Koedoe 20: 125–145 (1977)

SOME ASPECTS OF THE HISTORY AND POPULATION ECOLOGY OF THE TSESSEBE *DAMALISCUS LUNATUS LUNATUS* IN THE KRUGER NATIONAL PARK

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Abstract – The population trends and distribution of the tsessebe population of the Kruger National Park are evaluated in terms of the available data derived from records compiled in the developmental history of the Kruger National Park (KNP). The recent numerical status of the population is also given. A description of the habitats favoured by tsessebe in the KNP is presented as well as an analysis of the age structure and sex-ratio of the population. Aspects of the social organisation of tsessebe affecting the interpretation of the age structure and sex-ratio phenomena of the population, are also discussed.

Introduction

With the ever increasing human settlement along the boundaries of national parks and the colonization of hitherto uninhabited areas, the movements of wild animals have been severely curtailed and restricted to within park boundaries. Further limitations to the free movement of wild populations to and fro over the boundaries of protected areas have been brought about by the erection of game fences. It is a well known, albeit tragic, fact that most boundaries of conservation areas do not follow ecological barriers and the "closing" of such boundaries have almost invariably led to problems, especially with regard to migratory populations.

One of the major problems associated with the management of an animal community in a confined area is the accommodation of a number of different species in equilibrium with one another and their natural environment. The delicate balance between numerically differing populations poses one of the fundamental problems in this respect as competition for available habitat and natural resources, such as water and food, could lead to the gradual decline of less dominant species. Even an area the size of the Kruger National Park (KNP), Repub-

lic of South Africa, with its 1 948 528 ha, problems of this nature have cropped up and have led to the artificial reduction of some populations by means of culling, while all possible means are employed to increase the numbers of others. In the KNP the tsessebe *Damaliscus lunatus lunatus* (Fig. 1), falls within the category of the rarer antelope species and for various reasons – some of which will be dealt with in this paper -- it is vulnerable to competition by more abundant species.

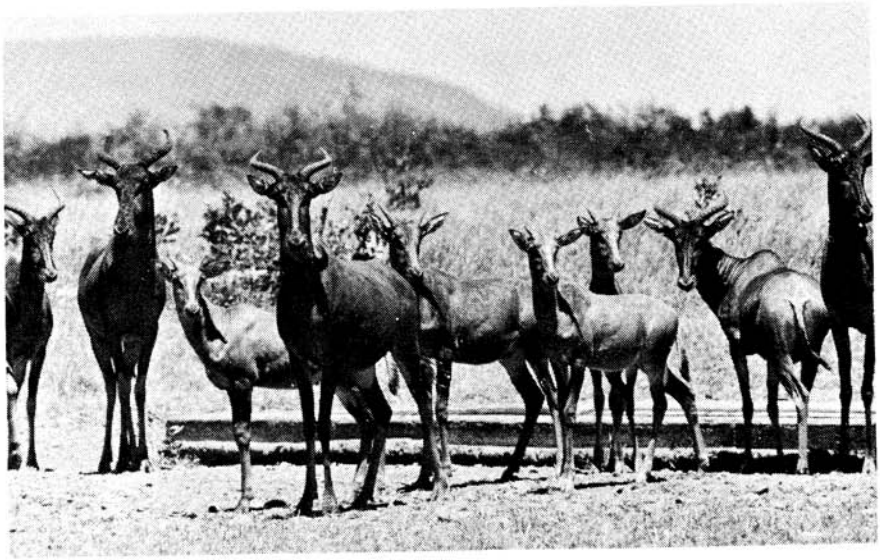

Fig. 1. A typical breeding herd of tsessebe in the Kruger National Park.

The results presented in this paper were collected over a four-year period from 1970 to 1973. Observations were mainly confined to the *Colophospermum mopane* flats in the north-eastern sector of the KNP as the majority of the small population of tsessebe occur on these flats.

A historical review

The period before 1965

South of the Olifants River

An accurate appraisal of the changes in the numerical status of the tsessebe population over the years is impossible as earlier reports give only vague indications of population trends. General terms, such as 'common', 'rare', 'on the increase (or decrease)', 'static', etc., were widely used to describe any changes (or imagined changes) in the various animal populations but could not be substantiated by any definite figures. Despite the vagueness of such descriptions, however, valuable deductions on population trends may still be made by comparing the localities

in which they were once described to be abundant, common or rare with the situation at the present time.

From the notes of the early hunters it is clear that tsessebe were once widely distributed and well represented in the area that comprises the present Kruger National Park. Kirby (1896) wrote that they were found ". . . throughout the Low Country". However, even at that early stage they were already being driven from their favoured open plain habitats to denser savanna-type habitats (apparently through exploitation by hunting parties) and were therefore ". . . commonly found in the bush about the Swinya (Sweni), Nguanetsi (Nwanetsi) and Timbabati (Timbavati) rivers" (Kirby 1896). Glynn (1926) found tsessebe in the company of roan *Hippotragus equinus* and sable *H. niger* antelope, waterbuck *Kobus ellipsiprymnus* and eland *Taurotragus oryx* in the area around Legogote in the 1870's.

In 1912 Stevenson-Hamilton (Warden's Annual Report 1912) estimated the number of tsessebe in the then Sabi Game Reserve to be 700 and in his Annual Report for 1925 Stevenson-Hamilton remarked that his estimate for 1912 was ". . . considerably under the mark, and since that time the total has increased at least fourfold". The total number of tsessebe in the Shingwedzi Game Reserve was estimated to be roughly half that of the Sabi Game Reserve at the time of the original estimate (1912), i.e. approximately 300.

If Stevenson-Hamilton's estimates are accepted it would mean that the Sabi Game Reserve had a total population of two to three thousand tsessebe by 1925. Even though this may have been a gross over-estimate the implication still remains that the tsessebe was by no means rare in the Sabi Game Reserve during the first quarter of this century. It is unfortunately also true that with the expropriation of the area west of Pretoriuskop in 1923 (Fig. 2) with the eventual consolidation of the old Sabi- and Shingwidzi Game Reserves and the proclamation of the KNP in 1926, the most favourable tsessebe habitat was excised from the KNP with the subsequent loss of a substantial proportion of the tsessebe population. The loss of this area to the KNP also adversely affected other game populations, notably the roan antelope and eland populations.

Subsequent to the loss of the western areas of the old Sabi Game Reserve little mention is made of the tsessebe population to the south of the Olifants River, other than to draw attention to the scarcity of these animals. In 1939 Stevenson-Hamilton summarised the position pertaining to tsessebe south of the Letaba River as follows: ". . . south of it (the Letaba River) they have always been rare, and the long drought drove most of those formerly found in the east of No. 4 (Tshokwane) and 5 (Satara) sections out westwards" and in 1944 it is reflected that ". . . neither of these species (roan antelope and tsessebe) ever existed in more than quite small numbers south of the Olifants River in the present KNP, though in the areas west in what was once part of the Sabi Game Reserve, they both were fairly numerous". No indication is, however,

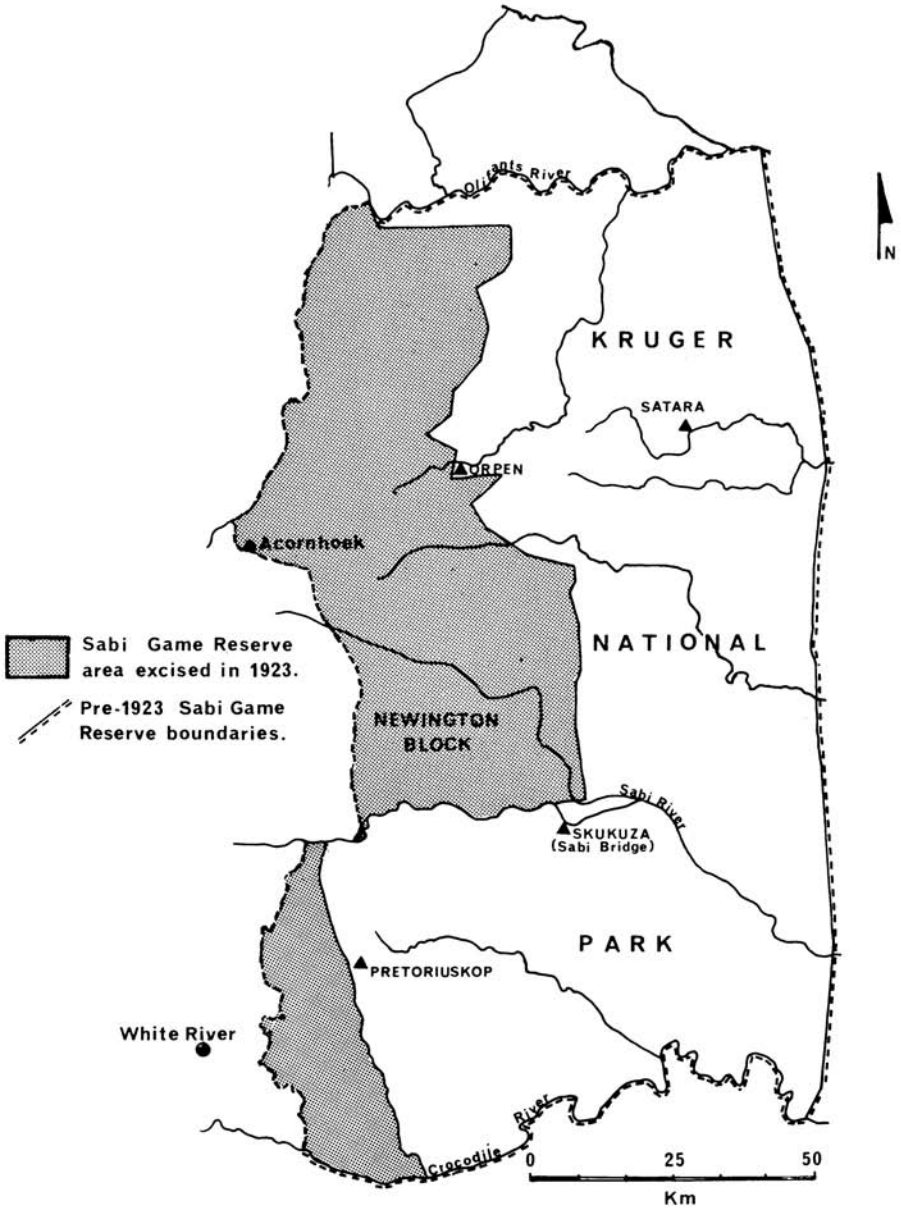

Fig. 2. Map indicating the boundaries of the Sabi Game Reserve and the area excised in 1923.

given of their numerical status and Sandenbergh (1946) only referred to them as being seen "in isolated small herds and single animals as far south as Tshokwane". Tsessebe did, however, still appear as sporadic immigrants in the area south of the Sabi River (Annual Reports for 1949 and 1950) although a population as such had already ceased to exist in this area.

In 1954 the first systematic census of animals was attempted and from the road counts a total of 75 tsessebe was obtained for the Central District in the KNP, i.e. the area between the Sabi and Olifants Rivers.

During the 1950's one of the strongholds of the tsessebe in this District was the Mnondozi dam area on the eastern Lebombo Flats of Tshokwane section. On one occasion no less than 24 of these animals were counted in the vicinity of the dam (August, 1955). During September 1957 a total of 25 were reported in the Tswiriri area along the western boundary. Whether this represented a temporary influx from outside the KNP is not known as two years later, in September 1959, Ranger J. J. Kloppers, who had kept meticulous record of all tsessebe sightings for the area since 1954, estimated the total for Tshokwane section at 90 with 65 in the Mnondozi area, 15 along the western boundary (Ripape) and 10 spread over the rest of the section.

At the conclusion of the period under consideration Pienaar (1963) estimated their numbers to be between 100 and 120 in the Central District of the KNP, while they had become extinct in the area south of the Sabi River.

North of the Olifants River

From the time of the proclamation of the old Shingwidzi Game Reserve at the turn of the century the extensive *Colophospermum mopane* flats to the west of the Lebombo Mountains proved to be the stronghold of the tsessebe. When, in 1912, Stevenson-Hamilton estimated the population for the Sabi Game Reserve to be about 700 he contended that the corresponding figure for the Shingwidzi Reserve would be roughly half that of the former, i.e. approximately 350. In spite of the severe droughts suffered during the 1920's and 1930's and the adverse effects they had on the game populations, the reports on tsessebe were almost invariably of a favourable nature and they were frequently referred to as being "numerous" and "flourishing".

Once again, however descriptive these terms may be, they are of no assistance in terms of the actual numbers of the animals and only in 1954 were their numbers estimated to be in the region of 525. This figure was derived from probably the first systematic game count of the area. Nine years later Pienaar (1963) estimated the total tsessebe population between 500 and 550.

The period since 1965

With the development of more reliable and accurate censusing

methods, more satisfactory and less subjective results have also been obtained in determining the population totals of the various larger herbivores in the Park. Since 1968 a combination of intensive aerial and ground censusing has been employed and in Table 1 the results of the tsessebe counts for the period 1968 to 1973, excluding 1972, are given.

Table 1

Derived totals of the tsessebe population of the Kruger National Park, as determined by means of aerial and ground censusing, for the period 1968 to 1973, excluding 1972

AREA	POPULATION TOTALS FOR THE PERIOD 1968 TO 1973				
Central District	1968	1969	1970	1971	1973
Tshokwane	70	60	60	35	40
Kingfisherspruit	25	25	25	15	30
Satara/Nwanedzi	3	3	8	10	10
Total	98	88	93	60	80
Northern District					
Letaba	5	6	10	10	
Mooiplaas	120	120	135	150	220
Mahlangene	55	50	50	49	60
Shingwedzi	150	145	180	110	160
Shangoni	70	65	65	45	45
Punda Milia	110	110	100	70	70
Total	510	496	540	434	555
Total for K.N.P.	608	584	633	494	635

In Table 1 the Central District represents the area to the south of the Olifants River while the Northern District represents the area to the north of it.

The present distribution of tsessebe in the Kruger National Park

Attempts to reintroduce tsessebe into the Southern District of the KNP, i.e. the area to the south of the Sabi River, have included the erection of a game proof enclosure to the south of Pretoriuskop rest camp and the introduction of a small breeding nucleus of tsessebe into the enclosure. Since the release of a bull and two cows into the enclosure during 1973 the herd has increased to six (July 1975).

The objective is to release more animals into the enclosure and maintain a breeding nucleus at the optimal stocking rate of the enclosure from where the surplus animals may be transferred to suitable habitats outside the enclosure on an annual basis. In this way it is hoped to re-establish the tsessebe in those areas of the Southern District from which they have become extinct and which are considered to meet their habitat requirements.

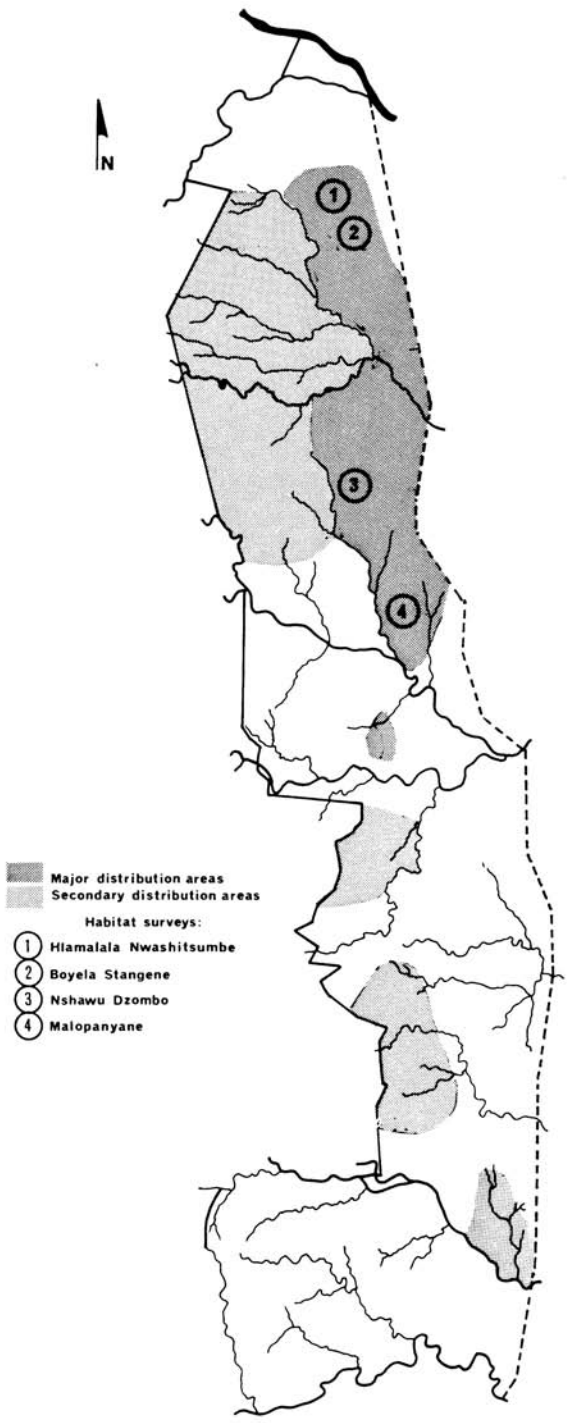

Fig. 3. Map of the Kruger National Park indicating the primary and secondary distribution areas of tsessebe.

In the Central District tsessebe are still distributed in isolated pockets along most of the western boundary area (Fig. 3). Scattered herds persist in the Mshatu pan-Swartkops-Shiyanamane-Mzanza area, the Mondzweni-Sweni-Mzanzene complex and the Ripape-Lugmagdam-Sundwini-Tinongane area. A few scattered herds also still exist in the Mnondozi-Saliji-Rietpan complex of the eastern Lebombo Flats. North of the Nwaswitsontso River tsessebe are extinct on the Lebombo Flats.

Between the Olifants and Letaba Rivers tsessebe are extremely rare and are represented by probably no more than one or two scattered herds.

The bulk of the KNP's tsessebe population is to be found to the north of the Letaba River and especially on the north-eastern Lebombo Flats (Fig. 3). In the mixed *Colophospermum mopane/Combretum* spp. communities of the western half of the area small isolated pockets still occur over a wide area. Tsessebe are absent in the mountainous terrain of the extreme northern areas of the Park as well as the Levubu River Basin in the north-east.

Due to their social organisation, based on a territorial system amongst the bulls and fixed home ranges amongst the harem herds (Joubert 1972) and their partiality for particular habitat-types tsessebe in the KNP are sedentary and individual herds may be observed in the same area for several years. Individual herd movements to more suitable areas have been observed but even on a local scale movements out of established territories are exceptional.

Habitat selection

The tsessebe is characteristically a species of open grasslands and tall woodland or tree savanna ecosystems (Kirby 1896; Glynn 1926; Stevenson-Hamilton 1947; Roberts 1951; Smithers 1966; Pienaar 1974). The major components comprising optimum tsessebe habitat appear to be open stands of healthy grasslands with easily accessible shelter in the form of trees and shrubs either as an ecotone to the grasslands or sparsely scattered about in savanna fashion (Child, Robbel and Hepburn 1972; Grobler 1973). Being strictly grazers they feed in the grasslands and lie-up in the shade of the trees during the day.

Optimum tsessebe habitat is rather restricted and patchy in the KNP and is best represented on the north-eastern Lebombo Flats, to the north of the Letaba River. Generally the area is slightly undulating and is dissected by a number of grass covered, shallow and broad drainage lines. The vegetation is sustained by a layer of heavy dark soil of basaltic origin (0–2 m deep) overlaying a deep and largely impervious calcareous substrate. The mopane *Colophospermum mopane,* is the overall dominant and occurs in varying densities ranging from open tree savanna to shrub thickets. The mopane is, furthermore, found in both tree and shrub forms with the latter extending over most of the area. Associated trees and shrubs include *Lonchocarpus capassa, Combretum imberbe, Acacia nigrescens, Sclerocarya caffra* and *Acacia tortilis.* The shrub stratum is

well represented by, among others, the following: *Colophospermum mopane, Dalbergia melanoxylon, Commiphora* spp., *Acacia exuvialis, Ormacarpum trichocarpum, Dichrostachys cinerea, Ehretia* spp., *Grewia* spp., *Albizia harveyi, Ozoroa paniculosa* and *Maytenus heterophylla.*

The rich soils support a well developed grass stratum with *Panicum coloratum, Themeda triandra* and *Cenchrus ciliaris* as the important dominants. Other species of importance include *Heteropogon contortus, Schmidtia pappophoroides, Digitaria* spp., *Enneapogon cenchroides, Setaria woodii, Eragrostis* spp., *Aristida* spp. and *Bothriochloa insculpta.* Probably due to the restricted resources of permanent water on the Lebombo Flats, the numbers of larger ungulates utilizing the flats have always been relatively low and consequently there has been no significant disturbance of the habitat.

Pienaar (1963) distinguished between two main wildlife habitats in this area, i.e. mopane scrub and tree savanna and grassland plains and 'dambos'. The former comprises by far the larger habitat of the two and is typically as described in the preceding paragraphs. The only true grasslands in the KNP are restricted to the broad drainage valleys in the *Colophospermum mopane* Community. The most common grasses of these depressions include *Sporobolus robustus, S. schlechteri, S. nitens, Ischaemum brachyatherum, Sorghum versicolor, S. verticilliflorum, Cynodon dactylon, Chloris virgata* and also a number of sedges. Trees and shrubs are largely absent from these grasslands though the following may be encountered: *Hyphaene crinita, Acacia xanthophloea, Lonchocarpus capassa, Combretum imberbe* and *Acacia polyacantha* (Pienaar 1963). Though these grassland habitats comprise only relatively small areas they play an important role in the ecology of the plains loving species such as tsessebe, roan antelope, eland and reedbuck. The edges of these grasslands are usually skirted by a well defined ecotone of mopane scrub and tree savanna. Similar habitats in central southern Africa are usually referred to as 'dambos' (Rhodesia, Zambia) or 'mulolas' (Angola).

In addition to the two major habitats there are also a number of *Acacia nigrescens* open tree savanna areas within the mopane scrub and tree savanna habitat. These areas consist mainly of medium to large sized knobthorn trees widely dispersed and provide excellent open savanna habitats. The tree and shrub strata are dominated by *Acacia nigrescens* although trees and shrubs of the typical mopane community may also occur. The grass stratum is dominated by *Setaria woodii, Panicum coloratum, Cenchrus ciliaris* and *Themeda triandra* with the species of the surrounding areas also represented. The most notable occurrences of this sub-habitat are in the Hlamalala-Nwashitsumbe-Stangene and Tihongonyene areas.

Tsessebe have a strong predilection for young green grass shoots and readily concentrate on burned areas after the appearance of the "green flush". Attraction to such burned areas is, however, limited to local movements within the favoured tsessebe habitats and has not been observed to result in even medium (5 km–10 km) or long distance movements such as are common for zebra and wildebeest.

In an attempt to augment the largely subjective descriptions of tsessebe habitats, the physiognomic and structural features of favoured tsessebe habitats on the north-eastern Lebombo Flats were analised. Visibility readings were taken at 0,5 m intervals up to a height of 4 m by means of a "density board" (Wight 1938 *In:* De Vos and Mosby 1963). Measurements were also taken of the distances between trees, crown diametres and the heights of trees and shrubs (only shrubs one metre and higher were taken into account). By assuming that the crowns of trees and shrubs are circular in shape, the relative crown cover could be determined from the crown diameters (Joubert *In prep.*).

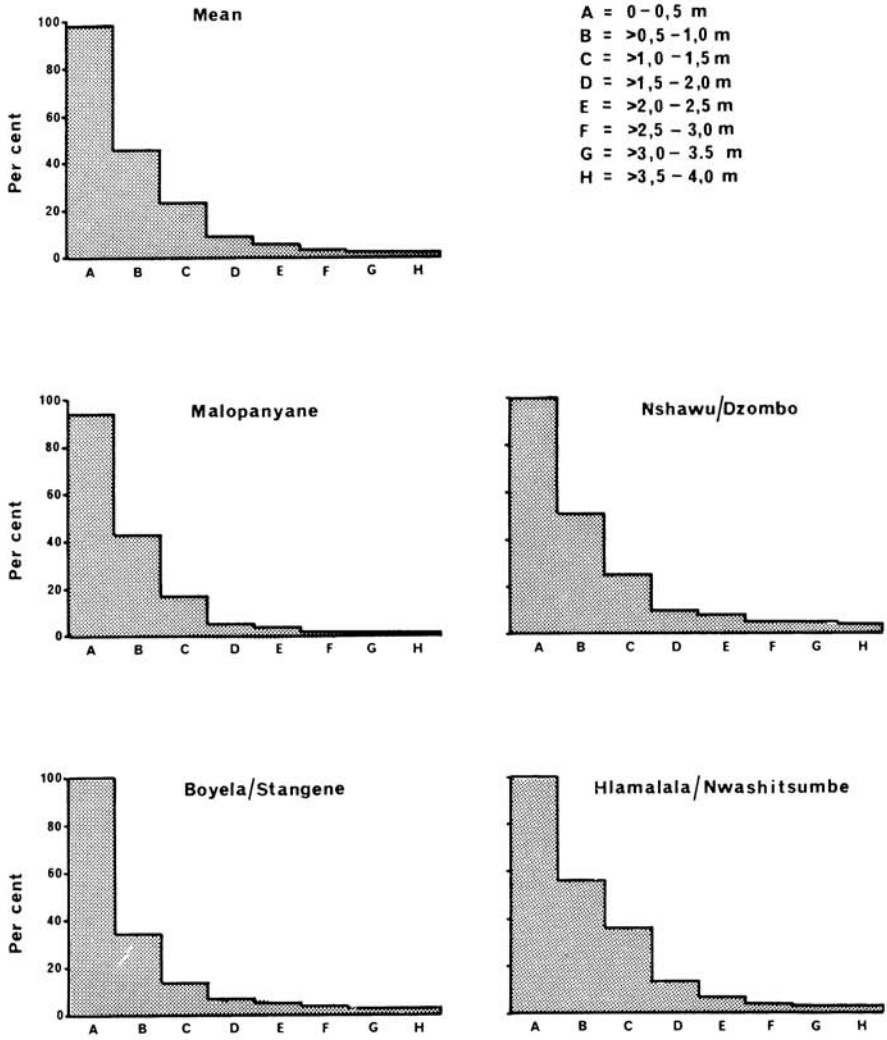

Fig. 4. The percentage obstruction to vision by vegetation in eight 0,5 m height intervals in four tsessebe habitats in the Kruger National Park

The percentage obstruction to vision in eight height intervals is presented in Fig. 4. while the results presented in Fig. 5 reflect the relative number and relative canopy cover of trees and shrubs in four height

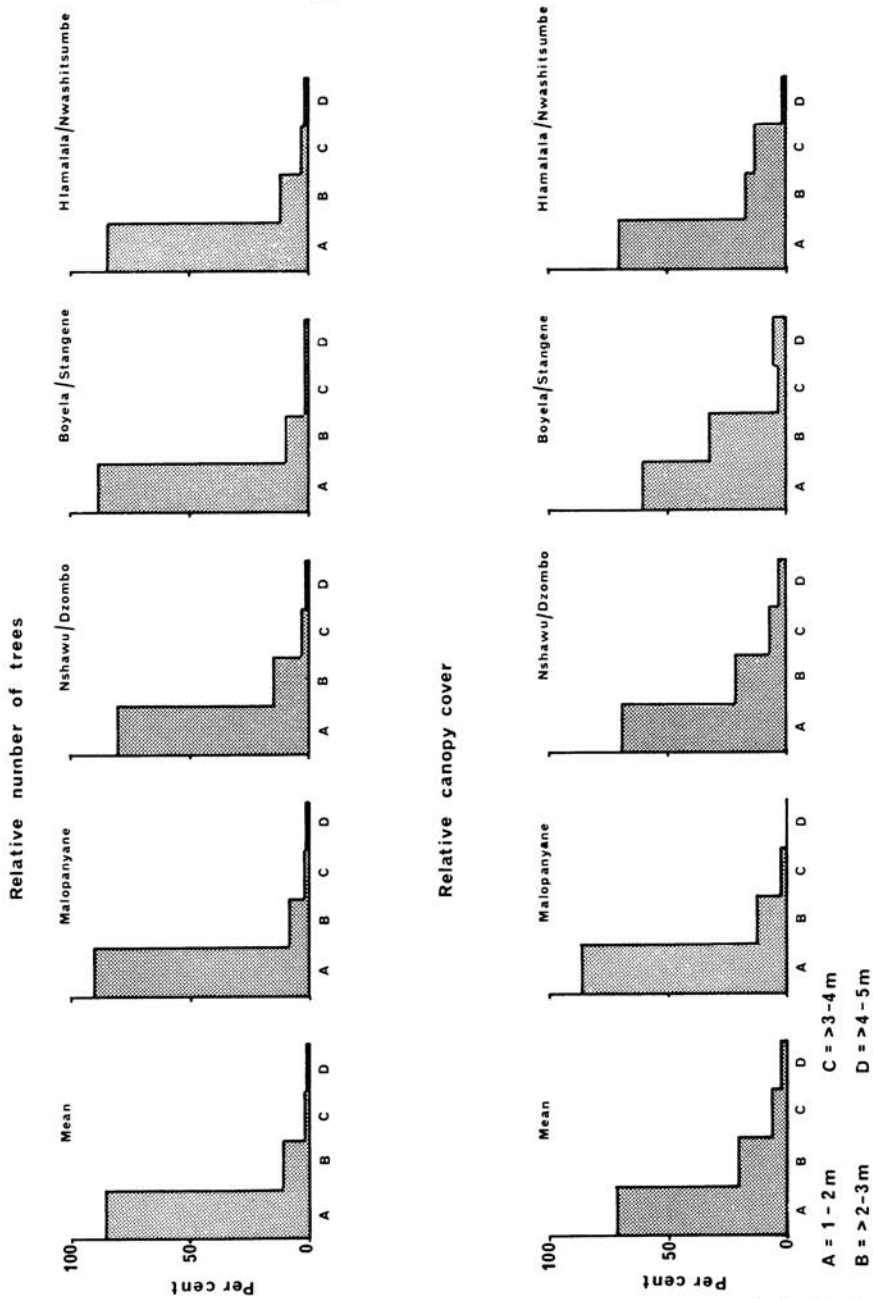

Fig. 5. The relative number and relative canopy cover of trees and shrubs in four height intervals in four tsessebe habitats in the Kruger National Park.

intervals. From these results it is clear that most of the cover in tsessebe habitats is confined to height levels below 2 metres. The results in Fig. 4 further indicate a high degree of cover in the 0–0,5 m height interval (which includes the grass stratum) but with a rapid decline in vegetative cover in the higher categories. The same tendency is borne out by the results presented in Fig. 5. The results from these surveys thus clearly reflect the "openness" of tsessebe habitats.

Social behaviour and population structure

Social Behaviour

For an interpretation of the population structure of tsessebe it is imperative to have a thorough knowledge of the social organisation of the species.

Walther (1968), Huntley (1970), Child *et al* (1972), Grobler (1973) and Joubert (1972), have indicated that tsessebe adhere to a social organisation based on territoriality throughout their range. There are, however, also indications that the form of territoriality may differ from one area to another with males defending a fixed territory and harems entering and leaving territories at will, on the one hand, and males defending territories which incorporate the fixed home range of a particular harem, on the other. In the case of the latter form it leads to the establishment of stable herds which occupy a fixed area for a prolonged period (Huntley 1970; Joubert 1972). In the KNP territorial bulls frequently patrol their boundaries and are not only involved in skirmishes with territorial neighbours but also defend their territories from intrusion by evicted young males.

Some form of dominance hierarchy seems to exist between the females in a harem and Huntley (1970) has stated that "the harem herd is a very closely knit association seldom if ever breaking up after its formation". On the few occasions where a 'strange' cow happened to enter an established harem group it unleashed aggressive displaying towards the newcomer. This has led us to believe that established harem groups are largely exclusive and that the assimilation of a new cow to the group is not of frequent occurrence. Because of the fixed territories and permanency of herds this phenomenon has been borne out by observations which indicate that 'new' cows are only rarely accepted in established herds. However, some exchange of cows does take place and this appears to be especially true with the formation of new herds. A reduction in the number of adult cows in a few herds has been observed and though this may, in part, be due to mortality there is also sufficient evidence to suggest that a number have formed the nucleus of new harems. In an area where tsessebe numbers have attained their greatest density per unit area in the KNP it has also been found that new herds are established by young territorial bulls gaining control over yearling heifers.

Over the study period of three years the average number of individuals per herd (i.e. territorial bull, cows and young) has remained re-

markably constant at an average of 8,1 per herd after ten surveys (ranging from 6,7 to 8,8: see Table 2). This clearly suggests that the group dynamics of tsessebe are innately regulated to maintain an optimum group size. Though some of the mechanisms of the regulating process have been suggested in the previous paragraph some still remain obscure. It is not clear why some of the yearling females leave the breeding herds with the yearling males and neither are the factors determining the number of cows in a group fully understood.

Eviction of young males commences shortly before the onset of the calving season and continues to the middle or end of January when all but the very exceptional yearling males have been ousted (Joubert 1972). In the KNP the eviction of yearling females has been observed but is regarded as exceptional. In the area of the highest tsessebe density two herds, each consisting of a young territorial bull and two yearling heifers, were found during December, i.e. when the eviction of yearlings reaches completion. In the enclosed area in the Percy Fyfe Nature Reserve where Huntley (1970) was of the opinion that the tsessebe population might have reached its saturation point, the ousting of yearling females from the harem herds occurred at almost the same frequency as that of young males. There can be no doubt that the territorial bull can distinguish between the sexes of the yearlings and there does not seem to be any ready explanation for the eviction of yearling females. If the eviction of young females is, in fact, density dependent it would imply that the bull is primarily responsible for determining herd size.

Young males which have left the harem herds aggregate together in small bachelor groups varying from two or three to as many as 12 individuals. The size of these groups will probably vary with population density and in Botswana Child *et al* (1972) found up to 31 together and Grobler (1973) as many as 22 in some high density areas in Rhodesia. Most of the members of such bachelor groups consist of yearlings and two-year olds and apparently only rarely older adults.

The bachelor groups are not tolerated in the territories of territorial males – in contrast to what Grobler (1973) found in some areas of Rhodesia – and are vigorously chased out when they do intrude. The tendency is therefore for these males to roam about on the outskirts of established territories.

A very close mother-calf relationship exists between the tsessebe cow and her calf. This relationship persists beyond weaning – which takes place at approximately six to seven months (cf. Huntley 1970; Child *et al.* 1972) – and is only culminated with the birth of the next calf or severed with the eviction of the calf from the herd. Walther (1963) differentiated between two broad systems amongst ungulates in rearing their young, based on the mother-calf relationship, i.e. the Nachfolge-(follower) and Ablieger-(concealing) types. In the former the calf follows its mother from the time of birth with no tendency of concealing itself while the mother pursues her daily activities, while in the latter the calf remains concealed in some cover until the mother calls it up for

nursing. In general, tsessebe calves are of the "follower" type and move about with the cows. It has also been observed, however, that young calves may conceal themselves while the herd moves off to a waterhole, thus reflecting some characteristics of the "Ablieger" type. On one occasion a group of young calves was found lying low in the company of a cow while the rest of the herd was approximately 2 km away at a drinking hole. On another occasion a herd with seven cows – all with calves as judged by their large udders – was found at a waterhole. After following the herd for about 1,5 km the calves, all seven of them, emerged from where they were lying down and joined their mothers. As in most other gregarious species the youngsters tend to form nurseries and often lie up with one of the adult cows while the rest of the herd is further afield. At the slightest sign of danger, however, the cows run to their calves and if the herd moves off each calf follows its mother.

Huntley (1970) found that four of 15 calves he observed were raised in typical "Ablieger" fashion where the calf remained concealed in tall grass and was visited by the cow only for suckling. The rest followed their mothers in the normal way. On the other hand Child *et al* (1972) found that "there was no apparent attempt to conceal even the smallest calves", though they also observed small nurseries bedding down close to their grazing dams.

Population Structure

Table 2 shows the population structure of the KNP tsessebe population at various times during the study. Surveys were largely confined to the north-eastern Lebombo Flats where the majority of the tsessebe population is concentrated. The structure of the tsessebe population is also graphically illustrated in Fig. 6 for two breeding seasons during the study period, i.e. the 1970/1971 and 1972/1973 seasons. In each case two separate surveys were required to determine the various age classes and/or sex ratios. It was found that during the period December and January a clear distinction could be made between yearlings and adults but that the sexing of young calves was almost impossible; conversely, towards April the sexing of young calves provided no problems but yearlings became more difficult to distinguish from adults with a reasonable amount of accuracy.

The preceding notes on the social organisation of this species will suffice to illustrate the caution with which an analysis of the population structure should be approached. In the further discussion of the population structure cross reference will therefore be made to social organisation to point out any possible sources of error.

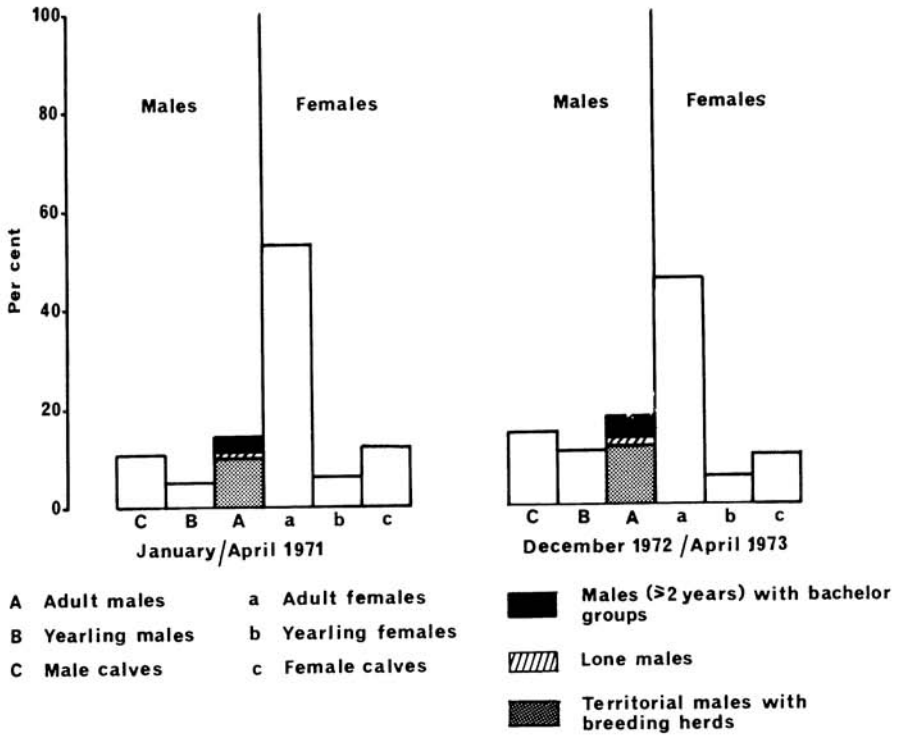

Fig. 6. The population structure of tsessebe during the 1970/1971 and 1972/1973 breeding seasons in the Kruger National Park.

Table 2

The population structure of tsessebe at various intervals between October 1970 and December 1973 in the Kruger National Park

Time	Sample total	BREEDING HERDS																			
		Tot. in harems	Ave. herd size	Adults					Yearlings (12–23 months)							Calves (0–11 months)					
				♂♂	% ♂ in harems	♀♀	% ♀ in harems	Total	% in pop.	% in harems	♂ in harems	% ♂ in harems	♀ in harems	% ♀♀ in harems	Total	% in pop.	% in ad ♀♀	♂	% of harems	♀	% of harems
Oct. '70	102	99	8,3	11	11,11	44	44,44	12	14,71	12,12	7	7,04	5	5,05	32	31,37	72,72	—	—	—	—
Nov. '70	59	54	7,7	7	12,96	29	53,70	5	18,52	9,26	2	3,70	3	5,55	18	24,07	44,83	—	—	—	—
Dec. '70	83	74	6,7	11	14,86	37	50,00	9	19,28	12,16	3	4,05	6	8,10	17	20,48	45,94	—	—	—	—
Jan. '71	126	115	8,8	12	10,43	56	48,7	9	11,11	7,83	1	0,87	8	6,96	38	30,16	67,86	—	—	—	—
Apr. '71	150	142	8,8	16	11,28	90	63,38	—	—	—	—	—	—	—	34	22,67	37,78	16	11,27	18	12,67
Dec. '72	216	187	8,5	20	10,70	97	51,87	19	15,28	10,16	7	3,74	12	6,42	51	23,61	52,58	—	—	—	—
Feb. '73	253	223	8,0	28	12,56	126	56,50	—	—	—	—	—	—	—	68	26,90	53,97	—	—	—	
Apr. '73	179	153	8,1	19	12,42	86	56,21	—	—	—	—	—	—	—	48	26,82	55,87	27	18,62	18	12,41
June '73	193	164	7,5	17	10,37	97	59,15	—	—	—	—	—	—	—	52	26,94	53,61	30	18,29	22	13,41
Dec. '73	155	147	8,2	18	12,24	66	44,89	17	12,26	11,56	1	0,68	16	10,88	46	31,29	69,70	—	—	—	—

Time	Sample total	NON BREEDING HERDS											
		Total in N.B.G.	% of pop.	Lone Bulls			Male Herds						
				Total	% in pop.	% of N.B.G.	Total	Total 2 yr.	% of ♂ groups	% of total population	Yearling ♂♂	% in ♂ groups	% of total population
Oct. '70	102	3	2,94	—	—	—	3	—	—	——	3(1 ♀) ♂♂ : 2	100,00	2,94
Nov. '70	59	5	8,47	—	—	—	5	—	—	——	5(1 ♀) ♂♂ : 4	100,00	8,47
Dec. '70	83	9	10,84	—	—	—	9	2	22,22	2,4	7(1 ♀) ♂♂ : 6	66,67	7,22
Jan. '71	126	11	8,73	2	1,59	18,18	9	4	44,44	3,17	5	55,56	3,97
Apr. '71	150	8	5,33	1	0,67	12,50	7			4,67 = yearlings + two-yr. olds			
Dec. '72	216	29	13,43	2	0,93	6,90	27	13	48,15	6,02	14	51,85	6,48
Feb. '73	253	29	11,46	7	2,77	24,14	22	—	—	—	22	100,00	8,70
Apr. '73	179	26	14,53	4	2,23	15,38	22	2	9,09	1,12	20	90,9	11,17
June '73	193	29	15,03	9	4,62	31,03	20			10,36 = yearlings + two-yr. olds			
Dec. '73	155	8	5,16	—	—	—	8	6	75,0	3,87	2	25,0	1,29

Sample size

Sample sizes varied between 59 and 253 individuals representing a range of 9% to 39% of the total population of the KNP, which is calculated to be 640 animals. Of the 10 surveys only two were below 15 per cent. However, these two samples did not differ markedly from the larger samples and may therefore be regarded as representative of the population structure of tsessebe.

Population Analysis

1. Non-breeding Groups

Among the non-breeding groups are considered lone territorial males without harems and bachelor groups. These groups are the most difficult to sample reliably due to the following factors:

(a) bulls classified as lone territorial bulls may in fact be harem bulls patrolling their territory (see social behaviour);
(b) bachelor groups do not have territories but are harrassed on entering established territories and consequently occupy peripheral areas where they are difficult to locate and may therefore be overlooked in a survey; and
(c) the known territories of breeding herds were often traversed until the herd was located but this did not apply to bachelors as there were no definite areas in which to search for them.

Both (b) and (c) point to an under-estimate of the non-breeding segment of the population while (a) would indicate a slight over-estimate. However, the error caused by (a) is believed to be minimal while the misrepresentation caused by (b) and (c) could be of a much higher order.

The adult sex ratio of tsessebe reflects a preponderance of females over males of the order of 3,1:1 (Jan. 1971), 2,8:1 (Dec. 1972) and 2,8:1 (Dec. 1973). However, among calves the male to female ratio was found to be almost 1:1 (1:1,2) in 1971 and 1:0,7 in 1973. Amongst yearlings the sex ratio was 1:0,7 during 1970 and 1:0,6 in 1972. A higher proportion of males would thus be expected in the adult segment. The discrepancies in the sex ratios of adult and immature segments are not easily explained and direct proof of the cause(s) of the differences proved extremely difficult to obtain. The following are, however, believed to be some of the main contributing factors:

(i) biased sampling favouring females as explained under (b) and (c);
(ii) differential mortality of the sexes after the age of one year. Considering lion predation, Pienaar (1969) found from an analysis of carcass returns in the KNP ". . . that the rate of predation on adult male animals (in general) is much heavier than on the breeding female segment of the population", and concludes that "differential

predation on the sexes may in fact be the most important factor responsible for the disproportionate sex ratio which is apparent in the adult segment". Prey species thus affected included impala, waterbuck, kudu, wildebeest, buffalo and giraffe. In the Kafue National Park, Zambia, Mitchell, Shenton and Uys (1965) also found that males in a wide variety of different species were killed in excess of females.

In the KNP tsessebe killed by predators (mainly lion and only occasionally leopard and cheetah) constitute only approximately 0,20% (1966–1972) of the animals killed annually. The sample of carcasses of adult animals recovered between 1966 and 1973 is therefore small, i.e. 20, but of these only six were females. The kill sex ratio of adult tsessebe is therefore 1:0,43. It may therefore be concluded that differential sex mortality due to predation may contribute quite significantly towards the disproportionate sex ratio in the adult segment of the population.

From the 10 surveys conducted during the study period non-breeding groups averaged 9,59% of the total population ranging from 2,94% to 15,03 per cent. Lone bulls averaged 2,14% of the population while bachelor groups comprised 8,69 per cent. In the bachelor groups an average of 40,34% were two-years old and older while 59,66% were yearlings.

2. Breeding Groups

Provided the sample size is adequately large there are no other apparent sources of error in obtaining a true reflection of the age and sex relationships within this segment of the population. Due to the difficulties experienced in obtaining a reliable sample of the non-breeding segment it would therefore lead to an over-representation of the breeding segment relative to the total population. In the 10 surveys breeding groups ranged from 84,9% to 97,0% of the population with a mean of 90,31 per cent.

(a) Herd size

Herd size varied from two or three individuals (a bull and one or two cows) to as many as 21. However, the average size of the herds remained remarkably constant throughout the study period and ranged between 6,7 and 8,8 individuals (mean 8,06) with no notable seasonal fluctuations (Table 2; Fig. 6). In the adult segment of the breeding groups the male : female ratio varied in the 10 surveys from 1:3,91 to 1:5,71 with the overall average 1:4,86 (yearling females were regarded as adults in these calculations as they become indistinguishable from adult cows before they reach the age of two years). Huntley (1970) recorded one bull to five cows as the average harem size in the Percy Fyfe Nature Reserve while Grobler (1973) estimated the average herd size in Rhodesia

at seven. In Botswana the year round group size averaged 3,6 females, ranging from 2,0 to 5,3, with smaller groups immediately after the rut (Child *et al* 1972).

(b) Harem bulls

Each harem herd is customarily accompanied by one adult male only while in exceptional cases a yearling male was also encountered with a herd. Harem bulls comprised between 8,8% and 13,2% (mean 10,7%) of the total population and an average of 11,89% of the breeding groups varying between 10,43% and 14,86 per cent. The fact that the non-breeding groups constitute a mere 9,59% (mean) of the total population as compared to the 10,7% of harem bulls may be a reflection of the under representation of the lone males and bachelor groups as discussed above. Alternatively, it may also indicate a high differential mortality rate amongst the non-breeding segment, indicating that mortality is not only higher amongst males but more specifically so amongst the non-breeding males. Such an assumption would lend further support to the findings of Mitchell *et al.* (1965) and Pienaar (1969) though further data is required to make a firm statement regarding the tsessebe.

(c) Adult females

Adult females make up almost half of the entire population (mean 46,65%, range: 42,5% to 60,0%) and just over half of the harem groups (52,88%, range: 44,44% to 63,38%). Reference has already been made to the remarkably constant bull:cow ratio (mean 1:4,86) in the breeding herds.

(d) Yearlings

As the yearling class represents the segment entering from the juvenile stage into the adult segment, it is essential that this class is well sampled in any consideration of the population dynamics of the species. Young males are evicted from the harems at the age of a year whereafter a reliable sample of their status is difficult to obtain; young heifers remain, on the whole, with the harems but from the age of 16 to 18 months become increasingly difficult to distinguish from the adult cows. The most appropriate time for sampling the yearlings would therefore be just prior to the calving season when eviction is being initiated and the youngsters are easily recognised.

Surveys during December, i.e. towards the end of the calving season, of 1970, 1972 and 1973 revealed 7,2%, 5,5% and 10,3% yearling heifers in the population, respectively. Mortality is believed to be low amongst females after their first critical year and it could therefore safely be assumed that the recruitment rate of females to the adult segment would vary between roughly 4% and 10% in normal years.

(e) Calves

Huntley (1970) found that among 38 calves born in the Percy Fyfe Nature Reserve the male:female sex ratio was 1:1,53 while Child *et al* (1972) could find no significant difference between the sexes of calves in Botswana. Of 34 calves sexed in the KNP during 1971 (April) 16 were male and 18 female, giving a sex ratio of almost 1:1 while a sex ratio of 1:0,67 (27:18) was obtained from 45 calves during April 1973.

Young calves made up 30,16% of the total population in 1971 (January), 26,90% in 1973 (February) and 31,29% in the 1973/74 season. Assuming that females reach sexual maturity early in their third year (i.e. as two year olds) and that the recruitment rate to the adult cow segment is 6,53% per year (mean for three seasons) this would represent a calf to adult cow ratio of 1:1,37, 1:1,74 and 1:1,35 for the three seasons respectively.

Conclusions

With the proclamation of the Kruger National Park in 1926 some of the most favoured tsessebe habitat in the Transvaal Lowveld was lost to conservation. This also had a significant effect on the tsessebe population south of the Letaba River as most areas where they still occurred, sustained only a small and struggling population. This position has persisted through the years with no notable improvement, and in fact led to the eventual extinction of tsessebe south of the Sabie River. North of the Letaba River sufficient habitat is still available and water provision in hitherto waterless areas and a notable increase in their numbers with an accompanying extension of their range, has been noted over the last few years.

It is widely accepted that tsessebe favour open savanna or grassland, preferably short grass, vegetation types as their select habitats, but also readily utilize woodland savanna (Child *et al* 1972). From objective surveys of the physiognomic and structural aspects of the vegetation of tsessebe habitats, the degree of "openness" of favoured habitats could be illustrated. It must, however, be pointed out that the surveys conducted during this study reflect conditions considered as optimal in the KNP although they may, in fact, only fall within the category of 'acceptable' when compared with other habitats in which tsessebe have attained a considerably higher density (cf. Child *et al* 1972).

The population structure of the KNP's tsessebe population compares favourably with that of other tsessebe populations which have been studied (Huntley 1970; Child *et al* 1972; Grobler 1973) and the proportion of immature animals indicates a healthy population. From this point of view, the inference may be made that the areas inhabited by tsessebe in the KNP meet the basic requirements of the species.

REFERENCES

CHILD, G., H. ROBBEL and C. P. HEPBURN. 1972. Observations on the biology of tsessebe, *Damaliscus lunatus lunatus,* in northern Botswana. *Mammalia* 36(3): 342–388.

DE VOS, A. and H. S. MOSBY. 1963. Evaluation of habitat. *In: Wildlife investigational techniques.* Ed. H. S. Mosby. Michigan: Ann Arbor.

GLYNN, H. T. 1926. *Game and gold. Memories of over 50 years in the Lydenburg District, Transvaal.* London: Dolman Printing Co.

GROBLER, J. H. 1973. Biological data on tsessebe, *Damaliscus lunatus* (Mammalia: Alcelaphinae), in Rhodesia. *Arnoldia* 6(12): 1–16.

HUNTLEY, B. J. 1970. Observations on the Percy Fyfe Reserve tsessebe population. *Ann. Trans. Mus.* 27(11): 225–239.

JOUBERT, S. C. J. 1972. Territorial behaviour of the tsessebe (*Damaliscus lunatus lunatus* Burchell) in the Kruger National Park. *Zool. Africana* 7(1): 141–156.

KIRBY, F. V. 1896. *In haunts of wild game.* London: Blackwood and Sons.

MITCHELL, B. L., J. B. SHENTON and J. C. M. UYS. 1965. Predation on large mammals in the Kafue National Park. *Zool. Africana* 1(1): 297–318

PIENAAR, U DE V. 1963. The large mammals of the Kruger National Park – their distribution and present-day status. *Koedoe* 6: 1–37.

PIENAAR, U DE V. 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12: 108–176.

PIENAAR, U DE V. 1974. Habitat preference in South African antelope species and its significance in natural and artificial distribution patterns. *Koedoe* 17: 185–195.

ROBERTS, A. 1951. *The mammals of South Africa.* South Africa: CNA.

SANDENBERGH, J. A. B. 1945–1954. Unpublished Warden's annual report for the Kruger National Park.

SMITHERS, R. H. N. 1966. *The mammals of Rhodesia, Zambia and Malawi.* London: Collins.

STEVENSON-HAMILTON, J. 1947. *Wild life in South Africa.* London: Cassell and Co.

STEVENSON-HAMILTON, J. 1902–1944. Unpublished Warden's annual report for the Kruger National Park.

WALTHER, F. R. 1963. Verhaltensstudien an der Gattung *Tragelaphus* De Blainville, 1816, in Gefangeschaft, unter besonderer Berücksichtigung des Sozialverhaltens. *Z.f. Tierpsychol.* 21(7): 871–890.

WALTHER, F. R. 1968. Kuhantilopen, Pferdeböcke und Wasserböcke. *Grizimek's Tierleben* XIII: 437–471. Zürich: Kinsller Verlag.