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THE NUMBERS AND DISTRIBUTION PATTERNS OF LARGE MAMMALS IN THE RUAHA–RUNGWA AREA OF SOUTHERN TANZANIA*

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SUMMARY

(1) An aerial census of Ruaha National Park, Rungwa and Kizigo Game Reserves, and part of the proposed Mloa–Ilambi Game Controlled Area is described.

(2) Zebra, eland, sable, and hartebeest were virtually restricted to the miombo woodlands. Impala and kudu were most common in the rift valley sector of the census zone. Elephants, buffalo, and giraffe occurred throughout the entire area.

(3) The 31 500 km^2 census zone carried one of the largest elephant populations in Africa, an estimated 43 685 ± 9254 elephants, of which 24 625 ± 7132 were estimated to occur within Ruaha National Park (10 200 km^2 in area). The densities of elephants and the combined densities of the other large herbivores were highest in the National Park and lowest in the Game Controlled Area.

(4) Within the National Park, comparisons with earlier counts showed an apparent increase in elephant density of 8–10% per annum since 1965. Of the large herbivores, elephants alone showed a significant increase since the 1972 census and only elephant distribution was significantly affected by the distribution of human settlement and hunting. The increase in elephant numbers within the National Park is probably the result of the change in human distribution in the region and a period of higher rainfall.

INTRODUCTION

The Ruaha–Rungwa–Kizigo wilderness forms one of southern Tanzania's three main wildlife conservation regions (the other two being the Selous Game Reserve and the Rukwa area). The Germans recognized its importance when they created the Saba River Game Reserve. This was renamed the Rungwa Game Reserve in 1946 (Bjornstad 1976) and in 1964 part of the Game Reserve was declared the Ruaha National Park. In 1974 the Kizigo Game Reserve was established to the north and east of the Rungwa Game Reserve.

Elephants were known to be damaging trees even when the National Park was first declared (Savidge 1968). Reports by Savidge (1968) and Bjornstad (1971) indicated that woodlands were being destroyed rapidly and it was recognized that the Park was showing the symptoms of a classic elephant problem (e.g. Laws 1969; Caughley 1976). Initial data on the numbers of elephants were provided by a series of aerial counts in the worst affected areas of the Park (Savidge 1968) and by sample counts covering the whole Park in the dry season of 1972 and the wet season of 1973 (Norton-Griffiths 1975a). Elephants continued to damage trees and the Tanzania National Parks authorities became more

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concerned about the management implications of the Ruaha situation. Since more information was needed on the numbers and distribution of elephants, it was decided to carry out another census which would cover not only the area sampled in 1972 and 1973 but also as much of the surrounding area as costs would allow.

The specific objectives of this census, which was made in September 1977 (the dry season), were to: (a) estimate the numbers of large herbivores (paying particular attention to the elephant population) within the National Park and compare the new estimates with the earlier ones; (b) plot the distribution of large herbivores in and around the National Park; (c) estimate the numbers of, and plot the distribution of, large herbivores within the Rungwa and Kizigo Game Reserves, neither of which had been counted before; (d) assess the factors determining the distribution of elephants within the census zone; (e) estimate the numbers of elephants in the Msembe area of the National Park where an intensive study of elephant ecology was in progress (Barnes 1979); (f) provide comparative data for the continental I.U.C.N./W.W.F./N.Y.Z.S. Elephant Survey.

STUDY AREA

The census zone covered the Ruaha National Park, the Rungwa and Kizigo Game Reserves, and a part of the proposed Mloa–Ilambi Game Controlled Area to the south and east of the National Park (Fig. 1)—a total area of 31 500 km². The south-east of the census zone lies in Pratt & Gwynne's (1977) ecoclimatic zone V (arid), and the western and northern parts lie in ecoclimatic zones IV (semi-arid) and III (dry humid to semi-arid).

The vegetation of the National Park has been described by Bjornstad (1976). The western half is covered by deciduous *Brachystegia* (miombo) woodlands. In the extreme

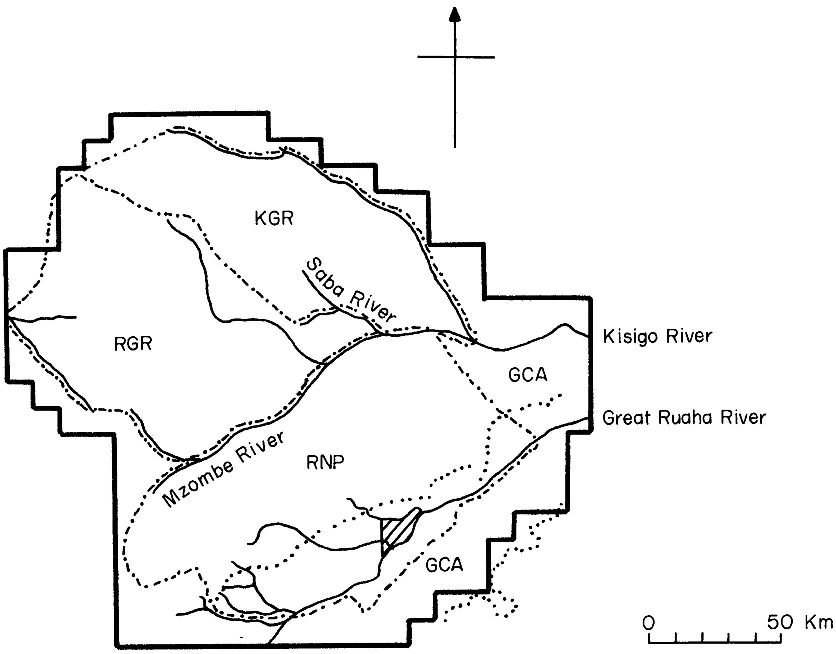

FIG. 1. Map of the census zone showing the Ruaha National Park (RNP), Rungwa Game Reserve (RGR), Kizigo Game Reserve (KGR), and part of the Mloa–Ilambi Game Controlled Area. The shaded part is the Msembe study area. ———, rivers; ...., escarpment; ▬▬▬, boundary of census zone; —.—.—, boundaries of National Park and Game Reserves.

western mountainous corner is an evergreen upland forest dominated by *Drypetes gerrardii* Hutch. The drier eastern half is dominated by *Commiphora-Combretum* woodland and bushland, while the north-eastern corner is dominated by *Acacia* bushed grassland. The south-eastern sector of the National Park lies in the Rift Valley, through which flows the Great Ruaha River (Fig. 1). The Msembe study area lies in this part of the *Commiphora-Combretum* zone on the north bank of the Great Ruaha River. A detailed vegetation map has been prepared by Bjornstad (1977). The mean annual rainfall recorded at Msembe Park H.Q. is 580 mm, of which 94% falls between December and April.

There are no descriptions of the vegetation of the Rungwa and Kizigo Game Reserves. They lie in ecoclimatic zones III and IV and have a variable cover of miombo woodland communities, except for the eastern and southern parts which are covered by *Acacia* bushland, *Commiphora* woodland, and extensive grassland plains.

The vegetation of the proposed Game Controlled Area has been briefly described by Strömquist (1976) and Johansson (1976) and is covered mainly by *Commiphora* woodland.

METHODS

Sample design

The census was designed to allow a comparison with Norton-Griffiths' (1975a) count of Ruaha National Park. A systematic design was chosen because data were required on distribution (Norton-Griffiths 1975a). A grid of 10 × 10 km squares was laid over a map of the census zone. The flight lines ran north–south through each grid square. The transects covered 3·1% of the National Park and Game Controlled Area, and 2·9% of the Game Reserves.

Data collection

Two aircraft were used simultaneously. One counted the National Park and Game Controlled Area while the other counted the Game Reserves. Methods followed Norton-Griffiths (1975b). Two back-seat observers counted all animals within their sample strips. Elephant carcasses and skeletons were recorded following the methods of Douglas-Hamilton *et al.* (1979). In each minute of flying time the front-seat observer recorded the following data: (a) vegetation type—miombo, *Acacia* woodland, *Commiphora* woodland, bushland, wooded grassland, or open grassland: (b) tree damage—estimated on scale from 0 (no dead trees seen) to 4 (>80% of the trees were pushed over): (c) human activity—huts, agriculture, abandoned agriculture, livestock, hunting, or logging activity.

After the census the two front-seat observers flew together down a long transect and independently made estimates of tree damage. The estimates were compared and a correction factor was calculated to standardize the estimates of one observer against the other. The mean value of the tree damage estimate was calculated for each grid square and was used as an index of tree damage. Transects were flown between 07.30 and 12.00 hours and between 15.00 and 18.00 hours. The census was completed in 3 days.

The Msembe study area (130 km^2 in extent) was counted by one aircraft in less than 3 h. Methods were as above, except that the fifteen transects were spaced 1 km apart and covered 31% of the study area (Fig. 2).

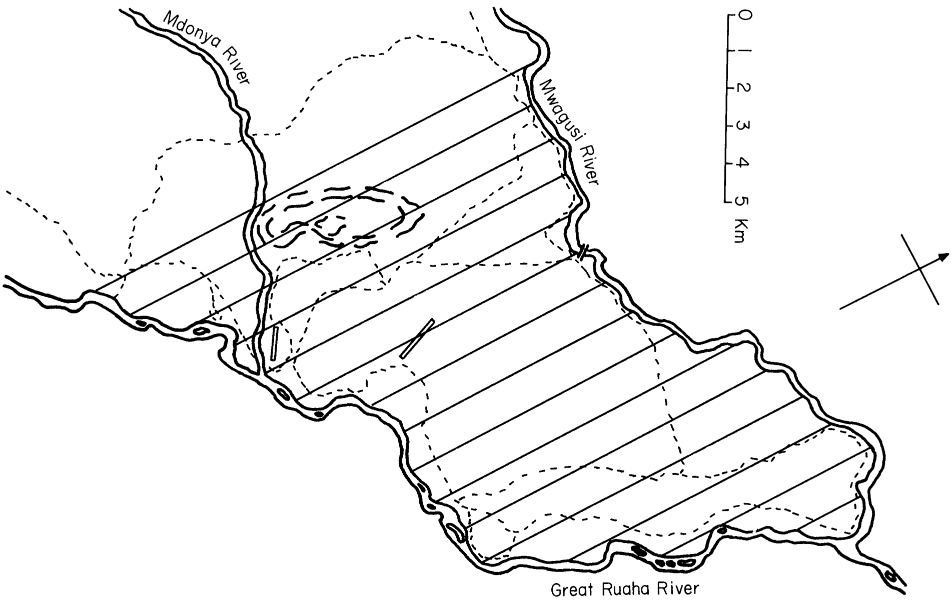

FIG. 2. Map of the Msembe study area showing flight paths. ═══, rivers; ------, tracks; ▭, airstrips; ——, flight paths.

Data analysis

Data analysis followed Norton-Griffiths (1975b). Population estimates were calculated separately for the National Park, Game Reserves, and Game Controlled Area. Each of these sub-zones was stratified into miombo, rift valley, and *Acacia/Commiphora* strata. The number of animals in each transect was summed. Corrections were made for under-counting by dividing the elephant transect totals by 0·928, the buffalo transect totals by 0·697, and the impala transect totals by 0·601 (Norton-Griffiths 1975a). The area of each transect was calculated from the product of the strip width (measured for each observer by calibration flights) and the transect length (measured from the map). The population estimate, variance, and 95% confidence limits were calculated by Jolly's method for unequal-sized sample units (Jolly 1969; Norton-Griffiths 1975b).

The numbers of dead elephants were expressed as a percentage of all elephants seen, both dead and alive. This was called the carcass ratio and was used as an indicator of elephant mortality (Douglas-Hamilton & Hillman 1981). The 1972/73 and 1977 population estimates for each species in the National Park were compared by a *d*-test (Norton-Griffiths 1975b):

$$d = \frac{(\hat{Y}_1 - \hat{Y}_2)}{\sqrt{\text{var}(\hat{Y}_1) + \text{var}(\hat{Y}_2)}}$$

where $\hat{Y}$ and $\hat{Y}_2$ are the population estimates to be compared, and $\text{var}(\hat{Y}_1)$ and $\text{var}(\hat{Y}_2)$ are their respective variances.

Distribution maps were plotted for each species. While the densities are shown as densities per 20 × 20 km grid square (Fig. 4), an analysis of the factors determining distribution cannot be made using these grid square densities because the results are a function of the size of grid square chosen. The following method of analysis was recommended by Dr M. Norton-Griffiths (personal communication). The census zone was stratified according to the variable in question, and the density calculated for each transect segment passing through each stratum. Differences between strata were tested using a one-way analysis of variance.

RESULTS

Numbers

Population estimates

Population estimates, 95% confidence limits, and density estimates for the National Park, Game Reserves, Game Controlled Area, and Msembe study area are shown in Tables 1, 2, and 3. The whole census zone carried an estimated 43 685 ± 9254 elephants, of which 24 625 ± 7132 were found in the National Park. The National Park had a higher

TABLE 1. Population estimates ($\hat{Y}$) and 95% confidence limits (CL) for Ruaha National Park, Rungwa and Kizigo Game Reserves, and part of the proposed Mloa–Ilambi Game Controlled Area

Species	National Park		Game Reserves		Game controlled area	
	$\hat{Y}$	CL	$\hat{Y}$	CL	$\hat{Y}$	CL
Elephant *Loxodonta africana* (Blumenbach)	24 625	7132	14 528	5524	4532	3782
Buffalo *Syncerus caffer* (Sparrman)	18 393	17 569	24 412	19 378	1216	1121
Impala *Aepyceros melampus* (Lichtenstein)	9075	6598	1179	–	5131	–
Zebra *Equus burchelli* (Gray)	3761	1775	8099	3484	344	–
Giraffe *Giraffa camelopardalis* (L.)	3478	1861	2464	1087	1603	1374
Eland *Taurotragus oryx* (Pallas)	1755	1155	1788	–	124	–
Kudu *Tragelaphus strepsiceros* (Pallas) and *T. imberbis* (Blyth)	438	413	33	–	754	541
Sable *Hippotragus niger* (Harris)	470	–	4757	3045	188	–
Roan *Hippotragus equinus* (Desmarest)	313	–	303	–	596	–
Rhino *Diceros bicornis* (L.)	94	–	371	–	31	–
Hartebeest *Alcelaphus lichtensteini* (Peters)	250	–	2261	1395	0	–
Carcass ratio	5·5%		9·7%		9·4%	
Area (km²)	15 400		10 200		5900	

TABLE 2. Estimated density of each species in each of the three sub-zones

Species	Density (km⁻²) National Park	Game Reserve	Game controlled area	*F*
Elephant	2·41	0·94	0·77	7·72**
Buffalo	1·80	1·59	0·21	2·64
Impala	0·89	0·08	0·87	0·46
Zebra	0·37	0·53	0·06	1·23
Giraffe	0·34	0·16	0·27	6·39**
Eland	0·17	0·12	0·02	0·66
Kudu	0·04	<0·01	0·13	1·14
Sable	0·05	0·31	0·03	4·12*
Roan	0·03	0·02	0·10	–
Rhino	0·01	0·02	<0·01	–
Hartebeest	0·02	0·15	0·00	–
Tree damage index	2·34	1·73	1·22	13·85**

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$.

TABLE 3. Population estimates ($\hat{Y}$), 95% confidence limits (CL) and density estimates for the Msembe study area (130 km²)

Species	$\hat{Y}$	CL	Density (km^{-2})
Elephant	534	195	4·11
Buffalo	2686	–	20·66
Impala	794	740	6·10
Zebra	38	–	0·29
Giraffe	61	51	0·47
Kudu	16	–	0·12
Rhino	19	14	0·14
Carcass ratio		3·8%	

elephant density than either the Game Reserve or the Game Controlled Area, and the Msembe study area had an elephant density of over 4 km^{-2}. The carcass ratio suggested that the highest mortality rates were in the Game Reserve and Game Controlled Area, and the lowest were in the Msembe study area.

Comparison with earlier estimates

Between February 1965 and November 1966 Savidge (1968) made thirteen aerial total counts in the Rift Valley stratum of the Park. His counts covered the area between the Great Ruaha, Mdonya, and Mwagusi Rivers, and the Ndanyanya escarpment. He estimated the area to be approximately 410 km², but this estimate would have been based on the earlier maps of the Park. Maps drawn since then were used by Bjornstad (1976; Fig. 3) to compile a new map which gives this part of the Park an estimated area of 295 km². This figure and Norton-Griffiths' (1975a) correction factor for undercounting elephants give a dry season density estimate of 1·53 ± 0·66 km² for 1965 (Table 4). A comparison with the 1977 density estimate (4·11 ± 1·47 km²) for the Msembe study area, which lies completely within the area counted by Savidge, suggests an 8% per annum increase between 1965 and 1977.

The 1965 density estimate of 1·53 ± 0·66 elephants km^{-2} can also be compared with the Rift Valley stratum estimates for 1972 and 1977, which were respectively 1·65 ± 0·62

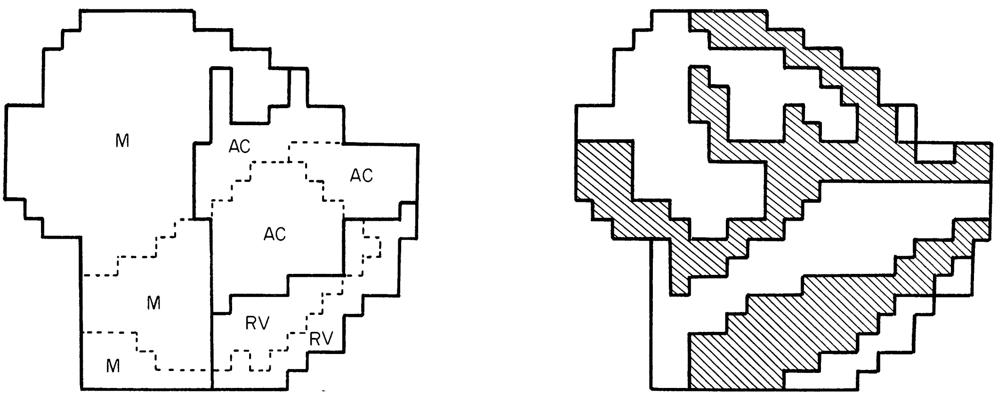

FIG. 3. (a) The three vegetation strata: miombo (M), *Acacia–Commiphora* (AC) and Rift Valley (RV). ——, census zone boundary and boundary between vegetation strata; ------ , census boundary of National Park. (b) The two water strata: the river stratum (shaded) and the non-river stratum (unshaded).

TABLE 4. Savidge's (1968: Appendix A) counts of the area between the Great Ruaha River, Mdonya River, Mwagusi River, and the Ndanyanya escarpment for the dry season months only. The numbers of elephants seen were corrected for undercounting (Norton-Griffiths 1975a)

Date	Total elephants seen (n)	Corrected total ($n \div 0{\cdot}928$)	Density (km^{-2})
June 1965	386	416	1·41
July 1965	535	577	1·96
August 1965	603	650	2·20
September 1965	–	–	–
October 1965	267	288	0·98
November 1965	–	–	–
November 1966	300	323	1·09

Mean = 1·53; SE = 0·24; 95% confidence limits = ±0·66.

TABLE 5. Comparison between 1972/73 and 1977 population estimates for Ruaha National Park

Species	Population estimate 1972/73	1977	d	P
Elephants	16 355	24 625	2·31	<0·05
Buffalo	13 972	18 393	0·51	NS
Impala	13 228	9075	1·00	NS
Zebra	6025	3761	1·17	NS
Giraffe	2430	3478	1·01	NS
Eland	2080	1755	0·49	NS
Kudu spp.	797	438	0·91	NS
Rhinoceros	447	94	–	NS

(Norton-Griffiths, personal communication) and 4·56 ± 2·61 suggesting a mean rate of increase of 9% per annum but with most of the increase having occurred after 1972.

The 1972 dry season elephant population estimate for Ruaha National Park was 15 966 ± 2297 (Norton-Griffiths 1975a) and in 1977 it was 24 625 ± 7132 (Table 1). This difference, which is significant ($d = 2{\cdot}38$, $P < 0{\cdot}05$), represents a 54% increase in 5 yr, or an exponential increase of 9% per annum (if the increase is due to reproduction) or a mean increase of 1732 elephants per annum (if the increase is due to immigration).

None of the other species showed a significant change between 1972/73 and 1977 (Table 5). There was no consistent trend in large herbivore numbers (Wilcoxon matched-pairs signed-ranks test, $T = 17$, $n = 8$, NS). Note that the rhino estimate had dropped to one-fifth of the 1972/73 estimate. This could be a consequence of the heavy rhino poaching within the Park.

Distribution

Distribution of each species

Over the whole census zone, the highest elephant densities were recorded within the National Park (Fig. 4, Table 2) and the lowest densities were around the edges of the census zone. There were significant differences in elephant density between vegetation type, river and non-river strata, and subzones (Tables 2 and 6). Within the National Park elephant densities varied significantly between vegetation types (Table 6), being highest in the Rift Valley stratum (Fig. 4).

TABLE 6. Results of statistical tests for differences between strata

Species	Complete census zone		National Park		Game Reserves		Game controlled area	
	Between vegetation strata *F*	Between river and non-river strata *t*	Between vegetation strata *F*	Between river and non-river strata *t*	Between vegetation strata *F*	Between river and non-river strata *t*	Between vegetation strata *F*	Between river and non-river strata *t*
Elephant	3·17*	2·16*	3·94*	1·06	2·59	0·96	0·01	1·55
Buffalo	0·05	1·92	0·99	0·81	1·95	1·93	0·65	1·21
Impala	6·32**	1·91	2·69	1·50	0·46	–	0·93	–
Zebra	8·62**	1·87	2·19	1·67	9·72**	0·84	–	–
Giraffe	1·92	0·84	2·54	1·34	1·54	1·34	1·26	1·40
Eland	2·49	0·07	1·79	1·06	–	0·49	1·35	–
Kudu	4·50*	1·28	0·96	–	–	0·25	1·63	0·55
Sable	–	0·55	–	0·95	4·15	0·92	–	–
Roan	–	–	–	–	–	–	0·42	–
Rhino	–	–	–	–	–	–	–	–
Hartebeest	–	–	–	–	–	1·49	–	–
Tree damage	2·98	1·32	0·55	0·08	0·36	0·43	2·52	1·94

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$.

For the whole census zone, and then for each division of the census zone (National Park, Game Reserve and Game Controlled Area), an *F*-test was used to test for a difference in the density of each species between the three vegetation strata (miombo, *Acacia-Commiphora*, and Rift Valley), and a *t*-test was used to test for a difference in the density of each species between the stratum with a major river (river stratum) and without a major river (non-river stratum). No tests were carried out when a species was restricted to only one stratum or when the animals were so sparsely distributed that most sample units contained none. Note that in a Table with sixty-two statistical tests, three are likely to be significant at the 5% level of probability by chance alone.

Buffalo were distributed throughout the census zone in large herds or small groups (Fig. 4). Densities were lowest in the Game Controlled Area (Table 2) but there were no significant variations in buffalo distribution. Few impala were seen in the Game Reserves (Fig. 4, Table 2). This was because impala densities were significantly higher in the Rift Valley stratum (Table 6) which did not fall in the Game Reserves. Zebra densities were significantly higher in the miombo zone (Table 6), and within the Game Reserves this was the only species to show significant variations in distribution. No zebra were seen in the eastern half of the census zone. Giraffe were recorded throughout the census zone (Fig. 4), but there were significant variations between sub-zones with the highest densities in the National Park and the lowest densities in the Game Reserves. Eland were seen most frequently in the miombo zone (Fig. 4). Kudu occurred mainly in the eastern half of the census zone (Fig. 4) and showed a significant difference between vegetation types, with the highest densities in the Rift Valley zone. Sable were seen only in the miombo (Fig. 4), resulting in a significantly higher density in the Game Reserve (Table 6). Hartebeest were also restricted to the miombo zone (Fig. 4). Roan were very sparsely distributed. Of the few rhino seen, most were in the miombo of the Game Reserve.

Tree damage differed significantly between sub-zones (Table 2), the least damage being recorded in the Game Controlled Area. Tree damage was highest in the National Park, and particularly around the confluences of the Great Ruaha, Mdonya, and Mwagusi rivers, and in the central part of the census zone, but decreased towards the edges of the census zone. Thus the general pattern of tree damage corresponds with the distribution of elephants. This is what one would expect: since most tree damage is caused by elephants in the dry season (Barnes 1979), the tree damage index is a measure of elephant distribution

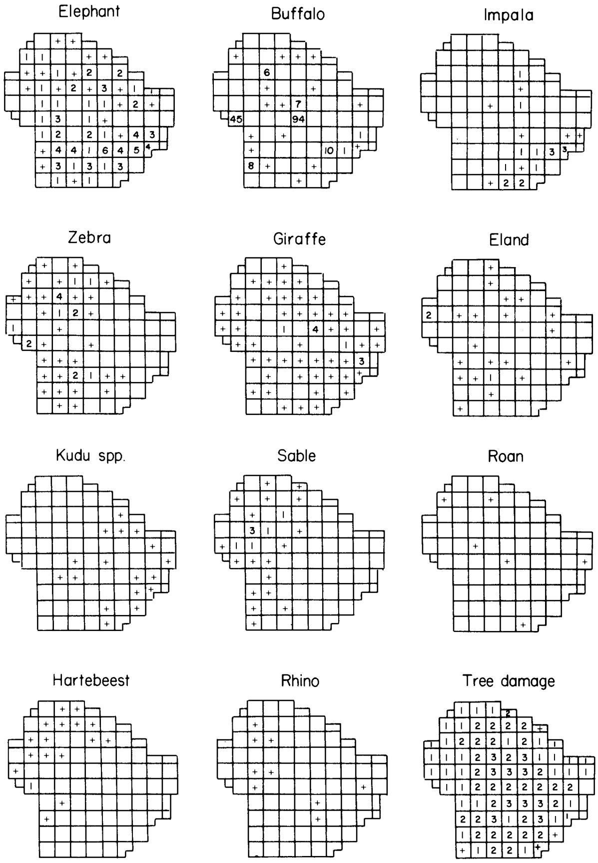

FIG. 4. The distribution of large herbivore species. The density of each species in each 20×20 km square is shown. A blank square signifies that no animals were seen. +, <1 km^{-2}; 1, 1–1·9 km^{-2}; 2, 2–2·9 km^{-2}; 3, 3–3·9 km^{-2}, etc.

over the whole dry season, and the elephant densities are an instantaneous measure of elephant distribution. The two measures are well correlated ($r = 0{\cdot}348$, d.f. $= 70$, $P < 0{\cdot}01$).

Variables influencing animal distribution

The distribution of zebra, eland, sable, and hartebeest can be explained by the distribution of miombo woodland. The distribution of impala and kudu can be explained by the distribution of Rift Valley vegetation. Elephant densities were higher close to water, but this does not explain why the elephant density was significantly higher in the National Park, or why elephant density fell off towards the edges of the census zone.

The distribution of elephants is best explained by the distribution of human pressures, as there is an inverse correlation between elephant density and human pressures (Table 7). Illegal hunting occurs in the Game Controlled Area where there are also some settlements. The Game Reserves are patrolled infrequently and the carcass ratio indicates that mortality, due largely to illegal hunting, is similar to that in the Game Controlled Area. There were no settlements in the Game Reserve. There were no settlements in the National Park which is patrolled more frequently than is the Game Reserve and has a lower

TABLE 7. Human pressures and herbivore densities in each of the sub-zones of the census zone

	Rift Valley sector of National Park	National Park	Game Reserves	Game controlled area
(a) Hunting	none	+	++	++
(b) Settlement	none	none	none	+
Total human pressures (sum of a and b)	none	+	++	+++
Elephant density (km^{-2})	4·56	2·41	0·94	0·77
Density of other large herbivores (km^{-2})	7·60	3·72	2·98	1·69
Tree damage index	2·20	2·34	1·73	1·22

TABLE 8. Comparison of elephant densities between the Rift Valley stratum of the National Park and the Rift Valley stratum of the Game Controlled Area

	Elephant density (km^{-2}) in Rift Valley stratum		
Species	NP	GCA	t (d.f. = 19)
Elephant	4·56	0·63	3·53**
Buffalo	3·20	0·33	1·56
Impala	3·49	1·68	1·23
Zebra	0·39	0·00	–
Giraffe	0·24	0·48	1·05
Eland	0·20	0·00	–
Kudu	0·08	0·21	0·36
Tree damage index	2·20	1·88	2·97**

** $P < 0{\cdot}01$.

hunting mortality according to the carcass ratios. In the National Park the level of poaching is lowest in the Rift Valley stratum, which contains the Park H.Q. and has a good network of tracks.

The effect of human pressures was tested by comparing the density of each species in the Rift Valley stratum of the National Park with those in the Rift Valley stratum of the Game Controlled Area. Both areas are on similar soils, carry similar vegetation, and are close to water. The main difference between them is that both settlements and poaching occur in the Game Controlled Area Rift Valley stratum, while the National Park Rift Valley stratum has no settlement and very little poaching. Table 8 shows that the elephant density and tree damage index were significantly higher in the National Park part of the Rift Valley stratum. The densities of buffalo and impala were higher in the National Park part of the Rift Valley stratum, but not significantly so, and zebra and eland were not seen in the Game Controlled Area part of the Rift Valley stratum. The combined density of all large herbivores excluding elephants was 7·6 km^{-2} in the National Park Rift Valley stratum, and 2·7 km^{-2} in the Game Controlled Rift valley stratum. This, together with the combined herbivore densities (excluding elephants) in Table 7, suggests that human pressures affect the distribution of species other than elephants. However, the effect on individual species appears to be less marked than it is for elephants.

Comparison with earlier distributions

While Savidge's (1968) elephants counts covered only part of the Rift Valley stratum, Norton-Griffiths' (1975a) counts covered the whole National Park. Norton-Griffiths counted elephant and buffalo only in his 1972 dry season count, but counted all large mammals in his 1973 wet season count. His elephant and buffalo distribution maps

TABLE 9. The distribution of elephant and buffalo in the National Park in 1972, 1973 and 1977, shown as the density in each stratum and the proportion of the total population in each stratum

Date of Count		Density (km^{-2}) in each stratum			Percent of total population in each stratum		
Year	Season	M	AC	RV	M	AC	RV
(a) Elephant							
1972	Dry	1·37	1·86	1·65	31	46	23
1973	Wet	1·28	1·80	2·37	28	42	31
1977	Dry	1·99	1·56	4·56	31	26	43
(b) Buffalo							
1972	Dry	1·00	1·30	1·79	29	40	31
1973	Wet	1·92	1·76	0·68	45	45	10
1977	Dry	2·84	0·05	3·20	59	1	40

The stratum sizes are 3800 km^2, 4100 km^2 and 2300 km^2 for the miombo (M), *Acacia-Commiphora* (AC) and Rift Valley (RV) strata respectively.

combined wet and dry season data, and the distribution maps for the other species were wet season distributions, so none of his distribution maps can be compared with the 1977 distributions. Instead, the densities of elephant and buffalo in each stratum in 1972 and 1973 (Norton-Griffiths, personal communication) are compared with the 1977 densities in Table 9.

Taking the percentage of the total elephant population in each stratum (Table 9a), a *G*-test (Sokal & Rohlf 1969) showed no difference between the 1972 dry season and 1973 wet season distributions ($G = 1{\cdot}52$, d.f. = 2, NS), but there was a difference between the 1972 and 1977 dry season distributions ($G = 11{\cdot}79$, d.f. = 2, $P < 0{\cdot}01$) with a higher percentage of the population in the Rift Valley stratum. This difference could be due to unseasonal rainfall in the month preceding the 1972 count. In October 1972 27·7 mm of rain fell at Park H.Q. whereas the October mean for the years 1967–77 was 4·1 mm. In 1977 no rainfall was recorded in August (the month before the count); the August mean is zero. Thus it is possible that in November 1972 elephants had dispersed away from the Rift Valley stratum because of the availability of water and green vegetation elsewhere, and so their distribution was similar to the wet season distribution. Thus the small apparent increase in the Rift Valley elephant density estimate between 1965 and 1972 and the larger apparent increase between 1972 and 1977 may be a result of the 1972 Rift Valley density being unusually low due to unseasonal rainfall. Another possible explanation is that the increase in elephant numbers has been accompanied by a change in the elephant distribution within the Park since 1972.

The distribution of buffalo (Table 9(b)) differed significantly between the 1972 dry season and 1973 wet season ($G = 15{\cdot}07$, d.f. = 2, $P < 0{\cdot}001$) and also between the 1972 and 1977 dry seasons ($G = 59{\cdot}01$, d.f. = 2, $P < 0{\cdot}001$). The greater difference between the 1972 and 1977 distributions than between the dry and wet season distributions of 1972 and 1973 again suggests that the 1972 distribution more closely resembled a wet season distribution.

DISCUSSION

The distribution maps show the importance to some species (zebra, eland, sable, and hartebeest) of the miombo woodlands, at least in the dry season. Ruaha National Park straddles the ecotone between the miombo woodlands and associated soils of south and west Tanzania, and the more recent volcanic soils of north and central Tanzania. It also includes the soils of the Rift Valley system. These three soil-vegetation types and their associated fauna make Ruaha National Park an important conservation unit, but its existence at the time of the census was threatened by the high elephant density and the rapid changes in the woody vegetation (Barnes 1979). The data presented here show that the elephant population was increasing. The higher elephant population estimate in 1977 could be due to reproduction, immigration, or observer bias. Observer bias (the failure to count all the animals falling in the sample strips) is one of the most important sources of error in aerial censusing (Pennycuick & Western 1972; Caughley 1974; Caughley & Goddard 1975; Norton-Griffiths 1976). The 1977 observers were more experienced than were the 1972/73 observers, and so would be expected to see a higher proportion of the animals in their sample strips. If so, then all species would be expected to have a higher population estimate in 1977. Table 6 shows that this was not the case: some population estimates had increased while others had decreased, and only elephants showed a significant change. Therefore the higher 1977 population estimate is taken to represent a real increase in elephant numbers, although part of the increase could still be due to improved observer efficiency.

Elephants were the only species to show both a significant increase between 1973 and 1977 and a significant difference in density between areas of high and low human pressures. This suggests that the increase in elephant numbers within the National Park was caused by immigration due to increasing human pressures outside the Park. Elephants may suffer more than other species from increasing human pressures because of their devastating crop-raiding habits and their ivory.

Before 1946 over thirty settlements were scattered through the area which was to become the National Park (Savidge 1968). These settlements were all close to water, so elephants were denied access to potential watering sites. Instead they made fleeting nocturnal visits to the river and then travelled long distances to spend the day far from human disturbance (Barnes 1979). Between 1946 and 1964 these settlements were moved out of the Park and relocated to the east and south (Savidge 1968). This resulted in a change in the distribution of human pressures, although there may have been no change in the total number of elephants and people within the area. Before 1946 it is likely that human pressures were sparsely distributed throughout the area covered by the census zone, whereas after the resettlement programme they were concentrated round the edges. This would have caused elephants to move away from the areas of high human pressure and into the National Park. After the human population left the Park, elephants had unrestricted access to water sources within the Park. The long marches, which had previously been necessary between water sources and feeding areas, were no longer necessary. This may have resulted in an increase in juvenile survival, as Laws (1969) suggested happened at Tsavo.

The creation of the Park and the change in the distribution of human pressures coincided with a period of higher rainfall. Rainfall records for Ruaha National Park date from 1967, but rainfall records have been maintained at Madabira (about 60 km from Park H.Q.) since 1924. Taking the rainfall totals for the climatic year (September–August), there was a high correlation between the Ruaha National Park and Madabira for the years 1967–76 ($r = 0{\cdot}910$, d.f. $= 7$, $P < 0{\cdot}001$). Assuming that the correlation between the two stations has remained high during the last fifty years, the Madabira rainfall records may be used as an index of the Ruaha National Park rainfall. Between 1955 and 1970 there was a period of higher rainfall (mean = 877 mm) compared with the years before 1955 and the years after 1970 (mean = 614 mm) (Fig. 5). Since primary

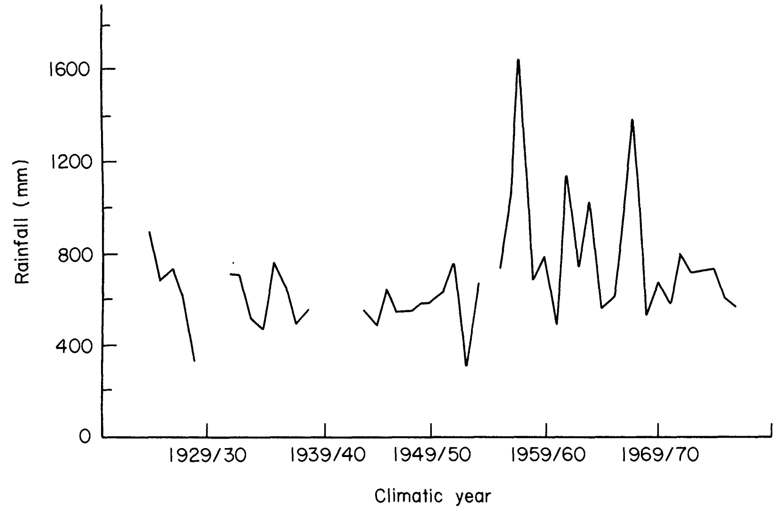

FIG. 5. The Madabira rainfall figures for the years 1924–1977. The rainfall for each climatic year (September to August) is shown.

production is proportional to rainfall (Rosenzweig 1968) there was an increase in the food supply between 1955 and 1970. This would result in higher conception rates, shorter mean calving interval, lower age of puberty, and possibly higher juvenile survival (Laws & Parker 1968; Laws 1968). Except for the severe dry season of 1976 when an unusually large number of elephants died (Barnes 1979), we know of no droughts which might have caused mortality (e.g. Corfield 1973; Phillipson 1975) to counter the 15-yr period of improved reproduction.

The combined result of the change in human pressures and the period of higher rainfall would have been a movement of elephants into the Park and a higher rate of reproduction, causing a gradual increase in the elephant density from 1946 onwards. Against the immigration hypothesis is the evidence that the increase in dry season elephant density in the Rift Valley stratum was much greater between 1972 and 1977 than between 1965 and 1972. Legal hunting stopped in 1973, and the Government's *ujamaa* policy moved people away from outlying hamlets into bigger settlements further away from the Park boundaries, so a decrease in immigration would have been expected between 1972 and 1977 compared with the 1965–1972 period. On the other hand, a change in elephant numbers in the Rift Valley stratum could represent a change in total elephant numbers within the Park, or a change in distribution within the Park. The most likely explanation is that the 1972 density in the Rift Valley stratum was lower than usual for that time of year because of the unseasonal rainfall in the month preceding the 1972 count.

The 4% carcass ratio in the Msembe study area probably represents the level of natural mortality since there was no hunting in the study area. Note that this figure may change seasonally since live elephants move while dead elephants do not, and dead elephants may be visible for several years. In any event, the overall carcass ratio of 7% for the whole census zone is very low relative to that found in elephant populations in Kenya, Uganda, and northern Tanzania during the 1976–77 period (Douglas-Hamilton & Hillman 1981) and suggests that poaching was relatively low at the time of the census.

CONCLUSION

The Ruaha elephant problem must be seen in the wider context of man/elephant interactions within East Africa, where the problem of 'compressed' elephant within National Parks has been superseded in its most classic examples, such as Tsavo and Kabalega, by the onset of massive poaching for ivory (Douglas-Hamilton 1979). Culling elephants can be an appropriate form of management as practised in Zimbabwe and South Africa, and has been discussed by Barnes (1979) for Ruaha, but only if poaching is entirely under control. The population of elephants defined by this census is one of the largest in Africa, comparable to that of the Selous Game Reserve in Tanzania of 109 000 (Douglas-Hamilton 1976) and the Luangwa Valley in Zambia of 35 000 (Douglas-Hamilton *et al.*, 1979). As such, the elephants of Ruaha represent a substantial potential asset, both economically and aesthetically. Yet the habitat damage which they cause also has wide implications.

The causes of the increasing Ruaha elephant population have important implications not only for Park management but also for those concerned with land use planning and regional development. If events inside the Park (increasing elephant densities and higher rates of tree loss) are a function of events outside the Park (the changing pattern of human activities) then the conservation of the Park's flora and fauna becomes more complex. For instance, management inside the Park (such as culling) could be off-set by further immigration from outside the Park, caused by forces over which the Park managers have no control.

The National Park and the two Game Reserves form a large part of the drainage basin of the planned Mtera dam lower down the Great Ruaha River. But the woodlands of the Park are rapidly disappearing (Barnes 1979) bringing the danger of soil erosion and higher sediment loads in the Great Ruaha and Mzombe Rivers which will drain into the new man-made lake. Park managers need to work with land managers outside the Park, and a management plan for Ruaha National Park should form part of an integrated land use development plan for the Mbeya, Iringa, Dodoma, and Chunya administrative regions of south-central Tanzania.

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REFERENCES

Barnes, R. F. W. (1979). *Elephant ecology in Ruaha National Park, Tanzania.* Ph.D. thesis, University of Cambridge.

Bjornstad, A. (1971). *A preliminary report on recent vegetation change in Ruaha National Park.* Report to Tanzania National Parks. Typescript, 2 pp.

Bjornstad, A. (1976). *The vegetation of Ruaha National Park, Tanzania. I. Annotated check-list of the plant species.* University of Oslo, Norway.

Bjornstad, A. (1977). *Vegetation map of Ruaha National Park eastern central area.* University of Oslo, Norway.

Caughley, G. (1974). Bias in aerial survey. *Journal of Wildlife Management* **38,** 921–933.

Caughley, G. (1976). The elephant problem—an alternative hypothesis. *East African Wildlife Journal,* **14,** 265–283.

Caughley, G. & Goddard, J. (1975). Abundance and distribution of elephants in Luangwa Valley, Zambia. *East African Wildlife Journal,* **13,** 39–48.

Corfield, T. F. (1973). Elephant mortality in Tsavo National Park, Kenya. *East African Wildlife Journal,* **11,** 339–368.

Douglas-Hamilton, I. (1976). *Selous elephant and wildlife survey.* Report to DANIDA/I.U.C.N., typescript 70pp.

Douglas-Hamilton, I. (1979). Why resurrect the dead elephant issue? *Africana,* **6,** 3–4.

Douglas-Hamilton, I., Hillman, A. K. K., Holt, P. & Ansell, P. (1979). *Luangwa Valley Elephant, Rhino and Wildlife Survey.* Report to I.U.C.N./W.W.F./N.Y.Z.S., typescript 57pp.

Douglas-Hamilton, I. & Hillman, A. K. K. (1981). Elephant carcasses and skeletons as indicators of population trends in low level aerial survey techniques. ILCA Monograph **4,** 113–129.

Johansson, J. (1976). Vegetation of the Mtera basin with reference to the impoundment. *Ecological Studies of the Mtera Basin.* SWECO, Stockholm.

Jolly, G. M. (1969). Sampling methods for aerial census of wildlife populations. *East African Agriculture and Forestry Journal,* **34,** 46–49.

Laws, R. M. (1968). Interactions between elephant and hippo populations and their environments. *East African Agriculture and Forestry Journal 33*: *Special Issue*: pp 140–147.

Laws, R. M. (1969). The Tsavo Research Project. *Journal of Reproduction and Fertility, Supplement,* **6,** 495–531.

Laws, R. M. & Parker, I. S. C. (1968). Recent studies on elephant populations in East Africa. *Symposia of the Zoological Society of London,* **21,** 319–359.

Norton-Griffiths, M. (1975a). The numbers and distributions of large mammals in Ruaha National Park, Tanzania. *East African Wildlife Journal,* **13,** 121–140.

Norton-Griffiths, M. (1975b). *Counting Animals.* African Wildlife Leadership Foundation, Nairobi, Kenya.

Norton-Griffiths, M. (1976). Further aspects of bias in aerial census of large mammals. *Journal of Wildlife Management,* **40,** 368–371.

Pennycuick, C. J. & Western, D. (1972). An investigation of some sources of bias in aerial transect sampling of large mammal populations. *East African Wildlife Journal,* **10,** 175–191.

Phillipson, J. (1975). Rainfall, primary production, and 'carrying capacity' of Tsavo National Park (East), Kenya. *East African Wildlife Journal,* **13,** 171–201.

Pratt, D. J. & Gwynne, M. D. (1977). *Rangeland Management and Ecology in East Africa.* Hodder & Stoughton, London.

Rosenzweig, M. L. (1968). Net primary productivity of terrestrial communities: prediction from climatological data. *American Naturalist,* **102,** 74–76.

Savidge, J. M. (1968). Elephants in the Ruaha National Park, Tanzania—management problem. *East African Agriculture and Forestry Journal,* **3,** 191–196.

Sokal, R. R. & Rohlf, F. J. (1969). *Biometry.* W. H. Freeman & Co., San Francisco.

Stromquist, L. (1976). Land systems of the Great Ruaha drainage basin upstream the Mtera dam site. *Ecological Studies of the Mtera Basin,* SWECO, Stockholm.

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