relatively easy to locate and count. Other large mammals have not been estimated in this paper because large proportions of them are likely to be missed in total counting. Gazelle have been grouped together because they are difficult to distinguish in aerial counting in the limited time available.

3. Sample counts

The results of the sample counts are shown in Table 4. The fiducial limits for each species have been calculated from the variance which is given by the expression:

$$V(\hat{Y}) = \sum_{strata} \frac{N_h^2}{n_h}\left(1-\frac{n_h}{N_h}\right)\frac{\sum_h (y-\hat{R}_h.x)^2}{n_h-1}$$

where $V(\hat{Y})$ is the variance of the estimated number of animals

$\sum_{strata}$ denotes summation over all strata

$\sum_h$ denotes summation over all the sample strips in a particular stratum h

N_h =total number of strips in stratum h

n_h =total number of strips sampled in stratum h

y =number of animals in a sample strip

x =area of that sample strip

$\hat{R}_h$ =estimate of the number of animals per unit area in stratum h.

The estimates of populations for all species have been derived from the expressions:

$$\hat{Y}_h = \frac{\sum_h y}{\sum_h x} X_h = \hat{R}_h X_h$$

where $\hat{Y}_h$ =an estimate of the number of animals in stratum h

X_h =total area of stratum h,

and: $$\hat{Y} = \sum_{strata} \hat{R}_h X_h$$

where $\hat{Y}$ =an estimate of the total number of animals of the species concerned in the area sampled.

These expressions were first proposed by G. Jolly (pers. comm.).

In sample counting no attempt was made to census domestic stock, and only the aforementioned large mammals, together with oryx, are thought to have been counted with sufficient accuracy to warrant an estimation of numbers. As can be seen from Table 4 it was not considered worthwhile to calculate fiducial limits in strata where less than nine samples have been flown, nor for species occurring at densities of less than ten per square mile. In these instances the confidence limits would be extremely wide and so estimates given without confidence limits must be treated with caution. This sample count demonstrates that the present sampling fraction is inadequate for most species in that unacceptably wide confidence limits are produced (see discussion.)

4. Comparison of total counts and estimates from sample counts

(*i*) *Blocks* 7 *and* 8 *of stratum* 1

Direct comparison is possible here, and the two sets of results are shown in Table 5. This satisfactory agreement should not be regarded as necessarily being a vindication of either method. The total count allows no estimate of the confidence interval (which is probably considerable) and the sample count gives rather wide confidence intervals which must be reduced. However it is encouraging that the two methods show comparable results.

(*ii*) *Blocks* 10, 12, 13 *and* 14 *in strata* 2 *and* 3

A second comparison of methods may be made here, as is set out in Table 6. Both these strata were completely sampled and estimates of the large mammal populations made (Table 4). Blocks 10, 12, 13 and 14, which were selected for the ease of location of their boundaries, were totally counted (see Table 3). Blocks 10, 12 and 14 are covered by open grassland, whereas block 13 is wooded. The density of the major species in these blocks has been calculated for woodland and grassland vegetation, and an estimate made of the total populations of strata 2 and 3, assuming that the blocks are representative of the whole strata. Table 6 shows a remarkably close agreement between the two estimates. However, fiducial limits for the sampled estimate are wide, and no limits may be set on the other estimate, and so this agreement must be treated with certain reserve (see discussion.)

5. Estimates of the large mammal populations of Loliondo Controlled Area

Table 7 sets out the final estimates from this census of large mammal populations for Loliondo Controlled Area, excepting the uncounted sector of the Loita hills. Because of the incomplete nature of some of the sampling and because, in general, insufficient samples were taken, it has not been possible to put confidence limits on to these estimates and wide limits must be assumed, probably in excess of 50% of the estimate (at a 5% level). Estimates for the cattle population have been arrived at by assuming the densities derived from the total counting in strata 1, 2, 3, and 7 are applicable over the rest of Loliondo Controlled Area to regions of comparable vegetation.

6. Costs

The costs of the census have been computed on the basis of flying time in the Cessna 185 aircraft at E.A.Sh.200/- per hour. Forty one hours were flown (including flying from and returning to Nairobi, and reconnaissance flying) totalling E.A.Sh.8,200/-. The census occupied pilot and observer for 10 d and the preparation of the report took one biologist 6 d. This adds a labour cost of 5,200/- to give a total cost of E.A.Sh.13,400/-.

DISCUSSION

1. Methods

The use of stratified sample counts is a

TABLE 4

Estimates of large mammals from sample counts

Stratum	Area sampled in km²	No. of samples	Sample in km²	Total area of stratum in km²	Width of sample strip in km	Altitude of working in m	Zebra N	Zebra D	Kongoni N	Kongoni D	Impala N	Impala D	Wildebeest N	Wildebeest D
Stratum 1 Blocks 7 & 8	155	10	16.8	805	274	91	0	—	240 (108–372)	1.55	1,855	11.97	0	—
Stratum 2	689	9	57.0	689	274	91	4,689 (2,837–6,551)	6.81	351	0.51	5,414 (1,002–9,826)	7.86	2,766 (757–4,775)	4.01
3	717	10	108.8	989	274	91	15,841 (6,527–25,055)	22.09	508	0.71	842 (210–1,474)	1.17	1,046	1.46
4	241	9	36.3	940	274	91	732	3.04	86	0.36	186	0.77	66	0.27
5	1,339	5	51.8	1,658	274	91	724	0.54	0	—	0	—	750	0.56
6	365	5	12.7	365	274	91	0	—	200	0.55	432	1.18	0	—
TOTALS	3,507	48	283.4	5,175			21,986 (10,820–33,048)		1,145		687 (1,830–11,378)		4,628 (2,619–6,637)	
Mean densities								6.27		0.33		1.96		1.32

Stratum	Area sampled in km²	No. of samples	Sample in km²	Total area of stratum in km²	Width of sample strip in km	Altitude of working in m	Gazelle N	Gazelle D	Buffalo N	Buffalo D	Giraffe N	Giraffe D	Eland N	Eland D	Oryx N	Oryx D
Stratum 1 Blocks 7 & 8	155	10	16.8	805	274	91	36	0.23	0	—	295 (164–426)	1.90	0	—	0	—
Stratum 2	689	9	57.0	689	274	91	1,814 (721–3,007)	2.63	0	—	437	0.63	532	0.77	0	—
3	717	10	108.8	989	274	91	4,824 (1,925–7,723)	6.73	0	—	144	0.20	1,162	2.32	0	—
4	241	9	36.3	940	274	91	578	2.40	0	—	133	0.55	25	0.10	0	—
5	1,339	5	51.8	1,658	274	91	20,783	15.52	0	—	0	—	0	—	233	0.17
6	365	5	12.7	365	274	91	0	—	0	—	58	0.16	0	—	0	—
TOTALS	3,507	48	283.4	5,175			27,999 (24,007–32,091)		0		777 (646–908)		2,219		233	
Mean densities								7.98		—		0.22		0.63		0.07

N = estimated number (the figures in brackets are the 5% confidence interval)

D = density per km²

TABLE 5

Comparison of total and sample counts in blocks 7 and 8

Species	Number counted	5% Confidence interval	Estimated from samples	5% Confidence interval
Impala	2,187	1,908–2,428	1,855	1,335–2,375
Giraffe	281	—	295	164–426
Kongoni	158	—	240	108–372
Topi	73	—	138	54–242
Ostrich	19	—	54	—
Gazelle	125	—	36	—
Zebra	29	—	0	—
Wildebeest	2	—	0	—
Buffalo	454	—	0	—

new technique for censusing East African mammals, first attempted in 1966 (Watson, 1967). For this reason it is useful to discuss the value of the method. Such fiducial limits as have been computed are wide, and it is clearly desirable to reduce these. It is felt that the large number of flying hours spent in reconnaissance (neither pilot nor observer was familiar with the area) and in total counting will, in future counts, be unnecessary. The number of hours spent on the actual sample counting was in fact under 13, and future counts could well increase the number of samples by a factor of two or three, which would be expected to reduce the variance of the estimates considerably.

The stratification of this census was also less than optimal, and has contributed to the wide confidence interval. Now that Loliondo Controlled Area is better known from the air it should be possible to improve the stratification.

The close agreement of density estimates for most herbivores from sample counts over a whole stratum and from total counts of four small blocks (Table 6) requires further comment. This may indicate that the heterogeneities of distribution of some herbivores are on a small scale, and that effort could profitably be expended in an exploration of the exact mathematical nature of spatial distribution patterns of a number of large herbivore species, with a view to proposing more efficient sampling procedures.

The satisfactory agreement between total count estimates and sample count estimates suggests that the method of total counting employed in this census was effective, although far from economically practicable.

2. Results

A discussion of the results of this census concerns two distinct viewpoints. In the first instance the economist will wish to know what bearing the results have on the maximum sustained yields from these animal populations. In the second instance the ecologist will wish to test the results against the ordered pattern of his discipline, and ultimately to use them to reinforce or expand that pattern, possibly even to alter it.

(*i*) *Maximum sustained yields*

The results of this census have produced estimates of the numbers of large herbivores in Loliondo Controlled Area in February 1968. At this stage no maximum sustained yields for exploitation of these animals can be suggested because information on the other parameters required for a sustained yield equation is not available. However, from more detailed knowledge of other herbivores (Watson, 1967; Laws and Parker, 1968) it is unlikely that the removal of an annual crop of 10% of the known populations will exceed the sustained yield. Proper handling of the results of such cropping will eventually provide all the information necessary for the correct solution of a sustained yield equation.

The estimates produced in this paper must be treated with some caution because of their wide confidence limits, and because the boundaries of the Loliondo Controlled Area are far from being ecological boundaries. An attempt was made not to count any of the Serengeti migratory wildebeest population, large numbers of which were occupying the area at the time of the count, but for other species there is at this stage no way of determining the nature and importance of movements across the boundaries of the Controlled Area. In view of these two factors the present estimates must be under constant review, and a series of counts will be

TABLE 6

Comparison of sample counting and partial total counting of strata 2 and 3

Block No.	Area in km²	Vegetation	Zebra N	Zebra D	Kongoni N	Kongoni D	Impala N	Impala D	Wildebeest N	Wildebeest D	Gazelle N	Gazelle D	Eland N	Eland D	Giraffe N	Giraffe D
10, 12, 14	127	Open grassland	3,306	26.06	55	0.42	105	0.81	260	2.05	1,013	7.99	493	3.90	—	
13	41	Wooded	195	4.63	37	0.88	389	9.38	130	3.13	72	1.74	4	0.10	7	0.15
Of strata 2 & 3, 759 km² are open grassland and 648 km² are wooded. Therefore using the density figures derived from total counts in blocks 10, 12, 14, 13 above we arrive at populations of:																
	759	Grassland	19,940		330		630		1,560		6,069		2,947		0	
	648	Woodland	3,046		568		6,078		0		1,125		62		125	
		Total	22,986		898		6,708		1,560		7,194		3,009		125	
From sample counts of strata 2 and 3 these estimates are derived (Table 4):			20,530		859		6,254		3,812		6,638		2,194		581	

N=estimated numbers
D=density per km²

TABLE 7

Final estimates of large mammals in Loliondo Controlled Area

Large mammal species	Zebra	Kongoni	Impala	Wildebeest	Cattle	Gazelle	Buffalo	Giraffe	Elephant	Eland	Oryx
Total-counted	701	834	4,883	140	13,820	680	3,031	701	123	108	—
5% Confidence limits	—	—	4,310–5,456	—	11,085–16,555	—	2,877–3,185	—	—	—	—
Sampled	2,942	126	490	441	—	1,784	—	81	—	334	—
Estimated from samples	21,986	1,145	6,874	4,628	—	27,999	1,569	772	—	2,219	233
5% Confidence limits	10,920–33,052	—	1,830–11,918	2,519–6,737	—	23,883–32,115	—	—	—	—	—
Estimated from mean densities for areas not counted	8,454	850	3,019	1,095	78,790	9,050	—	747	—	764	—
Estimated total in Loliondo Controlled Area (except Highlands)	31,051	2,849	14,776	5,863	92,610	37,729	4,600	2,220	123	3,091	233
Estimated density in Loliondo Controlled Area in animals per km²	5.40	0.50	2.59	1.04	16.21	6.60	8.11	0.39	0.02	0.54	0.04
Density in the Serengeti ecosystem (Watson, 1967)	8.88	—	—	11.19	—	8.88	1.27	—	0.07	—	—

Where an area has been sampled and total-counted, the sample results only are used needed to establish the year-round productivity of the area which must ultimately determine yields.

(ii) Ecological implications

Part of the Loliondo Controlled Area lies in the Serengeti ecosystem and the same range of rainfall and vegetation types occurs in both areas. The relative areas of woodland and grassland types are of the same order in the two regions. The similarities in biomass densities for Loliondo Controlled Area and the Serengeti ecosystem are therefore to some extent predictable (Table 2). The position of cattle in the biomass density situation is of considerable interest. In Loliondo cattle have replaced wildebeest as the dominant large mammal contributor to the secondary producer biomass, which suggests that there is a large degree of overlap between the requirements of wildebeest and cattle.

The overall biomass densities of the two areas are very similar and do not in themselves suggest that the presence of large numbers of cattle necessarily reduces secondary productivity. This is of some relevance when the problems of multiple use of land, in particular the joint grazing of cattle and wild herbivores, are considered. The general habitat preferences of the large mammals censused in this survey are confirmed from their distributions. The densities of these herbivores are shown in Figure 5. It is apparent that buffalo and oryx are more specialized in their requirements than the other species, since the latter occur throughout the area wherever some type of woodland or grassland is to be found.

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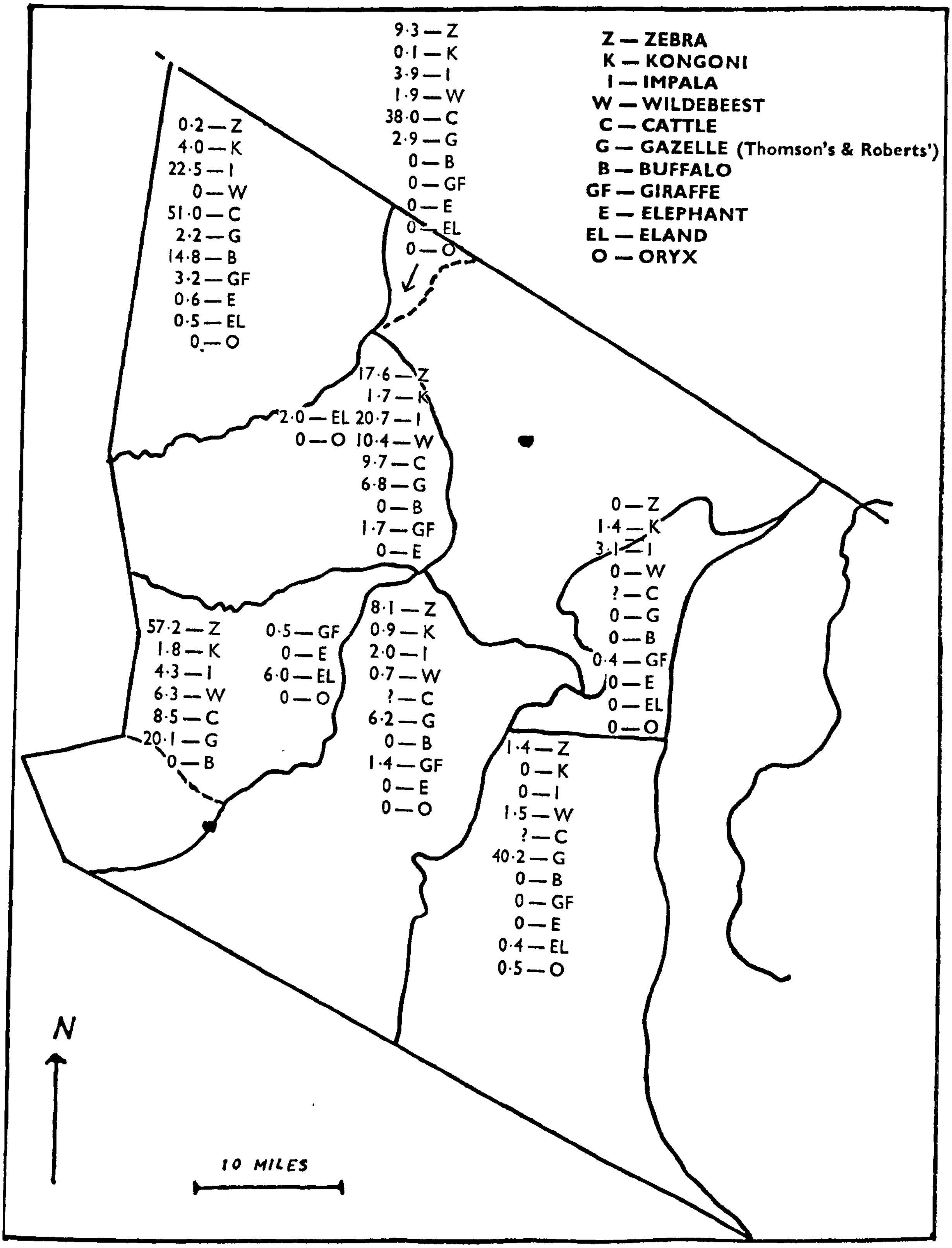

Figure

Densities (in numbers per square mile) of the large mammal species in Loliondo Controlled Area for each stratum reflecting the general habitat preferences of the species (cf. Figure 2).