

Observations on Ecology and Behaviour of Lechwe, Puku and Waterbuck along the Chobe River, Botswana

By GRAHAM CHILD and WOLFGANG VON RICHTER

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Introduction

The ranges of three species of the genus *Kobus* overlap along the southern bank of the Chobe River in the northeastern corner of Botswana. The present paper analyses observations on lechwe, *Kobus lechwe*, puku, *K. vardonii* and common waterbuck *K. ellipsiprymnus*, made during an ecological survey of the Chobe National Park and surrounding parts of North-Eastern Botswana in June 1965 through June 1967.

The study compared the ecological requirements and gross behaviour patterns of the three species in order to determine the similarities and difference which may occur in three closely related antelope using the same ground. Particular attention was paid to lechwe and puku as Prof. W. ELDER, a Fullbright Scholarguest of the Botswana Government, was doing a detailed study of waterbuck simultaneously. In addition, lechwe and puku were recognised as species deserving particular attention, as the lechwe population was reported to be declining and the small puku population had become isolated from other puku. A better understanding of their ecological needs and general behaviour seemed necessary as a basis for action to ensure their survival in the Park.

Methods

Numerical data on herd structure and physical condition were obtained during routine road counts, designed to indicate seasonal fluctuations in the number of large mammals along the Chobe river. The route extended 20 miles west along the main road from the Park headquarters to Ihaha, returning via three loop roads which sampled the flood plain. Counts were made by two observers in the cab of the vehicle between 14.30 hours and 15 minutes after sunset. Once game was sighted the vehicle was stopped and the animals were counted using binoculars or a twenty power scope and this was sometimes facilitated by climbing onto the bed or bonnet of the truck. Counts were discontinued during the flood season when the loop roads became impassable, but otherwise there were between five and thirteen per month by the authors or senior field staff of the Game Department.

Visibility on the flood plain remained similar throughout the study, but along the main road varied seasonally as vegetation came into leaf during the rains. Changes in visibility did not influence lechwe counts and only affected those of puku significantly once they began leaving the flood plain. The influence on waterbuck counts was more pronounced although the species favoured open areas in the scrub and the highest numbers were in fact recorded in December 1966, when visibility was poorest. Seasonal changes in the depth of visibility were similar in 1965/6 and 1966/7, allowing a comparison of numerical trends in the two years.

As many groups as possible were classified into sex and age classes by the senior author who assessed the physical condition of adults according to the method des-

cribed by RINEY (1960) and CHILD (1965). Puku and waterbuck were aged according to standards similar to those suggested by DE VOS and DOWSETT (1966), except that their two youngest classes were lumped under calves, and lechwe were aged according to ROBINETTE and CHILD (1964). Lechwe males were also aged from horn development as these authors showed that growth continued until they were about five years old and this was accompanied by changes in shape. Calves (0–11 months) either had no horns or simple spikeshaped horns up to 15 cm in length, these became bowed in yearlings (12–23 months) and reached 28 cm. The shape was similar in two-year-olds (24–35 months), but the horns were longer and up to about 57 cm. The horns of most older animals were lyrate and in any case were longer and heavier. Skulls from predator kills from all these classes had tooth formulae which correlated with ageing criteria determined by ROBINETTE and CHILD (1964).

Mid September 1965 and the end of September 1966 were taken somewhat arbitrarily as the beginning of the peak in calving for the purpose of classifying lechwe herds. From these dates well grown calves were termed yearlings, yearlings became two-year-olds etc. Some difficulty was experienced in assigning a number of small animals into the calf or yearling class and with deciding whether the horns of some males were fully adult or not, but in the total sample of 4,461 head these doubtful cases amounted to about two per cent. There was also a small number (1.3%) of animals within large herds which could not be seen clearly enough to classify.

Feeding preferences in the multispecies grassland were determined by direct observation. Each observation represented on individual animal's feeding from one species of plant in an area no more than 25 cm across, this being close to the maximum area in which a puku or lechwe could feed without stepping forward and having to select a new plant. In areas grazed by more than one species, the animals were watched from a vehicle to pinpoint the exact location at which an individual fed. It was then necessary to accept only very freshly bitten off plants so that an hour's work often yielded eight or fewer observations. Slowly settling detritus was a useful guide to the paths taken by animals feeding on emergent vegetation in shallow water.

Heavy grazing on the flood plain during the dry season meant most grasses had to be identified from vegetative features and then transplanted to seed boxes to mature, before they could be named by the National Herbarium of Rhodesia in Salisbury.

Study Area

The study took place mainly along the Chobe river between Kasane and Ngoma. Here the river forms the boundary between the Chobe National Park in North-Eastern Botswana and an area devoted to scattered village settlement in the Eastern Caprivi Zipfel of South West Africa (fig. 1).

The river meanders through an extensive flood plain which to the north stretches almost unbroken to the Zambezi river, while in the south it gives way abruptly to a sand ridge composed of a basaltic core overlaid by Kalahari sand. The Chobe receives much of its water from the Zambezi, which overflows its southern bank seasonally between March and June, so that the Eastern Caprivi is largely swamp or flood plain grassland, subject to more or less extensive annual inundation. Similar grassland occurs in a narrow strip and between the meanders of the river on the Botswana side. It is backed by a narrow riparian fringe along the foot of the sandridge, or along the edge of the Pookoo flats, an ancient flood plain between a curve in the sandridge and the present flood plain.

Rainfall is seasonal, falling mainly between November and March and has averaged 690 mm (range 363 to 1396 mm) over 43 seasons. The maximum and minimum

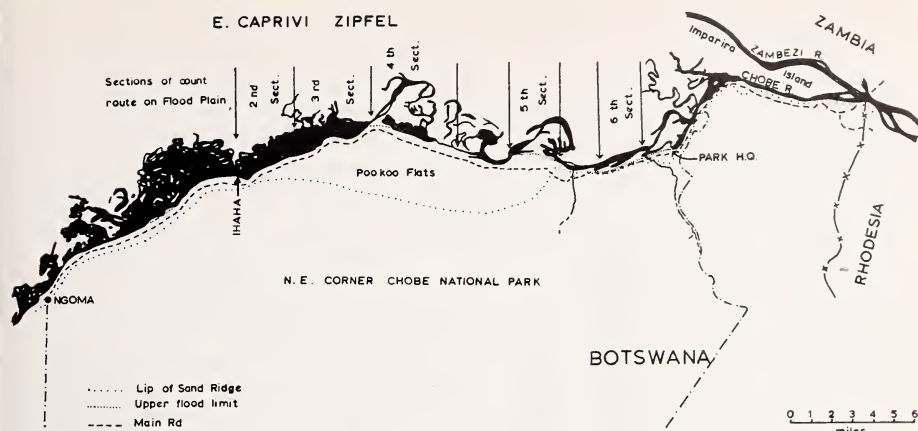


Fig. 1. Map of Study Area based on aerial photographs taken in June 1962 when the floods were still high and covered much of the flood plain along the Chobe River. The area subject to seasonal inundation spreads north from that shown, most of the way to the south bank of the Zambezi.

average monthly temperatures are then around 31 and 19°C before declining to the winter minima in June or July when they are 26 and 9°C respectively. Temperatures reach a maximum in October just before the rains when the average maximum over 24 years has been 35°C and the minimum 19°C.

These climatic conditions result in dry marginal habitats along the edge of the flood plain. The slight sandy elevations on the plain support a variety of riparian trees, but lesser vegetation has been sensitive to past land use which has led to some deterioration in the perennial grasses and to bush encroachment. The riparian strip has also been modified by past land use and elephant damage is extensive, while bush encroachment and a general decline in perennial grasses are wide-spread on the Pookoo flats and in Kalahari woodland on the sandridge.

The Chobe flats on the Botswana side of the river are subject to considerable use by over a dozen large browsing and grazing mammals, particularly late in the dry season, while grazing by domestic stock is fairly intensive on the north bank where there is also some village cultivation.

Distribution and Movements

The ranges of the three species overlap along the south bank of the Chobe. There is a relict population of puku inside the Park, although within historic times this was the southern limit of a bulge in the species range, which extended southwards across the Caprivi. It has, however, disappeared from the north bank of the Chobe during the past 40 years and from the last stronghold on Imparira Island, at the eastern tip of the Caprivi, since 1947, chiefly as the result of human settlement since 1958.

There are two more or less distinct populations of lechwe in Botswana. One is in the Okavango swamps, while the second occurs along the Linyati/Chobe system on the Caprivi border, and includes the herds which enter the north-east of the Park. In the latter area waterbuck have been recorded only in a narrow band some two to four miles wide along the Chobe. Elsewhere in Botswana they occur along the Rhodesian and Transvaal borders, along the Linyati swamps and in the eastern fringe of the Okavango swamps (CHILD, 1968).

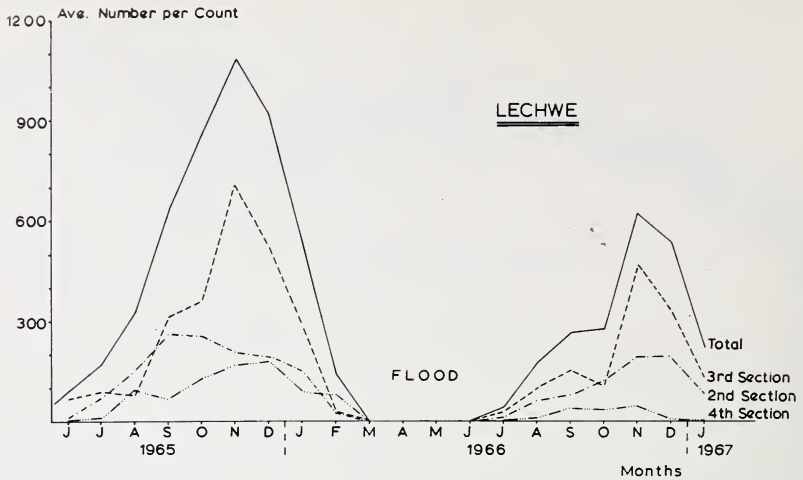


Fig 2. Mean monthly counts of lechwe along the standardised route, and along sections of this route

Puku and waterbuck were resident in the study area, but lechwe moved north into the Caprivi during the flood season. They were first noted on the count route in mid June 1965 and numbers reached a peak in November (fig. 2) before the whole population, with the exception of the two calves discussed below, returned to the Caprivi for the 1966 floods. The pattern was similar in 1966 and early 1967, although the initial build up was less rapid and began a month later, due to the higher floods in 1966. The floods were intermediate in 1967, but the lechwe did not appear until July.

The first groups generally contained a high proportion of males, including adults and juveniles (table 1). The calculated average number of males per count then increased to November, but fell away rapidly during December and January in both

seasons indicating a trend towards males leading the seasonal drift to and from the Chobe.

Excitement in a population is a characteristic prelude to movement and this would explain the marked increase in sexual excitation and rutting behaviour in males observed during November and early December, before the proportion of males declined. Sparring and some attempts at mating were observed in all months, but the incidence and intensity of this behaviour and of "flehmen" behaviour increased

Table 1

Relative Numbers of Male and Female Lechwe by Months, exclusive of calves

Season Month	Sample	♂ ♂ : 100 ♀ ♀
1965/66 July	59	111:100
Aug.	63	92:100
Sep.	386	76:100
Oct.	161	83:100
Nov.	618	72:100
Dec.	404	33:100
Jan.	565	45:100
1966/67 July	30	No females
Aug.	49	227:100
Sep.	597	31:100
Oct.	191	54:100
Nov.	109	42:100
Dec.	197	31:100
Jan.	54	26:100

greatly during this period, although no successful copulations were noted. Males of all ages were involved and seven calves, estimated as between two and four months old, were seen attempting to mount full grown females, probably their mothers, judging by the dispersion of the individuals in the herd and by the fact that one calf after several attempts at mounting then suckled.

This false rut was observed in October through November in the Caprivi by WILHELM (1933), who apparently mistook it for the peak rutting period, as this would explain the discrepancy between the length of the gestation period and the interval between the rut and calving seasons he describes, and commented upon by ROBINETTE and CHILD (1964).

The lechwe moved ahead of the rising water and in exceptional flood seasons such as 1957 and 1958 moved over 50 miles. A survey of the eastern Caprivi in November 1965, revealed few lechwe and the many villagers interviewed confirmed that the bulk of the population was then confined to a narrow band along the Chobe, seldom over a half mile wide on either side of the river. A similar distribution was observed by HEPBURN (*pers. comm.*) during a helicopter patrol of the area on July 29, 1966.

Here they favoured low lying areas near the banks of the river, although minor elevations, some of which supported sparse *Acacia* scrub, were frequently used as resting sites. This explains the distribution pattern shown in fig 3, as the second and third sections of the count route sampled extensive sections of low lying flats, the most favoured habitat in the Park. However, during November and December more lechwe moved onto the slightly higher sandy areas, to graze the maturing perennial *Eragrostis rigidior*. This was especially marked in the fourth section, although the local drift from adjacent lower lying areas does not reflect significantly in fig. 2.

Fair numbers of lechwe remained on the south bank of the Chobe when the Zambezi waters broke through, across the Caprivi in March 1966, causing the Chobe to rise sharply and so flood much of their most favoured habitat. The animals were then forced on to the slightly elevated Pookoo flats, before all, except the two calves swam the widening river back to the Caprivi. This short period of about one week was the only time when lechwe were contacted regularly off the flood plain, although there were sporadic observations between August and December, particularly in the mornings and towards the west of the Study Area, of herds in fringing scrub along the abrupt edge of the flood plain.

It was interesting that an adult female flushed in thick scrub during the March period sought refuge in a small pan about one foot deep and nowhere over six yards across and, standing in the middle of the pan, allowed an observer within 40 yards of her. Others disturbed during this period escaped away from the river and sometimes

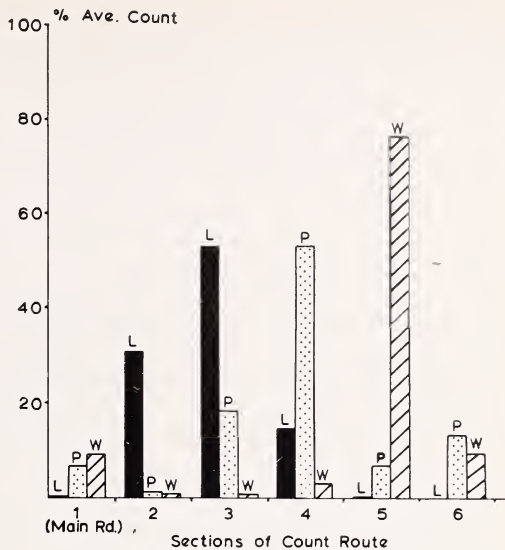


Fig. 3. The relative proportionate distribution of lechwe (L), puku (P) and waterbuck (W) along different sections of the count route. Note: some parts of the flats sampled by section 6 were visible from the main road (section 1) so that there is some overlap between these two sections

entered dense thickets, whereas those flushed in the scrub fringing the flood plain at other times of the year immediately made for the flood plain and eventually the banks of the river, which they crossed without hesitation if pressed. There were several observations during the dry season of poachers' dogs chasing lechwe on the flood plain and without exception, the animals made for and crossed the river, which was then shallow enough in most places for them to bound across and few had to swim more than a few yards.

These observations confirm that lechwe favour shallow water for escape, but indicate they are at a disadvantage when the water is deeper, although the species can swim well and often feeds in the water.

Lechwe were numerous on the flood plain, south of the river from shortly after dawn, but during late evening showed a strong tendency to cross into the Caprivi. Observations at night by means of a powerful spot light early in the dry season (June to August) indicated that many slept along the water's edge on the north bank, whereas there were very few on the south bank. Later in the season this behaviour became less marked and by October/November there were many lechwe at night scattered over lower lying parts of the flood plain south of the river.

The two lechwe calves which did not return to the Caprivi in March 1966 were interesting as each became associated with groups of waterbuck and lived with them until at least May 1967. They apparently made no attempt to rejoin the lechwe or to cross into the Caprivi during the 1967 flood and seemed to have been imprinted by their foster associates. Their behaviour indicated that small numbers of lechwe could survive if limited to waterbuck habitat on a year around basis in this area, as their physical condition was as good or better than that of many similar aged lechwe which returned from the Caprivi in 1966.

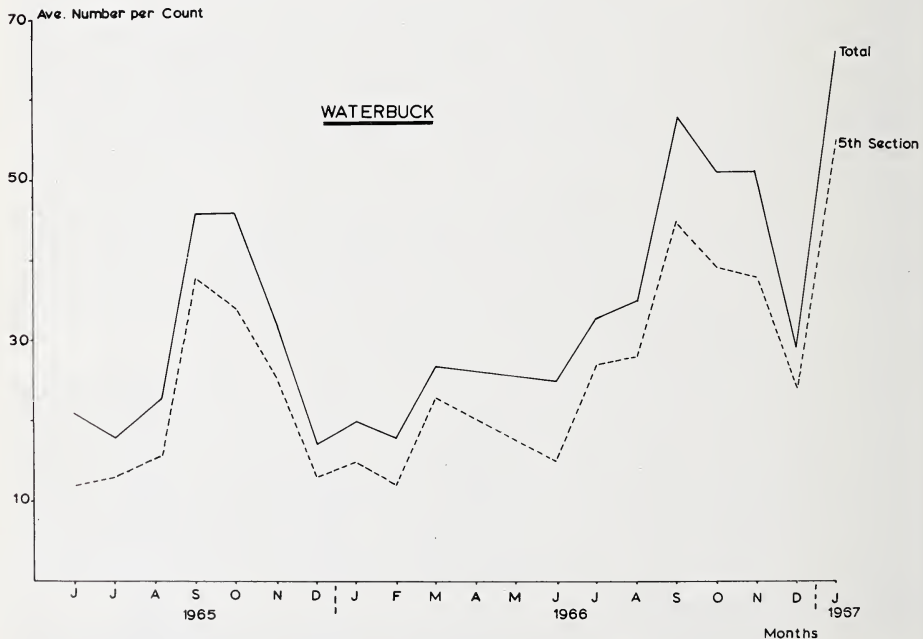


Fig. 4. Mean monthly counts of waterbuck along the standardised route showing the strong preference of this species for the eastern end of the Pookoo flats sampled by section 5 of the count route

Waterbuck were not recorded in the Caprivi opposite the Chobe National Park, but their range extended all along the south bank of the river between Kasane and Ngoma and in the east spread into Rhodesia beyond that of puku and lechwe, while in the west it was similar to that of lechwe. In the study area they favoured areas such as the eastern end of the Pookoo flats (section 5, fig. 1) where past disturbance and heavy trampling of the vegetation favoured the spread of the grass *Cynodon dactylon*. They were not recorded over a mile south of the lip of the sandridge and in spite of better visibility across the flood plain there were fewer recorded here than in openings in the scrub near its edge.

They did, however, tend to emerge on to the flood plain or into an abandoned rice paddy during the afternoon, especially during the dry season, and were one of the most common species observed there at night. The greater use of the flood plain and of open areas with *C. dactylon* during the dry season, explains the September/November peak in 1965 and 1966 (fig. 4), but the only apparent reason for the sudden increase during January 1967 was an influx of animals along the count route. Puku occurred on the flood plain and adjacent parts of the Pookoo flats and the only three observations from beyond these limits were of young individuals, apparently dispersing from the parental home range. The species often occurred with lechwe and less frequently with waterbuck on the flood plain during the dry season, although they were commonly with waterbuck on the Pookoo flats, to which most of the population became confined during the flood season. The third and particularly the fourth section of the count route (fig. 3) skirted elevated portions of the flood plain, where there were large trees, which were much favoured by puku. Here and elsewhere they made use of the low lying areas of the flood plain, but generally showed a distinct preference for areas near higher ground, while on the Pookoo flats they were usually in open areas amongst the scrub, where *Cynodon dactylon* and short annual grasses frequently dominated.

Fig. 5 reflects the seasonal drift of puku between the flood plain and the Pookoo flats. At the height of the 1965 dry season many of the females and juveniles were between the meanders of the river and were not visible from the count route. The species became more conspicuous along the edge of the flood plain from November when early rain caused grasses on the Pookoo flats to flush and some of those, which grew mainly during the flood season on the flood plain, to rot. Numbers declined in February and March as animals apparently moved south of the road and away from

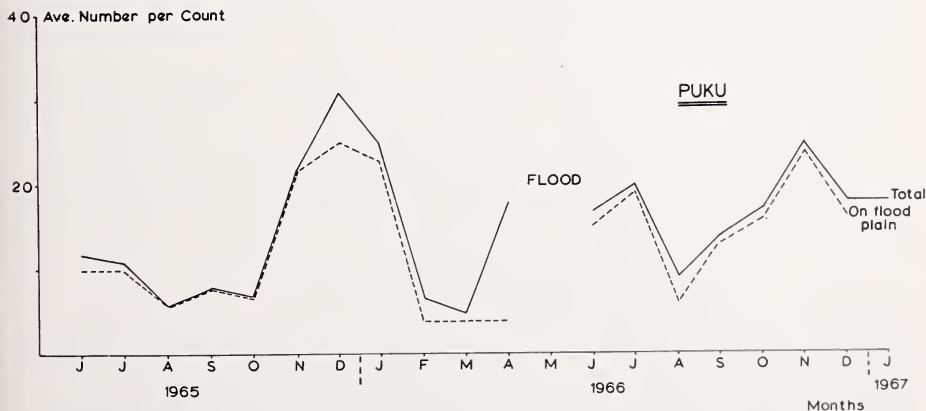


Fig. 5. Mean monthly counts of puku along the standardised route showing the relative numbers observed on the flood plain

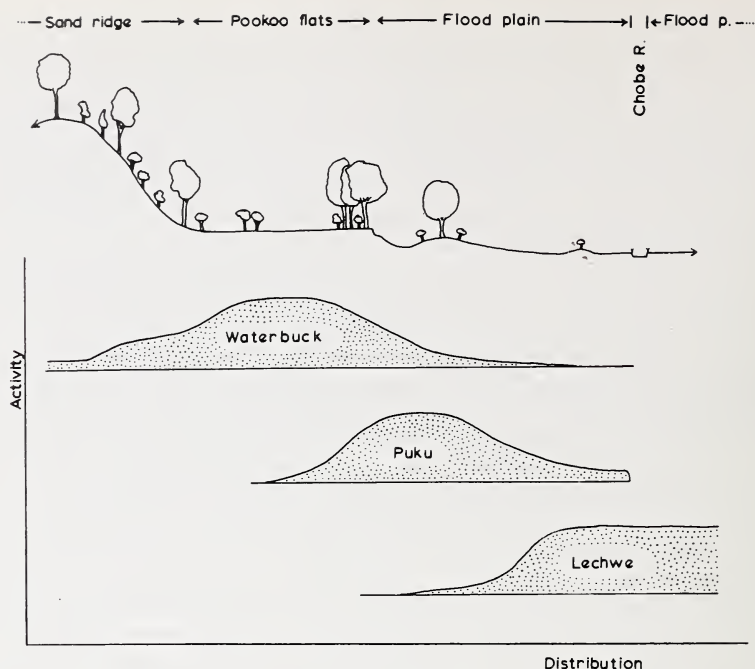


Fig. 6. Relative year round activity of puku, lechwe and waterbuck on a theoretical line from the top of the Sand ridge to the Chobe river

the edge of the flood plain. They were plentiful along the edge of the Pookoo flats in April through July, before moving north out or to the flood plain and repeating the pattern observed the previous year. The northward movement in 1966 was somewhat delayed by high floods, compared with the low floods in 1965.

The dispersal mechanism in puku appears to be similar to that described for impala by CHILD (1965) and to involve wellgrown sub-adults, as these were the only individuals observed outside the normal range of the species. Two young males were noted over five miles east of the nearest resident puku and in unsuitable puku habitat on September 11, 1965, and during the day covered a further $3/4$ of a mile along a road. Two similar aged females were noted in the same area on October 7 and by the following morning had moved another $1\frac{1}{2}$ miles away from the centre of the population. About this time a male and a female in this age group took up residence five miles east of other resident puku in an area in which the species had not been seen for at least three years. These animals were not observed during the 1966 flood season, but during the following dry season this area of about $1/4$ sq. mile was occupied by a group of five animals, including an adult male, three adult females and two immature animals.

Feeding Behaviour¹

Feeding preferences of lechwe, puku and waterbuck were observed on the Chobe flood plain within the National Park in December 1966 and January, July and

¹ M. KILEY's paper (1966) discussing the use of faecal analysis for investigating feeding preferences, unfortunately could not be considered, as the authors only became aware of it after the present paper went into print.

August 1967. Similar observations were made on the last two species in March 1967, when the lechwe were in their flood season habitats, which were visited in May. The total of 5,538 feeding observations are summarised in table 2, showing that all three species fed mainly on perennial grasses on the flats, where there was considerable overlap in the year round use made of some of the most favoured species.

Lechwe was the most numerous of the three species and made heaviest use of the pastures on the flood plain. In December they utilized 20 plants, of which the perennial grasses *Eragrostis rigidior*, *Brachiaria latifolia* and *Setaria sphacelata*, made up 62.1% of the feeding observations. With *Vossia cuspidata*, a species not recorded for lechwe at this season, although important at others, these grasses provided 67.5% of puku food, while *B. latifolia* and *V. cuspidata* contributed 67.2% of the feeding observations of waterbuck. Waterbuck grazed *Echinochloa stagnina*, on the flats fairly heavily but this species was used only sparingly by lechwe and was not recorded for puku. Unlike the other two species, waterbuck did much of their feeding off the flats, where *Cynodon dactylon* was much favoured.

Lechwe made considerable use of the sedge *Vetiveria nigriflora* during December, when it provided 5.5% of the observations, but these were limited to young leaves sprouting in recently burnt areas. Waterbuck used the plant in July and August, but were not observed feeding on it in December, when their range did not extend into the burns. The three Cyperaceae, *Cyperus digitatus*, *C. esculentus* and *C. articulatus* and the forbs *Polygonum limbatum* and *Ipomoea coptica* were taken by lechwe at this time of year in small but significant amounts, totalling 7.6%.

Twenty food plants were recorded for lechwe in January, although there were important differences from the feeding preferences observed the previous month. Less use was made of *E. rigidior*, although the three species most favoured in December still contributed 61.4% of the food, due mainly to the added emphasis on *S. sphacelata*. *B. latifolia* was clearly the dominant puku food in January, by which time most of the *E. rigidior*, which grew on sandy elevations, had matured. Both lechwe and puku made increasing use of young annual grasses and to facilitate this puku began feeding in glades on higher ground adjacent to the flats.

In January waterbuck favoured *Paspalum commersonii* (56.3%), but this occurred mainly in an abandoned rice paddy and although puku were regularly observed in the area, they did not apparently eat it. *B. latifolia* was also important to waterbuck so that all three species made considerable use of it at this season and this continued through into March for puku and waterbuck. By then large areas of the flats were becoming submerged and several plants favoured during the previous month had matured or ceased growing in the gradually rising water in which the old leaves decayed. The rising water did not act as a mechanical barrier as waterbuck were repeatedly observed standing up to their bellies in water feeding on emergent aerial parts of plants.

Digitaria remotigluma was relatively important to waterbuck in January, the only month in which its use was recorded for all three Kob. Waterbuck continued to make heavy use of *Cynodon dactylon* in areas adjacent to the flood plain, but although more use was made of annuals the switch to these grasses was less perceptible than for either lechwe or puku. In May lechwe fed mainly on species that were either not available or hardly used during the dry season, along the Chobe. It was, therefore, interesting that they made greater use of *C. dactylon*, although the grass was plentiful in their summer range. Much of the grassland of the Eastern Caprivi was still submerged in May, and the lechwe did much of their feeding in the water during the day, although, as to be expected, they bedded on higher ground, where they fed in the early mornings. The food plants preferred in these two situations are compared in table 2, but although they spent longer feeding on the seven species of emergent

Table 2

Seasonal Observations on the Feeding Preferences of Lechwe, Puku and Waterbuck, Expressed as a Percentage of Monthly Observations

Food Plants	Lechwe			Puku			Waterbuck					
	Dec. (1951 observ.) u/o	Jan. (1859 observ.) u/o	May (914 observ.) u/o	Jul/Aug. (219 observ.) u/o	Dec. (269 observ.) u/o	Jan. (519 observ.) u/o	Mar. (79 observ.) u/o	Jul/Aug. (727 observ.) u/o	Dec. (67 observ.) u/o	Jan. (197 observ.) u/o	Mar. (37 observ.) u/o	Jul/Aug. (72 observ.) u/o
Perennial Grass												
<i>Eragrostis rigidior</i>	21.6	14.6	1.2 ²		57.2	5.0		34.5				29.2
<i>Brachiaria</i> sp. aff.												
<i>B. latifolia</i>	21.4	17.9		51.1	10.0	52.8	92.4	0.3	35.8	24.3	72.9	9.7
<i>Setaria sphaeculata</i>	19.1	28.9			7.4	5.8		0.4				
<i>Eulalia geniculata</i>	7.9	7.5										
<i>Hemarthria altissima</i>	7.0	3.1			1.1	3.5			1.5		13.5	
<i>Echinochloa stagnina</i>	3.2	4.4							26.9	2.0		2.8
<i>Cynodon dactylon</i>	2.0	0.2	5.5 ²									
<i>Sporobolus pyramidalis</i>	0.6											
<i>Brachiaria humidicola</i>	0.2				1.1	22.7			1.5	1.5		
<i>Digitaria setivalva</i>		2.2								2.0		
<i>Digitaria remotigluma</i>		0.8				0.6				10.1		
<i>Fimbristylis hispidula</i>		0.4	4.2 ²									
<i>Acalypha indica</i>		0.2										
<i>Brachiaria nigropedata</i>		0.3										
<i>Burnatia emeandra</i>			20.6 ¹									
<i>Sacciolepis africana</i>			18.3 ¹									
<i>Trichoneura grandiglumis</i>			13.1 ¹									
<i>Acroceras macrum</i>			11.5 ¹									
<i>Eleocharis</i> sp.			5.7 ¹									
<i>Cymbopogon validus</i>			5.3 ²									
<i>Brachiaria brizantha</i>			3.8 ¹									
<i>Eragrostis gangetica</i>			0.5 ²									
<i>Vossia cuspidata</i>				48.9	14.9	1.7	3.8	1.4	31.4	1.5		15.3
<i>Eragrostis</i> sp.					2.2							4.2
<i>Phragmites mauritanus</i>					0.7							4.2

[illegible]

¹ Emergent species. — ² Species on higher ground.

grasses than on the 10 species on higher ground, the sampling did not permit of a numerical evaluation of the relative importance of the grasses in the two situations.

Small groups of lechwe returned to the Park in the second half of July and first half of August. The lower parts of the flood plain were still submerged and they fed mostly in shallow water, although the vegetation on many of the elevations, which had still not dried out, was heavily trampled.

B. latifolia and *V. cuspidata* were apparently the only grasses eaten, but both were actively growing and it was as yet too early in the season for significant competition from other grazers, including puku and waterbuck. By then puku were again making heavy use of *E. rigidior* (34.5% of observations) and with *E. lappula* and *Brachiaria brizantha* it made up 72.8% of their food. Waterbuck were also eating large amounts of the first and last and a small sample indicated that they contributed about half the food taken on the flats. Elsewhere waterbuck continued to eat considerable amounts of *C. dactylon* and as the puku were still mostly feeding off the flood plain there was probably some competition between these two species along the edge of the Pookoo flats.

Social Organisation

AS DE VOS and DOWSETT (1964) note, all three species are gregarious to some extent. The tendency was most marked in lechwe where loose aggregations of over 400 head were common, although there was a constant splitting and reuniting of groups during the dry season, which involved all sex and age classes. Waterbuck herds were smaller and more discreet and in 183 complete groups totalling 1035 animals, ranged between 1 and 37. The sample was somewhat biased by the greater ease of determining the sexes and ages of all individuals in small groups, but if 63 lone animals are excluded, this gives a mean herd size of 8.1. Puku classified on a year around basis yielded 221 complete groups, with an aggregate of 761 head, in units of one to 28. If individual animals are again excluded the average is 5.5 per herd.

These observations indicate more similarity in the sizes of groups of puku and waterbuck than between either of these species and lechwe. This is in general agreement with the conditions in Zambia reported by DE VOS and DOWSETT (1964).

Group Structure

The herd structure of the three species is compared in table 3. Irrespective of sampling bias it was clear that single males featured prominently in all three species, but especially in puku and waterbuck, in which male territorialism has been described by DE VOS (1965) and KILEY-WORTHINGTON (1965). DE VOS and DOWSETT (1964) reported similar behaviour in lechwe.

The low number of single females in all three species indicate their general gregariousness, and this also explains the low number of pairs. Groups composed of only full grown females were not common among puku where the adult females were usually accompanied by young animals. The incidence was higher in lechwe where there was a strong tendency for similar aged females, or females with similar aged calves to group together on their own or in large herds, while in waterbuck this was the second most common grouping observed.

Groups consisting of females with young and a single adult male were the most common association in puku. They were rare in waterbuck, but were also common in lechwe, although once again this unit tended to be masked by the presence of several such aggregations as well as more or less discreet groups of adult, two-year-old and yearling males in many of the large classifications. This and the general tolerance of

Table 3

Herd Structure Showing Frequency of Occurrence of Various Sex and Age Class Combinations

Herd Components	Puku		Lechwe		Waterbuck	
	Contacts	%	Contacts	%	Contacts	%
Single Ad ♂	84	39.1	42	18.3	55	30.0
Ad ♂♂	12	5.6	12	5.2	17	9.3
Ad ♂(♂) + immo ♂(♂)	10	4.7	8	3.5	18	9.8
Ad ♂(♂) + imm ♂(♂) & ♀(♀)	3	1.4	4	1.7	11	6.0
Single ad ♀	4	1.9	11	4.8	5	2.7
Ad ♀♀	7	3.3	11	4.8	21	11.5
Pair (ad ♂ + ad ♀)	8	3.7	5	2.2	4	2.2
Ad ♂ + Ad ♀♀	6	2.8	25	10.9	15	8.2
Ad ♂ + Ad (♀)♀ + imm ♂♂ & ♀♀	34	15.8	19	8.3	4	2.2
Ad ♂♂ + Ad ♀(♀) + imm ♂♂ & ♀♀	0	—	66	28.7	7	3.8
Ad ♀(♀) + imm ♂(♂) & ♀(♀)	19	8.8	22	9.6	11	6.0
Ad ♀ + calf	3	1.4	3	1.3	2	1.1
Imm ♂(♂)	25	11.6	0	—	8	4.4
Imm ♀(♀)	0	—	1	0.4	1	0.5
Imm ♂(♂) + Imm ♀(♀)	0	—	1	0.4	4	2.2
Total	215		230		183	

breeding males towards sexually inactive males of all ages, probably accounts for herds comprising groups of different aged males with females and calves being the most common arrangement found in lechwe. More than one adult male at a time with adult females was not recorded for puku, where aggressive behaviour between rams in adjacent territories similar to that described by DE VOS (1965) was frequently observed. In waterbuck this association was seen on seven occasions, when territorial males tolerated mixed groups of other males on their ground, although in this species fighting can be vigorous. One such fight lasted at least ten minutes and ended with the vanquished male being chased 0.4 miles before being lost to sight.

The incidence of the above associations observed in the three species along the Chobe was similar to that reported by DE VOS and DOWSETT (1964).

Herds of one or more adult males with female juveniles or juveniles of both sexes were most prevalent in waterbuck. On no occasion was an adult male lechwe seen with juvenile females away from a herd, but several males occasionally mixed with the young of both sexes.

Groups of young males made up 11.6% of the puku and 4.4% of the waterbuck contacts, but were not recorded outside mixed herds of lechwe, although within the herds, different aged males tended to run together. DE VOS and DOWSETT (1964) observed this association only once for puku in 386 groups, but the frequency for lechwe and waterbuck was similar to that observed along the Chobe. Young females on their own were seen once each in waterbuck and lechwe which agrees with the findings of these authors who also noted it once in waterbuck. There was also one mixed group of young animals in lechwe and four in waterbuck.

Two or more adult males on their own were noted with similar frequency in puku and lechwe, and slightly more often in waterbuck, which showed a strong tendency for the sexes to segregate into herds from an early age. This explains the relatively high proportion of groups of adult and juvenile males, which also occurred to some extent in lechwe and puku and on two occasions a territorial male puku tolerated young well grown males on his ground.

Territorial Behaviour

It was not planned to analyse detailed behaviour patterns in the three species, although routine observations were in general agreement with results obtained by previous workers. However, observations over a two-year period, on the territorialism described by DE VOS (1965) in male puku provided some fresh information on this topic.

Puku observed during regular standard game counts were accurately plotted and showed a neat pattern of territories occupied along the route. There was one easily recognised male with a broken horn which had left an unmistakable shaped stump, which was observed between July 1965 and the end of April 1966 along the same 1.3 miles of road (mileage 4.7 to 6.0) and was usually on the flood plain in the late afternoon, although in the mornings he was sometimes in clearings in the fringing scrub up to 500 yards from the edge of the flats. There were three more territories along the 0.8 miles east of that occupied by the one horned male, and all four had overlapping boundaries. A group or groups of 11 to 28 females with calves and juveniles of both sexes moved between the territories and beyond and while in a territory were accompanied by the resident male. For a short time a bachelor group of 6 well grown young males moved through the area and were not challenged by the territorial males. These rams were forced out of the greater part of their territories by the 1966 floods, but similar areas were occupied during the subsequent dry season, although not by the same animals in the same locations. The area that had been used by the one horned ram in 1965 was occupied by a different male in 1966, while the one horned ram took up a territory some 2.5 miles east of his previous area.

This behaviour differed from that of a recognisable male waterbuck, with very bowed horns, one of which had a deflected tip, who lost a portion of his tail during the study and who was never observed outside an area which did not exceed 27 acres during 24 months. Only a small portion of this area became flooded compared with the large portions of the puku territories which were inundated. The whole dry season range of lechwe was flooded so that choice of habitat may be significant to the varying degrees of territorialism in the three species described by DE VOS and DOWSETT (1964).

Status and Trend in Populations

Wild populations are seldom stable and are subject to more or less extensive fluctuations, which may be considerable, especially in marginal lands where habitats have been modified by changing patterns of land use. Any study of comparatively short duration of a species' ecology or gross behaviour should take into account these general numerical trends as a basis for a better understanding of the current status and behaviour of the population. This applies particularly where the results of such a study are to be translated into practical management.

During the present study the general trends in numbers of the three Kob populations along the Chobe were determined from interviews, in which the use of leading question was avoided, with old residents who had known the area for 20 or more years. Their conclusions were checked against information obtained in the Study Area.

Lechwe

Available evidence indicated that the lechwe population was declining rapidly. SELOUS (1928) hunted it in this area in July 1874 when lechwe were plentiful, although it is difficult to judge the extent of the population from his account. It was clear, however, that the species' effective range had decreased west of the Park, as it has

Table 4

Summary of *Lechwe* Classified into Sex and Age Classes along the Chobe River, between July 1965 and April 1967

Season	Month	Sample	Males			Females			Calves		Tot.	Unclass
			Ad.	2yr.	Juv.	Ad.	Juv.	Tot.	♂ ♂	♀ ♀		
1965/66	July	67	13	3	16	—	—	28	2	1	8	0
	Aug.	102	—	—	18	—	—	39	9	13	27	0
	Sept. ¹	48	—	—	9	—	—	24	3	—	6	1
	Sept. ²	398	82	45	127	153	42	195	—	—	39	14
	Oct.	191	42	16	58	51	37	88	—	—	23	7
	Nov.	753	87	91	178	—	—	359	—	—	132	3
	Dec.	609	36	33	69	—	—	304	—	—	196	9
	Jan.	776	89	39	128	—	—	389	—	—	194	17
	Feb.	12	2	0	2	—	—	7	—	—	3	0
	July	52	—	—	30	—	—	0	13	9	22	0
1966/67	Aug.	63	—	—	34	—	—	15	10	3	13	1
	Sept.	677	—	—	118	—	—	457	24	50	74	6
	Oct.	251	29	25	54	113	11	124	—	—	59	1
	Nov.	131	20	3	23	—	—	77	—	—	22	0
	Dec.	262	30	5	35	—	—	150	—	—	65	0
	Jan.	65	11	0	11	—	—	43	—	—	11	0
	Apr.	20	1	0	1	—	—	14	—	—	5	0
	Total	4477	442	260	911	317	90	2313	61	76	899	59
	% ³	—	12.5	7.4	20.3	37.7	10.7	51.7	44.5	55.5	20.1	1.3

— = class not recognised in particular month.

¹ Before peak in calving started in 1965. — ² After peak in calving started in 1965. — ³ Calculated from samples in which sex or age class was recognised.

virtually disappeared from the Lake Liambezi area where Selous remarks on its abundance, and old residents indicated that this had taken place during the previous 40 to 50 years.

HEPBURN (Dept. Record) estimated over 2500 lechwe on the flood plain along parts of sections two and three of the count route during the 1962 dry season. In 1965 the highest count was 1,414 while in 1966 it was only 778 and in both years at least 20 to 25% of these animals were beyond the main concentration areas where Hepburn made his estimate. This downward trend is substantiated by numerous unanimous reports from all over the Eastern Caprivi and adjacent Botswana, and by the low numbers observed by HEPBURN, on a helicopter flight between Kasane and Lake Liambezi, while searching for locusts in July 1966.

Sex and age class determinations of lechwe along the Chobe had certain limitations for determining trends in the population, but with the assessments of the physical condition of full grown animals were in accordance with the above observations.

Lechwe apparently calved throughout the year with a marked peak around the end of the year. Very young calves were recorded in all months between July and January, while lechwe were plentiful in the main Study Area. However, the incidence of small calves increased rapidly from mid September 1965, and reached a peak in November and January and most calves were born between October and January in 1966 (table 4). This is similar to the calving behaviour observed by ROBINETTE and CHILD (1964) for the Kafue flats lechwe where a few calves were probably born in all months, although there was a decided peak in December and January.

The results of these classifications are summarised by months in table 4, which gives an overall sex ratio of 52 males : 100 females exclusive of calves. However, as already noted, this ratio varied considerably from month to month, mainly as the result of the tendency for males to arrive first and leave first from areas along the Chobe, but the proportion of males was significantly higher in 1965/6 (59:100) than in 1966/7 (41:100) ($\text{Chi}^2 = 11.157, P > 0.01$). This could indicate a reduction in the proportion of males, similar to that described by CHILD (1965) in a declining population of impala, especially as ROBINETTE and CHILD (1964) calculated a proportionally higher mortality in males than females, from "found" carcasses, among desely populated lechwe on the Kafue flats. On the other hand DE VOS and DOWSETT (1964) had a smaller proportion of males (24:100) in a sample of 493 lechwe classified along the Chobe in September 1964, than that observed in this month in either 1965 or 1966.

The young calf to well grown female ratio in the three months with most calving was (50:100) in 1965/6 and (42:100) in 1966/7 but this difference was not significant ($\text{Chi}^2 = 2.479, \text{N. S.}$)² and compares with a ratio for similar aged calves along the Kafue (51:100) in 1962 (ROBINETTE and CHILD, 1964). But females approaching one year of age could still be separated from older animals in late September through October 1965 and represented about 28% of all females. It is, therefore, probable that a similar proportion of the females in the November to January samples were in this age class and could not have calved during these months, as ROBINETTE and CHILD (1964) found the earliest pregnancies in females which calved for the first time when about two years old. This gives about 70 calves : 100 potentially mature females compared with the birth rate of 82:100 computed for the Kafue population.

There were 12% non-breeding aged females in the early 1966/7 dry season sample, which if projected to the peak calving season gives approximately 47 calves : 100 breeding females, which indicates much lower calving in 1966/7 ($\text{Chi}^2 = 11.549, P > 0.01$)². These results suggest a low calf crop, compared with the calculated birth rate on the Kafue flats, in 1965/6 and an even crop in the 1966/67 season.

² calculated from original sample in table 4.

Nothing is known of the extent of calving during the 1964/5 season which led to 50 juveniles : 100 adult females returning to the Chobe during the early 1965 dry season. However, the 1965/6 calves apparently suffered a heavy subsequent mortality as there were 109 males and females about six to ten months old with 472 older females (23:100) in July through September and 24 with 124 females (18:100) in October, by which time most of the adult females to reach the Chobe had probably done so.

The physical condition of 192 adult males and 940 full grown females was assessed along the Chobe river and with the exception of a male with damaged testicles, all were classed as poor and the majority were poor in the extreme. VON RICHTER examined lechwe in their flood season range in the Caprivi in May 1967, and found they were in better condition than they had been along the Chobe during the previous October through January. This difference was probably not caused directly by the season of observation but by differences in conservation values of the habitats. These were assessed according to the standards described by RINEY (1963). Habitats along the Chobe were generally down-graded, particularly on the sandier elevations on the flood plain and although similar elevations in the Caprivi were also in a poor state, the extensive intervening areas of grassland had a healthy perennial grass cover in the area where the lechwe were observed in May 1967.

The poor physical condition, apparent low replacement rate and the marked decline in the number of lechwe observed in 1966/7 compared with the previous dry season are in accordance with a declining population and agree with the reduction in the distribution and abundance of the species reported by residents of the region.

Puku

SELOUS (1928) describes puku as numerous on the Pookoo flats in July 1874, when he saw groups of up to 50 and notes that the species extended west along the south bank of the Chobe for about 70 miles from the Chobe/Zambezi confluence. As already noted, this population is now isolated from those in the Caprivi and the range along the south bank of the Chobe has become limited to a stretch some 25 miles long commencing 10 miles upriver from the confluence.

In 1965 four men on foot counted the population for 25 miles west from Kasane twice, by walking back and forth across the narrow range of this resident species. The counts yielded 81 and 83, indicating that the entire population was under 100 individuals of all ages. These were mostly resident along a strip 10 miles long along the Pookoo and Chobe flats.

Table 5 summarises puku classified by sex and ages in June through January 1965/6 and 1966/7. The sample is almost certainly biased in favour of adult males (65:100 adult females) as the result of male territorialism along the count route. Nevertheless the adult sex ratio is similar to that obtained by DE VOS and DOWSETT (1964) in the Luangwa valley where they observed 61 males : 100 females in July and 67:100 in September/October. However, they report only 25:100 from the Kafue National Park in June and July.

The present sample contained 20 calves and 55 juveniles : 100 full grown females. The calf ratio was probably fairly representative of the population as only one calf, a male with 5 to 8 cm horns, was observed which was not in the company of an adult female. Juveniles on the other hand were sometimes on their own or with adult males. The overall proportion of calves observed along the Chobe was lower than that described by DE VOS and DOWSETT (1964), who found 30:100 females in the Kafue National Park in June and July; 36:100 and 20:100 in the Luangwa valley in July and September/October respectively. There were, however, 34:100 in June along the Chobe, where the September/October ratio was 46:100 and where the overall total

Table 5

Sex and Age Breakdown of Puku along the Chobe River, by Months

month	Adults		Juveniles	Calves	Juveniles + calves: 100 females
	♂ ♂	♀ ♀			
June	32	38	29	13	111
July	14	—	13	—	—
August	14	7	3	1	57
September	29	34	29	18	138.2
October	14	7	3	1	57
November	33	69	35	12	68
December	27	58	22	8	52
January	44	105	41	11	50
Total	207	318	175	64	Ave. 75

proportion of immature animals : 100 adult females was higher, being 75:100 compared with 47:100 in the Kafue National Park and 60 and 68:100 in DE VOS and DOWSETT's two Luangwa valley samples. This difference was even more marked in individual months, as in June it was 111:100, and in September/October 124:100 along the Chobe.

The physical condition of the adults was also better than in lechwe. Eighteen of 36 males and 10 of 33 females were classed as in fair condition, the remainder being in poor condition, although very few were as thin as the majority of the lechwe.

The puku population has obviously declined since Selous hunted along the Chobe, but, although old residents of the area have noticed a definite reduction in their range during the past 40 years, most indicated that numbers within the Park have remained essentially unchanged for the past 10 years or may have increased slightly since the proclamation of the sanctuary. Observations during the present study indicate a small but healthy population in which a marked increase in numbers may have been checked by the limited extent of suitable flood season habitat.

Waterbuck

SELOUS (1928) does not mention waterbuck along the Chobe, although his party saw and shot several near the Victoria Falls. The species appears to calve throughout the year and juveniles were plentiful, although social segregation from an early age made accurate classifications difficult. Few attempts were made to obtain a reliable measure of the proportion of immature animals in the population as it was being intensively studied by Prof. W. ELDER.

Nevertheless the species is reported by old residents to be expanding along the Chobe river inside the National Park, where the distribution is closely associated with that of the grass *Cynodon dactylon*, which is also spreading in disturbed areas and is eaten extensively by waterbuck. This agrees with the upward trend in numbers recorded on the regular counts between June 1965 and January 1967 (fig. 5), and with general observations of their physical condition. Most adult waterbuck were in poor physical condition during the 1965 dry season, although many, particularly towards the eastern end of the Pookoo flats where *C. dactylon* was plentiful, were in better shape than the majority of antelope concentrating along the river. In 1966, when

conditions were less severe, waterbuck were among the animals in best condition at the end of the dry season.

The status of the vegetation along the Chobe appeared to suit waterbuck and the population in the National Park was apparently increasing.

Discussion

Lechwe, puku and waterbuck are congeneric, predominantly grazing antelope whose geographical ranges overlap along the south bank of the Chobe river. Here there is some competition for food and space between puku and waterbuck, which are resident, and lechwe which move north of the river when the flood plain is inundated seasonally. The year round activity of the three species along a theoretical line from the top of the sand ridge, across the Pookoo flats and Chobe flood plain is shown in simplified diagrammatic form in fig. 6. Waterbuck occurred in all habitat types, but favoured areas between the flood plain and the crest of the ridge, puku occupied the Pookoo flats and the flood plain, but preferred higher ground on the flood plain, while lechwe seldom left the flood plain and were most active in the lowest lying areas.

These habitat preferences resulted in partial spacial separation of the three species and necessitated the type of seasonal movement patterns they exhibited. They may also have been significant to the important differences in their social organisation, which nevertheless showed basic similarities, such as would be expected in closely related species. Whereas waterbuck occurred in well wooded habitats and along the edge of the flood plain they were not resident in areas which were seasonally inundated, so that they were only marginally affected by flooding, while the area occupied by puku was greatly reduced and the whole of the lechwe dry season range was flooded.

There were also important differences in the feeding preferences, although there was considerable overlap in the grasses taken by the three species on a year round basis. The choice of slightly different food at the same time or of the same grasses at different times, while important between competing species, ensured greater efficiency of use of the vegetation where the species occurred together than in those where one or more was absent.

Habitats along the Chobe and throughout much of North-Eastern Botswana and the Eastern Caprivi have been modified by past land use. This has led to changes in the relative numbers in wild animal populations, including those of waterbuck, puku and lechwe, which may also have been affected by an increase in the hunting around the Park and protection inside it. Many lechwe were killed by people in the Caprivi who also poached on the flood plain in the Park and this hunting has been blamed for the decline in the population. Its significance to the decreasing numbers of lechwe across the international border between Botswana and the Caprivi requires further consideration, however, in relation to the importance of habitat changes. The flood plain on the south bank of the Chobe was heavily grazed by a dozen species of large mammals, had been downgraded by past land use was being further suppressed by fires associated with poaching activities. There was also serious deterioration of the habitats on higher ground in the Caprivi where lechwe became concentrated in years when the annual floods were high. Further evidence of the importance of deteriorating habitats in limiting lechwe numbers came from the poor physical condition of adults in a population with fewer young than were observed on a densely populated sector of the Kafue flats. It, therefore, appears that the reversal of the downward trend in the population requires greater protection and active management of the species habitats on both banks of the Chobe.

There has obviously been a decline in the number of puku along the Chobe and

numbers in the relict population in the Park were dangerously low. Nevertheless the population appeared to be in a healthy state and capable of expanding. The possible curb to such expansion resulting from the deterioration of the perennial grassland and scrub encroachment in their flood season habitats, particularly on the Pookoo flats, requires investigation with a view to increasing the suitable area available to the species at this season.

Waterbuck numbers appeared to have responded favourably to the current level of changes in the habitats and the use of low lying areas on the flood plain was generally most intensive where dry season lechwe numbers had declined or in areas no longer penetrated by the seasonal influx of this species. It is, therefore, probable that waterbuck were benefiting from the habitat conditions which were retarding the growth of the puku population and which were detrimental to the lechwe population.

Conclusion

Lechwe, puku and waterbuck are important species in the fauna of the Chobe National Park and the puku population in the Park is the only known occurrence of this species in the Southern African 300-geographical sub-region. Further investigation is needed into the ecology of the three species during the flood season as puku and lechwe population are then limited to a small portion of their range. This work should provide interesting information on the extent of overlap in the habitat requirements of puku and waterbuck at this time of the year and would be useful towards integrating lechwe management outside the Park with other forms of land use. The last would appear highly desirable in order to ensure the long term survival of the species in the Park and to provide the people of the Caprivi with a lasting source of protein and skins. It would also be desirable to have a better understanding of the year round interactions between members of this genus and other browsing and grazing ungulates.

Summary

Three species of the genus *Kobus*, lechwe, *K. lechwe*, puku, *K. vardonii* and waterbuck, *K. ellipsiprymnus* occur along the south bank of the Chobe River in North-Eastern Botswana. Puku and waterbuck were resident in this area where they were subject only to minor movements in relation to the seasonal flooding of the flood plain. Lechwe moved north out of the area ahead of the rising water during the flood season. The areas occupied by the three species during the dry season overlapped, although some separation resulted from the preference of lechwe for low lying areas and for waterbuck to use the highest part of the catina with puku predominating in the intermediate areas. There were also differences in the social organisation of the herds and in the behaviour of territorial males. All three grazed predominantly, often on similar grasses, but differed in the season in which some of these were preferred. A decline was observed in the lechwe population in which there were relatively few young and in which the adults were in poor physical condition. The small puku population had become isolated from the species range further north, but this relict population appeared to be in a healthy state while the waterbuck population was apparently expanding. Juveniles were plentiful and adults were among the antelope in best condition at the end of the dry season. It is suggested that changes in habitat, resulting from past land use, have been beneficial for waterbuck and detrimental for lechwe, and that limitations of flood season habitat may have restricted the growth of the puku population.

Zusammenfassung

Drei Arten der Gattung *Kobus*, die Lechwe-Antilope (*K. lechwe*), die Puku-Antilope (*K. vardonii*) und der Wasserbock (*K. ellipsiprymnus*) treten entlang des Südufers des Chobe-Flusses in Nordost-Botsswana auf. Puku und Wasserbock halten sich das ganze Jahr über im Untersuchungsgebiet auf und führen nur lokale Wanderungen durch, hervorgerufen durch die regelmäßige Überschwemmung der Chobe-Ebene. Lechwe dagegen ziehen nördlich vor dem steigen-

den Wasser aus dem Gebiet fort. Die drei Arten überschneiden sich in ihrem Auftreten während der Trockenzeit, obwohl eine gewisse Trennung zu beobachten ist. Die Lechwe-Antilope bevorzugt die tiefliegenden Gebiete, der Wasserbuck hält sich in der Regel in den höchstgelegenen Teilen des Untersuchungsgebietes auf und die Puku-Antilope ist dominierend in der Zwischenzone. Unterschiede sind auch in der sozialen Organisation der Herden und im Verhalten der territorialen männlichen Tiere festzustellen. Alle drei Arten sind vorwiegend Grasfresser; häufig äsen sie dieselben Grasarten, aber in verschiedenen Vegetationsperioden werden verschiedene Arten bevorzugt.

Die Lechwe-Population nimmt zahlenmäßig ab, relativ wenig Jungtiere wurden beobachtet, und die adulten Tiere sind in körperlich schlechtem Zustand. Die kleine Puku-Population ist vom Verbreitungsgebiet der Art im Norden isoliert worden; die so isolierte Population erscheint jedoch in einem gesunden Zustand zu sein. Der Wasserbuck hat sein Verbreitungsgebiet vergrößert. Jungtiere wurden in großer Zahl beobachtet, und die adulten Tiere wiesen unter den Antilopen die beste körperliche Verfassung auf.

Es wird angenommen, daß Veränderungen im Habitat, hervorgerufen durch Landnutzung in der Vergangenheit, die Verbreitung des Wasserbucks fördern, während die Lechwe-Antilope geeignetes Habitat verliert. Die Wachstumsbegrenzung in der Puku-Population ist wahrscheinlich durch den Mangel an ausreichendem Habitat während der Überschwemmungszeit hervorgerufen.

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Author's addresses: Dr. GRAHAM CHILD, F.A.O. Wildlife ecologist, Game Department, Gaborone, Botswana and Dr. WOLFGANG VON RICHTER, Mammal Research Unit, University of Pretoria, Pretoria, South Africa; formerly F.A.O.-Associate Expert, Game Department, Gaborone, Botswana

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