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TSETSE CONTROL HUNTING AS A MEASURE OF LARGE MAMMAL POPULATION TRENDS IN THE OKAVANGO DELTA, BOTSWANA

by

G. CHILD (1), P. SMITH, M. B. E (2), and W. VON RICHTER (1)

Cet article passe en revue les utilisations et les possibilités des résultats de 23 ans d'élimination des grands mammifères d'un territoire de 777 km², entreprise par les services de contrôle de la mouche tse-tse. Ces résultats donnent une base suffisante pour l'interprétation de l'évolution des populations. Leur analyse fournit aussi des informations sur la distribution, les déplacements saisonniers et la reproduction de plusieurs espèces animales dans une région importante du point de vue zoogéographique, mais peu connue. Il conclut que le programme d'élimination n'a pas atteint son objectif, que plusieurs espèces se maintiennent ou sont en accroissement dans la région effectivement chassée et que cette évolution est en général parallèle à celle des régions voisines.

INTRODUCTION

Organised hunting of game animals began in the early 1940's as one measure in a Government campaign to halt the spread of tsetse fly, *Glossina morsitans* then threatening Maun, the administrative headquarters of Ngamiland in northern Botswana. Elsewhere in the country anti-tsetse operations have relied upon the destruction of the most favourable habitats or spraying with insecticides.

Lewis and Krog (1962) and Brown *et al* (1963) outline the reinvasion of large areas from several small foci to which the fly had become limited by the turn of the century. They attribute the recession to the Great Rinderpest pandemic in Botswana in about 1896, decimating the ungulate populations on which the fly depended for food. The apparent correlation between the epizootic and the disappearance of tsetse from much of its former range prompted shooting operations in several parts of Africa, in an attempt to simulate the effects of the disease. Summers (1967) has, however,

(1) Department of Wildlife and National Parks, Botswana. The present study was undertaken while the first and third authors were engaged on an Ecological Survey of N. E. Botswana, carried out by F. A. O. on behalf of the Government of Botswana.

(2) Tsetse Fly Control Department, Botswana.

reviewed the historical record in detail and finds that the fly had receded from much of its former range in adjacent parts of Rhodesia several decades before the pandemic. In north-eastern Botswana the process was clearly discernible in the Kazungula/ Lesuma area some years before the disease and Summers concludes that the contraction in the tsetse belts was due to ecological changes associated with differences in land use or fluctuations in climate.

The present paper evaluates the records from hunting along the Maun Front (Fig. 1) with a view to determining whether it was achieving its objective of creating a game-free corridor of some 300 sq. miles (777 sq. km.). These records are the only numerical data on wildlife populations in Botswana that extend as far back as 25 years, so the opportunity has been taken to explore the uses and limitations of such evidence as an indication of the general biology of the populations sampled by the hunting.

A preliminary account of Tsetse Control Hunting along the Maun Front between 1942 and 1963 is given by Graham (1967). His conclusions are based mainly on the annual kills, whereas in the present paper these returns are incorporated into a syndrome which also uses monthly kills over a 10 year period, the details of the examinations of skulls of animals shot during hunting operations in 1965/6 and evidence of changing trends in populations reported by old residents in surrounding areas. This additional information is generally consistent with Graham's conclusions but it gives greater insight into the general biology of the important species hunted and of mechanisms applying within the populations in the area. A number of relatively minor discrepancies exist beween the kills reported by Graham and those used in the present paper, which is based as far as possible on the original field data sheets, as several errors were detected in the summaries of these sheets prepared for Graham.

THE STUDY AREA

Description

The Maun Front Tsetse Control Area is situated along the southern fringe of the Okavango Swamps in northern Botswana (Fig. 1). The swamps interdigitate with dry marginal areas, so providing a complexity of habitat types which support a remarkably varied large mammal fauna of which some 20 species were hunted during Tsetse Fly Control Operations.

The annual rainfall at Maun averages 463.7 mm and is generally

restricted to summer (November to March). Mean monthly temperatures are then around 32°C, before declining to the winter minimum of 15°C in June or July and increasing to 35°C at the end of the dry season.

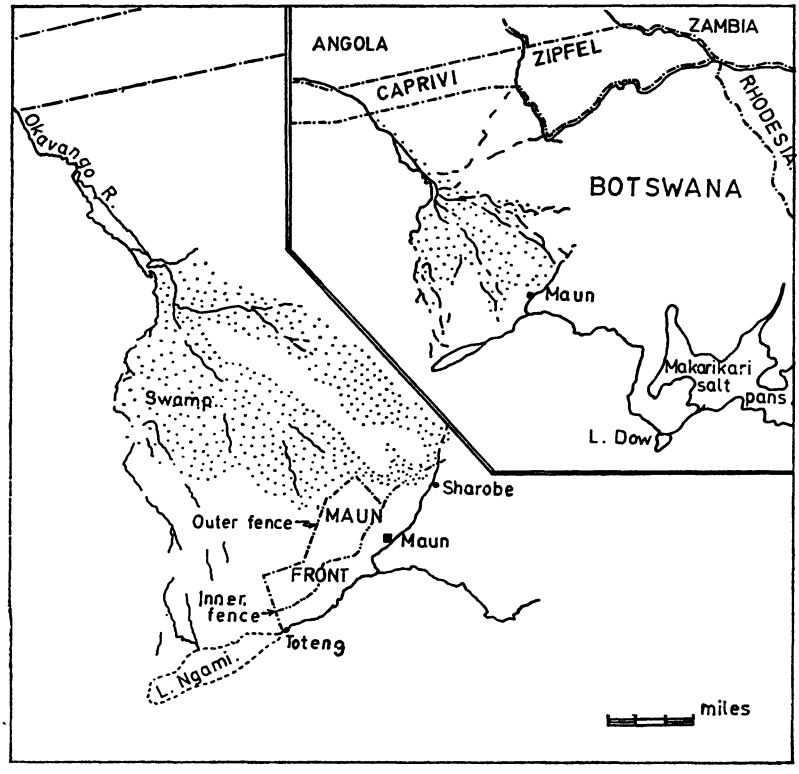

Fig. 1. — The situation of the Maun Front Tsetse Fly Control area in relation to the Okavango swamps and other geographical features (scale represents 30 miles).

The country is flat and minor undulations determine the courses of the ' molapos ' or open grassed drainage lines, which meander across the area from the swamps towards Lake Ngami. These drainages are subject to seasonal inundation from the swamps, which usually reach a peak in the area in June or July, although the pattern of flooding is variable from year to year.

Many molapos are fringed by riparian vegetation which is particularly dense along the lower Nxaragha (Fig. 2). This strip is often backed by *Acacia giraffae* woodland in which *A. tortilis* is a co-dominant in a tongue of sandveld penetrating the west of

the area. *A. giraffae* is also conspicuous on light sandy soils in the mosaic of open woodland between the molapos and here mopane, *Colophospermum mopane,* is often dominant. The geographical limit of mopane ends rather abruptly and cuts across the Hunting Area east of the Matsibe Molapo.

The area was grazed by livestock prior to the reinvasion of the tsetse fly and habitats have been further modified by the cutting of all trees in a 300 yard wide belt along part of the inner fence (Fig. 1) ; the ring barking of *Acacia* spp., particularly of *A. giraffae* in areas with a dense fly population and through the effects of regular burning, early in the dry season, associated with the hunting.

History of hunting operations

This account is based upon a thorough search of all existing Tsetse Fly Control Department records, and on the verbal evidence of old employees. There are some periods, however, particularly between 1950 and 1954, when the history is somewhat incomplete.

The earliest hunting associated with Tsetse Fly Control was a game drive held in 1916. The next attempt to reduce game took place in 1939 when parts of the Maun Front were thrown open to sportsmen, but it was not until 1940 that local tribesmen were specially recruited as hunters. Macauley (1942) did a survey of the tsetse and animal trypanosomiasis situation in Ngamiland between 1940 and 1942, and during 1940 and 1941, 1,887 head of game was shot, mainly along the north bank of the Nghabe river (Fig. 2).

Hunting was properly organised in 1942 and continued along similar lines until 1967. Initially it was concentrated around Maun in the hope that the disturbance would drive game north through gaps in the inner fence, then under construction. This failed and by 1945 an increasing number of hunters were active over the whole area enclosed by this fence and the Thamalakane and Nghabe rivers from Sharobe to Toteng. Hunting was discontinued in the eastern sector in about 1949, after shooting began between the inner and outer fences in 1947/48. At the same time the effective area hunted along the north bank of the Nghabe river was reduced to approximately that area now enclosed by the game and cattle fences (Fig. 2) and hunted until October, 1967.

The area was surrounded by a series of game fences supplemented by cattle fences in which it was hoped to create a game and cattle free zone denying the fly essential vertebrate blood. The

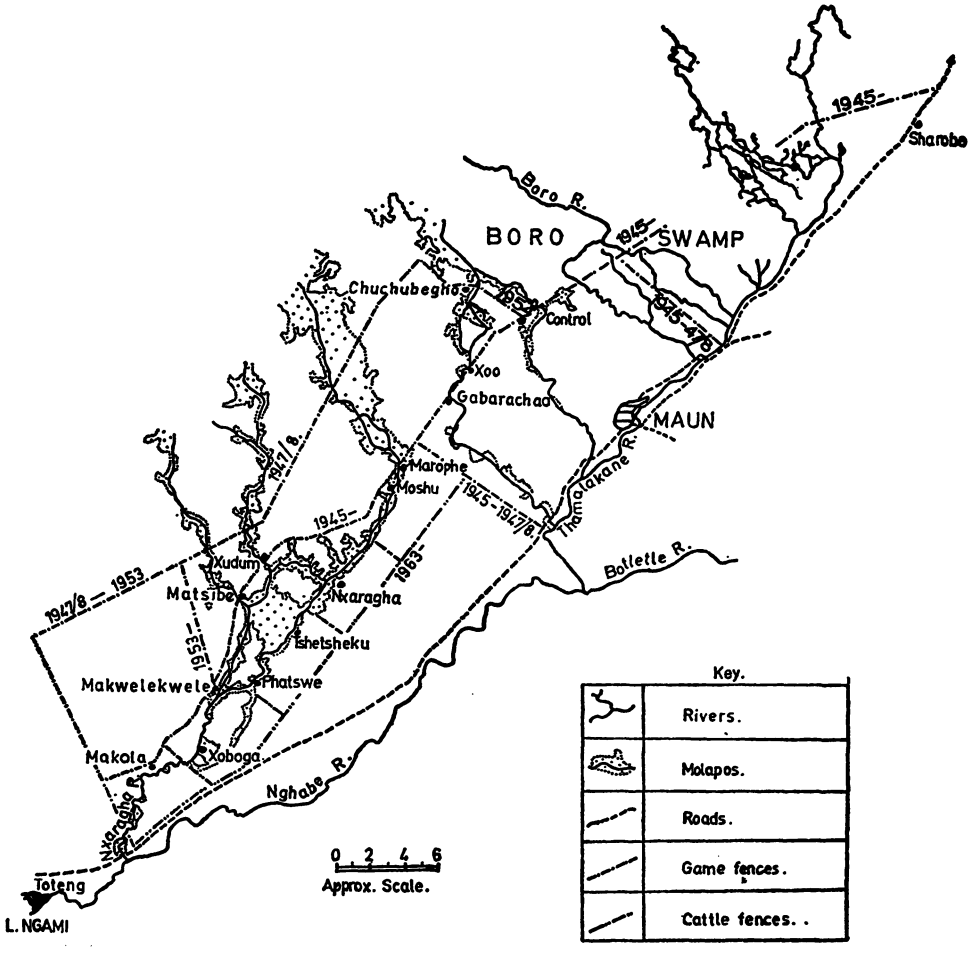

Fig. 2. — The Maun Front Tsetse Fly Control area showing the distribution of water courses, the location of hunting camps and the position of the game and cattle fences (scale in miles).

dates of completion and, where applicable, demolition of these fences are shown in Fig. 2. The Game fences consisted of five to eight strands of high tensile steel wire 10 to 16 ins. (25-40 cm.) apart, with the top strand about seven ft. (2.1 m.) from the ground. Wooden droppers were spaced at 12 ft. (3.6 m.) intervals and there were three of these between successive wooden poles along the outer fence and five between the poles on the inner fence, but these fences were only a partial barrier to large species. The veterinary fences enclosing the south of the area were standard cattle fences with steel standards and droppers.

ORGANISATION OF HUNTING OPERATIONS

The organisation of hunting on the Maun Front was essentially similar to that in a Rhodesian Tsetse Area which is being described in some detail elsewhere (Riney and Child, *Ms.*) so that it is appropriate here to outline the method only briefly. Most of the hunting was done by regular African hunters armed with ex-army .303 rifles and stationed in groups in semi-permanent camps scattered over the area in places where game was locally most plentiful or most likely to break into the area. This hunting was supplemented to a limited extent by that done by the supervisory staff and to a greater extent by men patrolling the fences to prevent concentrations of game from building up along them. Animals were also shot by hunters employed to provide meat for gangs of labourers eradicating tsetse habitats.

Usually from two to four regular hunters were stationed in each camp and operated on foot, alone or in pairs. Generally, these men returned to their camps during the heat of the day so that hunting intensity diminished rapidly over a few miles from the camps. At the end of each month the hunters gathered at the area headquarters to be paid and to hand in the tail and ears as proof of each animal shot. A system of bonuses for killing certain species was tried, but proved ineffective in promoting a greater sustained offtake from these species.

TABLE 1

Results of a three month comparison between the results of regular day hunting and night hunting with shotguns

	Night Hunters	Regular Hunters
No. Hunters	3	2
Animals shot :		
Buffalo		7
Kudu	2	4
Warthog		20
Reedbuck	10	5
Duiker/Steenbuck	34	10
Others	2	2
Total	48	48
Rounds used	96	163
Av. rounds/kill	2.0	3.4
Av. kills/Hunter	16	26

Night-hunting, as a means of improving the effectiveness of hunting certain species, was also tried on an experimental basis as reports from Rhodesia suggested that it was useful against such species as bushbuck. A group of three hunters was armed with shotguns and torches and the results of the first three months trial are compared with the kills from a control group of two regular hunters in Table 1. There was a lower overall success rate per night hunter, although the number of shots per animal was considerably better. The method was, however, abandoned after a further trial as it was ineffective against warthog, the primary source of tsetse blood meals in three areas on the edge of the swamps (Table 2).

TABLE 2

Results of analysis of tsetse fly blood meals from the Maun Front — 1960 to 1963 (*)

Species (U = Unidentified)	Blood Meals No.	%
Warthog	186	43.3
Kudu	45	10.5
Bushbuck	10	2.3
Reedbuck	20	4.7
Duiker	2	0.5
U. Antelope	9	2.0
Buffalo	22	5.1
U. bovid	44	10.2
Giraffe	1	0.2
Hippo.	3	0.7
Antbear	1	0.2
Man	14	3.3
U. primate	11	2.6
Horse	1	0.2
Dog family	1	0.2
U. mammal	34	7.9
Ares	8	1.9
Reptile	1	0.2
Total Positive	413	96.0
Total Negative	17	4.0
Total	430	100.0

(*) Blood meal identification by Lister Institute of Preventive Medicine, London.

Game drives, in which all the hunters systematically swept across a portion of the area, were also tried. The first such drive led to the killing of high numbers of kudu and duiker but was correspondingly less satisfactory against other species. Three such drives were held and the results are summarised in Table 3, which shows that successes were lower in subsequent drives, even for some of the most susceptible species.

Uses and limitations of hunting returns

Unless noted to the contrary, the present paper restricts consideration to the period 1942 to 1964 for annual kills and to the ten years ending June, 1965, for the detailed monthly returns of the numbers of animals shot by various classes of hunters and of the number shot from individual camps.

The first set of records, together with supplementary reports, provides useful information on the species that occurred in the area over a 23-year period, while the monthly camp kills indicate

TABLE 3

Results of three game drives on the Maun Front

		Species shot									
Date	No. Hunters	Kudu	Impala	Wildebeest	Reedbuck	Steenbuck	Duiker	Warthog	Gemsbok	Zebra	Total
Aug. 1959	21	47	1	18	13		97	9	2		187
Dec. 1959	17	7	1		2	7	23	5			45
Dec. 1962	27	8		4	9	35	47	15		1	119
Total	65	62	2	22	24	42	167	29	2	1	351

the relative seasonal distribution over the Hunting Area of the important species. These continuous records therefore provide valuable zoogeographical data from a poorly known region. Their usefulness as a measure of the effectiveness of Tsetse Control Hunting in eliminating or reducing game along the Maun Front could, however, be questioned on the grounds that the organisation of the hunting was not constant throughout the period. Riney and Child (*Ms.*) examine this problem in relation to Tsetse Hunting records from Rhodesia and conclude that it is not a serious objec-

tion provided the changes are taken into account and, more especially, provided conclusions are based upon changing trends in hunting success over a number of years. These conclusions are strengthened if a syndrome capable of only specific interpretation can be built up using the hunting returns along with other types of information.

The same conclusion was reached from the detailed analysis, species by species, of the Maun Front records. Before proceeding to a discussion of the effects of hunting and the influences of changes in its organisation on individual species, it is pertinent to review factors which may have prejudiced the value of the hunting returns from all species.

The impact on a given species may have varied with overall hunting intensity, if hunters tended to concentrate on more favoured species when the hunting pressure was low. There is no evidence that this affected the trends in a hunter's average annual kill, although an influx of buffalo into the Hunting Area sometimes coincided with a drop in the number of small antelope shot in individual months, but this did not affect the trends of annual kills significantly.

The extent to which hunters are supervised could influence the numbers of animals shot, but frequent attempts to improve supervision, reported in Departmental Reports, produced no more than minor temporary upward deflections in the graphs of annual kills. Lack of adequate supervision during the 1950 to 1954 period may have contributed to the crest in the number of animals shot, but marked changes in the organisation of the hunting were probably more important. Fewer regular hunters were employed, but other employees were armed, and their hunting was not confined to the Hunting Area, nor were they classed as hunters, although their kills were added to the total which accounts for the apparent improvement in hunter efficiency. These crests were also influenced by the introduction of from one to three specialised European rangers, who hunted from vehicles, and who were more effective against certain species. It is therefore necessary to ignore these years when interpreting the trends in kills over the 23 year period. The subsequent trough shown by the graphs of most species was thus related to the reorganisation of the hunting.

Policy decisions as to whether a species should or should not be hunted in a particular year would obviously be reflected in the shape of the graph, as for example in the case of reedbuck before 1952, when the species was subjected to uneven attention, or small antelope, which were not shot by regular hunters in 1954. Most policy decisions caused only temporary deflections of the overall

trends, although these were sometimes marked, as in the case of the increased kill among small antelope, and a corresponding drop in some other species, associated with game drives. Variations in rainfall and the extent of flooding in the swamps were probably as significant as most such decisions, as the 1947 peak in the average hunter's success coincided with a very dry year and the 1954/55 trough with exceptional flooding.

Animals shot for rations by specially employed hunters were included in the overall annual totals, although many were shot outside the Hunting Area. This hunting became significant from 1955, when the programme of eradicating tsetse habitats was embarked upon, and was intensified with the introduction of specialised hunting patrols during 1961. Where significant numbers of a species were shot for this purpose, the animals killed by regular camp hunters are graphed separately ; but with the possible exception of buffalo, show a similar trend to that of the total kills.

Regular camp hunters also poached outside the prescribed Hunting Area, but the extent of this activity probably did not vary much over the years, as the pattern of kills from the various camps with different hunters was similar in successive years, giving distribution patterns for the various species which fit in with their known habitat requirements and movement patterns. Its main effect would therefore have been to extend the effective hunting area, which would not have clouded the broad conclusions reached in this paper. Even a lack of ammunition in February, 1958, did not affect the annual kill for that year to a marked extent, although it necessitated appropriate adjustment when collating seasonal differences in hunting successes.

It has been suggested that the average hunter's success was lower than that recorded as hunters probably procured ears and tails from villages in surrounding areas. If this were significant it would produce a regression line with a positive number of kills for zero hunters, whereas the limited sample based on the last nine years of hunting, when conditions were standardised, indicates a straight line correlation, with the opposite tendency, between the numbers of hunters and the kill. Further, this source of tails and ears would have been limited and would not have increased proportionately with the enrolment of additional hunters, which would have detracted from the apparent linear relationship and would tend to induce a trend opposite to that shown. It may therefore be assumed that the hunters did not obtain significant numbers of tails and ears from unofficial sources.

TABLE 4 Total annual kills from tsetse

Year	Average Number of Hunters	Buffalo	Warthog	Kudu	Reedbuck	Impala	Tsessebe	Wildebeest
1942	—	58	81	335	15	36	55	43
1943	—	210	133	163	—	61	78	68
1944	54	274	242	377	18	145	177	128
1945	86*	502	436	477	52	152	299	242
1946	102	548	340	563	40	208	161	268
1947	55	111	132	506	14	140	98	364
1948	41	201	427	167	23	74	23	190
1949	48	200	670	229	87	85	64	108
1950	29	200	612	230	76	80	38	165
1951	29	280	422	276	3	173	116	108
1952	35	467	865	298	67	257	119	319
1953	21	414	394	252	152	342	62	158
1954	26	375	221	286	131	300	56	78
1955	33	380	220	238	104	126	29	23
1956	42	499	501	430	167	229	66	16
1957	41	362	597	601	188	176	19	139
1958	40	577	455	383	196	248	66	168
1959	46	373	557	703	353	194	47	69
1960	45	357	613	563	321	204	42	40
1961	44	522	463	330	235	304	49	19
1962	45	439	587	340	265	312	53	38
1963	55	668	511	348	266	590	34	26
1964	57	618	916	385	531	617	40	50
Total		8,635	10,395	8,479	4,304	5,053	1,791	2,827

control hunting on the Maun Front

Annual Kill									
Small Antelope			Large Antelope			Various			
Duiker	Steenbuck	Total	Lechwe	Others	Total	Zebra	Others	Total	Total
		281			22	16	38	54	980
		313			36	27	202	229	1,291
		385			63	34	256	290	2,099
		666			126	108	131	239	3,191
		772			284	126	802	928	4,112
		840			63	39	769	808	3,076
		319			25			62	1,511
		384			40			120	1,987
		199			11			119	1,730
		447			28			328	2,181
		657			15			290	3,354
		449			26			248	2,497
		6			13			150	1,616
140	122	265	7	22	29	27	79	106	1,520
470	262	732	25	46	71	60	43	103	2,814
341	247	588	52	13	65	5	179	184	2,919
497[1]	27[1]	524	35	29	64	42	23	65	2,746
950[1]	106[1]	1,056	14	22	36	41	1	42	3,429
492	369	861	28	22	50	27	—	27	3,078
385	303	688	37	28	65	36	6	42	2,717
535	389	924	26	17	43	31	40	71	3,072
1,024	419	1,443	28	9	37	46	47	93	4,016
1,067	376	1,443	28	13	41	38	23	61	4,702
—	—	13,242	280	221	1,253	703	2,639	4,659	60,638

[1] Some steenbuck recorded as duiker.

TABLE 5 Distribution of

Total kill July

Camp	No. (hunters/month)	Buffalo No. (%)	Wart hog No. (%)	Zebra No. (%)	Kudu No. (%)	Reedbuck No. (%)	Impala No. (%)	Tsessebe No. (%)	Wildebeest No. (%)	Hartebeest No. (%)
Chuchubegho	398 (3.5)	427 (13.7)	737 (14.3)	44 (15.9)	224 (6.4)	512 (21.6)	374 (16.3)	103 (30.9)	28 (5.5)	
Control	244 (2.1)	212 (6.8)	327 (6.3)	12 (4.3)	123 (3.2)	478 (20.1)	155 (6.8)	36 (10.8)	7 (1.4)	
Xoo	254 (2.2)	128 (4.1)	569 (11.7)	14 (5.1)	161 (4.2)	241 (10.2)	118 (5.2)	25 (7.5)	18 (3.5)	
Gabaracha	215 (2.0)	151 (4.8)	416 (8.1)	22 (7.9)	147 (3.9)	132 (5.6)	138 (6.0)	43 (12.9)	7 (1.4)	
Marophe	272 (3.1)	276 (8.8)	533 (10.4)	15 (5.4)	159 (4.2)	155 (6.6)	173 (7.6)	27 (8.1)	12 (2.4)	5 (19)
Moshu	243 (2.0)	207 (6.6)	316 (6.1)	9 (3.3)	166 (4.4)	86 (3.6)	113 (4.9)	20 (6.0)	12 (2.4)	
Nxaragha	395 (3.2)	180 (5.7)	347 (6.8)	5 (1.8)	354 (9.7)	164 (6.9)	126 (5.5)	12 (3.6)	26 (5.1)	
Xudum	319 (2.7)	415 (13.3)	417 (8.1)	27 (9.8)	191 (5.0)	127 (5.4)	311 (13.6)	23 (6.9)	35 (6.9)	3 (11)
Matsibi	289 (2.5)	317 (10.1)	328 (6.4)	41 (14.8)	211 (5.6)	98 (4.2)	258 (11.3)	13 (3.9)	18 (3.5)	2 (7)
Tshetsheku	382 (3.0)	171 (5.5)	336 (6.5)	11 (3.9)	347 (9.1)	139 (5.9)	137 (6.0)	6 (1.8)	89 (17.5)	2 (7)
Phatswi	375 (3.3)	143 (4.6)	235 (4.6)	5 (1.8)	488 (12.8)	90 (3.8)	93 (4.1)	4 (1.2)	67 (13.2)	1 (4)
Makwelekwele	264 (2.2)	195 (6.2)	178 (3.5)	37 (13.4)	268 (7.1)	34 (1.4)	122 (5.3)	8 (2.4)	53 (10.4)	3 (11)
Xoboga	376 (3.2)	125 (4.0)	180 (3.5)	15 (5.4)	630 (16.6)	90 (3.8)	95 (4.2)	6 (1.8)	56 (11.0)	1 (4)
Makula	245 (2.1)	161 (5.1)	219 (4.3)	19 (6.9)	312 (8.2)	27 (1.1)	71 (3.1)	7 (2.1)	81 (15.9)	10 (37)
Total	4,274 (36.2)	3,108	5,138	276	3,801	2,373	2,284	333	509	27

kills by Hunting Camps

1955 - June 1965

Lechwe No. (%)	Gemsbok No. (%)	Eland No. (%)	Sable No. (%)	Roan No. (%)	Bushbuck No. (%)	Small Antelope: Duiker No. (%)	Small Antelope: Steenbuck No. (%)	Small Antelope: Total No.	Ostrich No. (%)	Others No.	Total
108 (44.4)	2 (3)	2 (10)	1 (3)			178 (3.3)	56 (2.5)	234	3 (2.8)	11	2,830
84 (34.6)					1 (8)	137 (2.6)	50 (2.2)	187	7 (6.5)	10	1,639
17 (6.9)		1 (5)	1 (3)	9 (18)		188 (3.5)	98 (4.3)	286	18 (16.6)	21	1,627
2 (0.8)	1 (2)	1 (5)	7 (23)	2 (4)		189 (3.6)	100 (4.4)	289	4 (3.7)	8	1,370
6 (2.5)		2 (10)	1 (3)	5 (10)		200 (3.8)	109 (4.8)	309	5 (4.6)	6	1,689
2 (0.8)						262 (4.9)	113 (4.9)	375	4 (3.7)	11	1,321
	4 (6)	2 (10)		1 (2)	3 (23)	678 (12.7)	192 (8.5)	870	4 (3.7)	18	2,116
5 (2.1)	1 (2)	2 (10)		2 (4)		260 (4.9)	107 (4.7)	367	3 (2.8)	9	1,938
7 (2.9)	2 (3)	2 (10)	4 (13)	8 (16)	1 (8)	272 (5.1)	120 (5.3)	392	4 (3.7)	16	1,722
3 (1.2)	3 (5)	3 (14)	2 (6)	8 (16)	1 (8)	729 (13.7)	280 (12.3)	1009	17 (15.7)	12	2,269
4 (1.6)	6 (10)	1 (5)	1 (3)	3 (6)	4 (31)	829 (15.6)	289 (12.7)	1119	3 (2.8)	27	2,294
2 (0.8)	14 (22)	2 (10)	1 (3)	5 (10)	1 (8)	334 (6.3)	173 (7.6)	507	15 (13.9)	14	1,496
1 (0.4)	12 (19)		3 (10)	4 (8)	1 (8)	674 (12.7)	335 (14.8)	1009	9 (8.3)	14	2,252
2 (0.8)	18 (29)	3 (14)	10 (32)	2 (4)	1 (8)	389 (7.3)	247 (10.9)	636	12 (11.1)	7	1,598
243	63	21	31	49	13	5,319	2,269	7,588	108	184	26,141 *

* In addition 7 lion and a cheetah were shot.

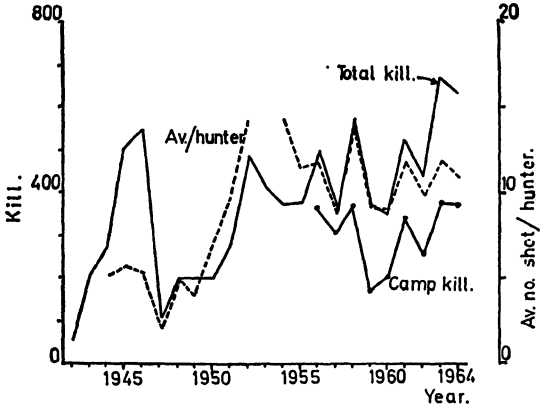
800
400
0
Kill.
20
10
0
Av. no. shot/ hunter.
Total kill.
Av./hunter
Camp kill.
1945
1950
1955
1960
1964
Year.

Fig. 3.

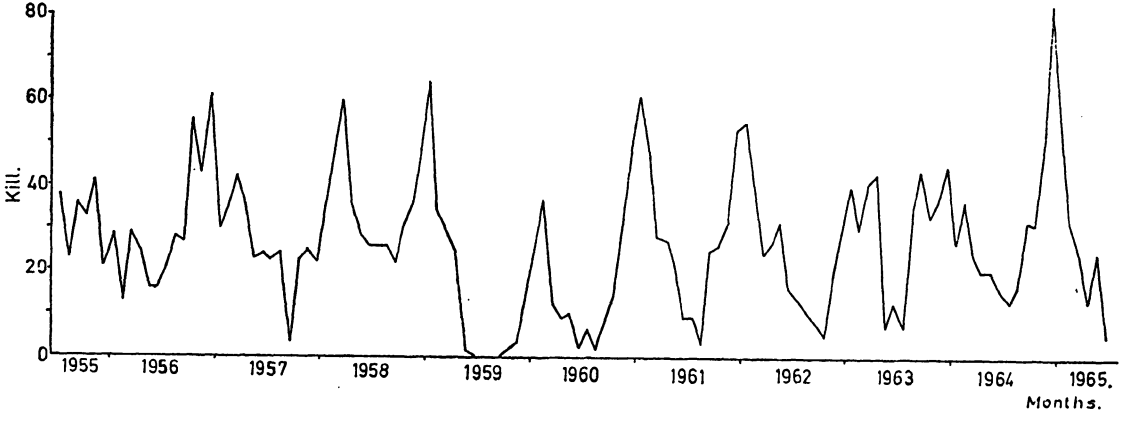
80
60
40
20
0
Kill.
1955
1956
1957
1958
1959
1960
1961
1962
1963
1964
1965.
Months.

Fig. 4.

RESULTS

The hunting returns for the 23 years under review are summarised in Table 4, in which a number of species have to be considered together, as they were unfortunately grouped under composite headings in the records from a number of years. Table 5 gives a detailed breakdown, by camps, of the animals shot by regular hunters during the ten years ending with June, 1964.

This information provided the basis for assessing trends that were valuable for gauging the effectiveness of the hunting. It also provided a picture of the distribution and relative abundance of large mammals in an area on the fringe of the Okavango swamps as well as an indication of seasonal movement patterns and other aspects of their biology.

BUFFALO

Buffalo, *Syncerus caffer,* were shot from all camps in the Hunting Area, although there was a distinct tendency for the highest kills to be from camps near the outer fence on the molapos crossing the area (particularly Chuchubegho in the north-east) and lowest kills from the lower Nxaragha (Table 5).

Annual kills showed the usual initial bulge between 1942 and 1946 as more and more hunters were enrolled into a fresh area (Fig. 3), and a low between 1947 and 1950 which coincided with fewer hunters, changes in the Hunting Area, and very dry conditions in 1947 and 1949. Following the 1950 to 1954 period the total kills showed a general upward trend towards a peak in 1963/64. The pattern of the kills from the camps was similar, although the upward trend was less well developed and the 1956 and 1958 crests were less marked. This was due mainly to the strengthening of the hunting patrols, from an average of 3.5 to an average of 8.9 men per month, in July, 1962, as their activities extended outside the area and were chiefly responsible for animals shot by non-camp hunters.

Many fluctuations in the annual kills can be traced to recorded changes in the hunting pattern, while others apparently had a

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Fig. 3. — Shows the total number of buffalo shot, the average number shot per regular hunter and the number shot from hunting camps between 1956 and 1964.

Fig. 4. — Shows the monthly distribution of buffalo kills from hunting camps during the 10-year period ending June 1965.

biological basis. Monthly kills from the camps show a regular seasonal periodicity (Fig. 4), with a wet season peak and a dry season low, which, with the distribution of kills over the Hunting Area, is in accordance with the general movement of buffalo away from the swamps during the wet season, and is related to the availability of seasonal surface water. The dry season troughs and the intermediate peak were lower than usual in 1959/60, following poor rains which apparently restricted the movements of buffalo in this area.

Fifty-one buffalo skulls were collected from the hunting operations and, in the absence of established ageing criteria, were assigned into arbitrary age classes based on the stage in tooth eruption and the relative wear on the adult teeth (Table 6). Animals that had not yet cut their third molar were classed as calves ; those with this tooth and subsequent molars erupting but no permanent tooth replacement in progress were termed juveniles, while those with the permanent teeth replacing were classed as sub-adults. If the cusps of the adult teeth were sharp, wear was described as light ; if they were rounded or smooth, as moderate ; and if wear had extended into the body of the teeth, as heavy.

TABLE 6

Breakdown by sex and age classes of buffalo skulls, collected April, 1966 to April, 1967

Age class	Number	Sex ♂♂	Sex ♀♀	Sex ?	% of Total
Calves	3	1	2		6
Juveniles	16	2	13	1	32
Sub-adults	15	5	10		30
Adults, Lightly worn teeth	4	4			8
Adults, Moderately worn teeth	11	4	7		22
Adults, Heavily worn teeth	2	1		1	4
Total	51	17	32	2	

Very few small calves were shot compared with the number of juveniles and sub-adults, which together accounted for 62 per cent of the sample. As hunters tended to select large animals, when offered a choice of targets, the high numbers of young indicated that this age group entered the Hunting Area in larger numbers than any other. The age distribution in this sample suggests that

the juveniles and sub-adults represented a dispersing age class moving away from the parental home range into new areas, similar to that found in other mammals (Howard, 1949 ; Riney, *Ms.*, and Child, 1965 and 1968).

The trends in the hunting successes indicated that hunting was not reducing the number of buffalo reaching the Hunting Area, and that there may even have been an increase in buffalo. This would confirm statements by old residents, of a general increase in buffalo in northern Botswana. Stigand (1923) discusses the game occurring between Toteng and the Linyanti Swamps, but does not even mention buffalo where they are now one of the most conspicuous species.

WARTHOG

Warthog, *Phacochoerus aethiopicus*, occurred throughout the Hunting Area, most being shot from camps in the east or along the largest molapos crossing the Area (Table 5). Annual kills generally increased from 1942 to 1952 and then, following a trough, increased

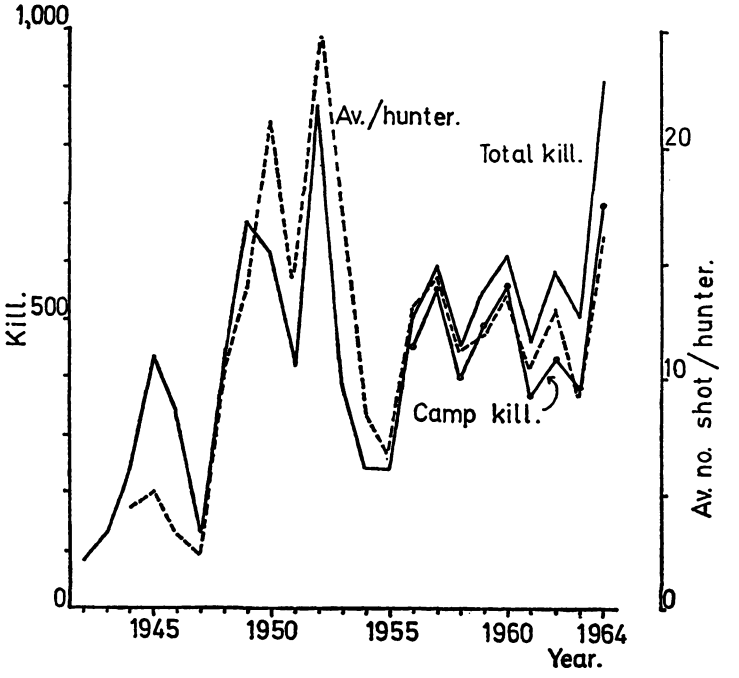

Fig. 5. — Shows the total number of warthog shot, the average number per regular hunter and the number shot from hunting camps between 1956 and 1964.

again from 1955 to 1964, when a record number was shot (Fig. 5). There was the usual initial bulge, as the hunting programme settled down, followed by a crest in 1948/49, which merged with the crest associated with the different hunting practices between 1950 and 1954. The first part of this crest was probably associated with the increased emphasis on hunting between the inner and outer fences as this area contains a lot of good warthog habitat. When hunting returned to normal there was a distinct upward trend following a low in 1954/55 and this is also shown by the numbers shot by regular camp hunters and the average hunter's success.

There was a correlation in most months in the 10 years ending with June, 1964, between warthog kills and general hunting conditions and intensity, as gauged from the total number of all other species shot. The relationship varied seasonally from about 20 warthog per 100 other kills from camps in August through March (Fig. 6a) to about 32 per 100 in May and June (Fig. 6b). In some

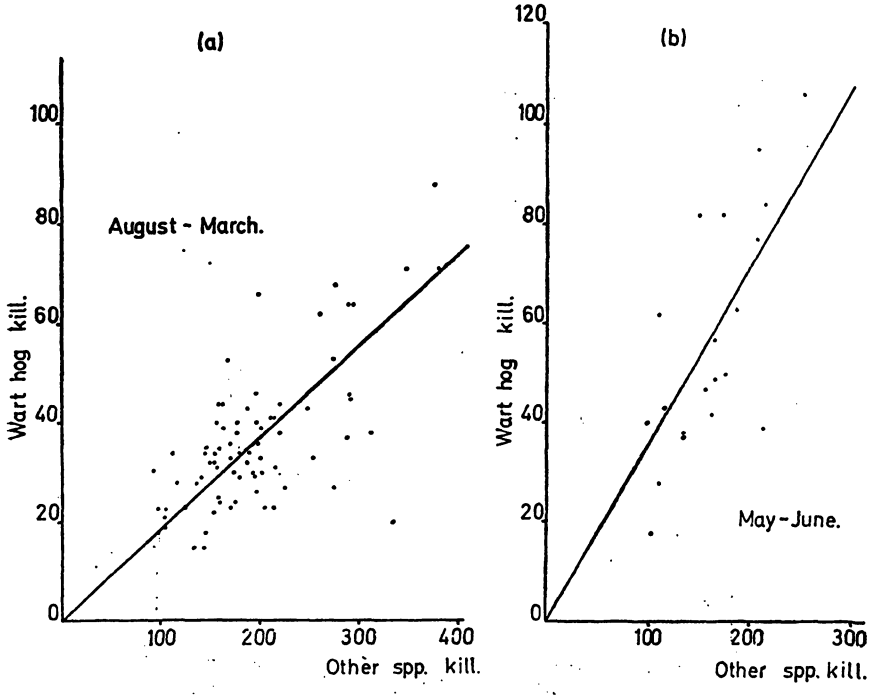

Fig. 6. — The correlation between the number of warthog and all other species shot by months in the 10 years ending June 1965.
a) shows that about 20 warthog per 100 other kills were shot in August through March, while —
b) indicates this number increased to about 32 in May and June.

years the April and July figures tended towards the latter relationship while in others they tended towards the former, suggesting that they were influenced by annual climatic differences or variations in the pattern of flooding in the area.

The monthly totals showing most discrepancy from the seasonal relationship could all be explained by changes in the hunting pattern. For example, only 37 warthog were shot in August, 1959, which was low compared with 277 other kills, but this coincided with a game drive which was especially effective against small antelope. Similarly, high numbers of duiker and steenbuck were shot in November, 1962 and November, 1963, and this applied to buffalo in October, 1956, and reedbuck in October, 1957, all months when the relative number of warthog was down.

TABLE 7

Breakdown by sex and age classes of warthog skulls, collected April, 1966 to April, 1967

Age class	Number	Sex ♂♂	♀♀	?	% of Total
Suckling	41			41	32.3
Yearling	42	22	17	3	33.1
Two-year-olds	28	12	15	1	22.0
Adult	16	9	5	2	12.6
Total	127	43	37	47	

Table 7 summarises the sex and age class breakdown of a sample of 127 skulls from hunting operations, aged from the state of tooth replacement, according to Child *et al.* (1965). This sample of kills does not appear to be representative of the structure of the population. Theoretically the first and second age classes would have to be at least adequate to sustain the offtake, leaving enough animals to replace the next age class. In the present sample, this would mean over 70 yearlings, the precise number depending upon the proportion of two-year-olds needed to replace three-year-olds in the adult class. Similarly, there would have to be a minimum of 111 sucklings, but the maximum theoretical reproductive potential in a sample of unborn litters was 270:100 mature females (Child *et al.*, 1968). The present sample contains only 20 females old enough to have farrowed the previous year, as females farrow for the first time at about 24 months of age. Thus at least twice the number would have been needed to provide the suckling class,

ignoring any natural mortality, which is generally high among young warthogs. This in turn would increase the number of sucklings and yearlings needed to replace older age classes, so that it is obvious that only a small proportion of these classes and of sexually mature females was represented among the sample of kills. The same probably applied to the males, as the sex ratio among animals over one year old approaches parity, and Child (1965) found a similar ratio in two other warthog populations, using different sampling methods.

A summation of this evidence indicated that hunting was not effective against the warthog population, whether or not the entire population was resident in the area. The number of warthog shot at different times of the year was related to the effort directed against the species and to some regular seasonal variant which made hunting easier in mid-winter. It may also have been related to seasonal behavioural characteristics such as behaviour associated with the rut, which in Rhodesia takes place between late April and mid-June, or it may have been related to restrictions on movement, resulting from the flooding of the molapos, or from the burning of the grass making hunting easier. The hunting removed a relatively small proportion of the animals available from each age class, so that the regular periodicity and general trend towards higher and higher annual kills, followed closely by the kills from the camps and the increasing average hunter's success, is good evidence that the population was at least maintaining itself.

It is not surprising that a warthog population can withstand this type of hunting as Riney and Child (*Ms.*) and Wilson (*Ms.*) have found the same in Rhodesia and Eastern Zambia. Child *et al.* (1965) and Child *et al.* (1968) have warned against the species resilience to hunting on account of the rapid population turnover that is possible resulting from the fast rate of growth and maturity and the high reproductive potential. Child (1965) describes some behavioural characteristics which make the species difficult to eliminate and enhance a rapid build up in a population under favourable habitat conditions. This could result after a population had been reduced or through suitable changes in the habitat. Mitchell (1963) has suggested how changes in the species composition of grasses, resulting from the misuse of fire, especially annual burning early in the dry season, such as usually accompanies a hunting programme, can favour more palatable forms.

There have been marked changes in the vegetation along the Maun Front as the result of the clearing and ring barking of the tsetse habitat, and of burning to improve the visibility for hunting. *Cynodon dactylon,* a grass often associated with disturbed soils

and much favoured by warthog (Child, 1968), is widespread particularly along some of the molapos. Nevertheless it was not possible to determine whether Mitchell's suggestion applied in the area, although some such mechanism could account for the general increase in warthog over the past 20 years, as reported by people living around the fringe of the Okavango swamps, where the species is very numerous. The conservation values of habitats in this region are generally deteriorating through past and present mismanagement of livestock and fire, and in some localities through over-population of wild ungulates. The widespread occurrence of the phenomen of deteriorating veld temporarily favouring a species, and its implications, are discussed by Riney (1963).

KUDU

Most kudu, *Tragelaphus strepsiceros*, were shot from Xoboga and Phatswe (Fig. 2) which contributed 15.9 and 12.2 per cent, respectively, of the kills from the camps (Table 5). These

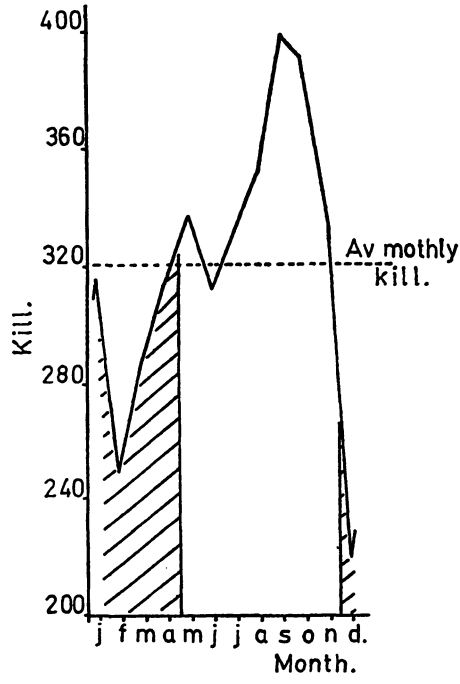

Fig. 7. — The average number of kudu shot by calendar months in the 10 years ending June, 1965.

two camps and Makwelekwele, had dense bush flanking open molapos and Xoboga tended to be cut off as an island by the seasonal floods, making hunting easier, although floodwaters restricted the hunters around Makwelekwele.

Most kudu were shot during the dry months, especially in August to November, between 1955 and 1965 (Fig. 7). Annual kills and average annual hunter's successes (Fig. 8) showed the usual early bulge followed by a marked drop in 1948. A second bulge between 1957 and 1960 followed the resumption of normal hunting but gave way to a low which lasted until 1964. The possibility therefore exists that hunting was effective in reducing the population after 1960. The average number of animals shot per regular hunter was not significantly different during the last four years compared with that before 1950 but there was an abrupt drop between 1960 and 1961. An average of 12.9 per hunter (range for 5 years ending 1960, 10.0 to 15.5) gave way to an average of 7.8 (range for 4 years 1960/64, 7.4 to 8.2), which is highly significant ($Chi^2 = 38.5 > 0.01$), and the decline was accompanied by a breakdown in the previously rhythmical pattern of monthly kills.

TABLE 8

Breakdown by sex and age of kudu skulls collected between April, 1966 and April, 1967.

Age class	Number	Sex ♂♂	♀♀	?	% of Total
Calf	4	2	1	1	5.6
Yearling	13	5	7	1	18.1
Two-year-old	25	14	10	1	34.7
Adult	30	17	13		41.7
Total	72	38	31	3	

A sample of 72 skulls collected in April 1966 through April 1967 was aged according to Simpson (1964) (Table 8). The age structure of this sample shows a high proportion of adults, even considering that older yearlings are difficult to distinguish from them in the field. There were 14 young animals (19:100) which had not yet cut the third molar compared with 24 in a sample of 75 skulls (32:100) obtained from the first year of hunting in the Nagupande Tsetse Control Hunting Area in Rhodesia (Child, 1965). This suggests either that successful reproduction was low and most animals

shot in the effective hunting area entered from outside, or that there was a strong tendency to shoot only well grown animals. Neither alternative would indicate that the hunting was the primary cause for the decline in the population suggested by Fig. 8. It seems probable that this resulted from factors other than those directly connected with the hunting and that the number shot each year reflected the general decline in the kudu population reported by many old residents of the region as a whole.

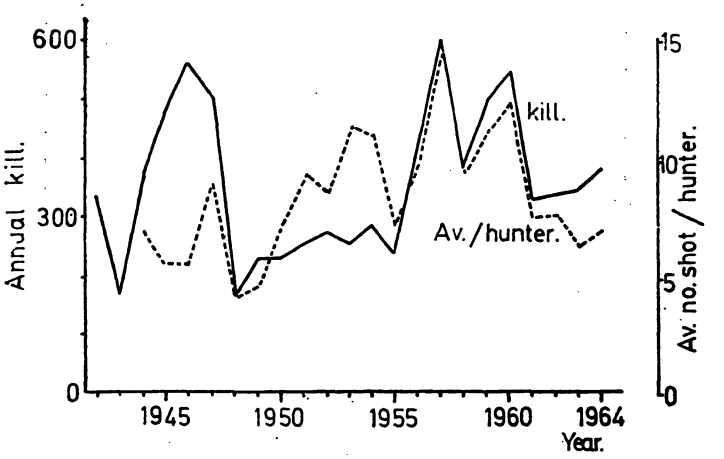

Fig. 8. — Shows the number of kudu shot and the average number shot per regular hunter between 1942 and 1964.

Reedbuck

Reedbuck, *Redunca arundinum*, occurred throughout the Hunting Area, but were most numerous in the largest molapos, especially towards the north and east. Hunting of this species was not emphasised until about 1952, and prior to this was subject to several policy changes which account for the fluctuations and general lowness of the annual kills (Fig. 9). After 1953 there was a steady increase in the number shot each year, with a crest in 1959/60 and a marked upward deflection in 1964. Inspection of the monthly hunting returns revealed a seasonal pattern reflecting the density of cover.

Many of the kills were young animals (Table 9) and the average number shot per hunter per year rose indicating the population was increasing in the way Riney and Child (*Ms.*) observed in Rhodesian Tsetse Control Hunting Areas. Whether this was stimulated by hunting or habitat changes requires further inves-

tigation, but it is significant that old residents in several parts of north-eastern Botswana reported an increase in reedbuck.

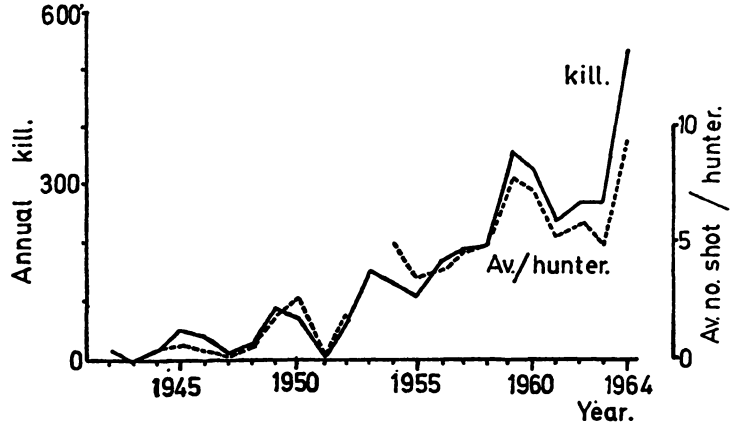

Fig. 9. — Shows the number of reedbuck shot and the average number shot per regular hunter between 1942 and 1964.

TABLE 9

Breakdown by sex and age classe of reedbuck skulls collected April, 1966 — April, 1967.

Age class	Sex ♂♂	♀♀	?	Total
Calves - up to those with lower M_2 in	8	6	2	16
Juveniles - lower M_3 erupting to all decid. teeth changed	14	9		23
Young adults - all perm. teeth - wear light	7	3		10
Adults - all permanent teeth - moderate wear	13	13		26
Old adults - all perm. teeth - heavy wear	1	2		3
Total	43	33	2	78

Impala

Table 5 shows that fewer impala, *Aepyceros melampus,* were generally shot from the south and west of the area than elsewhere and that most came from the northern camps on the largest

molapos crossing the Hunting Area. Annual kills increased initially from 1942 to 1946, but this was not reflected by the average hunter's success (Fig. 10). Following the usual 1950 to 1954 bulge kills increased steadily to a peak in 1964.

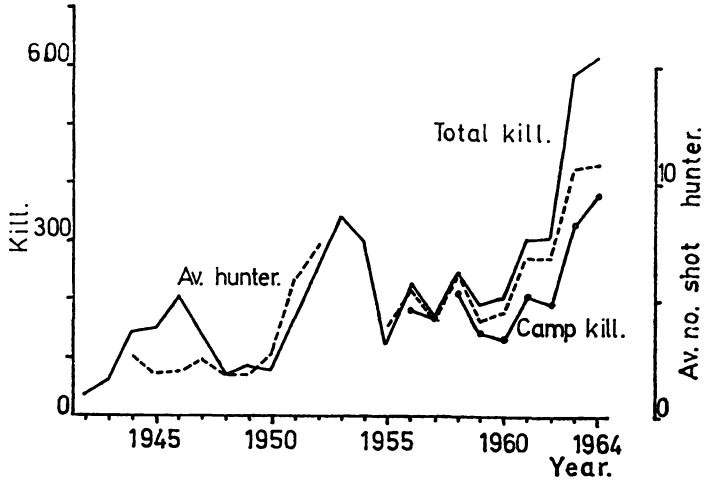

Fig. 10. — Shows the number of impala shot, the average number shot per regular hunter and the number shot from hunting camps between 1956 and 1964.

Fig. 11 summarises the definite periodicity in the numbers shot from the hunting camps in different months in the nine years from January, 1956, to December, 1964. The April/May peak was evident in seven of the nine years, while the subsequent trough, usually in June or July, was apparent in eight years ; the later peak was also present in eight years, but was accentuated in 1957, 1960 and 1963. The September/October low followed by a crest in the succeeding month, shown in the summary was clearly defined in eight years, but varied between October and December, thus tending to smooth out the two deflections in the summary.

The last two deflections coincided with the strict calving season, which lasts about six weeks and is reported to have varied over the years from September to December or early January. Before calving, females become much less gregarious and more secretive, while the upward deflection during the following month would indicate the emergence of the seasonal calves and the preoccupation of the females with nursing. The April/May crest was probably related to the rut when males become noisy and otherwise conspicuous and less aware of danger. The crest in August may have been influenced by the level of the swamps, but more probably

had a sociological basis, such as a movement towards the area of dispersing individuals just before the calving season, when 10- to 12-month old animals leave the parental home range (Child, 1965, 1967).

TABLE 10

The sex and age class breakdown on a sample of impala skulls collected between April and September, 1966

Age class	May			Other Months			Total
	♂♂	♀♀	?	♂♂	♀♀	?	
Calf				6	4		10
Yearling	8	6		17	9		40
Two-year-olds	10	1	1	7	8		27
Adults : Lightly worn teeth	3			3	4	1	11
Adults : Moderately worn teeth	33	5		29	20		87
Adults : Heavily worn teeth	8	1		4	4		17
Total	62	13	1	66	49	1	192
Total mature (*)	54	13		43	45		

(*) ♀♀ calve for the first time at 24 months, and ♂♂ rut for the first time at 2½ years, i.e. most yearling ♀♀ and 2-year-old ♂♂ were sexually mature.

The sex and age-class breakdown of 192 skulls collected from hunting operations between April and August, 1966, and aged according to Child (1964) is given in Table 10. The collection sampled the early dry season peak and confirmed its relationship with the rut, as mature males made up 72 per cent of the 75 sexed skulls collected in May, when rutting reaches its peak, while this age-class constituted only 36.4 per cent of the skulls from other months, a significant difference ($Chi^2 = 13.61 > 0.01$).

The level of annual kills (Fig. 10) probably reflected changing trends in the population, which was apparently increasing due to environmental changes, some of which resulted from the Tsetse Fly Control Operations themselves. The relationship between the seasonal activities of impala and monthly hunting returns, and the fact that the majority of kills were of full grown animals presenting the largest targets and most meat, coupled with the marked trend towards higher annual kills, suggests that hunting had little effect

in depressing the populations. The apparent increase may have resulted from a number of causes.

Child (1965) describes the wide range of foods taken by impala, varying from almost pure grass to almost pure browse, which enables them to compete favourably with many other species in downgrading veld. Conservation values have been suppressed by past land use, augmented by too frequent early burning in several areas around the Okavango swamps, including the Maun Front, and reports from old residents indicate a substantial increase in impala in several such areas.

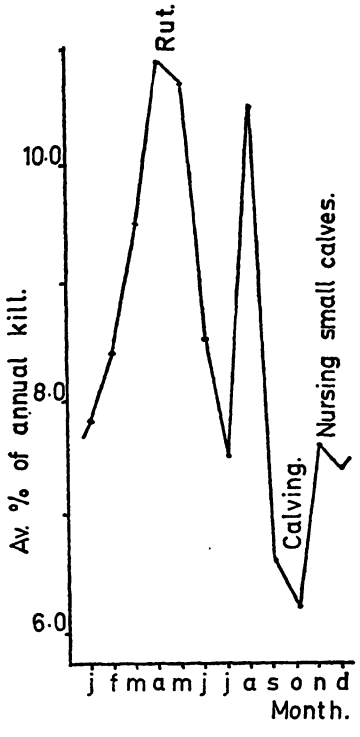

Fig. 11. — Summarises the seasonal periodicity of impala kills by calendar months during the 9 years ending June, 1965.

Lamprey (1963) describes impala as a species favouring the borders between woodland and open country and Child (*op. cit.*) has indicated how they were attracted by the edges of clearings when woody vegetation was cut in two areas in Rhodesia, including one in which the clearing was designed to eliminate tsetse habitat. It would therefore be useful to determine the importance to impala

habitats of the burning and clearing or ring barking of vegetation, associated with Tsetse Fly Control on the Maun Front.

Child (*op. cit.*) demonstrated a differential mortality pattern, based upon the co-ordinated seasonal social behaviour of a population, which favoured mature females and raised the reproductive potential per unit of surviving population after a set back due to environmental factors. A similar mechanism applies in the face of predation, as records published by Mitchell *et al.* (1965) indicate that more males than females are killed by the larger predators. The tendency on the Maun Front to shoot a high proportion of males, particularly around the time of the rut, simulated either or both of these mechanisms. The depressive effect of rutting activities on the physical condition of mature rams is very important for setting the stage for a differential mortality later in the dry season in critical years. It is therefore probable that hunting at the intensity practiced along the Maun Front equipped the impala population to expand rapidly if or when habitat conditions improved and in any case to regain any numerical strength lost through being hunted.

Tsessebe

Child *et al.* (*Ms.*) found that in north-eastern Botswana, tsessebe, *Damaliscus lunatus,* are usually associated with open grassland or neighbouring woodland such as occurs in the molapo country around the fringes of the Okavango swamps. As a result, most tsessebe hunted on the Maun Front in July, 1955 through June, 1965, were shot from camps towards the north-east of the Hunting area.

There was a general decrease in the total number and the average number of tsessebe shot per hunter after the first few years of hunting, followed by a minor crest during the 1950 to 1954 period and then a further decline towards 1964 (Fig. 12). Tsessebe are singularly easy to shoot and will stand, even after one or more of a group has been shot by an unconcealed hunter. Females will frequently stand by a fallen calf and on one occasion a yearling female lay down next to a dead one within 50 yards (46 m.) of the hunter and while a vehicle was driven up to the carcass. The only exceptions to this general rule are females accompanied by very young calves as these station themselves at some distance on the opposite side of a herd, furthest from potential danger, and flush more readily than other animals.

The combined hunting returns for the 10 years up to June,

1964, showed a slight tendency for most animals (233 of 333 head) to be shot between March and September ($Chi^2 = 3.19 > 0.10$), indicating an influx towards the area from the neighbouring swamps during these months. However, judging from the low returns from the western camps (Table 5) these movements were not very marked.

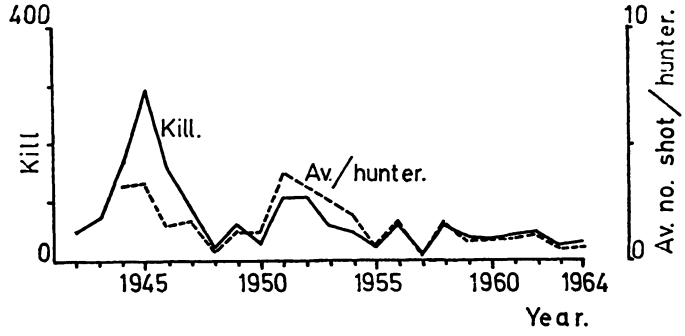

Fig. 12. — Shows the number of tsessebe shot and average number shot per regular hunter between 1942 and 1964.

The 13 skulls collected between April and August, 1966, included those of two adult males and an adult female with moderately worn teeth, those of three male and three female two-year-olds, and those of a male yearling and two male and three female calves, aged according to the criteria being developed by Child *et al.* (*op. cit.*). The sample is small, but includes a high proportion of sub-adult animals (77 per cent), especially two-year-olds (46 per cent), which may have represented a dispersing age class moving towards the area.

The behaviour of tsessebe when hunted, the trend in annual kills indicated in Fig. 12, and the high proportion of young animals in the kill, suggested by the sample of skulls, all indicate a decline in the tsessebe population along the Maun Front, possibly as the result of the hunting. This could be expected for a large and easily hunted species, associating in groups in open country and not subject to marked seasonal movement.

Wildebeest

Annual kills of wildebeest, *Connochaetes taurinus*, showed the usual initial bulge, with 364 being shot in 1947, but from them on until 1964, there was a general decline in the number shot (Fig. 13).

Two peaks interrupt this general trend. The first occurred during the 1950/54 period when the organisation of the hunting was on a different basis, but the second may have had some significance.

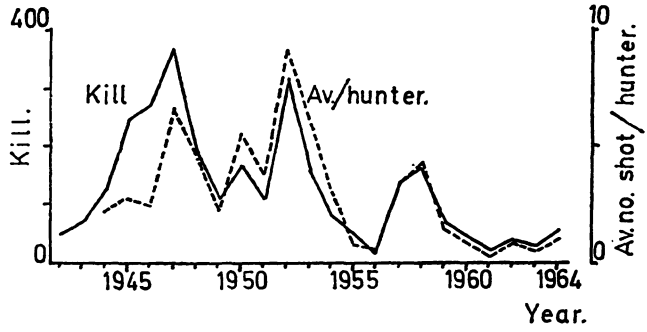

Fig. 13. — Shows the number of wildebeest shot and the average number shot per regular hunter between 1942 and 1964.

The species has often been described as migratory in Botswana, and, although any prescribed regular movements have yet to be demonstrated, there is no doubt that populations of the plains country to the south and southeast of the Okavango swamps are very mobile. Fig. 14 shows how most were shot on the Maun Front during the dry season (July-October) just before the restricted calving period. The distribution of the kills by camps (Table 5) illustrates that most were shot entering the Hunting Area from the south and west, when water was least available in the plains country and the swamps were in flood. Highest returns came

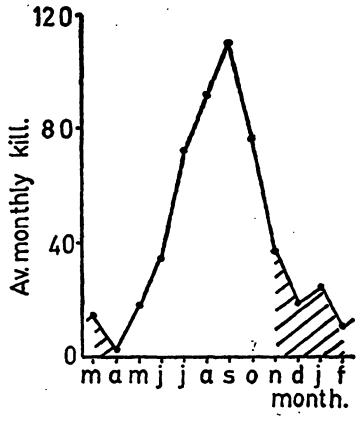

Fig. 14. — Summarises the seasonal periodicity of wildebeest kills by calendar months during the 10 years ending June, 1965, with rainy season months shaded.

from the camps where this influx was least impeded by flooded molapos, while the lowest were from camps lying nearest the swamps. This agrees with reports that wildebeest are generally scarce along the west side of the swamps, where numbers are augmented during the dry season by animals from waterless areas.

It is therefore possible that the downward trend in annual kills, especially after 1958, resulted either from effective hunting or from fewer and fewer animals reaching the area from the south or west, or both. Large gregarious plains species are generally easier to eliminate with high-powered rifles than secretive species of woody habitats, but on the other hand there was a very heavy die-off among wildebeest in central Botswana during the early 1960s, preceded by mass movements and heavy losses in the south-east of the country in 1957. Thousands died in localities as far apart as Sibanene on the Rhodesian border and Lake Dow in the south-western corner of the Makarikari system, and many deaths were noted or reported along veterinary cordon fences, particularly along the Kuki fence which runs east/west some 40 miles (64 km.) south of Lake Ngami.

Riney and Hill (1963) appear to have observed early stages in the die off in the Makarikari region during October, 1962, as although wildebeest were then still very numerous in this region, they found many carcasses. The main mortality in the Lake Dow area, however, took place during 1964 when Bachmann (1965 and pers. comm.) calculated that 14,000 head had died in an area of about 300 sq. miles (777 sq. km.) from June to mid-October. His calculation of the number of animals which died was based on the weight of bone recovered for sale from the area, in relation to the average weight of bone from 10 carcasses.

Wildebeest died along the cordon fences and east of the Botletle river in the same year and ten and twelve times the usual number of hides were offered for sale at the Nata Trading Post during 1962 and 1965, from animals dying along the Nata River. In the latter year Professional Hunters reported them as dying in groups of up to a dozen along the Kuki fence, and the marked decline in numbers between 1960 and 1965 is reported from much of central, eastern and north-eastern Botswana.

The population crash coincided with four particularly dry years, following a series of above-average rainfall years, and took place in many cases in areas which had been severely down-graded by past land use (Child, 1968). This probably contributed to the low numbers entering the Maun Front area after 1960, while the 1957/58 crest may have reflected similar mass movements from the Kalahari to those reported from the south-east of Botswana.

The decrease in the numbers of wildebeest shot on the Maun Front therefore probably reflected decreasing numbers reaching the area from the south and west and was not due to the hunting. The main effect of hunting was to reduce significantly the number which entered the Area, so that few penetrated to the camps in the north-east.

LECHWE

Lechwe, *Kobus leche,* were associated with seasonally inundated grassland along the edge of the Okavango swamps and must once have occurred along the molapos through the Hunting Area to Toteng, where the type specimen of the species was collected in 1850 (Ellerman *et al.,* 1953). Lechwe hunted before July, 1955 were recorded in the general category of large antelope, but during the next 10 years a total of 229 were shot from camps in the Area, while a further 102 were killed mainly by hunting patrols and for meat for labourers. Of the former 229, 183 or 79.9 per cent were from Chuchubegho and Control camps and a further 6.1 per cent were from Xoo, the third eastern-most camp (Table 5), while only two were shot at other camps after April, 1958. This would indicate that the limit of the species' effective range is now some 30 to 40 miles (48 to 64 km.) from Toteng in the direction of the swamp along the Boro river.

Apart from an unusual increase in the number of lechwe recorded towards the end of 1957, including 34 in December and another 14 the following January (the two highest months on record and possibly due to a recording error), the pattern of annual kills from camps changed very little over the 10 years. If the December, 1957 - January, 1958 crest is ignored then the hunting of lechwe followed the expected pattern, with most shot during the mid-year peak flood periods, when the population was forced out from the swamps towards the east of the Area. The variability in the height of these floods and the precise areas which they affect in any given year would account for the fluctuations in the annual kills. It is therefore unlikely that the hunting of the fringe of this population during later years was affecting its numerical strength significantly, although earlier hunting may have contributed to a reduction in its former range.

DUIKER AND STEENBUCK

Duiker, *Sylvicapra grimmia,* and steenbuck, *Raphiceros campestris,* are considered together as the hunting returns for the

two species were amalgamated until mid-1955 and again between March, 1958 and August, 1959. Both are small, more or less solitary antelope, and where separate returns for the two are available these indicate that both were more numerous towards the west of the Hunting Area (Table 5). Fewer of both were shot early in the year, when the grass was tall and when more favoured species such as buffalo were available, and Fig. 15 shows a remarkably similar pattern of hunting for the two species.

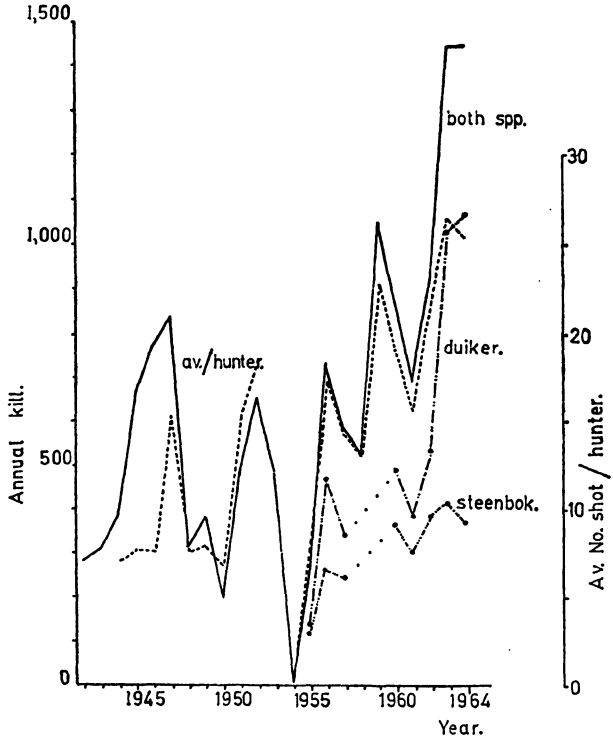

Fig. 15. — Shows the number of « small antelope » shot, the average number shot per regular hunter and the number of duiker and steenbuck shot in the years in which they were recorded separately between 1942 and 1964.

The recorded annual kills and the combined annual totals for the two species, together with the combined average hunter's successes, are summarised in Fig. 15. After an initial peak and following the 1950/55 period, when none were shot in 1954 and part of 1955, numbers increased steadily to a combined total of 1,443 in both 1963 and 1964. A similar trend was shown by the average

number shot per hunter. The peak for both species in 1959 was largely due to game drives held that year, as large numbers of « small antelope » were killed on the first two drives.

TABLE 11

Breakdown by sex and age classes of duiker skulls collected between April and August, 1966

Age in months (*)	Sex ♂♂	♀♀	?	Total	% of Total
0 - 6			10	10	17.0
6 - 12	2		4	6	10.2
12 - 18	8	2		10	17.0
18 - 22	4	4		8	13.6
Adult (22 months *)	14	11		25	42.4
Total	28	17	14	59	

(*) According to Riney and Child (1962).

TABLE 12

Breakdown by sex and age classes of steenbuck skulls collected between April and August, 1966.

Age class	Sex ♂♂	♀♀	?	Total	% of Total
Calves	1	5	3	9	27
Juveniles	3	5	2	10	30
Adults	7	7		14	42
Total	11	17	5	33	

The sex and age class breakdown of samples of skulls from duiker and steenbuck are summarised in Tables 11 and 12, in which duiker are aged according to Riney and Child (1962) and steenbuck are divided into arbitrary age classes from the state of tooth development. Animals with the second lower molar erupting or younger were classed as calves ; if this tooth was fully grown but permanent tooth eruption was not complete they were termed juvenile ; while all specimens with full mouths of teeth were classed as adult. In both samples there were 58 per cent of immature skulls which would indicate vigorous populations, as many of these young animals were well grown and therefore past the critical

period of rapid growth when natural mortality is high. Riney and Child (1964) have shown that duiker over six months of age are almost indistinguishable from adults and steenbuck classed as juveniles had well grown skulls.

The marked upward trend in kills and average hunter's success indicates that both populations were at least maintaining themselves and may have been expanding. This would not be surprising in the case of duiker, as Riney and Child (*Ms.*) describe similar trends from Tsetse Control Hunting Areas in Rhodesia, and both species survive well near settlements from which they are hunted. Child and Wilson (1964) give evidence that a duiker population studied by Riney and Child (*op. cit.*) had continued to increase for at least 27 months after hunting was suspended and Mr. I. Player, Chief Conservator of Zululand, South Africa (pers. comm.), described a population in what is now the Umfolozi Game Reserve, as having remained high for about seven years after Tsetse Control Hunting ceased.

Other species

At least eight other ungulates and several species from other groups were shot by regular camp hunters on the Maun Front. Previous to July, 1955, these were mostly grouped in a composite total, but after that the species were generally kept separate.

One waterbuck, *Kobus ellipsiprymnus,* and one springbuck, *Antidorcas marsupialis,* were shot in the Hunting Area, which was outside their normal ranges. Waterbuck are locally common around the north eastern fringe of the Okavango Swamps, but their effective range does not extend as far south as the Maun Front, while that of springbok ends abruptly some 20 miles (32 km.) west of the Hunting Area.

Red hartebeest, *Alcelaphus buselaphus,* and gemsbok, *Oryx gazella,* are species of the drier country to the south and west of the Hunting Area, which were shot in small numbers, mainly from the camps in the west. Eland, *Taurotragus oryx,* have a similar geographical range, but only 21 were shot by camp hunters, and all of these were in 1956 and 1958.

Sable, *Hippotragus niger,* have virtually disappeared from the west of the Okavango delta where numbers were reasonably large a generation ago, although the species is still fairly common on the eastern fringe of the swamps. Between one and nine were shot on the Maun Front in each of the seven years ending June, 1965. Roan, *H. equinus,* on the other hand, appear to have been elimi-

nated by early 1957 (when seven were shot in January, following a total of 35 the previous year), as none has been shot since then.

Zebra, *Equus burchelli*, were recorded separately between 1942 and 1947 and again between 1955 and 1964 (Table 4). Annual kills reached a peak in 1946, when 126 were shot in the original Hunting Area, but after 1955 the highest kill was 60 and no definite trend towards higher or lower kills was evident during the latter 10-year period.

A total of 13 bushbuck, *Tragelaphus scriptus*, were shot in the five years ending June, 1965, mainly along the lower Nxaragha Valley where there are well developed riparian thickets. It would be interes ing to know the reason for there being no earlier records, as this could signify important changes in the habitat.

In addition to these ungulates, seven lion, *Panthera leo*, one cheetah, *Acinonyx jubatus*, several jackals, *Canis* sp., and honey badgers, *Mellivora capensis*, were shot. The hunting of ostrich, *Struthio camelus*, was resumed in 1962, after a break of five years, when their blood was found to constitute a fairly high proportion of tsetse blood-meals. Sixteen were shot from camps in 1956 and 33 in each of the years 1962 and 1963 ; although only 13 were killed in 1964, so that the later hunting did not extend over a long enough period to show any significant trends.

DISCUSSION

An evaluation of the effects, on individual species, of Tsetse Control Hunting Operations along the Maun Front, indicates that, until 1964 it was not achieving its objective of creating a game-free corridor. With the possible exception of roan antelope, which were not common in the Area at the start of the control operation and which have declined in numbers in much of their former range in northern Botswana, no species was eliminated by 23 years of hunting. Only tsessebe, wildebeest and kudu were shot in reduced numbers during later years and there is evidence that the declining trends in the annual kills of the last two was due to factors other than hunting. All other species showed an upward trend, which. supported by other types of evidence, could not be reconciled with diminishing populations in the effective hunting area.

Similar results, involving some of the same species, were obtained by Riney and Child (*Ms.*) from an analysis of Tsetse Hunting records in Rhodesia. This means that such programmes are not efficient in the control of the tsetse fly, through denying it a source of vertebrate blood. It has been argued that hunting can

be effective against the fly, even if the host animals are not exterminated, but provided their numbers are reduced. It is argued that this will lead to a reduction in the fly-host contacts, which if below a given threshold can prove very detrimental to the fly population whose individuals must feed about every three days, depending on climatic conditions (Bursell, 1961).

To eradicate a fly population from an area would necessitate achieving this threshold for a significant proportion of the fly population in order to reduce it below the ' point of no return '. This would be difficult in a large area under field conditions, as a uniform hunting pressure is seldom achieved so that pockets of game ' survive ' owing to the nature of the country or distance from hunting camps, or through game entering the area from outside.

If the reduction in the fly population reported from parts of the Maun Front was due to hunting alone, then it would have been of short duration, unless host populations were held below a certain level. This might have prolonged hunting indefinitely, unless appropriate changes were induced in the habitat to render it unsuitable for the fly. In fact most species hunted from the Maun Front increased in numbers and this included forms such as warthog, which was the most favoured host of the tsetse fly (Table 2). This seems to invalidate Bursell's argument, at least so far as this tsetse area was concerned during this period of study.

Any long-term drop in a fly population, which can be attributed to hunting alone, under such circumstances, would have to have a cause other than the mere killing of animals. The rapidity with which most species adjusted to changes in the hunting pattern suggests that, if hunting can be shown to lead to a long term reduction in the fly population, but the host populations maintain themselves, the drop in the fly population may be due to the effects of the hunting on the behaviour of the game species.

The mechanism operating towards an increase in most game populations along the Maun Front was not always clear. It may have resulted from a shift in the sex and age structure of a population, leading to a more rapid turnover of individuals. But, whereas this could set the stage for a build-up in numbers, it is unlikely that it would lead to a continued rise in the annual kill over a number of years, unless accompanied by favourable changes in the habitat to accommodate the increase. Some species may have benefited from habitat changes resulting from the annual early burning by hunters in order to see game, or from the destruction of tsetse habitat through the clearing or ring-barking of woody vegetation. Nevertheless, the similarity between the pattern in the

trends in the hunting returns and those described by old residents from a far larger area, suggested that the hunting returns were in fact reflecting general changes in the wildlife populations in this part of Ngamiland. This is not surprising, as several species were subject to considerable movement and only entered the area seasonally.

TABLE 13

Weight of meat represented by animals shot on tsetse fly control on the Maun Front in 1964.

Species	No. shot	Mean dressed carcass weight lbs. (1)	Total weight of carcasses lbs.
Buffalo	618	650	401,700
Kudu	385	250	96,250
Wildebeest	50	263	13,150
Tsessebe	40	190	7,600
Impala	617	60	37,020
Reedbuck	531	85	45,135
Wart hog	916	70	64,120
Duiker	1067	21	22,407
Steenbuck	376	115	4,324
Lechwe	28	109	3,052
Zebra	38	418	15,884
Other large antelope	13	230 (2)	2,990
Total	4679	—	713,632

(1) Based on Roth (1966).
(2) Estimated.

The most likely explanation for the increasing trends in annual kills of several species may therefore be associated with the wide-scale habitat changes which have taken place in the region as the result of changing land tenure over the past century or more. Pole Evans (1948) reviews the documented history of the region, since Livingstone discovered Lake Ngami in 1849, stressing the obvious depressive effect which past land-use has had on conservation values, and Riney (1963) has illustrated how such changes can create eruptive oscillations in certain animal populations.

At the current level of oscillation, the populations sampled by Tsetse Hunting were very productive. In 1964 alone the regular hunters based in the camps shot over 350 tons (356 tonnes) of dressed carcass (Table 13). Although not all of these animals were resident in the 300 sq. mile (777 sq. km.) Hunting Area and a

little hunting may have taken place just beyond its limits, the figure nevertheless illustrates the type of productivity which can be achieved from a spectrum of wild animals around the fringe of the Okavango swamps.

This production, when considered in the light of the ineffectiveness of past control operations, emphasizes the need to be very clear on the cause/effect relationship between tsetse and game, before mounting tsetse control operations ; it also indicates the need to examine carefully the proposed benefits of reclamation as compared with the production that could be obtained through careful management of wildlife populations as a form of land use in its own right. It should be noted that these and other considerations have led to the suspension of hunting in tsetse control operations in Botswana.

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SUMMARY

This paper explores the uses and limitations of hunting returns, from Tsetse Control Hunting along the Maun Front in northern Botswana, for assessing the effectiveness of the hunting in eliminating large mammals from a 300 sq. miles (777 sq. km.) area in 23 years. It is concluded that the returns provide a sound basis for interpreting broad population trends, in conjunction with evidence from the skulls of animals shot and the general history of numerical trends in the populations in surrounding areas. The analysis of the returns also provides information on the distribution, seasonal movement patterns and reproduction in several species in this zoogeographically important, but poorly known region. It is concluded that the hunting programme was not achieving its objectives and that several species were maintaining themselves or increasing in the effective area hunted and that these trends were in general, in accordance with those in surrounding areas.

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