A STUDY OF THE SOCIAL BEHAVIOUR OF THE ROAN ANTELOPE, *HIPPOTRAGUS EQUINUS EQUINUS* (DESMAREST, 1804) IN THE KRUGER NATIONAL PARK

by

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S U M M A R Y.

An analysis of the social behaviour of the roan antelope (Hippotragus equinus equinus Desmarest, 1804) is presented in this thesis. The study commenced in July, 1967. A herd of 10 animals in an enclosure - 1,6 kilos. square and simulating natural conditions - provided ideal opportunities for intensive study. Further observations were made on free-roaming herds in the main roan habitat of the Park i.e. the Lebombo flats north of the Letaba river.

The basic discipline regulating the interactions between the members of a herd is the dominance hierarchy. According to this system the social standing of each individual in the herd is determined by its degree of dominance over other herd members. The position amongst males differs from that of the females insofar as the dominance - which allows for conditional tolerance towards other individuals - is replaced by total intolerance amongst adult males. This rules out any possibility of an amiable co-existence between adult bulls. A straight-line dominance hierarchy is evident amongst the cows. Characteristically the leadership of the herd is the function of the most dominant cow. Among the immatures dominance is determined by age and not sex. Rank positions among females remain unchanged in the transition from immature to adult. Dominant individuals assert their dominance over subordinates by means of the dominance display and low, moderate and high intensity fighting. Once established, the positions remain stable. The dominance hierarchy results in herd stability.

The/...

The characteristic mosaic pattern found in the distribution of roan herds may be attributed to both social and ecological factors. Socially, herd stability and the various zones occupied by a herd are the major factors. Adult roan bulls defend an 'intolerance zone' of approximately 600 m diameter. Other adult males are challenged upon entering this zone. Evidence of an intolerance zone and the difference between it and a territory proper is presented. The existence of a dominance hierarchy results in 'closed' social units (herds) and therefore inhibits other females from leaving one herd to join another. The area occupied by a herd throughout the year is referred to as the activity zone. The various herds' activity zones do not overlap. Activity zone marking is accomplished by both visual and olfactory means. Available activity zones in the Park are occupied and therefore the roan population is considered stable.

The mating behaviour of roan is described with an evaluation of the various phases viz. spacial relationship between bull and cow, dominance, smelling of the cow's tail and vulva, 'Flehmen', 'Laufeinschlag', standing firm of the female, copulation and post-copulatory behaviour.

A detailed account is given of the mother/calf and calf to calf relationships. The concealment behaviour of the calf during the first 6 weeks of life is given, with special emphasis on the means by which effective concealment is achieved. Other activities, such as playing, are also mentioned. Communication between mother and calf may be both visual and auditory. Auditory communication could not be confirmed but this may have been due to field conditions.

The/...

The survival value of the mother/calf relationship is tested against various decimating factors. The conclusion is that the mother/calf relationship is well adapted to prevailing conditions in the Park and that no abnormally high mortalities could be ascribed to this system.

A STUDY OF THE SOCIAL BEHAVIOUR OF THE ROAN ANTELOPE, HIPPOTRAGUS EQUINUS EQUINUS (DESMAREST, 1804) IN THE KRUGER NATIONAL PARK

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O P S O M M I N G.

'n Analiese van die sosiale gedrag van die baster-gemsbok (Hippotragus equinus equinus Desmarest, 1804) word in hierdie tesis aangebied. Die studie het gedurende Julie 1967 'n aanvang geneem. 'n Trop van 10 diere is in 'n wildskamp - 1.6 vk. kilos in grootte en getrou aan natuurlike toestande - geplaas. Hierdie kudde het ideale geleenthede gebied vir intensiewe studie. Waarnemings is egter ook gedoen op vrylewende kuddes in die voorkeur baster-gemsbok habitat van die Wildtuin t.w. die Lebombo vlakte ten noorde van die Letabarivier.

Die basiese sisteem wat die interaksies tussen die individue van 'n trop bepaal, is die dominansie hiërargie. Na aanleiding van hierdie stelsel word die sosiale status van elke dier bepaal deur die mate van dominansie van die betrokke dier oor die ander individue in die trop. Die posisie tussen die manlike diere verskil ietwat van dié tussen vroulike diere insoverre blote dominansie - wat toelaat vir kondisionele verdraagsaamheid teenoor ander individue - by volwasse bulle vervang word deur algehele onverdraagsaamheid jeens mekaar. Hierdie onverdraagsaam-heid skakel alle moontlikhede van 'n vreedsame naasbestaan tussen volwasse bulle uit. 'n Reguit-lyn dominansie hiërargie is die reël tussen die koeie. Die leierskap van die trop word op kenmerkende wyse deur die mees dominante koei behartig. Onder die jong diere word dominansie deur ouderdom - en nie geslag nie - bepaal. Die rangorde tussen koeie word nie beïnvloed deur die oorgang van die onvolwasse tot die volwasse toestand nie. Dominante

individue/...

individue bevestig hulle dominansie oor ondergeskiktes deur middel van die dominansie ritueel en/of lae, gemiddelde en hoë intensiteit twee-gevegte. Die rangorde tussen 'n groep diere word moeilik verander en lei tot trop stabiliteit.

Die kenmerkende mosaïese verspreidingspatroon van baster-gemsboktroppe word toegeskryf aan beide sosiale en ekologiese faktore. Sosiaal-gewys is die belangrikste faktore tropstabiliteit en die sones wat deur 'n trop bewoon word. Volwasse bulle verdedig 'n ‚onverdraagsaamheidsone' met ongeveer 600 m deursnee. Ander volwasse bulle word uitgedaag indien hulle dié sone binnedring. Bewyse van 'n onverdraagsaamheidsone asook die verskil tussen dié sone en 'n ware territorium word aangebied. Die bestaan van die dominansie hiërargie het „geslote" sosiale eenhede (troppe) tot gevolg en derhalwe word koeie geïnhibeer om van 'n trop weg te breek en aansluiting by 'n ander trop te soek. Die gebied wat oor 'n tydperk van 'n jaar deur 'n trop bewoon word, word na verwys as die aktiwiteitsone. Aktiwiteitsones oorvleuel nie. Die merk van aktiwiteitsones word bewerkstellig deur beide visuele en olfaktoriese middele. Beskikbare aktiwiteitsones in die Wildtuin is beset en gevolglik word die populasie as stabiel beskou.

Die paringsgedrag van die baster-gemsbok word beskryf met 'n bespreking van die onderskeie fases t.w. spasiëring tussen bul en koei, dominansie, ruik van die koei se stert en vulva, ‚Flehmen', ‚Laufeinschlag', vasstaan deur die koei, kopulasie en daaropvolgende gedrag.

'n Breedvoerige beskrywing van die koei/kalf en kalf tot kalf verhoudings word gegee. Die verstekingsgedrag van die kalf gedurende sy eerste 6 weke word beskryf,

met/...

met spesiale verwysing na aanpassings wat doeltreffende versteking moontlik maak. Ander kalf aktiwiteite, bv. speel, word ook beskryf. Kommunikasie tussen ma en kalf word moontlik deur beide visuele en auditêre wyses bewerkstellig. Auditêre kommunikasie kon nie bo twyfel vasgestel word nie as gevolg van die omstandighede waaronder dié navorsing gedoen is.

Die oorlewingswaarde van die koei/kalf verhouding is teen verskeie desimeringsfaktore getoets. Die bevinding is dat die koei/kalf verhouding goed aangepas is by heersende toestande in die Wildtuin en dat geen buitengewone mortaliteite toegeskryf kan word aan bogenoemde sisteem nie.

CHAPTER I.

I N T R O D U C T I O N

The roan antelope:

The roan antelope (Hippotragus equinus equinus, Desmarest, 1804) is one of the most conspicuous of the African ungulates due to its large size and also its wide range of distribution on the African sub-continent, south of the Sahara Desert.

Among the antelopes, it is second in size only to the eland (Taurotragus oryx) and may attain a height of 150 cm at the withers. Both sexes carry heavily ringed horns which curve backwards in the same fashion as those of the congeneric sable antelope (Hippotragus niger), though somewhat shorter. The most outstanding characteristic of the animal is centered around the head, viz. the striking facial colour pattern consisting of a black background with white snout and half-circles in front of the eyes, creating the impression of a mask. The exceptionally long ears - on the average from 25 to 30 cm long - immediately attract the attention. A well developed mane is present and the general body colour is roan (or greyish brown) while the legs are dark brown in colour. Large males may weigh from 250 kg to over 270 kg and adult females approximately 45 kg less.

Ecologically, one of the most important features of the roan antelope is the extensive range it inhabits. With the exception of the deep forest of the Congo Basin and the extreme arid zones it is met with almost anywhere south of the Sahara. Despite this wide range of distribution the importance of the species with regard to numbers or biomass varies considerably from one faunal community to the next.

Over/...

Over most of its range it occurs as small, scattered groups and may be regarded as one of the "insignificant" or "rare" species. However, in areas where conditions are most favourable it may also be found in considerable numbers and thereby constitute one of the dominant species, such as in the western half of Angola and also in North West Africa.

In their habitat preferences roan show a distinct partiality for open grassland savanna with easily accessible woodland to which they may revert to for shelter or in times of danger. These basic requirements are best met in the Brachystegia woodland country of Central Southern Africa. This area is characterized by numerous shallow, broad and grass covered drainage lines dissecting the tree woodland. However, most open grasslands or open tree savanna veld-types provide suitable habitat for roan.

Though their diet consists primarily of grass, roan also browse to a certain extent and the green leaves and young shoots of favoured shrubs and trees (e.g. Dalbergia melanoxylon, Lonchocarpus capassa and others) may provide an important food resource during the long dry winter months. They are dependant on a regular water supply and especially during the dry months visit their favourite waterholes at least once and at times even twice a day.

Roan antelope are semi-gregarious animals which associate in small herds of 5 to 12 individuals. Larger herds of 15 to 25 animals are also encountered and rarely even herds numbering between 50 and 80. In the Quicama National Park of Angola the author saw two herds of over 50 individuals and Capt. Robson (pers. comm.) reported temporary aggregations of up to 80 in Uganda.

However/...

However, the large herds are the exception with small groups - in which family ties play an important role - are the rule. All-male groups (bachelor herds) of 2 to 8 bulls and solitary old bulls are not uncommon.

Calves are dropped throughout the year though there appears to be some indication of a seasonal peak in certain areas. Young calves are rufous brown at birth and remain in concealment for the first few weeks following parturition. On assimilation into the herd, calves of the same age group tend to associate together and spend more time together than with their mothers. Weaning takes place gradually and is usually completed at six months.

The present study:

The Kruger National Park population of roan antelope represents the southern-most nucleus in the present-day distribution of the species. With the advent of man and the subsequent wanton killing of wild animals the roan antelope suffered severely and despite its erstwhile occurrence over the greater part of South Africa down to the Cape Province (Buckley, 1876) the herds surviving in the Kruger Park represent the only remaining population of any consequence within the Republic of South Africa. A small population - estimated at no more than 50-60 animals (Kettlitz, pers. comm.) - still persists despite great odds, in an inaccessible tract of country in the Northern Transvaal. Together, these two remnant populations total no more than 300 to 350 animals.

The already gloomy picture is further aggravated by the fact that roan antelope are highly susceptible to anthrax (Pienaar, 1960, 1961). During one epidemic no less

than/...

than 41 animals could be accounted for that had died from the disease in the Kruger National Park.

It is therefore little wonder that the responsible authorities are at present taking any (and all) possible steps to secure the future safety of this species in South Africa. Actions already in operation are of a dual nature, viz.

(a) the Transvaal Provincial Administration is gradually translocating the small group from the 'Belgium Block' in the Waterberg area of the Northern Transvaal to the Percy Fyfe Nature Reserve where they may be kept under close surveillance and

(b) in the Kruger National Park a specially built, game-proof enclosure has been erected into which a nucleus of 10 animals has been released for the sole purpose of enabling intensive scientific research to be carried out on the species.

The roan antelope project in the Kruger National Park commenced during July, 1967, and from the very onset the object of the study was to gain as much information as possible on all aspects concerning the species. It was hoped that by making a general study the various limiting factors pertaining to the roan would come to light and that subsequent recommendations could be made to neutralize or minimize the effects of these factors. As the study is still in progress it is the object of this paper to "introduce" the roan antelope, that is, to present some information on

the behaviour of the species and the interactions between the members of a group. Special attention has been given to those aspects in their behaviour which may exert a natural regulatory influence on the population or which may otherwise influence their ecology and management.

It is, therefore, the object of the present study to shed some light on the behavioural aspects of roan antelope.

Methods:

Basic equipment consisted of a four wheel drive Land Rover, a pair of 10 x 50 Halina binoculars and a 40 x 60 Hensoldt Wetzlar Dialyte telescope. Photographic equipment included an Asahi Pentax Spotmatic camera with 55 mm, 200 mm and 500 mm lenses.

Initially the herd in the enclosure was extremely wary and took flight when approached to a distance of 200 to 400 metres. However, the animals soon became accustomed to the vehicle and within 2 to 3 months the author was able to approach to within 40 to 70 metres of the herd without causing any undue disturbance. Later it was possible to approach even closer. However, the animals never lost their fear of man and observations were consistently done from the vehicle. This was by no means a handicap but rather an advantage as the terrain of the study area was of such a nature that it was easily negotiable by four wheel drive. It was thus possible to follow the herd wherever they moved about.

Observations were not only confined to the herd in the enclosure but were also extended to free roaming herds

outside/...

outside the camp. In a radius of approximately 24 kilometers of the camp there were 4 herds which provided favourable opportunities for observation. During the dry winter months these herds were regularly located at waterholes. They were much more difficult to find and observe during the rainy season due to

(a) an abundance of water in veld pans which tended to scatter the game and

(b) the denseness of the vegetation which made spotting the animals difficult and further effectively aided in their concealment from the observer.

Observations were generally confined to the early morning (sunrise to about 1000 hrs) and again during the late afternoon (1600 hrs to dusk). It was soon established that the animals rested during the midday heat and therefore did not necessitate observations. The time spent observing the herd in the enclosure alone totalled well over 1200 hours.

The great advantage of having a nucleus herd in an enclosure which in all respects - but for size - represents the natural habitat of roan is quite obvious and enables direct comparison of restricted and free-roaming individuals.

During the capture of the 10 roan which were released into the camp, each individual was marked by means of plastic eartags of various colours and combinations which assisted in the immediate and easy recognition of each animal. Because of the pugnacious nature of the roan the sharp horn tips were removed during the capture process and the horns fitted with pieces of rubber hose. Soon after release some of the rubber fittings became undone and once it was noted

which/...

which animal(s) had lost both, left or right horn pipings, these rubber fittings, or lack thereof, provided an additional means by which individuals could be recognized.

The roan antelope population and study area:

A. Roan antelope enclosure and its population:

With the erection of an enclosure in which to keep a nucleus group of roan antelope it was hoped to achieve at least two important ideals, i.e.

(a) that it would provide the necessary data on which to base a scientifically sound management programme to the benefit of the Kruger Park's roan population in general and

(b) that the nucleus herd in the camp could serve as breeding stock and that their offspring could gradually be released in small herds to augment the 'free-roaming' population.

To realise any of these two objectives it was clear that the camp would have to meet with the following requirements:

(i) the construction would have to be of such a nature that it could effectively withstand the onslaught of other wild animals from outside. Such animals included elephant, carnivora - from lion to jackal, zebra and various antelope species;

(ii) it would have to be as "natural" as possible to avoid any bias in the collection of data and

(iii) it would have to be large enough to allow sufficient freedom of movement and an expansion in the population without causing deterioration of the food supply.

To/...

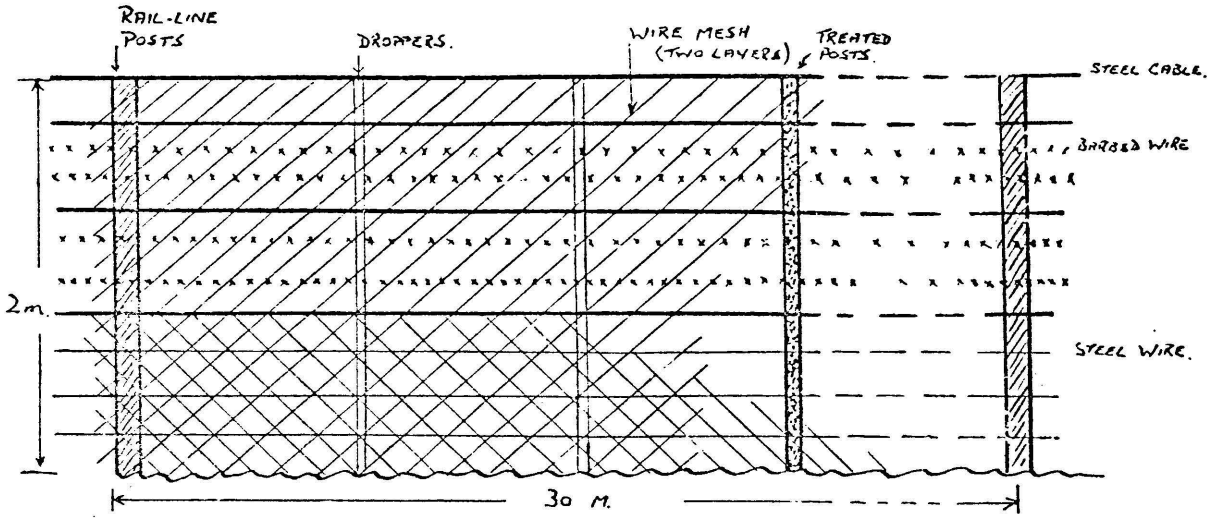

Fig. 1: Construction of the fence of the roan antelope enclosure at Nwashitsumbe.

Fig. 2: Attaching the second layer of wire mesh to the roan antelope enclosure.
Nwashitsumbe, January, 1968.

To satisfy these requirements the following programme was adhered to:

Construction of the fence:

To date the fence has proved quite satisfactory as a game (including elephant) barrier and was constructed as follows:

Lengths of railing erected in concrete, 30 m apart; treated posts, 12½ cm in diameter, planted in concrete at 10 m intervals between railings;

2 treated posts, 7½ cm in diameter, used as 'droppers' between the larger treated posts;

4 strands of 125 mm diameter steel cable at heights of 192 cm, 177 cm, 142 cm and 110 cm above ground level;

4 strands of barbed wire between the steel cables;

8 lengths of steel wire, bound in bundles of 3 strands each, at heights of 77 cm, 55 cm and 25 cm;

2 layers of wire netting, each 2 m broad; the first attached to the fence to a height of 1 m and the other half buried approx. 15 cm beneath ground surface and extending to the 'outside' of the enclosure, the second layer of netting is attached to the fence for its full length.

Selection of the site:

To ensure that the enclosure would be erected in true roan habitat an area was selected which

had/...

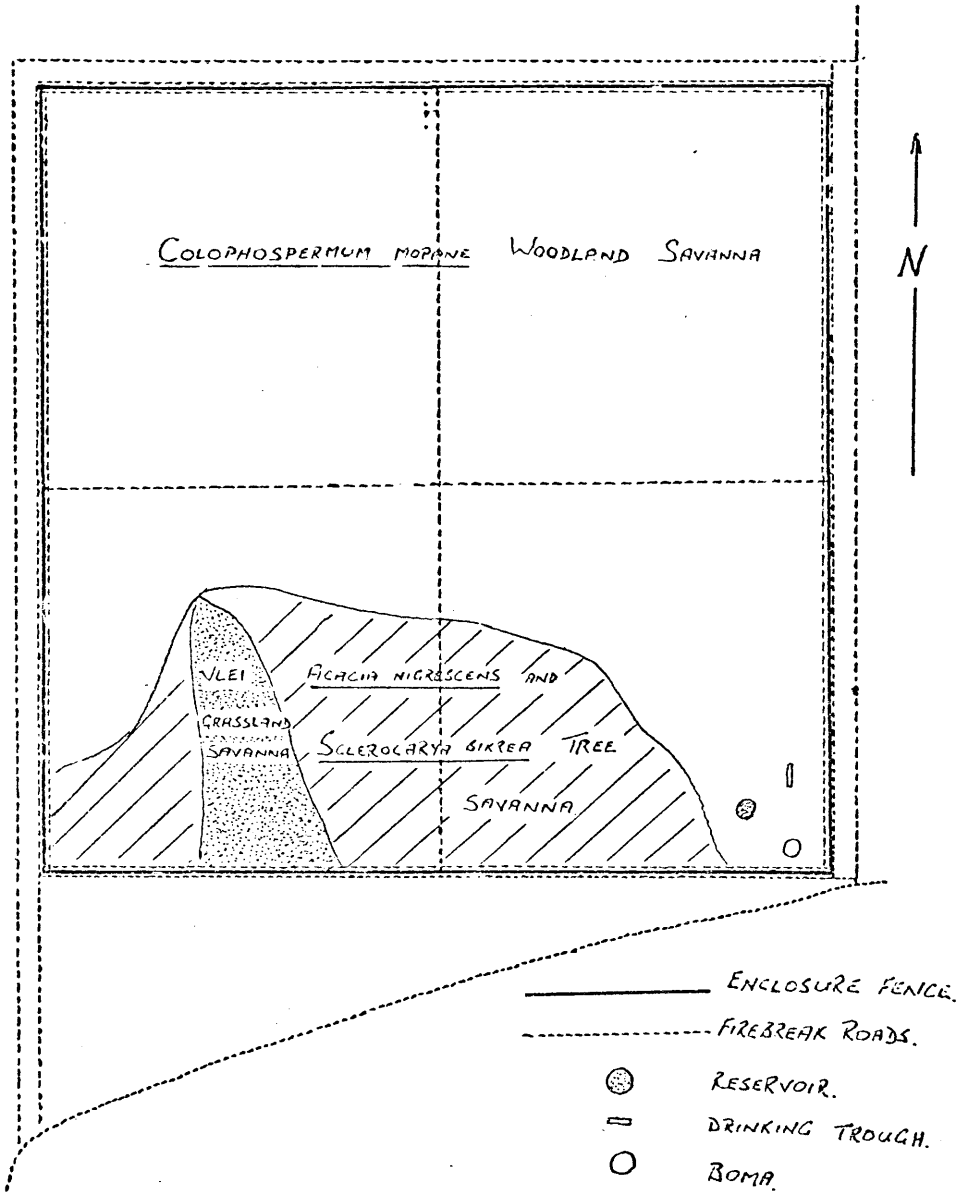

Fig. 3: Diagrammatic map of the roan antelope enclosure at Nwashitsumbe.

had been known for many years previously to be favoured by these animals. For this purpose a site in the Nwashitsumbe area proved to be the most suitable and was decided upon.

Size of enclosure:

To reach a reasonable compromise between size, expenditure and the labour necessary for the erection of the camp, and keeping into consideration the species to be contained in the camp, it was decided to make the camp 1 mile square (or 302 morgen) in extent (1.6 kilometer square). At present there are 26 roan in the camp and it is expected that the number could quite easily be trebled with no inconvenience to the animals or damage to the vegetation.

The habitat provided in the enclosure:

As already inferred the vegetation type in the camp has been a select spot for the species for many years and may therefore be regarded as true roan habitat.

Physiognomically and in species composition it is possible to differentiate between 3 more or less distinct vegetation types, viz.

(a) Mopane (Colophospermum mopane) woodland savanna: this vegetation type covers the largest area in the camp, i.e. the entire northern half and large portions down both the eastern and western fences. The most conspicuous and dominant plant in the tree

and/...

and shrub stratum is the mopane (Colosphospermum mopane) in the form of small trees (4 to 6 metres high) but predominantly in the shrub form. Associated trees and shrubs include Sclerocarya birrea, Combretum imberbe, Dalbergia melanoxylon, Lonchocarpus capassa, and Grewia spp. The grass cover consists mainly of Themeda triandra, Panicum coloratum and Schmidtia bulbosa while other important grasses include Heteropogon contortus, Cenchrus ciliaris, Digitaria stolonifera, Eragrostis spp, and Aristida spp.

The amount of tree and shrub coverage varies considerably from a fairly open aspect to rather dense stands of shrubs and trees on the rocky outcrops.

(b) Grassland savanna in vlei area:

This vegetation type covers a relatively small area in the south-western section of the camp, and includes the source of a shallow drainage line. Characteristic of the area is the stand of rank grass dominated by Setaria woodii and Panicum coloratum with sub-ordinates such as Sporobolus robustus, Sporobolus sp. Chloris sp., Sorghum versicolor, etc. Woody growth is mainly-restricted to a few large Acacia nigrescens trees, and thick stands of shrub growth of Colophospermum mopane and Combretum imberbe.

(c) Sclerocarya/...

(c) Sclerocarya birrea and Acacia nigrescens Tree savanna:

Two separate areas in the camp, one to the east and the other to the west of the vlei, fall within this category. Both areas are rather small but are favoured by the roan during certain periods of the year and are therefore important. The large trees (10 metres high and more), primarily Sclerocarya birrea, and the few shrubs with a well developed grass layer represent ideal roan country. Major grass species are Cenchrus ciliaris, Schmidtia bulbosa Heteropogon contortus, Urochloa mossambicensis Digitaria stolonifera, Eragrostis spp.

Water provision is in the form of a reservoir and drinking trough in the south-eastern corner of the enclosure. During the summer rains a number of depressions in the camp are filled and as long as these contain water the roan avoid drinking at the trough. This priority given to veld pans is in accordance with the behaviour of most other species (including roan) to vacate regular drinking places and to disperse with the onset of the first spring rains.

Special measures are taken to ensure the protection of the camp against uncontrolled veld fires from outside. Two firebreaks run through the centre of the camp and thereby divide it into four equal sections while firebreaks also run along the

inside/...

inside and outside perimeters of the fence. An additional firebreak was cleared parallel to, and 50 metres from, the fence and the intermitent strip of veld is burned regularly every year in the dry season.

The population in the enclosure:

During July, 1967, a total of 10 roan were immobilized and transported to the Nwashitsumbe camp where they were subsequently released (Pienaar). No mortalities were suffered during the capture and subsequent release of the animals. Soon after their introduction into the enclosure they settled down to a fully natural, if somewhat confined existence.

The sex ratio and age structure of the animals caught was intended to simulate the position normally found among the species. This ideal was achieved with the capture of 2 mature bulls, 4 adult cows, 3 heifers and a male calf.

The more dominant of the 2 males took possession of the females and immatures while the other bull was evicted from the newly formed herd. The following table gives the particulars of each animal caught and also the initials by which each individual will be referred to in the text:

TABLE I/...

Fig. 4: Roan cow BY. Nwashitsumbe, September, 1968. Note the ear tags and streamers in the ears. In the illustration both (B) ears have yellow (Y) streamers and hence the initials BY.

TABLE I:

ANIMALS CAUGHT AND RELEASED INTO ROAN ANTELOPE ENCLOSURE:

Date of capture	Sex	Approx Age	Locality	Ear markings	Initials
21.7.67	♂	5-6 yrs.	Hlamalala South	Right: Red	Herd Bull
22.7.67	♀	18 mnths.	Nwashit-sumbe	Left: Red	LH
22.7.67	♀	21 mnths.	Nwashit-sumbe	Both: Red	BH
24.7.67	♀	6-7 yrs.	Boyela N-E	Right: Yellow	RY
24.7.67	♀	7½ yrs.	Boyela N	Left: Yellow	LY
25.7.67	♀	15-16 mnths.	Boyela N	Both: Yellow	BY
25.7.67	♂	3 yrs.	Boyela N-E	Right: Grey	Lone Bull
26.7.67	♂	12 mnths.	Nwashit-sumbe	Left: Grey	LG
26.7.67	♀	10 yrs.	Stangene	Both: Grey	BG
27.7.67	♀	3 yrs.	Nwashit-sumbe	Right: Red Left: Yellow	LYRR

After the first 27 months in the enclosure no less than 15 calves had been born of which 4 succumbed to unknown causes and 11 have been reared successfully. To differentiate between the various calves each was given a name - mostly of colleagues who were responsible for the erection of the camp fence - and as many of these are referred to in the text, the following table provides their vital statistics:

TABLE II/...

TABLE II:

CALVES BORN IN THE ROAN ANTELOPE ENCLOSURE:

Mother	Calf	Sex	Born
LY	Fransie	♀	6.2.68
	Don	♂	28.11.68
	Young Bull	♂	29.9.69
RY	Stoffel	♂	8.10.67
	Lenie	♀	12.7.68
	Calf dead	Undeter.	15.5.69
BG	Nel	♀	12.9.68
	Betsie	♀	2.8.69
LYRR	André	♀	11.11.68
	Calf dead	Undeter.	Sept. 69
BH	Calf dead	♂	11.7.68
	Dirk	♂	14-15.5.69
LH	Hennie	♀	16.5.69
BY	Mike	♂	8-10.5.69
?	Dead	Undeter.	22.1.68

B. The entire study area:

Despite their occurrence (in recent times) in other areas of the Kruger Park, roan antelope have consistently shown a preference for the extensive mopane flats north of the Letaba river, immediately to the west of the Lebombo mountain range. This area includes two main game habitats which Pienaar (1963) has referred to as "grassland plains and 'dambos'" and the "mopane scrub and tree savanna of the northern Lebombo flats". A remnant population - numbering approximately 30 to 35

animals/...

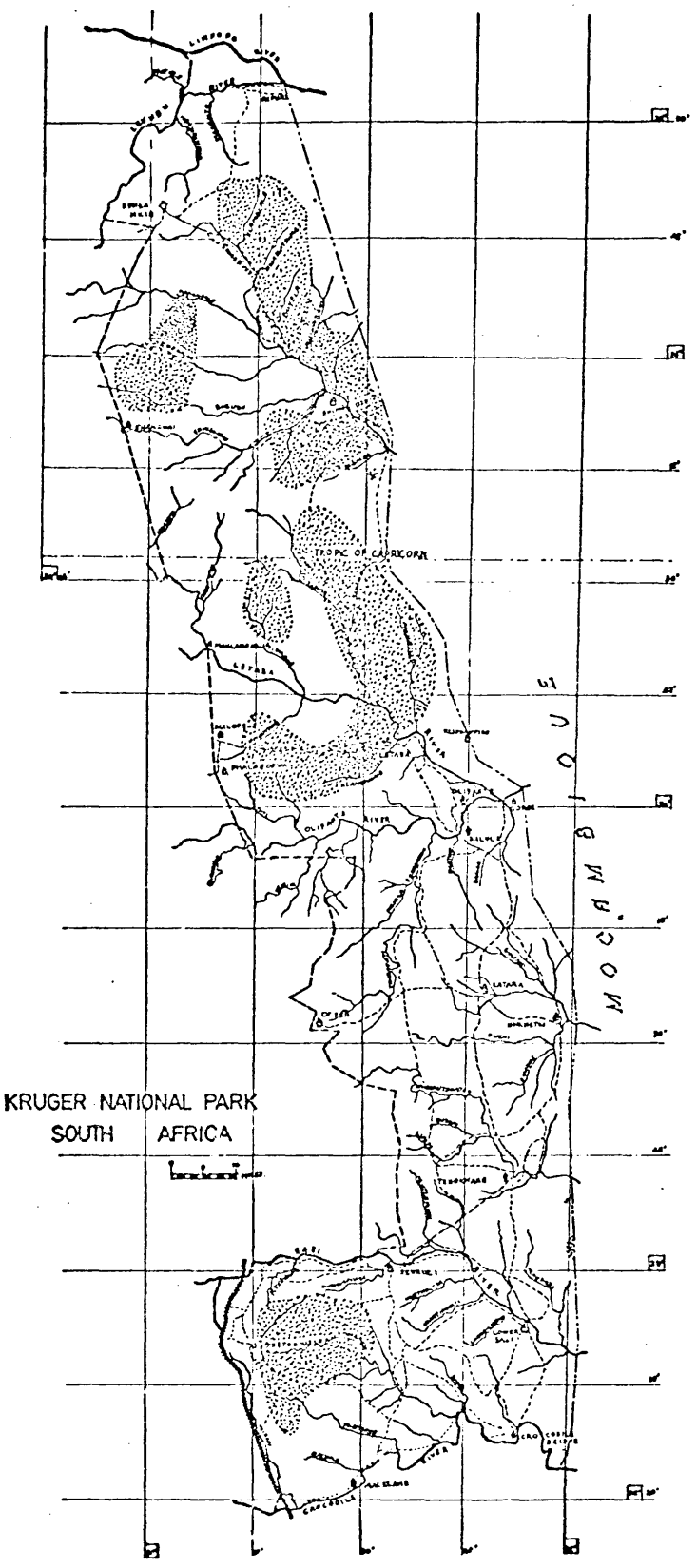

Fig. 5: Present distribution of the roan antelope population of the Kruger National Park.

animals - still persists in the Pretoriuskop area which falls within the long grass savanna woodland and tree savanna zone. A few herds are also resident in the mixed mopane-Combretum associations in the north-western area of the Park. However, both these latter areas are of little consequence when considering the habitat preference of this species and the general description of roan habitat presented here is restricted to the Lebombo flats:

Soils:

The characteristic black, clay soils of the Lebombo flats are derived from the underlying igneous basaltic rock formation. The depth of the top soil varies considerably, viz. from a few centimeters to a meter or more in the low-lying drainage lines. Immediately below the 'turf' soil a hard and poorly drained calcareous layer follows which is probably one of the major causal factors for the shrub growth-form of the dominant tree species, Colophospermum mopane.

Rainfall:

Climatologically the area may be subdivided into 2 main seasons, based on the pattern of rainfall, viz. the dry winter months extending from early May to the end of September with little or no rain, and the humid and hot summer months from October through April-May. These 2 seasons have a profound influence on game movements and concentrations with the majority of the game concentrated around the isolated natural and

artificial/...

artificial watering points during the dry season and a general dispersion of animals after the first good downpours in early summer.

Vegetation:

All the vegetation types described for the roan enclosure are represented in Pienaar's (1963) two main categories for the study area and need little further elaboration. By far the most important of the two habitat types, with regard to roan antelope, are the "grassland plains and 'dambos'". The broad, grass covered drainage lines, characteristic of the Central Southern African region, are absent in the Kruger Park but are represented by somewhat similar grass covered water courses draining large areas of the Lebombo flats. In addition to the plants already mentioned, Pienaar (1963) also lists the following as important: the Mlala-palm (Hyphaene crinita) and various grasses, such as Ischaemum brachyatherum, Cynodon dactylon, Bothriochloa insculpta, Dactyloctenium aegyptium, Cyperus spp. etc.

The mopane scrub and tree savanna extends over a considerably larger area than the previous vegetation type but is also unfortunately of much less importance to roan.

The roan population is not randomly distributed over the whole area but herds are conspicuously attached to the grassland valleys. No signs of

nomadism have been detected in the population and herds show a definite preference for certain favoured localities, where they may be encountered year after year.

Other important species which share the same habitat as the roan are elephant (Loxodonta africana), buffalo (Syncerus caffer), zebra (Equus burchelli antiquorum), sable antelope (Hippotragus niger), tsessebe (Damaliscus lunatus), eland (Taurotragus oryx), reedbuck (Redunca arundinum), wildebeest (Connochaetes taurinus), and to a lesser extent kudu (Tragelaphus strepsiceros).

Previous studies on roan antelope and general behavioural studies of African antelopes:

The roan antelope with its wide range of distribution is sure to have attracted attention at some time or another and no wonder that it is mentioned - with some superficial notes on its behaviour - in most papers dealing with game in general.

No intensive or long term study on its ecology and/or behaviour has as yet been undertaken. Child and Wilson (1964) have drawn attention to some aspects concerning its ecology and behaviour from observations made in Rhodesia and Zambia during Tsetse control operations.

(Dr. R.D.) Estes, an American zoologist, is at present doing a general ethological/ecological study of the Hippotraginae but the author is aware of no other project where the roan antelope has or is being singled out for study.

Behavioural studies of many of the African antelopes are steadily increasing and notable papers have already been published on many of the gazelles (Brooks, 1961; Walther, 1964 a and b, 1965, 1968, Estes, 1967), oryx (Walther, 1958), the genus Tragelaphus (Walther, 1963), wildebeest (Estes, 1968), reedbuck (Jungius, 1969), Uganda kob (Buechner, 1961, 1963; Buechner and Schloeth, 1964 and Leuthold 1966), waterbuck (Kiley-Worthington, 1965); Hartebeest (Backhaus, 1959), Spinage, 1969, 1969a; Herbert, unpubl. thesis, etc.

CHAPTER II.

DOMINANCE HIERARCHY IN ROAN ANTELOPE.

One of the least known aspects of the social life of African ungulates is the intricate regulation of the interrelationship among the members of a group. The study of social systems has increasingly shown that what once appeared to be loose aggregations of "individuals" now actually prove to be members of a highly organized group or herd, or, as Tinbergen (1965) asserted: "aggregation is usually but the mere prelude to closer co-operation". Not only may a population as a whole be governed by a particular social system, viz. territoriality, but quite often the members of a group are also subjected to some form of discipline in which the degree of dominance and subordinance of each individual plays an important role. A social hierarchy probably exists to a greater or lesser degree in most gregarious species.

In roan antelope there is a well developed, straight line dominance hierarchy which provides a rank for each individual in the herd. Full grown, mature roan bulls rank

above/...

above all cows and calves and further demand the submission of all members of the same sex entering their particular area of occupation. For a better understanding of the hierarchical system and its functioning in roan antelope the following analysis may be made concerning the position occupied by each individual and the maintenance of its "social standing":-

Position among bulls:

Roan bulls go through various complicated stages from the time of birth until they reach the ultimate in dominance i.e. total intolerance toward other mature males and the acquisition of a harem:

(i) for the first 30 to 36 months the young bull remains with the herd in which it was born and is tolerated by the herd bull. During this period the role played by the young male is no different from that of any other herd member of its own age. Though the influence of its social ranking order at this age is of no consequence to the older members of the herd, the young bull nevertheless holds its own particular position among the immatures where rank is determined primarily by age and not sex (see below).

(ii) following its eviction from the herd, a young bull enters a period in its life which may last for approximately 3 to 4 or more years, and at the end of which his intolerance toward other mature males becomes apparent. Small bachelor groups of 2 to 5, but as many as 9 individuals, are the rule during this "interphase"

period/...

period of roughly 4 years. Each of the bachelors in the group has its own degree of dominance within the group, the most dominant ones periodically breaking away from the group to establish themselves within a particular area to the exclusion of other mature males. Bachelor groups are excluded from these "activity zones" so that they are compelled to resort to marginal habitat areas where they are free from the persecutions of the dominant bulls.

(iii) The final phase is reached when a bull becomes intolerant toward other mature males. The intolerance of these males towards one another rules out any possibility of an amiable co-existence between 2 or more males beyond the age of 5 or 6 years. This implies that males in this category either lead a solitary life, if unable to compete for a harem, or become herd bulls by ousting a male from his herd

One of the functions of a hierarchical system is certainly to ensure that a group of wild animals may live a disciplined and organised life together to the mutual benefit of all members of the herd.

Though the herd exists as a unit the individual members only tolerate one another as long as subordinates acknowledge the supremacy of those more dominant than themselves. In this respect it is quite remarkable that the only true break in the line occurs between the fully mature bull and his subordinates in the "interphase". Total intolerance is exerted by the herd bull over all young males

except/...

(except those still with the herd) and this represents the one instance in which the "conditional tolerance" of the hierarchical system is replaced by absolute intolerance. Whether the gap between a herd bull and younger males is ever bridged - even after a bull has been ousted from his herd by a more competent male - is rather doubtful as the author has never encountered old males in bachelor groups.

The relationship between bulls defending 'activity zones' is based on the same principles as those between a mature bull and young males of the "interphase" stage i.e. the herd bulls are totally intolerant towards one another, therefore excluding any possibility of an amiable co-existence between them.

Among the members of his herd the roan bull is the undisputed dominant, or alpha animal and he also frequently exerts his dominance over his subordinates. Also, the cows and young animals of other roan herds acknowledge the dominance of a herd bull and customarily submit to him whenever in his presence. The dominance of a herd bull over his subordinates is developed to such a high degree that physical contact between the bull and one of his inferiors is limited to exceptionally rare cases only (see: maintenance of ranking order). However, though the dominance of the bull is not contested by his subordinates, his primary function is the maintenance of his herds' 'activity zone' and not the leadership of the herd, which is the function of a dominant cow.

Hierarchy among cows:

Though the bull is dominant over all cows and young animals, i.e. he can at any time elicit the submissive

attitude/...

attitude from any herd member, there also exists a definite social ranking order among the cows and juveniles with the leadership of the herd the sole responsibility of a dominant cow.

Observing a small herd of oryx, (Oryx gazella) (an old bull, 2 cows, W1 and W2, and a 2 year old bull calf) in the Münchenen Tierpark Hellabrun, Walther (1965) found that the old bull was dominant over all the others. He also mentions that the dominance of the bull did not necessarily imply that the bull was the leader of the herd. Of the other 3 animals the young bull was the junior and frequent skirmishes between it and one of the cows (W2) were observed. From this he concluded that W2 was subordinate to W1. However brief these observations may be, they clearly resemble the position found in roan antelope as discussed below:

(i) The leader-cow:

The leadership of the herd is clearly based on dominance amongst the cows and is therefore performed by the most dominant female. Backhaus (1959) also mentions the leadership of a dominant cow in a small herd of roan antelope he observed in the Garamba National Park of the then Belgian Congo. In a herd with several old cows, where the dominance of the leader-cow is not as pronounced as in herds with merely one or two aged cows to fulfill the functions of leader, a group of more than one cow may to some extent share the responsibilities of leadership. However, notwithstanding the competition from subordinates, a single cow may clearly be identified as the

leader of the herd.

The influence of the leader-cow may easily be recognised as paramount in all forms of activity which may have a bearing on the herd as a whole, i.e. in determining movements from one area to another, location of grazing and guidance to and from watering points. It is true that one or more of the cows of inferior position, with regard to the leader-cow but of high ranking order in the herd may also influence the activities mentioned above (see below).

In guiding the herd to water the alpha cow characteristically takes the lead with the others following behind - in no particular order and not necessarily in a straight line either. Occasionally the leader-cow may lag behind on approaching the water with one of the other cows advancing ahead of the herd. The bull occupies no particular position in the herd when moving about and is frequently found in the centre though more often than not in the rear.

The leader-cow's influence is also clearly discernible in the choice of grazing grounds. Roan herds generally appear to be of a rather loose nature due to a large individual distance (5 to 10 metres) between mature individuals. This is especially noticeable when a herd is grazing during early morning or late afternoon.

Herd/...

Herd members disperse over a large area with as much as 200 metres or more between animals on the outskirts of the herd and there is seemingly little or no unison among the various members. However, observation has revealed that they seldom move far away from the leader-cow who constantly remains the focal point of the herd. It is therefore amply clear that the determination of the daily routine of activity - especially movements - is dependent on the guidance of the leader-cow and in this way she is also responsible for the plotting of both the "home range" of the herd over a short period of time and also the herds' "activity zone" over a more extended period, covering the different seasons of the year.

In many respects the leader-cow plays a stabilizing role in the herd. Roan antelope are inherently nervous and wary animals and show a definite inclination to flee at the first sign of danger. From observations made, it appears as if the dominant cow has a greater ability to evaluate a position in terms of danger and act in the best interests of the herd. The first reaction of a herd to approaching danger, e.g. a motor vehicle, is for the younger animals and also some of the cows to mill around or run away. The leader-cow will immediately focus her attention on the source of disturbance and gaze in its direction until she

has determined its exact nature. The fact that the leader-cow does not flee immediately after detecting a potential danger has a profound reassuring influence on her subordinates who soon become calm, turn about and inspect the situation more carefully. Should the position surpass her tolerance threshold she will turn about and - depending on the situation - make off at a stiff legged trot, tail swishing from side to side and ears turned up and directed backwards which is a sign for the herd to flee (prancing action). This appears to be the position at low intensity disturbance while sudden danger may be greeted by a snort from one or more animals in the herd and the fast retreat of the entire herd (high intensity disturbance). The behaviour of the leader-cow under situations of stress certainly reminds one of the age-old warning under any conditions demanding caution i.e. "stay calm".

When a roan herd retires after a period of activity the individuals lie down one after the other with the mature cows spaced out as sentinels for the safeguarding of the herd. Once again the leader cow becomes quite prominent in that she is the last, or one of the last, cows to lie down in the majority of cases.

Despite his arch position in the social ranking system, it is quite clear from the above account that the harem bull plays a completely inferior

role in herd activities and submits freely to the leadership of the cow(s). This then also accentuates the widely different roles played by the 2 most dominant members in the roan hierarchical system i.e. the herd bull and the leader-cow.

The major activity of the herd bull is centered in maintaining a zone around the nursery herd free from intrusion by other mature males. This ensures that each nursery herd is attended by only one adult male at any specific time. This system may have definite advantages for the species as only healthy and superior males participate in reproduction while the maintenance of "intolerance zones" provides for an equal dispersion of the population throughout their available habitat, thereby avoiding over-utilization of the range.

In direct contrast to the bull the leader-cow exercises her dominance and experience to the best possible benefit of the cows and juveniles subjected to her authority. The safety and survival of her followers is clearly the main concern of the leader-cow.

(ii) Other mature herd cows.

Roan herds normally consist of a number of adult cows and the possibility of a number of old cows together sharing the various responsibilities of the herd leadership has already been mentioned.

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It is therefore clear that the character distinguishing one as the leader and the rest as subordinates is no more than one acquired merely through age and physical strength, which renders one cow more dominant than the others. This line of dominance runs from the leader-cow down the line to the most inferior cow, thereby providing each female with a particular position in the social ranking system. This being the case it is once again quite comprehensible that the qualities encountered in the leader-cow should also be exhibited to some degree by the cows lower down the scale.

The more mature females there are in a herd - especially ageing cows - the more strife and competition there will be for the leadership of the herd. The position may thus arise where one or 2 cows may acquire sufficient dominance to "share" the leadership. This becomes apparent when a cow of lesser rank than the leader temporarily takes the lead of the herd in situations normally dominated by the leader-cow e.g. leading the movements of the herd to water or while grazing, etc. More important, and of greater ecological consequence, is the fact that divided leadership may give rise to the formation of groups within the herd (see below).

Mature cows of all standing contribute generously toward the safeguarding of the herd from outside

dangers/...

dangers by their general alertness and their special distribution in the herd. The role played by so-called sentinels in various species of ungulates has long been a matter of dispute but in roan antelope there can be little doubt that all mature cows act as sentinels and are characteristically found on the perimeter of the herd - both while grazing and when resting. Certainly, one of the most radical changes in the behavioural pattern of a roan cow is her transformation from juvenile to adult status. The change is brought about during her first pregnancy - especially the last stages - and the period immediately following the birth of her first calf. Prior to adulthood the young heifer roams about with the herd fulfilling no apparent function. During the late stages of pregnancy the young cow gradually isolates herself from the main body of the herd by remaining on her own on the perimeter of the herd. Immediately prior and for a few days after giving birth she remains on her own and once she rejoins the herd she assumes her new role as a sentinel. It is during this period of isolation, and parturition of her first calf, that the young female acquires an intense alertness and the responsibility of safeguarding her newborn. Once mother and calf rejoin the herd the cow retains these 'maternal' characteristics which enable her to fulfill her role as a herd sentry.

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It was probably to these young cows that Sclater (1868) was referring when he wrote: "I have frequently remarked that the main body of the herd is protected while grazing by one or more of the party, who act as sentries and give alarm at the approach of danger".

Estes (1969) noted the same behaviour, that is the tendency for cows to remain on the outskirts of a herd, for sable antelope in the Shimba Hills of Kenya. As in the case of roan, these animals proved to be particularly wary and were generally also the first to detect danger. Once a cow has reached this stage she has basically all the necessary requirements for leadership, though under normal conditions she is withheld from this position by the presence of more dominant cows in the herd.

Ranking order among immatures:

The dominance and submission pattern in roan antelope operates from the very earliest stages of life and is quite evident among calves as young as 2 months and upward. For the first 6 weeks of life the young calf "lies up" and cannot be considered a member of the herd. It is therefore also most probable that a calf of this age does not yet qualify for the hierarchical system. However, once the calves "join" the herd they are immediately "placed" and once the sorting out has gained full momentum at the age of 4 to 6 months there is no more doubt as to the position of each calf.

During/...

During this stage and up to $2\frac{1}{2}$ or 3 years calves of both sexes are present in the herd. No difference at all has emerged between the two sexes and young bull calves are equally dominant or submissive toward inferior and superior heifers respectively. This position is retained until the bull calf is ejected from the herd by the herd bull. The relationship between the herd bull and the male calf will be referred to in detail in chapter 3. By the time the young bull is ousted from the herd (at $2\frac{1}{2}$ to 3 years) his social standing among his 'fellow herd members' is no different to what it was when he joined the herd as a calf, that is, he readily submits to all of the mature cows and also to his dominant heifer companions.

For the young heifers there is little change in their social pattern and each one's status, relative to the others, is carried over into the adult stage.

Determination of rank in the social system:

From the preceding comments on the position and functions of the various members of the herd in the hierarchical system it has clearly emerged that the position occupied by each individual is determined by two factors viz. age and sex.

(i) Age:

Undoubtedly age is the overall determining factor regulating dominance and subordinance among the members of a herd. This is especially true of the younger animals - or 'lower ranks' - where competition for a more dominant position is not as severe as among the animals in the 'higher ranks'. Despite continual fighting among animals of all ages in their efforts to retain their position

or/...

or gain higher status, the ranking order appears to remain fairly constant once it has been established. In the marked roan herd in the camp, the position of each individual could be determined quite easily and from the very beginning it was obvious that their positions were age - specific e.g. the following sequence was evident from the leader-cow down to the most inferior individual:

LY(1); BG(2); RY(3); LYRR(4); BH(5); LH(6); BY(7); LG(8); Stoffel(9) and Fransie (10).

The above line of dominance follows the age structure of the herd - with the possible exception of the leader-cow and BG. Though no specific ageing criteria were used to age the 2 old cows the general appearance of the 2 would suggest that BG is older than LY. However, both cows fall within the "leader" class and as LY was the first of the 2 to be released in the camp she was probably in a better position to establish herself as leader. During the capture process BG suffered a back injury which hampered her movements for at least the first few weeks and this further swung the scale in the favour of LY.

Age also plays a role in the frequency and intensity of intimidations and fighting for social rank with light skirmishes among the lower

ranks and fights of the highest intensity among old cows. Casual skirmishes occur with the highest frequency and serious fighting only rarely (see Maintenance of Social Rank).

(ii) Sex:

In discussing the initial stages in the establishment of the social hierarchy among immatures it was pointed out that there is no discrimination against either sex in the first 3 years of life. At this stage young males leave the herd and only re-enter a nursery herd when they are able to evict and replace the herd bull.
A herd bull is immediately dominant over all cows and sub-adults though he may in actual fact be younger than some of the cows in the herd. The total dominance of a bull over a cow in the mating ceremony plays an all-important role (see: Mating Behaviour) and therefore it is possible to believe that a bull cannot attain the status of a herd bull until such time that he can exert his dominance over all cows in a herd.

Whether a mature male could be considered a true member of a roan herd is a debatable point. Attention has already been drawn to the different purposes for which the bull and the leader cow exert their dominance over their sub-ordinates, which clearly indicates that the bull is not a fully integrated member of the herd but rather occupies a "reserved" position in the herd

and/...

and cannot be considered on a par with the other members of the herd. This 'sex-determined' dominance of the bull is probably also the result of his superior physical powers - especially weight - which is acquired toward the fifth or sixth year of life.

Among the bulls dominance according to age is the rule during the inter-phase period but to compete for a nursery herd the determining factor changes to physical strength. If this was not the case there would be virtually no competition from the younger bulls for nursery herds, in fact, it is difficult to conceive whether such a system could be maintained at all in the absence of some form of competition other than that based on age. If this was the case young bulls would not only have been deprived of the ability to compete with older bulls in the defence of an 'intolerance zone' but would not have been in a position to establish themselves within an activity zone in the first place.

Maintenance of the hierarchical system:

The hierarchical system in roan antelope plays an all-important role in the species as it governs each individual's response towards others of its kind and is evidenced in every form of social activity in the herd. It is therefore quite feasible that the maintenance of the system should be one of the conspicuous features in the activities of the herd members. Dominance and subordinance form the

basis/...

basis of the system which includes each member of the herd. Though age appears to be the most important factor in determining the position of each animal, it does not exclude or eliminate the constant friction occurring between members of a herd. Fighting and sparring takes place between all the herd animals but varies considerably in duration and intensity, and depends largely on the position of the participating individuals in the social scale. The intimidation of a lower ranking individual by a senior animal by means of the "Dominance display" is usually sufficient to endorse the status quo between the two individuals. Backhaus (1959) has also commented on the frequency with which the dominance hierarchy is maintained merely by dominance ("Imponieren") displays as contrasted to actual fighting. Actual contact is most frequent in low intensity sparring among low ranking individuals while serious clashes are generally found in the higher placed animals. The different phases, or sequences, that may be distinguished in the fighting contests include low, moderate and high intensity dueling.

It must also be pointed out here that though the dominance hierarchy is maintained by threats and duelling, the one important function of this form of social organization is to minimize and control unnecessary and destructive fighting (Scott, 1962). Almost synonymous with the roan antelope are the scores of references by old hunters and naturalists of the ferocious nature of the beast and the high frequency of fighting among the members of a herd (cf. Lyell, 1910). Despite all the aggression, the occurrence of serious injury due to fighting is conspicuous

by/...

by its almost total absence. In the roan camp the leader-cow lost one of her horns in a duel; a large bull was seen with a torn ear (which may not have been the result of fighting) while some old bulls show one or more scars in the head region. Personal observations revealed no deaths resulting from fighting in the Kruger Park though fatalities have been recorded from elsewhere (cf. Blower, 1961). Scott's (1962) general remarks that "fighting may first arise in a playful form and a dominance relationship be formed without serious fighting taking place", comes remarkably close to the position found in the social relationship of roan; serious fighting being restricted entirely to those individuals at the top of the scale. Eibl-Eibesfeldt (1961) has also drawn attention to the lack of serious injury in the frequent intraspecific fights among vertebrates and suggests that, apart from causing little or no harm, they serve the important function of "spacing out the individuals or groups in the area they occupy".

(a) Low intensity fighting:

This form of fighting is usually associated with the young animals in the herd, i.e. immatures which occupy the lowest positions in the ranking scale. It may also occur among the younger cows of a herd and also in situations where there is a large difference in the "seniority" of the 2 contestants, viz. between a mature cow and one of the immatures.

Typically, 2 individuals stand face to face and leisurely rub their horns and faces together.

They/...

Fig. 6: Two immatures engage in a bout of low-intensity fighting. Nwashitsumbe, 1969.
The dominant animal on the right allows a subordinate to push horns with it.

They will frequently rub their muzzles together and also the sides of their faces, including the eyes and preorbital regions. They may then tilt their heads slightly to bring their horns into contact and stand waving their heads about gently, apparently in an effort to interlock their horns. Simultaneously the tails are whisked playfully from side to side and from time to time one or the other (usually the dominant animal) may exert some pressure and push his opponent's head down slightly. If the subordinate animal does not see fit to continue the duel he usually breaks the fight at this point by merely backing away from his adversary, turning around and running away a short distance.

If they do not end the fight at this stage the two usually fall onto their knees and may either proceed with rubbing their faces and horns together or may immediately 'come to grips' with their heads and start pushing at one another. The pushing contest normally signifies the end of the duel as the subordinate animal soon submits to the superior one by jumping up and giving way. Occasionally the dominant animal may remain on his knees for a few seconds after his victory before standing up.

The appearance of this fighting creates the impression of playfulness and at this low intensity level there is probably little difference between

playing/...

playing and fighting. Without exception however, it is possible to predict the "winner" of such a duel which points to the importance of the dominance/subordinance relationship between individuals from the very earliest age.

Low intensity fighting may also occur between young adults and takes the same form as that between immatures. When 2 individuals of different social standing compete with one another it sometimes appears as if the dominant animal tries to entice the younger one to "fight" with it, only in the end to push the weaker one out of the way. During such duels the dominant animal may fall onto its knees in typical fighting position and allow the younger one to rub and clash horns with it, or the younger animal may be on its knees with the older one co-operatively holding its head close to the ground for the younger one to butt at. In both instances the dominant animal eventually tires of the "game" and pushes the younger one aside.

Such fights are the most frequently observed in the herd and mostly occur in early morning or late afternoon when the herd is actively grazing. Sparring may last for only a few seconds or it may be extended for 5 or more minutes. On the average low intensity fights probably run for 30 to 90 seconds and though certain sequences have been described the fighting may be culminated at

any/...

Fig. 7: The Herd bull assumes the Dominance display posture, directed at a young male on the outside of the enclosure. The subordinate male drops his head in the head-low threatening posture. Nwashitsumbe, September, 1968.

any stage or it may proceed with the omission of a certain sequence e.g. 2 animals may immediately fall onto their knees, clash horns and end the fight, etc.

(b) Moderate intensity fighting:

Both low and high intensity fighting are immediately evident and clearly differ from one another. On the contrary, moderate intensity fighting does not differ much from low intensity fighting and is therefore more of a subjective classification based on the seriousness of the conflict. Whereas low intensity fighting is generally associated with immature animals, fighting of a more serious nature is commonly observed among higher ranking adults. Such fights also occur at considerably lower frequency than the less serious duels but are similar in duration.

The basic fighting is very much the same though face rubbing and the seemingly gentle horn rubbing of the younger animals is mostly absent with fighting (or contact) reduced to a fairly severe pushing duel with both contestants on their knees. Once a fight has broken up, it is not as readily resumed as is the case in younger animals.

(c) High intensity fighting and displays:

Highly placed individuals in the social ranking system are rarely involved in actual contact

fighting but more commonly exert their dominance over subordinates by the "Dominance display". Disputes at a high level are characterized by short but high intensity fights, and are restricted to the herd bull and the top 2 or 3 cows.

Strictly speaking the fights between bulls and their subordinates or male rivals should also be considered under this heading but as their rivalry is of a more specialized nature and involving only the males it will be more appropriate to give their relationships detailed consideration in the next chapter.

Dominance postures may be displayed by the herd bull and the 2 or 3 senior cows in the herd or by any member toward a subordinate. Displays by the bull and cows are identical though the response they elicit from subordinates varies with the dominance of the animal displaying. The bull is the undisputed "senior" in the herd and his displays are sufficient to force any member of the herd, including the leader-cow, into submission. On only 2 occasions did the bull actually clash with a cow, the leader of the herd, and a younger cow, during the courting and mating ceremony.

Initially the bull and the leader-cow only rubbed their foreheads together and while on

their/...

their knees the bull pushed the cow back a few paces (low to moderate intensity fighting). Shortly afterwards the bull and cow were again involved in low intensity rubbing of the foreheads and light skirmishing. The cow jumped away from the bull and as he again approached her the cow fell onto her knees. With head held low the bull clashed horns with the cow simultaneously uttering a loud guttural "roar" upon which the cow jumped up and moved away from the bull (high intensity). Dominance plays an all important part in mating and it is therefore quite significant that dueling should have taken place between the bull and the most dominant cow in the herd. (See chapter on Mating Behaviour). Both prior and subsequent to the clash described above the leader-cow had been seen to succumb to the displaying of the bull.

Among the cows the 'Dominance display' is frequent between high ranking females and animals of lower social standing. Cows in the 'top level' are more equally matched and more often than not mere displaying does not force a slightly less dominant cow into submission and the result is a high intensity fight. Clashes of this nature, however, are very rare - especially concerning the leader-cow - and usually last for no more than a few seconds.

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In high intensity fighting one or both of the contestants makes a short but determined charge at the other. The 2 cows fall onto their knees and strike the basal portions of their horns together with such force that the clash may be heard a long distance (200 to 300 metres) away. If one of the two cows does not acknowledge defeat with the initial clash the two will stay on their knees and amidst loud guttural noises, attempt to push each other off the mark. The defeated cow soon jumps up and evades the dominant one by running off a few metres and then resumes grazing.

In many cases a cow may make a short and determined charge (10 to 20 metres) at a lower ranking individual in which case the subordinate evades the charge by quickly giving way to one side. If the charge is directed at a higher ranking cow the superior animal will receive the charge by dropping onto her knees and clashing horns with her pursuer. In such cases the weaker of the two again jumps up and runs away.

The 'Dominance display' clearly demonstrates the superiority of the displayer i.e. the postures assumed leave no doubt as to the dominance of the animal displaying: the neck is slightly arched and the head held high with the tail well away from the body (Imponier verhalten, Walther, 1958). The ear on the side of the subordinate

animal/...

animal is held somewhat horizontal while the ear on the other side is outstretched and above the horizontal plane. The animal displaying in this manner may take in a broadside (lateral) position in front of the one being subjected to the intimidation, that is, displaying its side to the submissive individual ('Lateral dominance display'). While in this lateral display position the head, and horns, are typically held at an angle toward the submissive animal and the displayer may take a few "lateral paces" toward the lesser animal. If it does not move away fast enough it may lead to an actual clash with the horns.

As characteristic as the 'Dominance display' is also the attitude adopted by the submissive animal. Whenever a dominant individual succeeds in intimidating a subordinate the following basic behavioural pattern is manifested: The latter animal immediately drops its head with ears outstretched above the head and pulls its tail tightly between its legs or else swishes it from side to side (Kopf-tief-drohen, Walther, 1958). In this way it approaches its intimidator from about 5 to 10 metres distance and passes 2 or 3 metres from the dominant one. As the submissive animal passes, it may jerk its head a few times and then run past the dominant animal in a semi-circle. Once it is about 5 to 15 metres from the intimidator it resumes its normal posture

again/...

again. The dominant individual is passed in the direction of the head to the tail and as it passes the dominant individual follows the submissive one with its head and may make a casual sweep or butt at its buttocks as it passes.

As could be expected in a situation where an animal is being forced into submission through the dominance ritual that this is the ideal setting for the release of displacement activities. In the dominance - appeasement ceremony the 2 most frequent displacement activities appear to be scratching - with the hind foot - and grazing. Roan normally scratch themselves in the fore-quarters with their hind feet in normal 'comfort behaviour' when molested by biting flies and other insects. As the dominance ritual usually occurs when the animals are actively grazing, it could not be stated without any doubt that either one of these reactions is actually a true displacement activity, though the situation during the displaying is of such a nature that these activities could, if anything, be looked upon as displacement activities.

The stability of positions in the hierarchical system:

The fact that no positional changes were noted in the tame herd at Nwashitsumbe over a 2-year period is sufficient proof that once each member of the herd has established its position it is not easily displaced by one of a lower rank. On the subject of the dominance hierarchy

Scott (1958) writes that "this kind of social organization is relatively stable and permanent....." which "is presumably due to the drastic and long-lasting emotional responses connected with fighting and avoidance.....".

In fights between 2 animals it was not always possible to determine the challenger but the impression was certainly gained that it was the more dominant animal of the two that initiated the fighting. This leads one to believe that in the ordinary rank and file members of a herd duelling primarily serves the purpose of endorsing the dominance of the senior animal on its subordinates and not the reverse in which a subordinate challenges a senior in the hope of gaining higher social status.

It has already been noted that the most intense strife and fighting occurs among the most senior members of a herd; this includes fighting for both "top" positions in the hierarchical system, i.e. the acquisition of a nursery herd in the case of males and leader of the herd amongst the females. It is also in these 2 positions where changes would necessarily have to take place from time to time. Again the indications are that once an animal has established itself in a position, it is seldom dispossessed of its dominance. During the late stages of pregnancy in the leader-cow (LY) of the marked herd, the 'second in charge' (BG) made a desperate effort to oust LY from her position. BG actually managed to push LY off the mark and it appeared as if LY had lost the leadership to BG. Late pregnancy probably represents the most vulnerable period for the position of a cow, especially as she then starts avoiding the herd and increasing her 'individual distance' from the

others/...

others, until she finally breaks away and isolates herself prior to and immediately after parturition. However, both in the case of LY above, who soon recovered her leadership, as well as the other cows in the herd it was never observed that any of them ever lost their ranking order due to pregnancy.

Some months after the incident described above, it was found that LY had lost her right horn - presumably in a fight with BG. Despite her handicap and the pain she must have suffered, LY stubbornly retained her leadership of the herd.

Even in the face of what might have been thought to be sufficient grounds for a "junior" to oust a "senior", exchange of positions has not yet occurred in the marked herd, and this is considered to be sound proof of the extreme stability of the 'ranks' in the hierarchical system.

In a group of black wildebeest (Connochaetes gnou), it was found that the senior cow lost her seniority due to weakness in the late stages of pregnancy and subsequent abortion of twins (Walther, 1964).

Ecological significance of the hierarchical system:

Roan antelope are semi-gregarious animals which form small herds ranging from a few individuals to as many as 20 or more. From the foregoing notes on the hierarchical system it is quite evident that roan groups are governed by certain principles (superordinate - subordinate relationships) which determine the relationships between the members of the group and thereby render it a stable and well organized association of a number of individuals, as contrasted to a loose aggregation of individual animals uncommitted to

one another. Stability of the herds was clearly demonstrated at a waterhole where 2 herds gathered to drink at the same time. Cows and calves intermingled freely though there was much evidence of dominance displays which made it quite clear that a total reshuffling and fighting for positions in the ranking scale would be necessary before the 2 herds could fully unite as one. When they departed from the water a number of cows from the one herd left with the other herd but by the following morning they had once again rejoined their own herd. This is but one of many examples which illustrate the close ties between members of the same herd and their reluctance to join a 'foreign' group. Apart from any other bonds, e.g. family bonds, which may influence the relationships between individuals, it is believed that the hierarchical system plays an all important role in establishing and maintaining the identity of a herd and dissuading its members from joining other herds.

In comparing the reactions of established groups of dogs to the introduction of a strange dog, King (1954) found that the rejection of strangers by a group reflected the rigidity of the dominance hierarchy within the group and concluded "that the more rigid the social hierarchy, the more exclusive the group". There is no doubt that this principle is also operative in roan antelope herds and that it is responsible not only for the relative stability of groups but also for their exclusiveness to strangers of the same species. Further, Collias (1944) in his review on aggressive behaviour among vertebrates, draws from the observations of various authors (amongst others Lorenz, 1931; Odum, 1941; Carpenter, 1942b; Alverdes, 1935) to formulate the statement

that/...

that "strangers among the vertebrates appear almost invariably to be attacked when they try to enter small groups organized on a hierarchical basis".

The benefits derived from a system which provides for group stability, coupled with the fact that a herd tends to occupy the same general area for any number of years, are quite evident. Under the leadership of the dominant cow, who also represents the cow with the most experience, the herd may exploit the most advantageous situations offered by the habitat for breeding, resting, grazing, watering, sheltering and other activities and avoid natural perils such as carnivora, droughts, veld fires, etc.

Herd stability described above does not infer that splitting up of herds does not occur. On the contrary, roan herds very frequently break up into one or more smaller groups - only to reunite again some time later. In the marked herd it was possible to determine the composition of the groups as they broke up and though the animals comprising each group did not necessarily always remain the same there was nevertheless a remarkable consistency in their composition. This is probably the most common manner in which new roan herds are formed and the way in which it is achieved conforms to the following pattern:
In herds consisting of a number of old cows in the "leader" category the competition for leadership gradually becomes so severe that the degree of dominance between the alpha cow and 1. or 2. of her immediate subordinates slowly diminishes until they are on more or less the same level of dominance.

In such cases the 'second' cow may break away from the main herd with a small following. This group may reunite with the herd and again break away. It probably gradually moves further and further afield until it is able to select its own home range and activity zone in an adjoining area and so form the nucleus of a new herd. What the particular bonds are that unite the members of the defecting groups is not quite clear, but they may be old family ties or bonds between certain members of a herd which are formed at an early age (see relationships among calves).

In the chapter on Spacial distribution it is pointed out that the network of activity zones (influenced by habitat preferences), and the social organization of roan herds, together exert a profound influence on the size and distribution of the population. Certainly, one of the most important functions of the dominance hierarchy is the formation of relatively small 'closed' groups (5 to 12 individuals on the average) which form the basis for the natural regulation of population size, and in this manner conform to the general statement that 'most simple and relatively closed societies are small' (Collias, 1944).

A further advantage of the ranking system is that the herd is consolidated by the leader-cow under situations of stress (see functions of leader-cow). The author has never had the opportunity of observing roan in the presence of dangerous carnivora, but assumes that it would be similar to their behaviour under other conditions demanding caution i.e. in the presence of a human observer. Under these conditions the leader-cow exerts a calming effect on all the herd members which would otherwise, as could be imagined,

lead/...

lead to disastrous results if a pride of lions should disintegrate the herd.

The system of declining dominance also provides for a 'second in charge', should the leader cow fall away. As the rank and file members of the herd are all subordinate to the "second" cow she can take over the leadership without any disruption in the herd.

The remarkable adaptation of the nucleus herd of roan to life in the enclosure at Nwashitsumbe, and the high reproductive rate of the animals, has surpassed all expectations and it may already be predicted with confidence - in the absence of any unforeseen set-backs - that small herds may be released from the camp into their natural environs within the next 3 to 4 years. To derive the maximum benefit from this experiment, the survival of the released animals is a first prerequisite and to meet this requirement it is pertinent to recognise and adhere to the natural social organisation of the species as outlined in this chapter. In accordance with this principle the following recommendations for the release of animals from the camp are suggested:

(a) that animals which have formed a stable group in the enclosure be released as a unit;

(b) that at least 1, but preferrably 2, old cows be included in the group to act as leader(s).

(c) That, as far as is possible, only females that have successfully reared a calf be considered for release. The motivation for this stipulation is derived from the behavioural changes

which take place in the transition from immature heifer to adult cow, with fully developed maternal instincts, which could prove to be one of the important factors relating to individual and group survival (see text).

(d) the release of immature animals can serve no useful purpose and it is therefore recommended that they be confined to the safety of the enclosure until they have gained maturity;

(e) for the sake of completeness, the following recommendation is also made though the reasons may be sought in greater detail in the next chapter: that groups of young males in the inter-phase period be released from time to time to avoid unnecessary friction and possibly even disruption of the herds as space is limited in the enclosure and contact between evicted young males and herd bulls would be difficult to avoid.

CHAPTER III.

SPACIAL DISTRIBUTION: ACTIVITY ZONES, HOME RANGE AND INTOLERANCE ZONE.

It has already been noted that the small roan antelope population of the Kruger National Park is widely and sparsely distributed over a considerable range, particularly in the Mopane (Colophospermum mopane) veld to the north of the Letaba river.

The preference for a particular locality by a herd has emerged as one of the characteristic features of the roan antelope (see below) and for the purpose of determining the factors influencing their spacial distribution it was deemed important to gain a better understanding of the interrelationships between adjoining herds.

Sufficient data have been accumulated to indicate that the distribution of roan herds is strictly in accordance with their pattern of social discipline and their rigid habitat requirements. Basically, the antagonism between adult males and the functioning of the dominance hierarchy lead to herd stability and the dispersion of the herds throughout the available habitat.

The occupation of an area by one herd to the exclusion of another approaches the position found in some territorial species. However, certain deviations from the definition of a territory are apparent in roan antelope and

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the author therefore wishes to suggest the term "Intolerance Zone" in preference to 'territory' as applied to the roan antelope.

As the 'Intolerance Zone' will be discussed in detail later in this chapter, it is sufficient to define it here as an area actively defended by an adult roan male against intrusion from other adult males, with a radius of approximately 300 to 500 metres around the male and his herd. There are no fixed boundaries, implying that the intolerance zone is defended wherever the herd may move about.

The following discussion will further clarify the position pertaining to roan and also shed light on its ecological importance:

Evidence of an intolerance zone in roan antelope:

By definition, the maintenance of an intolerance zone by a roan male implies that each nursery herd is accompanied by a single mature male only. Many of the characteristics of a true territorial species may therefore be expected to be found in the roan and the following discussion is intended to illustrate the distinction between the two:

(a) Herd composition:

Roan antelope are semi-gregarious animals and characteristically associate in small herds averaging between 6 and 10 individuals. Herd size may vary considerably and herds of up to 20 - or in exceptional cases up to 50 or more - have been recorded. Regardless of its size, the one distinctive

feature/...

feature in the composition of each herd is that it is accompanied by only one fully mature male (cf Blower, 1961). Young males are tolerated in the herds until they are $2\frac{1}{2}$ to 3 years of age, after which they are evicted from the group by the dominant bull and form small bachelor groups.

The fact that a herd consists of only one mature male is not in itself exclusive proof that the species adheres either to a territorial system or has an intolerance zone. This is clearly illustrated in the work done on the social organization of zebras by Klingel (1965, 1968, 1969). In his study of the plains zebra (Equus quagga) in the Ngorongoro Crater, he found that the zebra population consisted of small, stable family units accompanied by a single mature stallion. Though the stallion defended his mares viciously against other stallions he could find no evidence that the stallion defended a territory. A similar social organisation was also found in two species of mountain zebra, E. zebra hartmannae and E.z. zebra (Klingel, 1968).

An important feature of the social structure of the zebra is that it places no restriction on the movements of a family unit from one area to another within their preferred habitat.

The/...

The herd dynamics of roan differ significantly from both that found in zebra, on the one hand, and true territorial species on the other. Each herd of roan is confined to its own particular "activity zone" (see later) while true territories are not formed. It may therefore be concluded that the presence of a single adult male to each nursery herd cannot be regarded as proof of any of the three social organizations mentioned above. It may nevertheless be a good indication of any one of the three.

(b) Demarcation of intolerance zone:

Territorial demarcation by means of various marking devices has received much attention in other species and is certainly one of the activities most intimately associated with the maintenance of a territory. Despite the lack of boundaries, roan also mark their intolerance zones. Marking therefore occurs throughout the activity zone. Both olfactory and visual means are employed for the purpose of marking and are accomplished primarily through the following agents:

(i) Horning;

The vigorous beating of a small tree or shrub with the horns is not restricted to the adult males alone but may also be exercised by females and immatures.

However/...

Fig. 8: A Grewia sp. shrub after being horned by a roan bull. Note the defoliation and broken branches. Nwashitsumbe, 1969.

Fig. 9: Close-up picture of a Lonchocarpus capassa branch, illustrating debarking and other damage caused by tree-horning. Nwashitsumbe, September, 1968.

However, the frequency and intensity of this activity is notably higher in the herd bull and particularly during the oestrus period of a cow. The bull deliberately approaches a shrub and thrusts vigorously with his head and horns among the branches, thereby stripping many of the branches of their leaves; breaking many of the smaller branches and virtually debarking some of the thicker ones. These actions certainly simulate a high level of aggression and frequently the crushed remains of leaves and twiggs remain attached to the base of the horns. As early as 1910 Lyell wrote that "they (roan) are constantly rubbing their horns on trees... and the hollows between the ridges of the horns will always be found full of bark and often chipped in places".

Not all the actions are of the intense nature described above, but may also be accompanied by gentle rubbing of the face and basal area of the horns on shrubs or branches of trees. The preorbital region, especially, is rubbed against the branches, creating the impression that the animal is deliberately attempting to rub some substance onto the plant. A variation

of/...

Fig. 10: A young male horning the soil in the roan enclosure. Nwashitsumbe, November, 1968.

of shrub and tree horning is found in soil- and grass horning. Both these activities are basically the same as tree horning and are only directed at different objects. In soil horning the animals - both males and females - drop onto their knees and plough up the soil with their horns. Rubbing of the face in the soil has also been observed. On occasions animals have been seen with clods of mud, or even grass tussocks, clinging to their horns. Grass-horning has only been observed in immatures and is no different from any of the two activities described above.

The significance of horning in all probability has a two-fold function as a marking device i.e. visual and olfactory.

It is believed that the diverted aggression directed at an inanimate object (shrub, tree, soil) serves as an important device in advertising the bull's presence and further eliminates the chances of direct physical contact between two adjoining males. The redirected aggression in tree-horning is believed to serve as threatening behaviour to intimidate would-be rivals and limit actual fighting to the minimum.

Horning/...

Horning in roan generally occurs at random throughout their range of activity. This together with the fact that horning activity sharply increases during the oestrous period of a cow, may indicate that the dominance display associated with this form of activity is directed at both male rivals and the herd cows.

Trees and shrubs which are partially defoliated and/or debarked during horning sessions may in themselves serve the important function of zone demarcation In the closely related sable antelope horning and soiling has also been observed and Blaine (1922), quoted by Varian (1953), remarked that giant sable antelope bulls (H. n. variani) "have a habit of rubbing their great horns on the bark of saplings and small trees, the branches of which they break off..... The rubbed bark, broken branches, and sapling tops hanging downwards from the stem by a strip of bark, together with the furrows scratched in the soil are certain indications establishing the presence of sable....."

In his study of the gazelles, Walther (1968), found that the horning of grass and shrubs occurred frequently and was a ritualized display. He ascribes the

following/...

following functions to the display:

> the damaged branches, leaves, grasses, etc. may in themselves serve as markers and
>
> that the display also falls within the category of dynamic-optic (dynamisch-optischen) advertising.

With regard to (a) it is also believed by the author that the damage done to objects by individuals displaying in this manner serves as an important marking device in roan antelope.

Leuthold, 1966, related horning in the Uganda kob to the following functions:

> threat behaviour,
>
> an expression of aggression but a reluctance to engage in actual fighting with a contender due to a "subordinate feeling" and
>
> a "vacuum activity, releasing accummulated energy in the absence of an appropriate stimulus".

From the meticulous and careful rubbing of the pre-orbital region and base of the horns on twiggs and branches, it can be deducted that this also serves as a form of scent

marking. However, it is known that the Hippotraginae have poorly developed pre-orbital glands which consist merely of enlarged epidermis cells (Pocock, 1910). There is no fluid secretion which could easily be rubbed off and the only signs of a secretion consists of fine yellow grains spread over the surface of the gland. Seen in the light of the very poorly developed pre-orbital glands, this form of scent-marking in roan must be regarded as doubtful. What other functions the facial rubbing may fulfill, would be most difficult to explain though the possibility exists that it merely represents a phyllogenetic relict, suggesting that pre-orbital glands may have played an important role in the early evolutionary development of the species.

In many species with strongly developed pre-orbital glands (cf. Antilope cervicapra - Hediger (1949) Thomson's gazelle (Gazella thomsoni) - Walther (1964(a), 1968; Estes, 1967) the excretion is placed onto inanimate objects in the territory and serves the function of scent-marking. The habit of these animals to deposit the secretion on the same

objects/...

objects for a prolonged period results in the accumulation of the secretion in the form of spherical 'balls'.

(ii) Static-optic marking:

This form of territorial advertising is well-known for various species of ungulates (cf. Hediger, 1949, Estes, 1968, Jungius, 1969) and entails a territory proprietor making himself visible (or conspicuous) in his territory, and thereby discouraging would-be rivals from entering his domain. The apparent dozing stance of wildebeest bulls may be regarded as static-optic territory marking (Estes, 1968) and even more particularly the habit of tsessebe, and hartebeest (Backhaus, 1959) to stand on a slight elevation, e.g. termite mound, within their territories. Roan bulls frequently lie down though at times males have been encountered standing idly under trees. Though not as conspicuous as in some other species, this may however also be one of the means by which the bull advertises his presence. In the roan antelope enclosure the young and females of the herd showed a great liking for an old sand heap near their drinking place and frequently one or more would stand on the heap either before or after drinking. Contrary to what would have been expected,

Fig. 11. Cross-section of the front foot (left) and hind foot (right) of an adult roan cow, illustrating the well developed interdigital glands. Waterberg, Nylstroom Dist., May, 1970.

the bull showed no interest in the sand heap. Apparently sable antelope may revert to this form of territorial advertising as Roberts (1951) gives an account of a bull he observed standing on a termite mound "arching his neck and displaying his horns".

(iii) The role of Interdigital-glands:

Though the pre-orbital glands are poorly developed in the Hippotraginae, the pedal glands of both the fore- and hind feet are well developed in both sexes. The thick secretion is greyish in colour with a sharp and penetrating smell. The role of this gland for marking purposes and its role in the social organisation of the species in general, is not clear and its importance can only be speculated. During the entire period of observation foot scraping was observed on only three occasions and apart from this no other activity directed at the placement of the secretion onto inanimate objects was observed. It is quite feasible, though, to believe that the scent is continuously being rubbed onto objects in the normal daily routine of the animals, i.e. throughout the 'territory' and home range. Though unintentional but ever present, this may be one of the most

important/...

important means by which the area of any particular male may be marked.

(iv) Defecation:

Roan do not form dungheaps characteristic of many other ungulates viz. tsessebe, and it is not certain what - if any - role defecation may play in marking their activity zones. Estes (1969) found that sable bulls tended to defecate repeatedly in small heaps along roads while patrolling their territories. These 'small' heaps of feaces have subsequently been noted for roan in the Kruger Park and the number and regularity of dispersion of these heaps were quite obvious along roads shortly after heavy rains. Dung piles (not dung heaps as in other species e.g. tsessebe) are dropped throughout their range of activity and therefore appear to function in much the same way as horning and scent marking by means of interdigital glands.

When roan defecate they haunch slightly with their hind legs apart and when urinating the bulls straddle their legs to the rear. Defecation and urination are not necessarily simultaneous and no particular significance could be attached to the postures of the animals while engaged in these activities which could be related to social behaviour.

In certain other species, however, not only the faeces but also the postures adopted while defecating and urinating have been found to have definite advertising value, e.g. defecation and urination in male Grant's gazelle (Walther, 1968). Whatever role these individual dung piles may play, the author has never observed other roan taking any notice of them.

(c) Eviction of young males from nursery herds and the formation of bachelor groups:

The fact that roan herds are accompanied by a single mature male suggests that at some time in the life cycle young males must be driven out from the mixed herds until they are able to establish themselves as herd bulls. Young roan males accompany the nursery herd until the age of approximately $2\frac{1}{2}$ to 3 years when they are evicted from the herd by the herd bull. Adult males accompanying nursery herds are characterised by their strong physical build, i.e. thick-set neck, sharply contrasting black and white facial markings and are estimated to be at least 6 to 7 years of age. Following eviction from the herd the young male therefore enters the inter-phase period which may last for 3, 4 or more years before it can compete for a nursery herd. During this inter-phase the young males withdraw to the perimeters of

occupied areas to form small all-male groups varying in size from 1 to 9 individuals and probably even more. In her study of waterbuck in East Africa, Kiley-Worthington (1965) found that young bulls, estimated at approximately $2\frac{1}{2}$ years of age, resorted together in bachelor groups which frequented the less favourable peripheral areas of the choice waterbuck habitat and had not yet attained territorial status. This corresponds to the position found in the roan.

In the Kruger Park where roan are rare and dispersed over a wide range, male (or bachelor) herds are relatively uncommon and the largest recorded consisted of 6 individuals. In the Quicama National Park in Angola where roan are more numerous, bachelor groups were seen more frequently and also formed slightly larger groups.

It was interesting, however, to note that some of the males in these groups were only about 2 years old, and in some cases even slightly younger. This phenomenon could possibly be explained if it is accepted that young males are more prone to leave their nursery herds where company in the form of young males in bachelor herds is more readily available.

The absolute intolerance toward one another among adult roan bulls is not yet evident among young males reaching sexual maturity. Young

roan bulls probably reach sexual maturity at $2\frac{1}{2}$ to 3 years, i.e. the same age at which they are evicted from the herds. At this age the agonistic behaviour among males only enters its earliest stages of development and requires at least another 3 to 4 years to attain its peak.

In their study of the Ugunda kob (Adenota kob thomasi), Buechner, Morrison and Leuthold (1961) also found that the attainment of sexual maturity is followed by a period in which the young kob has to establish himself in the territorial system.

The bachelor groups to which the males resort during the inter-phase plays an important role in the development of the agonistic drive. As in the case of the leadership of the herd among cows the ability of a bull to establish an intolerance zone and maintain it, is based solely upon the dominance of the bull over other competing males. During the inter-phase the young males indulge in numerous bouts of sparring by which they are able to establish their own group hierarchy. Once the alpha male of such a group has succeeded in detaching himself from the 'juniors' by driving them to some other area he has established his own intolerance zone and hence also acquired full 'adulthood'.

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The eviction of a young male from a herd by the bull is a gradual and prolonged process which may take a number of months to achieve. In the main study herd in the roan antelope camp the entire process dragged on for months before the young bull finally broke away. The manner in which the herd bull eventually achieves a breach between the youngster and the herd is by gradually increasing the individual distance between the young bull and itself, i.e. the distance from the herd bull at which the young male will be tolerated. Before the rejection process actually commences the young male is tolerated up to a distance of about 8 - 10 metres from the herd bull before the dominance - submissive ritual is released. This is the normal dominance-submissive display between any dominant animal and a subordinate where the dominant one (in this case the herd bull) displays its dominant attitude by lifting his head, ears stretched to the sides and tail held slightly away from the body. The submissive animal (young male) lowers his head, twitching his ears and holds his tail tightly between his legs while passing the herd bull from front to rear. The bull normally pays no further attention to the youngster.

Gradually the distance releasing this display increases to about 15 metres. Once it has

reached/...

reached this stage, the ejection process is in full operation. While grazing the herd bull will suddenly look up, advance upon the young male with nose pointing forward, ears to the side. While still 15-20 metres away the young bull lowers his head and reluctantly attempts to evade the old bull by running away. The herd bull will usually pursue the younger one by charging after him and more often than not this develops into a "follow-the-leader" race with the herd bull hot on the heels of the youngster. The young male will never make the slightest attempt to resist the senior bull. During the chase the inferior male constantly attempts to rejoin the herd and seldom runs more than 200-300 metres away from the herd before turning back. The young male then retraces his steps and races back to and through the herd with young calves and cows dispersing in all directions. This pattern of running in circles repeats itself over and over until the young male moves about 200 metres from the herd and the herd bull ceases his persecution of the young bull.

Whenever the young male attempts to rejoin the herd he is again harassed by the herd bull. During this time the younger bull remains strictly along the perimeter of the herd until he finally breaks away from the herd and joins other young males. Similar behaviour was

observed/...

observed between an old and a 2 year old oryx bull in the Münchener Tierpark Hellabrun by Walther (1965). Whenever the young male approached the 2 cows he was harrassed and chased by the herd bull until he retired to the perimeter of the area normally occupied by the oryx in the enclosure. Had the herd been in the "wilds" the only conclusion to be arrived at is that the young bull would have been driven from the herd.

(d) Defence of the intolerance zone:

Following the eviction of sub-adult males from the mixed herds the logical conclusion to be drawn is that adult males will show aggression toward other adult bulls attempting to enter their defended area. The defence of intolerance zones in the case of roan and the fact that these areas do not have fixed boundaries as compared to true territories, limits peripheral conflicts to the minimum. The inhibitions placed upon neighbouring males from entering one another's 'activity zones' is explained elsewhere in this chapter. Nevertheless fighting between adjoining males does occur and the defence of 'boundaries' is probably as strenuous as in those species which are continually engaged in the defence of their territories.

The/...

The following example may be quoted from field observations to illustrate peripheral conflicts in roan: The waterhole at Nwashitsumbe windmill fell within the activity zone of a large bull. In the area adjoining his range were (2) young males in the inter-phase stage which readily joined a nursery herd when it moved out of its normal activity zone to drink at Nwashitsumbe waterhole. This nursery herd occasionally drank at Nwashitsumbe at the height of the dry season. When they approached the waterhole in the presence of the herd bull, he walked a few paces forward - apparently to his 'boundary'- and awaited their arrival. Each animal of the herd, including cows and immatures, "bowed" (head-low submissive posture) before the old bull before they passed to the water. The 2 young bulls also submitted to his dominance (typical dominance - submissive postures described elsewhere), but when the one lifted his head the old bull immediately knocked his horns against those of the younger bull - the latter resumed his submissive posture without any further resistance. On 24.9.1968 the 2 young bulls and a few cows of the visiting herd remained with the Nwashitsumbe bull's herd when they moved away from the waterhole. Later, during the afternoon, one of the young bulls was found back in his old haunts with his mouth agape and obviously exhausted after being chased out of the bull's

activity/...

activity zone. The herd bull had left the younger bull once he had crossed his boundary and was approximately 500 metres from his herd returning to harass the other bull which had also entered his domain. Similarly, there can be little doubt as to the aggressive behaviour of the camp bull in response to outside males. Whenever a bull approaches the camp fence from the outside the camp bull immediately shows interest if he is in the area, and attempts to assert his dominance on the "outsider" by means of the Dominance display. On only 1 occasion (21.1.1970) did conflicts through the fence go beyond displaying when the 2 bulls were involved in an intense fight "through" the fence. Unfortunately the author was unable to observe the actual conflict though the signs left no doubt as to what had taken place. The 2 males had obviously patrolled along the southern fence of the camp and had indulged in at least 2 bouts of lesser intensity before engaging in a high intensity fight. It was quite obvious from the signs, as would also have been expected, that the fighting entailed furious clashing of the horns and subsequent pushing bouts. The severity of the clash could easily be judged by the ploughed-up soil on either side of the fence and also the damage done to the fence, i.e. 6 strands of steel wire - bound together in 2 bundles of 3 strands each - were ripped apart

and/...

and a hole thrashed through the 2 layers of wire netting in the fence.

The occurrence of this fight coincided with a mid-summer drought, accompanied by a severe heat wave which forced roan herds from their summer range back to the artificial watering points around windmills. With the arrival of the "outside" herd along the southern fence of the roan enclosure the 2 bulls found themselves beyond their limits of tolerance and hence the ensuing fight.

Conflicts between the herd bull and the 'lone bull' in the roan enclosure were mostly averted due to the inferiority (subordination) of the lone bull. However, threatening and fighting occurred frequently whenever a female entered an oestrus cycle - thereby enticing the lone bull to within the intolerance zone of the herd bull.

Conflicts between the 2 males were generally initiated by the approach of the lone male to within 200-300 metres of the herd. At this stage the bull immediately adopted the Dominance display attitude and approached the lone bull. If the lone bull showed any signs of retreat the herd bull gave chase and charged after the retreating male in a very determined manner. In the ensuing fight the subordinate male most

frequently/...

frequently sought refuge in the water trough. This is the only watering point in the camp and the behaviour of the lone bull lead to the assumption that this area represents a "neutral zone" for the camp animals. There was no evidence of any territorial boundaries in the enclosure.

An example of an observed fight between the 2 males will best serve to illustrate the nature of the conflicts: At 1700 hrs. on 16.11.1968 the 2 bulls were found at the drinking trough. The lone bull was actually standing in the shallow water with the herd bull on the side. Upon arrival the 2 bulls had already engaged in fighting and for the 40 minutes before dusk the following sequences were observed:
HB (Herd bull) lunges forward and strikes LB (Lone bull) on the horns with his own. LB's head practically pushed under the water.
HB then withdraws and walks away (± 50 metres).
LB remains in the water, tail tightly withdrawn between his legs, head slightly below horisontal, ruminating. HB returns after few minutes, again they clash horns. As HB lunges forward he keeps his horns at a slight angle to those of LB and without fail their horns strike approximately in the centre (on the bulge).
HB withdraws 5 metres and lowers his head as if to graze but does not graze. Lifts his

head/...

head. HB approaches LB. LB drops his head to near waters' edge, tail between legs, ears held back along neck (exaggerated submissive posture). HB does not attack but walks away for 100 metres and appears as if he is going to rejoin his herd. LB leaves water and stands grazing alongside the trough. HB then returns and the 2 again clash horns.

This pattern of events repeated itself from the time the 2 males were first seen at the water (1700 hrs.) until observations were stopped at 1815 hrs. when the bulls were still engaged in their fighting. While fighting the flush distance of the 2 males is considerably reduced and it is possible to approach to within 20 to 30 metres without causing any disturbance.

From observations on the fighting of roan males (and also females - cf. hierarchical system) the following important ritualized displays are evident:

(i) Head-high threatening display:
(Kopf-hoch-Drohen, Walther, 1958). The challenger raises his head, neck slightly arched and the ears outstretched to the sides and 'facing' forwards. The tail is held away from the body. While displaying the threatening posture the senior animal may stand <u>face-to-face</u>

with/...

Fig. 12: The Herd bull displays the head-high threatening posture to the submissive Lone bull in the roan antelope enclosure.
Nwashitsumbe.

Fig. 13: In high intensity fights the two combatants lunge head-first at one another with the horns held at an angle to receive the blow. Nwashitsumbe.

Fig. 14: Actual fighting consists of a vicious pushing duel with the contestants on their knees. Nwashitsumbe.

with his subject or, more impressively, it may stand in front of its rival with its side turned to him (Lateral presentation). The 2 animals may also be in the reverse-parallel position, i.e. standing next to one another but with the head of one and the tail of the other facing one direction. Actual fighting may follow from the face-to-face or lateral presentation attitude but not from the reverse parallel stance. Animals in the reverse parallel position revert to one of the other attitudes before clashing their horns.

If the intimidated animal shows no resistance, it lowers its head and ambles past the dominating animal. As it passes, the intimidator may turn slightly and give a casual sweep with his horns in the direction of the passing animal.

(ii) Fighting:

Fighting amongst individuals, and at various intensity levels, is discussed under the hierarchical system. The manner in which 'fighting' is accomplished may be considered as a pushing duel between 2 contestants. On no occasion could the author find any indication that fighting was aimed at doing bodily harm to an opponent. On the contrary, 'fighting' is obviously more of

...

a psychological than physical nature. In determining the physical superiority of one individual over the other, the 2 animals clash their horns together and, falling onto their knees, engage in pushing one another until one of the two withdraws.

(iii) Head-low threatening display: (Kopf-tief-Drohen, Walther, 1958). An animal which is successfully threatened and intimidated by a more dominant one or is overpowered in a pushing duel, reverts to the head-low threatening posture i.e. lowers its head to near ground level, pulls its ears back along its neck and twitches them (nervously?) while withdrawing its tail tightly between its hind legs or swishing it from side to side. This posture represents a lower intensity of threat behaviour than the head-high posture and the animal displaying it normally evades the aggressive onslaughts of the more dominant animal.

True submissive behaviour was observed solely in the case of the lone bull during intensive duels with the herd bull in the roan enclosure. The inferior bull dropped his head to ground level and stood motionless with his ears drawn back tightly along his

neck, horns also held back along his neck and tail between his legs. This posture represents true 'Demutstellung' and one of its main characteristics is the complete reluctance of the animal to move. The acute form in which the submissive animal lies down, was not observed in roan.

(e) Herding:

A prominant feature of most territorial species are the attempts made by the territory proprietors to retain the nursery herds within their territorial boundaries. The 'herding' of females is conspicuous in species such as Thomson's and Grant's gazelles (Walther, 1968), waterbuck (Kiley-Worthington, 1965) and wildebeest (Estes, 1968). In contrast to these species, the males of which defend fixed territories, herding activity in roan is infrequent and apparently unimportant. This is believed to be due to the flexible nature of the roan bull's intolerance zone, which is maintained as the bull moves about with his herd and is not confined to a particular area.

Roan herds generally create the impression of being rather "loose", with the individuals, especially the cows, spaced widely around the perimeter of the herd. When herding, the bull does "the rounds" by walking, slowly but deliberately, up to a cow and when being approached the cow may run off to the main group without any resistance,

or/...

or the bull and cow may go through the normal dominance-submissive ritual before the cow runs off to the rest. Immatures and young calves are herded in the same way as the cows.

The 5 points listed above are all intimately associated with species adhering to the territorial system and clearly illustrate the similarity between the intolerance zone, as suggested for the roan antelope, and the true territory. The underlying differences, however, merit a clear distinction between the two systems. The functioning of the intolerance zone, both as a social system and an ecological factor, may be sought in the following considerations:

The spacial distribution of roan antelope herds:

The spacial distribution of roan herds is of such a characteristic nature that anyone familiar with the species can verify that it is possible to allocate a certain area to each herd. Superficially this is correct and the mosaic pattern obtained by their distribution is primarily due to the stability of herds and their habitat preferences. The habit of a roan herd to remain in a particular area for a prolonged period of time is a phenomenon that has been observed throughout their range of distribution. In East Africa the herd around Banagi hill in the Serengeti presents a classical case and has been observed in its usual haunts for the last 30 years or more (Moore 1938; Turner, pers comm; Walther, 1968). In the Kruger National Park individual herds have also become known to the field staff due to their preference for a particular locality e.g. a herd in the area of the Malopanyana windmill has been known in this area for at least the last 6 to 8 years or more. In their study of

the habits and ecology of roan and sable antelopes Wilson and Child (1964) found that a particular herd (it could easily be recognised due to a tailless individual) inhabited an area of approximately 30 sq. miles (77 sq. kilometer) for the total period of 10 months that it was kept under observation.

From the study by Wilson, et. al. (1964) in Zambia and observations of free-ranging herds in the Kruger Park, it appears that the average area covered by the activity of a herd in the course of a year is of the order of 25-40 sq. miles (64-104 sq. kilometers). Obviously this area is much too large to be effectively protected by one bull from intrusion by neighbouring rivals and the whole area can certainly not qualify as a single "territorium" at any one time. In a discussion of the factors affecting spacial distribution in roan antelope, and especially in the light of any ecological consequences this system may have for the species, it is also important to consider the annual movements and home range as background to facilitate a better understanding of both the activity- and intolerance zones. Taking into consideration the entire 80 odd sq. kilometers utilized at some stage or another in the course of a year (a year in this sense rather implying the different seasons of the year and their effect on the behaviour of the animals than mere calender months) the various herds' spacial activities may conveniently be divided into: (a) Activity zone; (b) Home range and (c) Intolerance zone.

(a) Activity zone:

The heading given here is a translation, intended to convey the essential meaning of Walther's (1967)

German/...

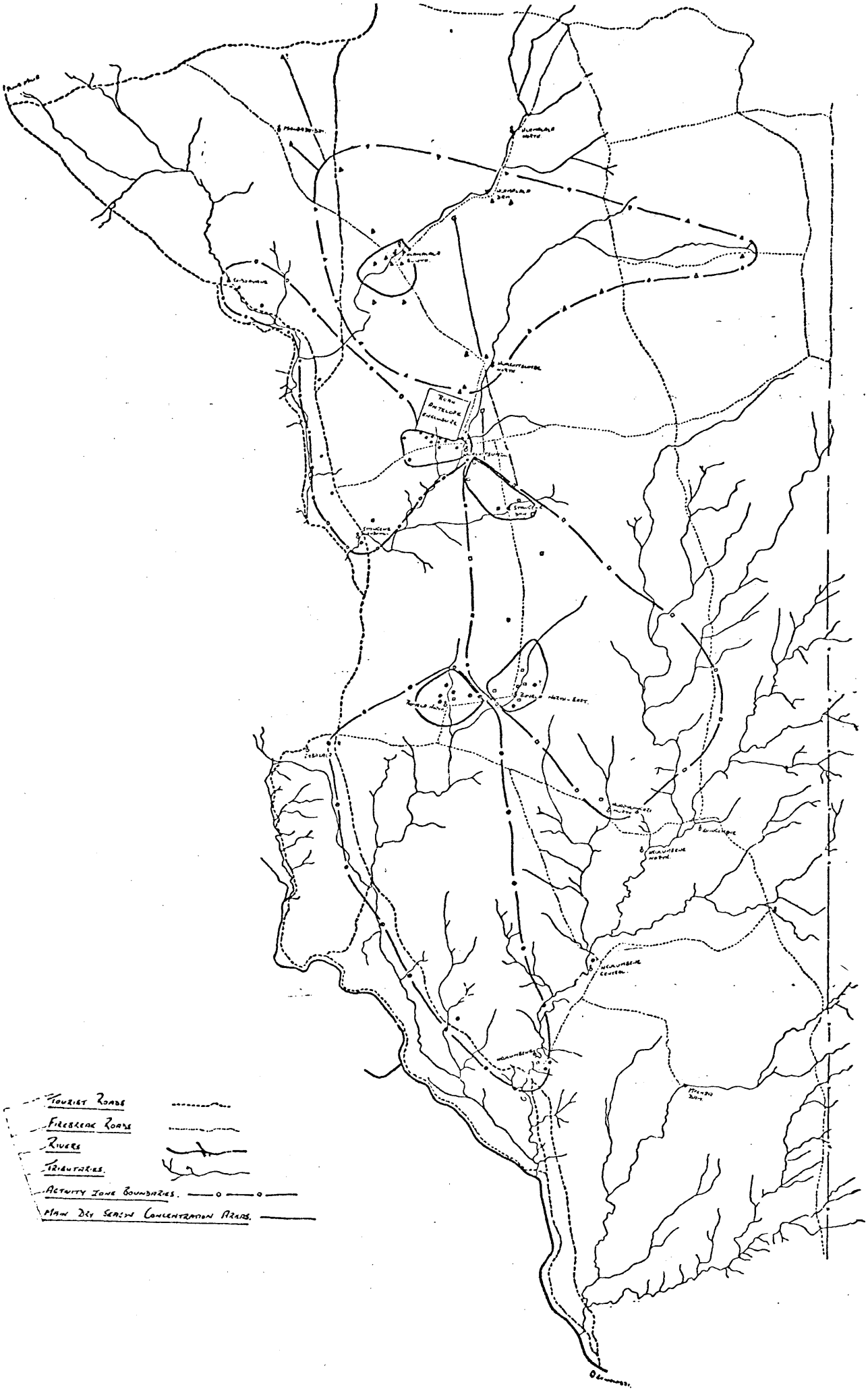

Fig. 15: Map of the Hlamalala- Nwashitsumbe- Boyela area in the northern district of the Kruger Park, illustrating the activity zones of four roan antelope herds during the period December, 1967, to April, 1970.

German title of "Aktionsraum". This category is intended to include all those areas which are utilized or occupied by an animal at some stage of its annual or life cycle and is best defined by Walther (1967) as: "das gesamte Gebiet, das ein Individuum oder eine ständige organisierte Gruppe (Rudel, Herde) während der Zeit ihres Lebens bzw. Bestehens überhaupt betritt. Hierin sind sowohl verschiedene Saison - Territorien und Aufenhalts-gebiete wie auch die Wanderwege zwishen diesen eingeschlossen".

Climatologically the Kruger Park has 2 distinct seasons viz. a hot summer season corresponding with the wet or rainy period which extends from October to March or April, and a dry winter season from May to September. The winter season, and especially the latter half from the end of June to September, imposes the greatest stress upon the herbivorous fauna of the Park as most of the natural waterholes dry up during this period and the bulk of the animals are compelled to resort to artificial watering points to quench their thirst.

As with most other species, roan too have developed a clearly rhythmic pattern of activity in accordance with the conditions prevailing during each season. With the first substantial summer rains the animals disperse from the perennial waterholes and seek more favourable grazing and living conditions

(i.e./...

(i.e. less competition and predator pressure) further afield. As the veld pans dry up progressively toward the dry season the animals are once again compelled to return to the various permanent pools. The degree to which the animals disperse during the favourable summer months varies considerably from species to species e.g. in the southern half of the Kruger Park the first rains stimulate the great concentration of blue wildebeest and zebra to migrate to their summer grazing grounds more than 100 kilometers from their winter haunts; a large percentage of the eland population of the Park can be regarded merely as temporary residents due to the fact that they disperse to areas beyond the limits of the Park during the summer months. The manner and degree to which the various species respond to the different seasons of the year not only determines the activity zones of the species but clearly represents one of the important ecological facets influencing the management of wild animal communities. Not all species, however, move such considerable distances away from their winter ranges and notably the territorial tsessebe and impala remain within a very limited area throughout the year. Roan antelope fall between these extremes as has been indicated by Wilson et. al. (1964) and by observations made during the course of the present study.

Though/...

Though the activity zone of roan antelope is by no means synonymous to a territory it is nevertheless quite significant that only rarely have 2 adjoining herds been found to overlap into one another's activity zone and due to this phenomenon the characteristic mosaic pattern in the distribution of roan herds is found. It has already been indicated that this "aktionsraum" is not patrolled and protected daily against intrusion from adjoining territorial males and does not therefore comply, in the strictest sense, with the definition of a territory. The explanation for the sole occupation of the activity zone by a single herd may be due to the following reasons: the activity zone consists of a definite summer and winter range; competition would therefore be for either one of the two but not for both areas at the same time. As the herd moves through its range the adults, but in particular the bull, mark the area by thrashing their heads in shrubs, defecation, interdigital gland secretions, etc. and thereby indicate their presence in a particular area. It is believed that in this way each herd's activity zone is scent- and visually marked and that this has an inhibitory influence on intruding herds. In this respect the function of the interdigital glands may play an important role.

Whereas shrub-beating with the horns, defecation and other marking methods are largely, but not

exclusively/...

exclusively, confined to the activities of the herd bull, both sexes, adults and immature animals have functional interdigital glands which must constantly be leaving a scent where the animals are active and this probably plays an all-important role in sealing off activity zones to particular herds.

In the discussion of the dominance hierarchy in roan herds it was pointed out that though the herds quite frequently break up into smaller units (see reasons) the roan herd is in actual fact a closed social unit which tends to discourage assimilation of strange members of the species. This must then be regarded as another factor which not only contributes toward herd stability but also in keeping herds separated from one another.

This discussion, and especially the conclusion that the activity zone in roan antelope is the almost exclusive 'property' of a single herd, does not imply that activity zone and territory are synonymous in either roan or any other species. In his definition, Walther (1967) clearly states that the activity zone includes both the territory and home range of a species.

The defence of an intolerance zone, which is maintained throughout the activity zone, is believed to be one of the major factors contributing toward the exclusiveness of the activity zone. The

author suggests that due to a herd bulls' intolerance toward other adult males, they (the adult males) not only avoid direct confrontation with the herd bull but are also inhibited from entering an area bearing his 'mark'.

Females, on the other hand, are barred from entering the activity zones of strange herds due to the social organization of the females which discourages mixing of the herds.

(b) Home range:

To avoid any confusion in the interpretation of the terms 'home-range' and 'intolerance zone' and the context in which they are used here it is only appropriate to give a short definition of what is considered to be a 'home-range'. Basically the term refers to what Dice (1952) has defined as "the area over which an individual animal habitually travels while engaged in his usual daily activities". Walther's (1967) definition is somewhat more circumscriptive: "Ein Gebiet, in dem sich ein Tier oder häufiger eine Gruppe von Tieren über einen längeren Zeitraum hinweg umherstreifend aufhält. Die Streifzüge schließen sich (wahrscheinlich) in Tagesrhythmus zu einem „Kreis". Eine gewisse Gliederung des Gebiete in Weideplätze, Tränken, Salzlecken, Ruhestätlen, Wechsel, usw. ist gegeben. Außerdem kann das Aufenhaltsgebiet (Home range) markiert werden. Verteidigt wird es jedoch ein allgemeinen nicht".

Roan are water dependent animals and under normal conditions drink at least once a day during the dry winter months. With the rather restricted water resources in the Park during this time of the year it is not surprising that the water holes form the focal point of their daily activities.

Normally, roan drink between 1000 and 1100 hours when, under Lowveld conditions, it is already starting to get fairly hot - even during winter. After drinking the herd slowly moves away from the water, grazing intermittently until they are roughly 400-800 metres from the water where they lie up in the shade of a tree or shrub or in open grassland during the hottest hours of the day. When the herd again becomes active and resumes grazing during the late afternoon it does not return to the water but gradually meanders further away from it while grazing. During this period before sunset the herd may move up to 2 or more kilometers away from the waterhole. After sunset there is not much activity and animals which had been observed in an area until dusk could be located in the same locality at sunrise the next morning. During the early morning active grazing once more commences and the herd leisurely works its way back to the same waterhole. This pattern may be followed for a shorter or longer period after which, for no apparent reason, the herd may move off to another waterhole only to

return/...

return to the original one after a few days. However, there is always one particularly favoured watering point where each herd usually drinks. The reason why the herd moves away from the water-hole to graze during the afternoon and morning may be of a two-fold nature i.e. for the benefit of obtaining more favourable grazing conditions and possibly also to escape the intense competition of the other herbivores concentrated around the waterholes. From time to time the herd may also change its direction of approach and departure from the waterhole.

The total area covered by the home range of a herd would, on the average, comprise approximately 2 to 4 square kilometers. This figure is attained if it is assumed that a herd may move 2-4 kilometers from its watering point and spread out an average of 500 metres along the line of its daily course.

The fact that roan adhere to one home-range for a period and then change to another naturally facilitates in leaving the "mark" of the herd evenly distributed over the activity zone of the herd to the exclusion of other herds.

(c) Intolerance zone:

A definition for the intolerance zone has already been presented at the beginning of this chapter. Essentially the intolerance zone represents that area in which a particular adult roan male will

not/...

not tolerate the presence of any other adult males. The resemblance between the two systems is quite obvious and only after careful comparison was it decided to differentiate between the two.
By definition a territory is:
"ein relativ kleines Gebiet, das nur von einem Tier oder einer ganz kleinen Gruppe unabhängig vor Fortpflanzungsperioden und dergleicen über sehr lange Zeit - eventuell zein Lebens - bewohnt, gegliedert, markiert und verteidigt wird" (Walther, 1967).

In the true sense of the word a territory is therefore a relatively small area with fixed boundaries which are within easy reach if they are endangered by the intrusion of an adjoining territorial male. For many ungulate species territories with rigid boundaries have already been described and therefore comply with the requisites of the definition e.g. Uganda Kob (Buechner, 1961, 1963; Leuthold, 1966), Grant's and Thomson's gazelles (Walther, 1964, 1965, 1968; Estes, 1967), waterbuck (Kiley-Worthington, 1965) and wildebeest (Estes, 1968), etc.

In roan antelope, however, no comprehensive proof could be found that territories are in fact delimited by definite and rigid boundaries. Rather, the herd bull actively defends an area around the herd within a radius of approximately 300-500 metres. It would therefore appear that the territory defended by a roan antelope bull is

closest/...

closest to the pseudoterritorial (Watson, quoted by Estes, 1968) or movable (Talbot and Talbot, 1963) type described for migrating wildebeest in which territorial activity was quite evident but could not be related to a fixed area. Estes (1968) in his detailed study of territoriality in wildebeest, confirmed the Talbots (1963) observation of territorial activity in migrating herds of wildebeest but found that actual territories, i.e. fixed areas, were in fact formed but were only of a very temporary nature - most bulls leaving their territories within 2 to 20 hours after having established them. It is therefore clear that this form of territorial activity also differs significantly from that found in the roan antelope.

The existence of an intolerance zone - and the consequent absence of a territory - was clearly illustrated in the roan enclosure during the course of 1970. The lone bull that had been totally subordinate to the herd bull, gradually started penetrating the herd bulls' intolerance zone. Initially the lone bull could not face up to the vicious attacks of the herd bull and retreated to 300 or 400 metres from the herd, where he was free of persecution. However, the lone bull persistently tested the superiority of the older male and eventually, after 2 or 3 months of continual skirmishes, succeeded

in/...

in ousting the old bull from the herd. During the entire process there was not the least indication of territorial defence in either of the 2 males. Subsequent to the eviction of the old bull, the herd and its new bull retained its customary activity zone in the enclosure while the evicted male withdrew to a few hundred metres of the herd. As before, neither of the 2 adult bulls has shown any inclination to defend fixed boundaries.

Once the intolerance towards other males is fully developed in a bull and he has successfully established himself with a nursery herd in an activity zone he maintains his intolerance zone throughout the year. This is similar to the position found in permanent or "stationäres" territories which are continually protected without any seasonal fluctuations.

Size of the intolerance zone:

That area which is actively protected and maintained free of intrusion by rival males is considered to be the actual intolerance zone. If there is an intruder in the vicinity of a herd the bull will leave the herd and face the rival though he may still be some 300 to 500 metres away from the herd. If the intruder happens to approach closer than this distance the herd bull immediately shows aggression toward his rival. This entails the usual routine of challenge (threatening) chasing and/or pushing horns. In the chasing that follows the herd bull pursues

his/...

his adversary until the latter is again about 500 metres from the herd before the dominant bull turns back to his herd. In the course of the eviction of young bulls from the nursery herds it was also pointed out that the individual distance between the herd bull and the rejected youngster becomes progressively larger and initially the younger male is harassed until he moves away 150-300 metres from the herd where the herd bull leaves him in peace. Once evicted from the herd he may also elicit aggression from the herd bull at a distance of 300 metres.

If then the area protected by the herd bull comprises a zone with a radius of 300 metres around his herd the actual size of his intolerance zone will be roughly .56 sq. kilometers. This, of course, is only a rough estimate as the absence of definite, fixed boundaries makes a more accurate calculation impossible.

Blower (1961) mentions that "the territory of any given (roan) herd is usually fairly well defined, and is restricted to an area of a few square miles". There may possibly be some confusion as to the interpretation of the term 'territory' in this case and in all probability Blower is here referring to what has been termed the activity zone in the present report. Nevertheless, this once again emphasises the remarkable consistency with which one herd occupies a particular area.

Duration of intolerance towards other adult males:

Direct evidence on the length of time that mature bulls retain their intolerance toward one another could not be obtained. However, the absence of old bulls from the bachelor herds may be regarded as an indication that once a

bull has become intolerant toward other males he retains the intolerance for the rest of his life. This does not imply that the bull retains the same activity zone - or even a nursery herd - throughout his adult life. In the Quicama National Park of Angola, with a particularly high roan antelope population, it was observed that very old bulls, obviously long past their prime, tended to withdraw to thickly wooded areas which were very sparsely populated by roan and represented all but true roan habitat. The obvious conclusion to be drawn from this phenomenon is that as the old bulls are replaced by younger, stronger males in the choice activity zones the older animals seek refuge in the less favourable areas on the perimeter of the roan habitat. The fact that these old bulls remain single in their old age is a further indication that though they are no longer capable of competing for favourable activity zones and nursery herds, they still do not tolerate other males and are disinclined to form groups with other old males.

Activity zones (intolerance zones and home ranges) in relation to habitat and its possible ecological significance on the roan population of the Kruger Park:

The successful establishment of an activity zone in an area depends entirely upon the nature of the habitat and although the habitat preferences of roan do not, strictly speaking, fall within the limits of a behavioural study, a brief discussion of their habitat requirements will suffice to illustrate the importance of the interrelationships between activity zones and habitat availability and its possible ecological influence on the species. (A detailed description of habitat requirements for roan will be the subject of a

later/...

later paper).

Roan antelope have been observed in 3 different vegetation types, viz.

(a) in the Quicama National Park, Angola:

This area represents one of the peaks in the density of the species throughout its range of distribution. The particular vegetation type especially favoured by roan is an open grassland savanna, dominated by Eragrostis superba, with sparsely distributed clumps of trees and shrubs. The ecotone between the grassland and the adjoining woodland is an open tree savanna with tall grass. In the open grasslands there are numerous grass-covered depressions which serve as catchment pools for run-off rain water and provide the game animals with drinking water and green grass shoots during the dry months.

(b) Bicuar National Park, Angola:

This Park is situated in the southern end of Angola and provides a totally different habitat to that of Quicama i.e. the main vegetation type is light to heavy woodland and thickets which are drained by broad, shallow drainage lines, variously referred to as "dambos" in Rhodesia and Zambia and "mulolas" in Angola. These dambos may be up to 400 to 800 metres wide and are grass covered and thereby represent an ideal grassland savanna, fringed on either side by open tree savanna which gradually merges into thick

woodland/...

woodland. It is these dambos which are frequented by roan - the adjoining woodland providing important shelter from the sun, carnivora, etc.

(c) Kruger National Park, South Africa:

The area which supports by far the greatest proportion of the roan population is collectively referred to as mopane - (Colophospermum mopane)-veld. The area is characterised by the shrub form of the mopane tree which occurs in stands of various density throughout the range. Interspersed among the shrubs is a good coverage of grasses. Somewhat in the fashion of the dambos described above the mopane veld is also drained by large, shallow, grass-covered drainage lines. By far the greater majority of roan herds known to have established activity zones in the Kruger Park are intimately associated with these open grass "plains".

From the very brief notes above it clearly emerges that optimum roan habitat has to comply with the following requirements:

(i) open grass plains,

(ii) easily accessible cover in the form of trees or shrubs and

(iii) open surface water.

The delicate balance between habitat selection and the social system of exclusive "activity zones" per herd probably comprises one of the most intricate natural

regulating/...

regulating systems operating on animal populations. The available roan habitat in the Kruger Park lies along the rather restricted open drainage lines in the mopane veld with a further restriction caused by the lack of sufficient surface water during the dry winter months. Roan antelope have been strictly protected in the northern mopane veld of the Kruger Park for at least the last half century since the proclamation of the area in the original Shingwedzi Reserve, which was later incorporated in the present Kruger National Park. Though meagre, the earliest reports indicate a low population density of roan in the area. As time progressed more accurate surveys confirmed the first reports of low numbers which have, with slight fluctuations, remained at a consistently low level through the years. The proclamation of the Shingwedzi Reserve followed a period of intensive hunting and most species, including roan antelope - suffered severely. In 1911 the Warden noted in his annual report: "being a buck (roan) partial to rather open bush country it is one of the first to be exterminated by hunters"[1]. To illustrate the history of the roan population in the erstwhile Shingwedzi Reserve and later Kruger Park the following extracts from the Wardens reports are of interest: (before 1926 the present Kruger National Park consisted of the Sabie Reserve - southern area - and the Shingwedzi Reserve - northern half).

1903: roan considered to be exterminated in both reserves though there were still "a good many" in the adjoining Portugese Territory.

1905/...

1905: animals (generally) increasing.

1911: "this formerly rare species is now increasing well and numerous small troops are to be seen....."

1912: "increasing largely in the parts of the Reserve favoured by them"

Estimates: Sabie Reserve: 300

Shingwedzi Reserve: 150.

(For the present consideration, only the animals of the Shingwedzi Reserve are of importance as the later decline in the Sabie Reserve population was due primarily as a result of changes in the boundaries of the Reserve in 1923).

1918: Estimate of the Game Reserves Commission: Shingwedzi Reserve: 500.

1925: "exists in considerable numbers north of the Olifants to the Limpopo river".

The warden further reports that "I have reason to believe that my calculations (1912) were then considerably under the mark, and since that time the total has increased at least fourfold.....".

1929: "Roan have always been scarce....."

A slight decrease in numbers was observed during a severe three-year drought prior to 1929.

1944: "the position of roan antelope north of the Olifants river continues to be favourable.....".

1946: "numerous in the northern sections".

1948/...

1948: "the Roan position seems to have deteriorated.....".

1949: Quite significant in the 1949 report is the following remark: "I do not think these animals are nearly numerous enough considering the favourable grazing and other conditions in the Park" and further: "in the Northern areas they seem to be just holding their own".

1954: Biologist's estimate of roan numbers in the Park: Northern district: 440 (Total for K.N.P. 477).

1955: Population in Northern district estimated at 400 to 500.

During 1959 and 1960 two anthrax epizootics raged through the roan habitat in the northern area of the Park and a total of 47 roan carcases could be accounted for (Pienaar, 1959, 1960) with an unknown number never found. The decimation caused by the anthrax outbreak, together with one of the most severe droughts ever suffered in the area, caused a decline in the roan population and in 1963 the total number in the Northern district was estimated at 200-220 (Pienaar, 1963). The latest estimate (1969) is that there are in the region of 250-300 roan in the Northern district of the Kruger Park.

The short survey of the history of the roan antelope given above is sufficient to indicate at least two important features of the population: viz.

(i) despite the critically small population at the beginning of the century their numbers rapidly

increased/...

increased until they reached their asymptote at approximately 400 animals between 1912 and 1918. Influx from the adjoining Portugese Territory may also have contributed to this total;

(ii) since reaching the 400-500 level the population has remained remarkably stable for at least the last half century. The many seemingly contradictory remarks in the Annual Reports (increasing, decreasing, static, etc.) appear to accentuate, and confirm, the normal fluctuations in numbers of a population that has reached its maximum. The only serious decline in the population since 1912 (i.e. a period of 57 years!) was caused by the anthrax epidemics mentioned above. The apparent inability of the population to regain its prior 1959 level may confidently be ascribed to the severe 10-year drought which commenced in 1960 and was partially relieved only at the end of 1968. The relative stability of roan populations has also been observed in other areas of its distribution range and Guggisberg (1966) writes that "in many areas it occurs in small, widely separated herds, which even under strict protection, do not show much increase in course of the years".

A few facts on the population dynamics of the species will further serve to shed some light on the conclusions to be drawn from the preceding discussion. At 3 years of age a roan cow may drop her first calf, 2 to

3 weeks after parturition she enters her first postpartum oestrus cycle and after a gestation period of 275 days she may have another calf at heel. Essentially, this means that every 10-10½ months a roan cow can give birth to a calf, and if it is accepted that the reproductively active life of a cow is of the order of 10 to 12 years, it becomes apparent that the reproductive potential of the roan antelope is quite considerable, measured by any standards for animals of similar size! In a period of 2 years 7 adult roan cows gave birth to 15 calves in the experimental camp at Nwashitsumbe! Needless to say that if the full reproductive potential of roan had to be realised, the Kruger Park would certainly not still be concerned about their low numbers.

The phenomena pointed out above, i.e. an animal species with a high reproductive potential yet with an apparent maximum population density at a comparatively low level, indicate an intricate, natural regulating mechanism operating on roan antelope. This mechanism, it is believed, operates along the following lines:

(a) the major features determining suitable roan habitat have already been outlined and using these prerequisites as a standard it is found that the Kruger Park in fact contains only very restricted areas suitable for occupation by roan. In this sense the Kruger Park must be considered as marginal country for this species and this is borne out by reliable authorities (see Wardens Reports) who have indicated that the former stronghold of this species in the Lowveld was along the foothills

of/...

of the Drakensberg mountain range. (The old Sabie Game Reserve, the southern half of the present K.N.P., was estimated to have twice as many roan as the Shingwedzi Reserve in 1912. With the formation of the Kruger National Park in 1926, a large portion of the Drakensberg foothills was reclaimed as European farming and Bantu trustland with the exclusion of the most favourable roan habitat. Today the once prospering roan population of that area is represented by a small group of 25-35 animals, only just holding their own!);

(b) the social organisation of roan antelope by which each herd inhabits a certain area (activity zone). When one considers that an activity zone may be as large as 64-104 sq. kilometers it becomes clear that there must be some means by which the animals must advertise their presence in an area to strangers from other areas. This is brought about by two means which have already been dealt with i.e.

(i) various marking devices (see text) are utilized to advertise occupied zones;

(ii) strangers are inhibited from entering the area by the fact that the females unite in a fairly exclusive group (based on social dominance) and males are discouraged from entering due to the intolerance nature of the proprietor male.

In/...

> In discussing the various functions of territoriality Etkin (1964)makes the following interesting remarks which are equally applicable in the case of the roan antelope: "....territoriality still seems to play a role in regulating animal economics in another way, namely, in acting as a population - regulating mechanism. Since territories are not indefinitely compressible it is clear that, as the population goes up, the range of the species is extended by the new individuals claiming territories peripheral to the group. In general, this entails less favourable areas. Thus the population in a given area would tend to be stabilized around the number of families that can be supported by the resources of the area for that species. Defended territoriality protects a species from such violent population fluctuations and illustrates the importance of the type of territorial behaviour for an animal's general ecology".

Though not territorial in the true sense of the word, the non overlapping activity zones of roan herds fulfill the same function in this species as defended territories in other species.

Davis (1952) in a review of the effects of social behaviour on reproduction in birds cites a number of examples in which territoriality apparently plays an important role in restricting the number of birds of a particular species which may inhabit a certain area, e.g. on an island in

Chesapeake/...

Chesapeake Bay only four pairs of Osprey, Pandion haliaetus, were successful in establishing nesting sites despite attempts by other pairs to nest on the island and also the apparent abundance of suitable nesting sites. According to Davis (1952) Moreau and Moreau (1938) found that territoriality placed a similar limitation on the population of the weaver finch, Euplectes hordacea.

It is proposed, therefore, that the "carrying capacity" of each habitat-type for roan antelope is determined primarily by (i) vegetation and (ii) social spacing and that once the maximum density has been reached the surplus animals are compelled to seek new activity zones elsewhere while basically the population level in the favoured habitat remains at a relatively constant level (cf. Errington, 1956). This point of view allows for an explanation of the thin scattering of roan herds along the western half of the K.N.P. which appear to be far less stabilized - both numerically and locality wise - than their counterparts in the preferred habitat. From this argument it may be concluded that the best way to ensure population growth would be the artificial manipulation of the habitat in accordance with the social and ecological requirements of the species.

CHAPTER IV.

M A T I N G B E H A V I O U R.

Roan antelope in a herd are seperated from one another by an "individual distance" of approximately 5 to 10 metres and therefore form a rather loose herd structure. Violations of the "individual distance" are normally followed by intimidations and/or fighting. In the mating process the distances tolerated between two individuals is reduced to zero and it is therefore of the utmost importance that the species find a way in which to neutralize agonistic tendencies aroused by an ignorance of the individual distance between the two animals. This has been accomplished by an elaborate and highly ritualized sequence of displays which effectively "bridge the gap" between the two and culminate in mating. The first impression gained from the observation of mating in roan is that each sequence follows upon the preceding one in fixed order. However, it soon becomes apparent that the various sequences do not necessarily follow one another in a rigid fashion but that there may be numerous minor variations of the same 'theme'. Despite these variations, the different steps followed in the courtship and mating behaviour are quite predictable and give rise to a very distinct pattern. It is also believed that the various behavioural patterns correspond to the basic steps in the oestrus cycle of the cow, which ensures a delicate synchronisation between coitus and ovulation and which in turn provides for the maximum possible chance of fertilization of the ovum.

In general terms, mating behaviour is initiated when the bull approaches a female in the dominance attitude

and/...

and attempts to nose the base of her tail. Touching the base of the tail inhibits the cow from moving away and she comes to a standstill. The bull will again smell the base of her tail or her vulva after which the cow reacts by lifting her tail and urinating. As she urinates the bull inserts his nose into the stream of urine for a few seconds, lifts his head and performs "flehmen" i.e. an olfactory analysis of the oestral status of the cow. Depending upon the result of the 'test', the bull may take one of two courses - he may either immediately commence grazing and take no further notice of the cow if she is not in oestrus or still in a very early stage of her cycle, or he may further pursue the cow and proceed to further stages in the mating ritual.

The initial stages in the mating behaviour, i.e. up to 'flehmen', are exclusively aimed at the determination of the oestral status of the cow. Should the cow be in oestrus the bull proceeds in attempting to kick up with his foreleg between the hind legs of the cow. This process has been termed "Laufschlag" by Walther (1958). If the cow is not receptive, she will continually evade the bull's attentions by turning around him in a tight circle, thereby rendering it impossible for the male to get in behind the cow. Beating with the foreleg may then be performed from the side under the cow's belly, or on the sides of her hind legs. Once the cow is receptive she will allow the bull to move in behind her, kick up between her hindlegs and, ultimately, also to mate with her. Post-coital association between the two animals consists merely of a smell of the cow's vulva by the bull after which both animals resume grazing. Copulation may

take/...

take place several times during a single oestrus cycle and the only pre-copulatory action that is performed without exception before each mating is "laufschlag".

From the very brief outline given above it is sufficiently evident that the mating ceremony consists of a number of definite phases, each with its own particular significance and contribution toward the successful mating of the two animals - and therefore also the propagation of the species. These phases, or stages, may conveniently be isolated and considered as follows:

The sequence in which each step is discussed, roughly follows the order as encountered in the courtship ceremony.

(a) Relation of bull and cow to one another in terms of space:

In the absence of an oestral female in the herd the bull occupies no definite position with regard to any of the members of the herd. The first obvious sign that a cow is in an oestrus cycle is the close attachment between the bull and the cow. This attachment develops once the bull has succeeded in establishing the oestral status of the cow and is the sole doing of the bull as the cow appears to have little interest in the bull. The 'attachment' therefore is nothing more than the sexual interest of the male in the female and which is not reciprocated by the cow. The "closeness" of the two animals to one another is brought about by the bull who tends to follow the cow during periods of

activity/...

activity or lies down to rest close to her during rest periods.

During the early stages of the oestrus cycle (pro-oestrus), the attendance of the cow by her suitor is not as accentuated as later in the cycle and it may frequently happen that the bull will move a long distance away from the cow; it has also been noted that a cow may break away from the herd, and the bull, during this phase of the oestrus cycle. However, whenever the bull comes into the company of the cow again he will immediately run (or walk at a fast pace) to where she is. During early oestrus the bull may also spend much time fighting off would-be suitors attracted from adjoining areas, but once he has asserted his dominance over them he immediately returns to the cow.

At this stage courtship behaviour is still restricted to occasional smelling of the vulva and 'testing' of the cows urine, after which the two animals part again. "Laufschlag" may be performed a number of times though courtship is dominated by "flehmen".

As oestrus proceeds the bull spends increasingly more time in the company of the female and seldom wanders more than 10 to 20 metres from the cow. When retiring to rest the bull lies down about 10-15 metres from the cow and once activity is again resumed the bull immediately approaches

and/...

and courts the cow. During this period courting has usually advanced to the stage where "flehmen" is of little importance and is more often than not omitted from the courtship activities - the emphasis being on "laufschlag" and copulation.

(b) Dominance:

In the discussion of the hierarchical system and its functioning in roan antelope, the all-important role of dominance in determining the social relationship between the different members of a group, was clearly illustrated. In mating behaviour the dominance of the bull over the cow is the overruling factor without which the bull would be incapable of courting and mating the cow successfully. This ensures that only the dominant herd bulls participate in the propagation of the species and clearly illustrates the integrated role that dominance plays in regulating social relationships in roan antelope.

When a roan bull approaches a cow which is in oestrus he invariably adopts an intimidating attitude and forces the cow into submission. The Dominance display performed by the bull is identical to that normally adopted by the bull or high ranking cows to confirm their dominance over subordinates i.e. head held high with the nose pointing forward; the ears cocked and pointing in the direction of the intimidated animal and the tail held a few inches away from the body. An

intimidated/...

intimidated female reacts by lowering her head, ears pointing backwards or twitching back and forth and her tail tightly drawn in between her legs. Once exhibiting submission, as described above, the subordinate animal rarely attempts to run away but either stands still awaiting the approaching bull, or slowly ambles on toward the bull itself. A dominant bull may at times release this reaction in a cow from a distance of up to 20 or 30 metres. This plays an extremely important role in the courtship phase as the normal reaction of the cow would be to evade the attentions of the bull and run away. If this was the case, the bull would not be able to approach the cow and sample the urine to verify whether she was actually in oestrus or not.

The function of the special "reserved" position occupied by the herd bull in the herd i.e. his undisputed dominance over all the other herd members, is clearly centred around reproduction and therefore differs markedly from the functions of the leader-cow who is socially orientated. Dominance is the vital factor required by a bull for the establishment and maintenance of an intolerance zone around himself and his herd. It has also now become apparent that dominance is the basic requirement if a bull is to participate in mating.

Observing courtship and mating behaviour in the

related oryx antelope Walther (1961) found that courting was initiated by "more or less playful fighting" between the bull and cow and by means of which the male asserted his dominance over the female. He also considers the dominance of the male over the female an important prerequisite for successful mating in this species. The manner in which the dominance of the male over the cow is attained, differs markedly in the two species as the Dominance display of the roan bull is quite sufficient to subordinate the cow and hence the absence of fighting in the courtship (or pre-courtship) ritual. The fighting - at a low intensity level - of the oryx may, of course, have been due to the fact that these animals were observed in captivity. To draw a distinction between the two species on this point would therefore be unjustified. In birds, too, dominance plays an important role in reproduction (mating) and Davis (1952) quotes Hochbauen (1944) as stating that the attempts of a non-territorial Canvasback, Aythya valisineria, to mate were frustrated by other drakes in the area. In this case, as in other territorial species, the acquisition of a territory depends largely upon the dominance of the competing male.

(c) Smelling the base of the tail and vulva:

The object of asserting his dominance over a cow in oestrous by the bull is to nullify the

individual/...

individual distance existing between the two and to enable him to approach the cow and smell (or nose) the base of her tail. The smelling of the base of the tail and the vulva is usually considered as a part of the flehmen process but it is such a distinct sequence in the pattern that it merits consideration on its own. Nosing the base of the cow's tail probably has a dual function viz. (a) to make the cow stand still if she starts moving away. The response to stand still if the vulva, or the root of the tail, is touched is present from birth and probably persists through life. If a roan mother wants to nurse her young she nudges at the tail root and the youngster responds by standing still and lifting its tail to be licked. Gosling (1969) also found that if he wanted young hartebeest calves to stand still he merely touched the base of their tails. (b) Once the cow is in a standing position the bull is able to smell her vulva, which obviously stimulates the cow to urinate. This behaviour, and that mentioned under (a) merely represent two aspects of the reaction to the same stimulus. As soon as the cow starts urinating the bull can make a urinalysis to determine her oestral condition. The additional function accorded to this sequence by Kiley-Worthington (1965) that the anal licking ".... stimulates the female according to her oestral status" does not apply to roan as it

appears/...

Fig. 16: A bull performs "Flehmen" after sampling the urine of a cow in oestrus.
Nwashitsumbe, 1968.

appears to have no - or alternatively, very little - stimulation to the cow other than that mentioned in (b). This sequence, however, plays an important part in the stimulation of the male and is more appropriately discussed in the next section.

(d) Flehmen:

The German word "flehmen" was first used by Schneider in 1930 to describe the reaction which many animals exhibit by lifting their heads and pulling their lips apart after making contact with a strange smell. Though flehmen may be released by various different scent stimuli and may be seen in females and immatures, it is the one reaction which is most intimately associated with the urinalysis of the oestral cow, and thus performed by the bull.

After the bull has smelled her perineum the cow squats slightly with her hindlegs and urinates. The bull then approaches from the rear and inserts his nose into the stream of urine. For a few seconds the bull will hold his nose to the stream and then lifts his head as high as he can manage. His mouth is held slightly open and the lips are retracted strongly to expose the gums. From all appearances the bull inhales when lifting his head and apparently "holds" his breath with his head in the air. Fraser (1968) has noted that "....inhalation and some exhalation, via the upper

respiratory passages, occur briefly during the reflex". The ears are pricked forward and the impression created by a bull in this attitude is one of deep concentration - especially when he sometimes slowly moves his head from side to side. The reflex may last as long as 10 seconds and when the bull lowers his head the movement is slow and deliberate while his tongue flicks rapidly in and out of his nostrils.

The actual functioning of the urinalysis has not been cleared up beyond doubt but it is believed that the Organ of Jacobson plays an important role in this regard; the basic idea being that certain oestral hormones are contained in the urine of the female and that the bull is capable of isolating these hormones and thereby determining whether the cow is in oestrus or not (Knappe, 1964). Apart from the fact that the male can determine whether a female is in oestrus or not by means of the urinalysis, it is also quite obvious that it is possible for the bull to establish in which phase of oestrus the female is. In the initial stages of oestrus (pro-oestrus) the bull takes little notice of the cow after performing flehmen, and thereby determining her reproductive status. During the pre-oestrus phase the courting sequences seldom progress further than flehmen, which clearly indicates that the stimulus received by the bull is not sufficient to arouse sexual

interest/...

interest beyond the initial stages.

As the oestrus cycle progresses the bull frequently approaches the cow and tests her urine. The closer she approaches the peak of the cycle (oestrus proper) the more important the next sequence in courting behaviour, viz. laufschlag, becomes with a corresponding decline in the performance of the urinalysis. In the final stages flehmen may be omitted altogether. It has never been observed that the stimulus received from flehmen has been sufficient to cause erection of the penis, as is the case in many other species (see Estes, 1968).

From a behavioural point of view the various oestral-phases are quite obvious and it is believed that these phases also coincide with the physiological changes taking place in the cow and therefore these observations are in agreement with Fraser's (1968) remark that "..... it is a reasonable assumption that oestrus cycle phasing may be recognizable to the male animal by the odour testing of the urine".

Despite the elaborate physical reaction accompanying flehmen it is merely regarded as a reflex released by a scent stimulus and is not a "display" in itself (Estes, 1968). In roan antelope, too, no obvious attention is paid to an animal performing "flehmen" and consequently no display value could be attached to it.

Neither/...

Fig. 17: "Flehmen" in an adult cow, immediately after smelling the ground where another cow had urinated.
Nwashitsumbe, December, 1969.

Neither is flehmen restricted to adult males alone but may be seen in cows, and even immature animals of both sexes - the reflex and performance being identical to that of the bull. It has already been mentioned that flehmen may be released by a wide range of scents and is not necessarily always linked with sexual behaviour. In fact, the context in which flehmen is performed provides the main difference between the adult bull and the cows and immatures. In the bull the stimulus is actively sought from cows by inducing them to urinate - a positive stimulus immediately giving rise to the initiation of mating behaviour and thereby rendering flehmen one of the important sequences in mating. In cows and immatures the stimulus is obtained from substances on the ground - apparently areas where other individuals have urinated - and releases no further action from the stimulated animal.

(e) Laufschlag or Laufeinschlag:

Once again a German word has been accepted in general usage to depict a further sequence in the mating behaviour and was first suggested by Dr. Fritz Walther (1958) who did much of the pioneer work in analysing and describing the mating rituals of ungulates (Walther, 1958, 1960/61, 1961, 1963, 1964(b) 1968). Laufschlag is the most advanced sequence in the courting ritual and immediately precedes copulation. It

consists/...

consists of the repeated beating up with the foreleg between the hindlegs of the cow and whereas flehmen is a test of the reproductive status of the cow, Laufeinschlag is a test of the state of receptiveness of the female. While in the dominant attitude, the bull attempts to gain a position directly behind the cow from where he could best perform the beating up of either one of his forelegs between the hind legs of the cow. This is not always possible as the cow continually evades his attentions by milling around the bull in a tight circle i.e. 1 or 2 metres from the bull. The circling of the cow around the bull has been referred to as Paarungskreisen or mating-whirl-around (Walther, 1958, 1961). While circling the dominance-submissive relationship between male and female is maintained by the dominance posture of the male (i.e. erect, head high, etc.) while the cow displays the submissive posture (i.e. head low, tail drawn in between her legs, etc.). In the oryx, Walther (1961) suggests that the head low posture of the female represents a threatening attitude in response to the demonstration of superiority by the male (Kopf-tief-Drohen). If the cow keeps on moving, the bull lifts his leg up from the side, beating her under the belly, or he may lift his leg up behind her while in the reverse-parallel position. It is quite obvious that the bull exerts the utmost care not to upset or disturb his partner in any way and rather than

"beating/...

Fig. 20: "Laufeinschlag" in the sable antelope.
Tsumanini, July, 1968.

"beating up" he lifts his leg under the cow's belly with extreme gentleness. His leg is never held quite straight but is usually loosely bent and only in the final stages is it straightened out but even then it is still somewhat bent.

Laufschlag obviously fulfills two indispensable functions in the mating ritual:

(i) it is the final sequence before copulation takes place and as such it is the display by which the bull determines the state of receptiveness of the cow. If the cow is not ready to accept the bull she will react to laufschlag by lowering her head and holding her tail between the legs (Kopf-tief-Drohen) and keep on turning around the bull; thereby preserving the reverse parallel stance between her and her suitor and avoiding at all costs that the bull moves in behind her.

Once she is ready for copulation she will stand still and allow the bull to perform laufschlag from the rear after which copulation soon follows. Walther (1960/61) has postulated the hypothesis that laufschlag might have originated from the primeval fighting postures of ungulates before they developed horns and that it has subsequently been

retained/...

retained and ritualized in the courtship behaviour. When one considers that the entire mating process (and its success) is based upon a dominance-submission relationship between the two partners and that the primary function of laufschlag is to prod the cow to keep moving until she is prepared to accept the bull, this hypothesis becomes quite feasible. In other species which apparently do not perform laufschlag in their courting ritual, its place is taken by various displays such as nudging at the tail with horns, pushing from behind with the shoulder or biting as in stallions (Fraser, 1968) which all may reflect their origin from primeval aggression. In the Tragelaphine antelopes laufschlag is replaced by ritualized neck-fighting (Walther, 1963).

(ii) Laufschlag not only reflects the oestral status of the cow but it also prepares the bull for successful mating by stimulating him into full erection. The stimulating effect of 'belly beating' on the bull is quite obvious and the degree of stimulation is also associated with the position of the bull in relation to the cow while performing laufschlag - the nearer the bull is in beating up from behind the cow the greater the stimulation. If the bull succeeds in gaining a position

behind/...

behind the cow from which to perform laufschlag his whole body becomes tense, head held high and frequently this attitude is accompanied by erection of the penis. If the cow is receptive the bull is in a position to accomplish successful copulation and in cases where the cow is not yet ready the bull may nevertheless be stimulated to such a degree that he will attempt to mount her from the side. From observations of the mating of Ugunda kob, Buechner and Schloeth (1964) suggest that laufschlag may serve the dual purpose of stimulating the male for copulation and also to determine the acceptability of the female for inguinal nuzzling by the male in post-coital behaviour.

(f) Firm stance of the female:

To ensure successful copulation it is essential for the cow to stand still and allow the bull to mount. Standing firm is a definite sequence in the mating ritual and is a positive reaction to the courting of the bull. The cow is receptive for coitus for only a short time in the whole courtship and mating cycle, which may conveniently be divided into a pre-coital and coital stage. During the precoital stage the bull performs an array of highly ritualized courting displays during which the female constantly attempts to avoid the attentions of her suitor. The reactions of the

bull/...

Fig. 21: Copulation follows upon belly-beating. The bull retains his dominant posture while the female remains in the head-low posture. Nwashitsumbe, December, 1968.

bull may therefore generally be considered as positive and those of the cow negative. The most positive step by the cow in the mating ceremony is when she stands firm and thus initiates the coital stage. Standing still by the female permits the bull to gain a position behind her from where he can perform laufschlag - which leads to full stimulation of the bull and probably also the cow - and eventually also coitus. Fraser (1968) in reviewing the vast amount of literature on mating behaviour in a wide range of ungulates, states that "it is recognised that firm standing in the female is a principal stimulus to male sexual behaviour" and further also that "firm standing is the positive response to nudging (laufschlag in the case of roan) by the male subject and provides reciprocal stimulation".

(g) Copulation:

Copulation is the next logical step and follows soon after the 'standing firm' response of the female. The bull stands directly behind the cow and continues to perform laufeinschlag until he rears up onto his hind legs and mounts the cow. Successful copulation, i.e. intromission of the penis and ejaculation, does not necessarily result from every mount and frequently 1 or 2 unsuccessful attempts at mounting precede actual coitus. Unsuccessful mounts may be with or without erection of the penis and in a bull that

is highly stimulated an attempt at mounting may even be performed at an angle from the side of the cow. Unsuccessful mountings seem to be most frequent in the early stages of the coital phase.

True copulation is very brief and is usually completed in 1-3 seconds. The bull mounts the cow from the rear and clasps his front legs round her haunches - his head held high and ears facing forward and his tail held away from his body. Once in position the bull gives 2 or 3 vigorous forward thrusts and dismounts.

While receiving the bull during copulation the cow remains in the head-low posture and may even occassionally nibble at some grass.

(h) Post-copulatory smell:

Immediately after dismounting from successful copulation the bull briefly smells the vulva of the cow, passes his tongue rapidly in and out of his nostrils a few times, after which both bull and cow then resume grazing again. The copulatory smell has never been observed after an unsuccessful mount and neither has the smell released the flehmen reaction in the bull. This last smell concludes the courtship and mating cycle and every subsequent mating is again characterized by all or some of the sequences described above.

Display/...

Displays and activities of the bull related to mating:

Many of the displays and activities of the bull which are prominent during the courtship period are also closely linked and/or form an integral part in the maintenance of the intolerance zone of the bull. This creates the impression that sexual jealousy may be one of the factors contributing towards the bulls' intolerance of other adult males. The existence of an isolation zone around the bull and his herd excludes other males from participating in mating activities. Adult bulls attracted by a female in oestrus may provide severe competition for the herd bull and it is therefore not surprising that displays of dominance and aggression are so evident during the courtship and mating cycle. Displays which are especially prominent during the courting ritual, but which are discussed more appropriately in the previous chapter, include agonistic behaviour (dominance displays and fighting), tree-horning, herding and foot-scraping.

The role of the bull and the cow in the mating cycle:

In the discussion of the various sequences in the courting and mating ritual the attention was for the greater part concentrated on the role played by the bull. This could be expected as the bull takes the initiative and plays an active part, as contrasted to the more subdued role of the cow. In an analysis of the roles portrayed by each member of the pair, the following points emerge as important:

(a) Role of the bull:

The bull displays a positive attitude toward courting and mating throughout the ceremony and

the/...

the most important single aspect characterizing his activities is the assertion of his dominance over the cow. Each and every advance made by the bull is accompanied by the dominance posture to which the cow submits, viz. the initial approach, smelling of the cow's vulva, Laufeinschlag, etc. To facilitate successful mating dominance is a prerequisite over both:

(i) the cow in oestrus and
(ii) competing suitors.

(b) Role of the cow:

If mating success is dependant upon the dominance of the bull over the cow it is only logical to expect that the role of the cow would be one of submission and therefore also more negative than that of the bull. It is further not extraordinary to note that the major activity of the cow is one in which she constantly attempts to evade the attentions of the bull until she is ready for coitus. In the entire courting and mating ritual the only positive reaction of the cow is the "standing firm" to permit the bull to serve her.

The submissiveness of a cow toward a courting male and her negative reactions towards his approaches has frequently, but briefly, been referred to in the text and merits more detailed expounding:

(i) Head-low threatening posture (Kopf-tief-Drohen):

The first reaction of the cow to the intimidating approach of the bull is to lower her head,

draw her ears back or twitch them to and fro and pull her tail tightly between her legs. This is the typical low-intensity threatening posture common to all individuals intimidated by a dominant animal. Once an animal has submitted to a superior animal it rarely attempts to make a break and run away but rather seems to be 'attracted' towards the dominant animal or else stand and await its approach. In this respect the lowering of the head by the female is in direct response to the dominating posture of the male and may therefore be regarded as a positive reaction. This leads to the following phase, viz.

(ii) Circling (Paarungskreisen, Walther, 1958): Circling, or also known as 'mating-whirl-around', is one of the characteristic phenomena of the courting ritual and is performed by the cow in an attempt to avoid the bull from gaining a position behind her from which he could mount her. The mating-whirl-around occurs in response to 'laufschlag' by the male and clearly reflects the unwillingness of the female to mate (cf. Beuchner and Schloeth, 1964). During the circling the cow maintains her head-low threatening posture and the bull his dominant attitude and due to the circling they remain in a reverse-parallel position in relation to

one/...

one another. During this phase the cow may give vent to displaced activities such as grazing or scratching the neck with a hind foot. After a few circles the cow usually tires and runs away from the bull. During the early stages of oestrus the bull may leave her in peace but as the cow approaches the peak of oestrus the bull continually pursues her and the performance is repeated several times.

(iii) Running away:

It has already been mentioned under (ii) that the cow may break away from the bull during the circling process and attempt to run away from him. Usually running away is not a very determined effort to avoid the bull and a cow seldom runs away more than 15 to 20. metres. If the bull is persistent in his courting attempts the cow may suddenly charge away for about 40 - or even more - metres in an attempt to escape his attentions.

(iv) Hiding:

Occassionally a cow may be so determined to discourage a courting bull that she will reverse into a shrub or thicket to 'hide' her hindquarters from her suitor. More frequently however, the cow retreats to a shrub or tree and circles around it in an effort to shake off the bull. Needless to say that

these efforts have little effect on a determined bull. In sable antelope a harassed cow may even lie down in an effort to evade the male. On one such an occasion the bull stood alongside the prostrate female and persistently scratched her withers with his forefeet in an attempt to make her rise. The male's actions simulated 'laufschlag' and left scratchmarks of dust on the female but failed to raise her. Similar markings on other females suggest that lying down as an evasive action of the sable cow occurs quite frequently. This type of behaviour has not yet been observed for roan antelope.

In Ugunda kob, Beuchner et. al., 1964, found that it was primarily young 'virgin' females which were inclined to lie down in response to the male's courting.

Phasing of the oestrous cycle:

In the preceding account of the behavioural characteristics in the courting and mating ceremony, the term 'oestrus' has frequently been referred to in a rather loose way, generally referring to that period during which a bull is sexually attracted to a cow. However, physiologically the oestrus cycle is accepted as a process involving various phases which follow one another in sequence and in which 'oestrus' relates to that phase during which ovulation takes place. From observing the "oestrus cycle" in roan antelope it is clear that different stages may also be recognized on

the/...

the basis of behaviour and may be founded on the behaviour of either the bull or the cow. Rowell (1963), as quoted by Fraser (1968), has suggested that the term oestrus be used in describing behaviour and not physiology. The following stages in the oestrus cycle are suggested for roan antelope as based on the behaviour of

(a) The bull:

(1) Pro-oestrus:

The major characteristics of this phase are:

(i) the assertion of the dominance of the bull over the cow;

(ii) the affirmation that the cow is entering a period of sexual activity (oestrus cycle) by means of the urine test;

(iii) in conclusion of the phase urine testing (flehmen) and nudging with the foreleg (laufschlag) are common.

Pro-oestrus therefore represents the initial stages of the ceremony and includes such steps as the intimidation of the cow by the bull, repeated flehmen performances, laufschlag and circling. Duration 2-3 days but may be longer.

(2) Oestrus:

Oestrus is the final stage in the mating behaviour with the one outstanding feature

that/...

that copulation takes place. Together with copulation, laufschlag, circling and the post-copulatory smell all occur during this phase. The duration of the oestrus-phase is estimated to be between 24 and 36 hours. Fraser (1968) quotes Eibl (1962) as stating that true oestrus in domestic cattle lasts 18 to 24 hours.

(b) The cow:

In the cow the same sequence of stages may be observed as in the bull. In early pro-oestrus the cow is more likely to evade the bull by running away or backing into shrubs while the degree of circling shows an increase during the later stages of pro-oestrus. It is noteworthy that during this phase the cows reaction toward courting is totally negative.

The oestrus or coitus-phase is distinctive by the positive 'standing firm' reaction of the cow and the consummation of the mating act.

For a better understanding of the courtship and mating process and the interactions between male and female the following example may be quoted from field observations:

13.2.68: During early morning LY approached the herd bull and the bull performed the lateral Dominance display while LY reciprocated with the head-low threatening posture (Kopf-tief-drohen).

As/...

As LY ambled past the bull he turned around and smelled at her vulva. LY moved away but the bull again approached her and attempted to smell her vulva. To evade the attention of the male LY turned around the bull in a tight circle (Paarungskreisen). The male then lifted his foreleg up gently and tried to beat up between her hind leg (Laufschlag). LY immediately bolted and ran 10-15 metres away from the male. However, he followed and once more reached for the cows vulva with his nose. Circling followed. During the circling the male retained the Dominance Posture while the female, head low, kept her Submissive Posture.

In response to the bulls' smelling, LY held her tail out, haunched slightly with hind legs apart, and urinated. The bull inserted his nose into the stream of urine and followed with the flehmen reaction. The male then followed with laufschlag. The bull again put his nose to the female's vulva though the cow did not urinate and neither did the flehmen reaction follow.

Intermittently the bull performed belly beating a number of times and then made a rather 'half-hearted' or undetermined effort to mount LY. LY reacted by immediately running away (10 metres) but the bull followed closely behind her. The bull again sniffed at her vulva and performed belly beating a few times before apparently losing interest.

No courtship or mating activity was observed during the afternoon and neither on the morning of 14.2.68.

19.2.68: At 1030 hrs. the herd bull and LY were found alone at the top end of the vlei with the rest of the herd out of sight. No courting behaviour was observed but the bull and cow remained close to one another for the rest of the day until the herd joined them in the course of the afternoon. (It was quite evident that the 'togetherness' of the two animals was solely due to the male that kept close to LY and not vice versa).

At 1730 hrs. the bull approached the cow and smelled her vulva, but she tried to evade his advances by running away. The bull pursued her and performed Laufschlag three times. LY started urinating, the male inserted his nose into the stream and after taking his 'sample' the flehmen reaction followed. Laufschlag (twice) followed after which both animals started grazing. The bull still remained close to LY but no more courting was attempted.

20.2.68: No courting behaviour was observed during the morning and afternoon though the bull attempted to smell the cow's vulva. LY was not very tolerant of her suitor and ran away a few metres. During the whole day the only evidence of courting behaviour was the fact that the bull remained

close/...

close to the cow and his attempts to smell her vulva.

21.2.68: No courtship was observed during the morning.

22.2.68: As LY arose from her afternoon rest at 1730 hrs. the male approached her and smelled her vulva. Laufschlag followed, the male beating up under LY's belly, the two standing reverse-parallel; circling (mating-whirl-around) took place until LY stood still and urinated. Flehmen from the bull followed. Belly beating again commenced on which LY bolted and ran away 20 metres. The bull followed and as he tried to smell her tail again, she once again ran away. Both resumed grazing.

Twenty minutes later the bull again approached LY but she ran away before he had reached her. The bull followed, smelled her vulva and LY again ran away. No further courting was observed.

23.2.68: At 0730 bull and cow were together again but LY kept evading the bull as during the previous afternoon. At 0845 the bull approached LY and smelled her vulva, beat up once with his foreleg and again smelled at the base of LY's tail. LY reacted by urinating; followed by flehmen from the bull. LY allowed the bull to stand behind her from where he performed Laufschlag (3 times). After he beat up the second time he

showed/...

showed erection of the penis. Immediately after the third 'beating' the bull mounted LY with full erection. Successful intromission was achieved and with the ejaculatory thrust LY took 1 or 2 steps forward. Copulation was completed in 2-3 seconds. LY stood with her head up, chewing while the bull mounted her. After copulation LY did not move but went on chewing for a few minutes before lying down. Immediately after dismounting the bull again smelt at LY's vulva before moving off 5 or 6 metres and vigorously shook his head in a Dalbergia melanoxylon shrub, after which he also lay down.

At 1630 hrs. the bull approached the cow and without any apparent preliminaries he mounted her twice in quick succession. The first time intromission did not take place but 5-10 seconds later the bull again mounted LY and copulation took place successfully. Before moving off to graze the bull briefly sniffed at LY's tail. A few minutes later the bull lay down close to where LY was grazing.

At 1710 hrs. the bull arose, approached LY and they rubbed their foreheads together. LY then fell onto her knees and the bull gently pushed her back a few paces. After LY jumped up, the bull again smelled LY's vulva, after which Laufschlag was performed 8 or 9 times. LY ran away 5 metres, followed by the male who again smelled her vulva

and/...

and beat up between her hind legs 3 or 4 times. The bull again mounted with erection but intromission did not take place and there was no ejaculatory thrust. Five to ten seconds later successful copulation was achieved. Smelling of the vulva followed dismounting - a certain indication that successful copulation had taken place.

After grazing a few minutes LY and the bull again rubbed their foreheads together and fell onto their knees in rather playful manner. After some 'gentle' skirmishing the cow jumped up and evaded the bull. When the bull followed her she moved away ahead of him. As he approached her again LY went onto her knees. The bull approached her with his head lowered and uttered a loud gutteral sound as he clashed horns with her. LY did not resist the bull but jumped up and ran away a few paces. Twice after this the bull attempted to smell LY's vulva but she persistently evaded him by running away. Shortly afterwards both shook their heads vigorously in Dalbergia melanoxylon shrubs.

On 25.2.68 all signs of courting and mating activity had ceased and the bonds between the bull and LY severed.

CHAPTER V.

MOTHER/CALF RELATIONSHIPS AND THE SOCIAL INTEGRATION OF THE CALF.

Social relationship between:

(a) Mother and calf:

A few days prior to parturition a cow isolates herself from the herd and withdraws to an area of sufficient cover for both herself - while alone - and for concealment of her calf. The mother remains on her own up to 5 days after the birth of her calf and during this time she usually remains in the neighbourhood of her recumbent calf. During the period of isolation the cow is particularly alert as is clearly evidenced by the continuous twitching of the ears and the repeated interruptions during periods of grazing when the cow abruptly lifts her head and gazes intently in all directions. The senses of smell, hearing and sight are all well developed in roan antelope and the cow uses them to their full in her close vigilance over her calf. For the 3 or 4 days following birth the cow normally does not move more than 400-500 metres away from the calf and apparently does not go down to drink.

There is some indication that the period the cow remains detached from the herd is in close

correlation/...

correlation with her standing in the order of dominance in the herd viz. the most dominant cow remaining in isolation for the shortest time while those of lesser influence remain on their own for a longer period. This is brought about by the fact that the dominant cow is the leader of the herd and though she may withdraw to calve the others soon follow her to her place of hiding.

However, the period normally spent in isolation by the cow varies between 2 and 5 days after which the cow again joins up with the herd.

Once a cow has rejoined the herd she remains conspicuously wary and alert and the close vigilance over the calf of the first few days is somewhat relaxed. This is quite inevitable as the cow again returns to the normal activity routine of the herd and accompanies it down to water, meanders further distances away from the calf while grazing with the herd, and generally spends the hours of resting further away from her offspring than in the beginning. The distance between mother and calf varies considerably during this stage and may be from about 50 metres to 2 kilometers or more away. If not disturbed the mother normally does not wander far away from her calf after nursing it in the morning, but if the herd should be disturbed and chased from the area where the calf is lying the mother will not return merely to be close to her calf. In fact, once mother and calf have parted

after/...

after the early morning nursing the cow will show no effort to remain in the neighbourhood of her calf.

Cows with young calves in hiding exert a definite influence on the other members of the herd and once again the degree to which the herd is affected is determined by the status of the particular cow. In general, the following pattern is adhered to when a young calf is in hiding: when the mother nurses her calf in the morning the rest of the herd graze in the vicinity and once the calf has taken refuge, they may wander off and eventually come to rest. Later during the day the herd moves away to drink and to graze. During the afternoon the herd may graze a long distance away from the young calf until late afternoon. During the last half hour or so before sunset the mother of the calf gradually starts moving towards the area where her calf is concealed. A dominant cow may attract the whole herd to follow her while a cow of lesser influence may wander off alone or in a small group only to rejoin the herd at a later stage.

At the time the young calf reaches the age that it remains with the herd throughout the day, the once close relationship between mother and calf is further relaxed and the association between the two is of a very 'loose' nature. From the age of 2 months the calf behaves quite independently

of its mother and associates much more freely with other youngsters of its own age than with its mother. In fact, the bond between mother and calf at this stage is so flaccid that unless a calf is observed suckling its mother it is nearly impossible to distinguish a cow and her calf in a mixed herd!

During the period that the calf suckles regularly i.e. to the fourth month, there is daily - or at least frequent - contact between cow and calf. With the decline in drinking frequency and its eventual culmination, contact between mother and offspring correspondingly becomes less frequent until at the age of 6 months when the calf is weaned it becomes, for all purposes, a fully fledged and independent member of the group. However, this does not necessarily mean that all bonds between cow and calf are severed at weaning age, and there is sufficient indication that the ties between mother and daughter may persist throughout life (or for many years). In the case of a male calf the relationship is broken once the youngster is driven from the herd by the herd bull. Evidence for the maintenance of family ties may be sought in the definite sub-groups within a herd, the existence of which becomes most apparent with the periodic splitting up of the herds into recognizable units.

Mother/...

Mother/calf relationships in other Hippotraginae:
One of the striking features in the mother-calf relationships common to all the Hippotraginae is the apparent 'looseness' of the relationship. The apparent independence of the calf of its mother and the possible 'lack of interest' of the mother towards her calf could probably be sought in the first few weeks of life when the calf remains concealed and on its own for a large part of the day while the cow moves further afield to graze and water. During this period contact between cow and calf is restricted to the brief periods of nursing whereas calves of the 'follower-type' (nachfolge) remain in constant contact with their dams and hence the intimacy of the relationship.

At this point it is necessary to draw attention to the fact that the term 'loose', here used to describe the bond between mother and offspring, is totally subjective and is only used in the absence of a better word. The term is used in this context to indicate an association apparently lacking intimate bonds between a mother and her calf but it is not intended that the term should reflect a 'degrading' light on the system as such. The possible advantages and disadvantages of this system will be discussed under ecological considerations.

At the close of the eighteenth century a congeneric form of the roan and sable antelopes in

South/...

South Africa, viz. the Blaauwbok (Dutch) or Blue antelope, Hippotragus leucophaeus, became extinct. This antelope inhabited an extremely localized area centering around Swellendam in the Cape Province. (For a detailed account of old reports by travellers and naturalists and an inspection of the few remaining museum specimens, see Mohr (1967)). Unfortunately most of the references to this antelope are purely descriptive with very little information to shed some light on its ecology. However, Mohr (1967) quotes Thunberg (1792) as stating that one of the reasons for the low numbers of the Blaauwbok was the poor mother-calf relationship which resulted in the loss of large numbers of calves to predators. For a species with such an extremely limited range of distribution the loose mother-calf relationship may quite feasibly have been one of the contributing factors leading to the total extermination of the species.

In the sable antelope the relationship between mother and calf is decidedly more intimate than in the roan. Observations on sable in the Kruger Park have revealed basically the same social organization in this species as in the roan antelope though the sable herds appear to be obviously more united and coherent than roan herds. Calves also club together in nursery groups but do not appear to detach themselves from the adult cows

as freely as their counterparts in the roan herds. Under conditions of stress - and probably when unable to keep up with the adults - the young calves may deviate from the main herd. During September, 1969, field staff were engaged in the capture of a number of sable for release in an enclosure. The animals were captured by means of tranquillizers and darting was done from a small helicopter. While operating on a small herd of 5.1 sable (♂ + 2♀♀ + 2 calves of approximately 8-9 months old) the 2 young calves suddenly made a break from the adults and darted off into thick cover on their own. One of the calves was subsequently caught and about an hour later the other calf was relocated close to the herd bull who had also parted from the cows.

Estes (1969) has remarked on the rather loose relationship between mother and calf in sable antelope and describes a case in which a calf was parted from its mother when the herd divided into different sub-groups. After a while the calf left its group, apparently in search of its mother, and was only reunited with her after a lapse of several days - with no ill-effect! No systematic study has as yet been undertaken on the remaining member of the Hippotraginae, viz. the oryx, under natural conditions though observations by Walther (1965) on a small herd in the Münchenen Tierpark Hellabrun, also reflect the same loose character as in the preceding roan and sable antelopes.

Especially/...

Especially during periods of grazing or playfulness the calf tended to drift from its mother.

(b) One calf to another:

Certainly one of the major characteristics in the composition of the roan herd is the close relationship between the young animals and especially those of the same age group. Young roan generally associate together in a closely knit unit or nursery in the close proximity of one or more of the adult cows, or at times even seek the company of the herd bull.

Age-specific influences appear to be the main factors governing the relationships between calves and may conveniently be divided into the following stages:

(i) Period of concealment:

Immediately following birth mother and calf remain isolated for a few days (see p 132) during which time there is usually no contact between the young calf and any other members of the herd. This period may vary from 1 to 4 or 5 days. After a few days the calf becomes more active and may follow its mother for short distances during periods of nursing in the early morning. If there happen to be 2 or more calves of similar age in the herd they are immediately attracted to one another and during their

brief period of nursing and playing in the early morning they may engage in playful bouts of running and frolicking. Initially they again part when lying up though they may conceal themselves quite close to one another. As they grow older, however, the relationship between the young calves becomes more intimate and they rarely part company. Gradually the time spent together increases while the time spent with the mother decreases and by the time they 'join' the herd after six weeks of lying up a firm bond between the two is established which probably persists throughout their lives in the case of females.

(ii) Relationship between calves lying up and older calves:

The predominant reactions released in older calves, i.e. calves over 6 weeks old to 2 years, by the 'discovery' of a new calf is one of curiosity and frequently exuberant playfulness. In all cases new born calves have proved to be a great attraction for the older calves and immediately after encountering a small calf the older ones attempt to smell it - in no particular area - and turn about it, often falling onto their knees in playfull fighting with one another and/or breaking into spells of running and jumping in follow-the-leader fashion. In one case 2 male calves

made several attempts to 'mount' a 5 day old calf but this was not observed in any of the other calves. The reaction of the cows toward the inquisitiveness shown by the older calves toward a newborn calf varies greatly. At times the same cow may show aggression toward calves approaching too close to her own while at others she may be quite tolerant towards them.

The influence a young calf exerts on older calves varies with the number and age structure of the calves in the herd. Basically the strongest bonds are formed between calves of the same age with the intensity of the relationship diminishing with the increase in the age gap between 2 calves. As roan antelope have no well defined calving season, calves of all ages may be encountered with the herd. These calves normally resort together though the closer groups of same-age animals are clearly discernable and illustrate the difference in intensity of the bonds between the various calves.

A particularly interesting observation was afforded by 2 young calves in the roan enclosure. The calves differed in age by two months and when the younger one was born the other had just joined the herd. In the absence of any other calves of similar age

(the only other calves in the herd were 5 and 9 months old), the elder of the two became very attached to the new born calf. The relationship developed to such an extent that the older calf regularly lay up with the young calf during the day. On numerous occasions the old calf was seen to detach itself from the herd and wander off on its own to the area where the younger one was in hiding and then conceal itself. This behaviour could be interpreted in two ways, viz.

(a) that the bond between the 2 calves was so strong - in the absence of calves the same age as the older calf - that the elder one of the two could not resist leaving the herd for the company of the younger one.

From observations on roan calves it has become amply clear that calves are much more inclined to 'befriend' a calf younger than themselves than a calf in an older age class. This is in all probability due to the strongly developed 'line of dominance' in roan antelope which is in operation from a very young age. If this is accepted it also explains why the older calf in the example above was more attached to the younger calf than the more dominant older calf of 5 months.

(b) at/...

(b) at the time of birth of the younger calf the older one had just started joining the herd and could have been stimulated to continue the lying-up behaviour by the example (or presence) of the newborn calf. Lying up in young roan is extremely well developed and may therefore be prolonged by the stimulus received from a younger calf, especially in the absence of other calves of comparable age in the herd to which it could attach itself.

In other cases where there were 2 or more calves of the same age group, the calves remained together and did not follow younger animals.

(iii) Relationship among calves older than six weeks: The six-weeks criterium used in this case was chosen as representing the age at which young calves become 'independent' members of the herd i.e. they do not conceal themselves during the day but follow the same activity pattern as the adults.

By the time the calves join the herd the bonds between them and the other calves in the herd have already been formed and the perpetuation of these ties largely depends on two factors, viz. age and sex.

(a) Age/...

(a) Age:

It has already been stated that calves of the same age form the closest ties between one another and that though there are bonds between calves of different age groups they are of a lower intensity - probably directly in relation to the difference in age between the two animals. Age-specific bonds are formed at a very early age - within the first 6 weeks of life - and are maintained for many years. Though the evidence is not conclusive, the author believes it is reasonable to suggest that the ties may be maintained throughout life. One of the characteristic features of a roan herd is the obvious close relationship existing between animals of the same age class, even into the adult stage, and this certainly plays a part in the formation of definite groups within a roan herd.

(b) Sex:

Sex itself exercises no influence on the degree of stability of the ties between calves and for the first 2 to 3 years there is no difference in the relationship between heifers, males or heifers and males. However, due to the intolerant nature of adult bulls young males are evicted from the herds at the

age/...

age of $2\frac{1}{2}$ to 3 years, with the severing of all ties between the calf and the herd. How long it takes a young male to break all contact with his herd is not yet fully established though it is quite clear that for at least several months after the young bull has been driven from the herd he will repeatedly attempt to rejoin it if given the opportunity i.e. in the absence of the herd bull.

The presence of bachelor groups with young males in the vicinity may also influence the time it takes to oust a young male from its herd as it may be more inclined to join other young males and therefore 'break' more easily from its herd than in the absence of such groups, in which case the young male may return to its family group more persistently when chased by the herd bull and thereby delay the inevitable final break.

In the case of bull calves leaving the herd together to be taken up in small bachelor groups of from 2 to 6 or more individuals, the bonds between the calves may thus be prolonged. However, once they also reach their full intolerance towards one another at the age of

approximately/...

Fig. 22: A mother nurses her young calf. During the first six weeks of life nursing consists of elaborate licking of the genitals, neck, ears and face.
Nwashitsumbe, May, 1969.

approximately 5 to 6 years the bonds between them are finally broken.

Nursing and suckling:

(a) Nursing:

For the first few weeks of life, during which the young roan calf is concealed, the only contact between mother and calf is during the brief periods of nursing and suckling. Once the calf has suckled and lies down the cow takes no further notice of her offspring and wanders off with the herd.

When a calf approaches its mother to suckle the first contact between the two is usually a cursory lick by the mother on the calf's head (distinctly not the naso-nasal greeting characteristic of many other species, cf. Grant's gazelle, Walther (1965) reedbuck, Jungius (1969)). The calf may then commence to suckle while the cow licks its anal area around the base of its tail. Elaborate and thorough ingestion of the excreta forms the major part of nursing and is performed with the calf holding its tail upright and swishing from side to side, and may take place either while the calf is suckling or standing idly alongside or in front of its mother. In males the penis is also thoroughly licked from between its hind legs or from the side. Licking is not only confined to the anal region but also the back, ears - especially around the base - and eyes, neck and forehead of the young calf

receive/...

receive careful attention from the cow. During the first week of life suckling and licking is the main form of activity when mother and calf are together. The cow may lick the anal region of the calf for 5 minutes at a time and this may be repeated several times during the 60 - 90 minutes that mother and calf are together in the morning. This is the only time nursing takes place during the hours of daylight - though further nursing periods probably occur after dusk in the evening.

This form of nursing by the mother corresponds closely with the period during which the calf remains concealed and thus unattached to the herd. In 4 observed cases the elaborate licking ceremonies were discontinued more or less simultaneously to the time that the calves joined the herd i.e. 7 to 8 weeks after birth. Even after the calf has become active and no longer resorts to hiding, it lifts its tail perpendicularly into the air while suckling as if to permit the cow to lick its anal region. The cow may respond by giving the tail, and at times also the head and ears, a cursory smell or lick but pays no further attention to the calf. This by no means suggests that calves stopped suckling at this age but merely that the licking of the mother ceased.

The benefits derived from the licking of the head, body and genitals may very well be of a dual nature i.e. hygienic and ecologic. The importance of stimulation in the young animal to urinate and

defecate has been pointed out by Hediger (1949). However, of interest in an ecological sense is the role licking may play to eliminate - or minimize - any odours which may be emitted by the calf during the period of concealment. Walther (1964a, 1966, 1969) has drawn attention to the close correlation between the elaborate licking of the young calf and the habit of the calf of 'staying out' for the first few days or weeks of life. On the contrary, the tendency to lick the calves in species where the youngsters follow their mothers almost from the time of birth, is poorly developed and occurs infrequently.

Whether young, hiding calves are actually odourless or not is an undecided matter. Altmann (1952) refutes the idea that young elk (Cervus canadensis) calves - also of the 'Ablieger' type - are without smell and bases her assumption on the fact that cows are able to smell the tracks of the calves to distinguish their own calf from the rest. To support her argument she cites Murie who found that dogs were able to find concealed calves. On the other hand Walther (1969) observed jackal and hyaena passing 10-30 metres from concealed Thomson gazelle fawns without detecting their presence.

Whatever the case may be, the available evidence points to the fact that all precautions are taken to limit any potential odours to the minimum.

The/...

The intensive and thorough licking of particularly the genitals of the young calves supports this statement. Further important evidence endorsing this point of view is the fact that many of the external glands are either poorly developed or non-functional in the young animal. Gosling (1969) found that in a tame Coke's Hartebeest (Alcelaphus buselaphus cokei) calf both the preorbital and pedal glands were non-secreting during the period that the calf would normally have been in concealment. To support this Walther (1969) reports that "testing the glands of the skin in very young gazelles (and several other species of horned ungulates) I found them obviously to be not yet in function. This seems to be especially important in regard to the interdigital glands". The author has not yet had the opportunity of determining the functional aspects of the skin glands in young roan antelope though the following important behavioural adaptation cannot be overlooked with regard to the avoidance of unnecessary "tell-tale" scent-trails which may disclose the position of a hiding calf: when a female calls up her calf to be nursed she does not go right up to her calf and neither does she accompany her calf to its place of concealment after it has been nursed. It does appear that the mother in this way deliberately avoids leaving a trail to her lying up calf which may later be followed by a predator. Walther (1969) has also referred to this phenomenon in Thomson's gazelle.

(b) Suckling/...

(b) Suckling:

For the first 5 to 6 weeks after birth suckling is restricted to the early morning, i.e. just after sunrise the young calf leaves its hiding place, approaches its mother and suckles. Observations extending from daybreak to dusk to ascertain whether there was no other feeding time during the day revealed that cows do not return to suckle their calves during this period. However, it was noted that during the late afternoon a cow with a calf in hiding will slowly graze towards the area where the calf was known to have taken refuge in the morning and it is very probable that the calf is nursed some time after nightfall. When cows are encountered just before, or shortly after, sunrise they are not accompanied by their calves and from this the deduction can be made that though there may be one or more feeding sessions during the night the calf does not remain with its mother throughout the hours of darkness.

Observations made on the post-natal relationship between mother and calf of the gemsbuck (a member of the sub-family Hippotraginae) revealed that the calf was frequently suckled during the night but that the mother paid no attention whatever to the youngster during the day (Thomas, 1961). The lack of nursing periods during the day corresponds closely to the author's observations on roan and this is especially significant in the light of the

remark/...

remark by Fraser (1968) that "there does not appear to be a physiological need for frequent nursing".

When mother and calf are together in the morning for approx. 60-90 minutes the time is almost exclusively spent in nursing and suckling. Apart from brief periods of grazing, the cow continually grooms and licks her calf while the youngster may suckle up to 3 times during their sojourn. When undisturbed, calves normally suckle more than once but are discouraged by their mothers to drink more than 3 or 4 times. When a cow does not want her calf to suckle, she merely gives a few paces forward when the calf attempts to drink.

The actual time spent in drinking varies from a few seconds to 5 or 5½ minutes at a time. At the age of 5 days one calf, André, drank for a total of 6 minutes and a few seconds between 0605 and 0705 hours, representing 3 periods of suckling of 5 min. (0605 hrs.) 1 min. (0640 hrs.) and a few seconds (0705 hrs.). On the morning of 20th November, 1968 - at the age of 9 days - the same calf was observed to suckle continuously for 5-5½ minutes. Once the calf has joined the herd it normally approaches its mother to drink shortly after activity is resumed following a rest period.

A group of young calves may have been resting any distance up to 100 or more metres away from their respective mothers. Once they resume activity the

calves/...

calves rise, wander about and graze for a few minutes before one or more of the calves may start off in the direction of its mother.

The calf may charge up to its mother at full gallop from a distance of 50 metres or more, drop onto its knees and without any preliminaries proceed to suckle. After a minute or two the mother moves forward a few paces - which spells the end of suckling. If the calf has had its fill it will rise, resume grazing and gradually move off towards its young companions. At other times it may follow its mother a short distance, again attempt to suckle and eventually drift off to the other calves. Calves drink regularly for the first 3 to 4 months after which the suckling frequency declines and becomes quite irregular. However, sporadic suckling is continued up to the age of 6 months when the calves are finally weaned. Weaning of calves appears to be quite natural in roan antelope and apparently the urge to suckle gradually fades away until the calf exhibits no more tendency to suckle. Weaning is not brought about by any form of aggression on the part of the cow towards her calf. Newly born calves stand on all fours while suckling but soon adopt the kneeling position once they have attained sufficient height to reach the udder.

Concealment/...

Fig. 23(a):

Fig 23(b):

Fig. 23 (a & b): A calf, only a few days old, lying-up in a stand of Schmidtia bulbosa grass. Nwashitsumbe, May, 1969.

Concealment of calves:

The behaviour of young calves of different species immediately after birth may be divided into two distinct categories, viz. those that follow the parent animal from the time of birth and those that conceal themselves for a varying length of time before joining the herd.

Roan antelope calves fall within the second category and remain concealed for roughly the first 6 weeks of their life. In the roan camp 7 calves were kept under close observation during their period of concealment and the major features arising from this characteristic are the following:

(a) Manner of concealment:

Due to the dense grass cover of the camp and the timidness of the species, the posture in which young calves lie down while hiding was observed on rare occasions only. A calf which lay down in relatively open burnt veld curled its legs in under the body while the neck and head were stretched out in front of it. The conspicuously long ears were outstretched to either side of the head and even in the open veld the calf blended so remarkably well with its surroundings that it was only with difficulty that it could be spotted. Another calf that was accidently found while driving through a clump of tall Themeda triandra grass lay in the same way.

A calf of a few days old which was found lying up in short grass lay in exactly the same way but

with/...

Fig. 24: Typical environment in which calves find concealment during lying-up period of six weeks.
Nwashitsumbe, January, 1968.

with the ears extended backwards along the neck.

This manner of lying-up appears to be most effective and despite the meagre cover in which 2 of the calves, mentioned above, were found they were extremely difficult to detect and visually most effectively concealed.

Other calves that are known to hide themselves during their first few weeks of life curl themselves up with the head and neck held in similar fashion (Gosling, 1969, Walther 1964). While resting the older calves and adult roan bend their necks backwards with their heads facing to the rear and it is more than possible that the young calves also take up this position while in hiding, though it has not been observed.

(b) Locality of concealment:

Sufficient cover is the major consideration in the choice of an area for concealment. Roan are on the whole an open savanna or plains-loving species which avoid dense thickets so that anything from long, dense stands of grass as in vleis or areas of long grass interspersed with shrubs or low trees may be implied by "sufficient cover". All these situations are provided for in the camp and ideally the most preferred areas for concealment appeared to be areas of rank grass and low shrubs. Cover in this form effectively conceals the calf from view while it also provides shade during the heat of the day. In such an area the calf selects

a/...

a clump of dense grass or low shrub where it lies down between nursing times. In roan the position is therefore essentially the same as what Gosling, (1969) has noted for Coke's Hartebeest, viz. "the only reliably consistent feature of the site is good cover of long grass or forbs which effectively conceals the calf".

The total area utilized by the calf in selecting its 'hiding' sites varies with the age of the calf. During the first few days (7-10) there is very little activity during nursing periods and if undisturbed the calf may seek concealment in an area of approximately 100 x 100 metres. As the calf becomes more active it also remains with its mother and the herd for longer periods during the morning and may wander away from its usual 'lying up' area. In the transitional period - immediately prior to joining the herd - the calf usually lies up close to the resting herd. More than one calf may occupy the same area simultaneously.

In Grants gazelle the 'lying up' area is of the order of 20,000 sq. metres (Walther, 1965).

(c) Selection of the concealment area:

The general area in which a calf is to be concealed is in the first place the choice of the mother when she isolates herself from the herd to give birth to the calf in some secluded spot. While

detached/...

detached from the herd, and especially during the process of giving birth, the cow is most vulnerable to predation and it is only reasonable to assume that she will select an area affording maximum cover and protection both for herself and later also for her calf. Birth and concealment areas fall within the activity zone of the herd.

It is evident that mother and young remain close together for the first few hours after birth, but for how long the author has been unable to determine. However, it appears that between 12 and 24 hours after birth the calf may conceal itself. Evidence for this was gained by observing newly born calves (in 2 cases no more than 1-2 hours old) with their mothers in the late afternoon (1500 hrs. and 1700 hrs.) but were concealed at dawn the next morning. Further, during the very first stages there may be some guidance from the mother to initiate lying up ('ablieger') behaviour in the calf in which case the cow selects the lying up site. From the second day after birth. the selection of a particular spot is the choice of the young calf itself. Once nursing and suckling is completed the youngster may walk up and down for a few metres in front of its mother a number of times and then meander off into the bush on its own. While walking away, head just below horizontal and ears backwards or twitching now and again, the calf follows neither a straight line nor

seems/...

Fig. 25: A calf utilizing the coppice growth of a mopane, Colophospermum mopane, shrub for concealment. Nwashitsumbe, August, 1968.

seems to be heading for any particular object. Suddenly the apparently aimless ambling of the calf ends when it disappears among some long grass or below a shrub where it remains concealed until it is again called by its mother. Walther (1968) mentions that gazelle fawns are attracted by "uprights" such as tree stumps, shrubs or high grass and by "moulds" such as shallow depressions in the ground, hollows between the roots of trees and in captivity even the feeding trough. Though the author has found a roan calf lying in short grass (approx. 15 cm high) their more general selection for sites alongside shrubs or in a clump of high grass substantiate the influence of "uprights" in the choice of a lying-up site.

(d) Daily activity of calves:

Despite all attempts and observation extending from sunrise to dusk, the only time at which young calves have been found with their mothers is during the early morning. Usually about 20 minutes after daybreak a cow will graze to within 10-20 metres of her calf upon which the calf makes its appearance and is nursed by its mother. Nursing may continue on and off for an hour or more during which time the calf also participates in such activities as playing and running about with other herd animals. Soon after this it departs from the herd, lies down and is not seen again until the following morning. This is especially true of

the/...

the first 3 to 4 weeks after birth (cf. oryx calf in the Lincoln Zoo, Thomas (1961)). Gradually however, the early morning sessions become more prolonged and the calf remains with the herd for longer periods. Even at this stage it is essentially in the early morning that the calf is seen with its mother and only rarely is it with the herd during the afternoon. The transition from the period of concealment to a fully fledged member of the herd is not abrupt but takes place gradually as the daily activity of the calf increases until it can follow the same pattern as that of the adults. The behaviour of the calf from the time of birth to recruitment to the herd, follows the general pattern outlined below:

First week: During this period the calf is still very weak and only makes a brief appearance in the early morning to nurse. Soon after suckling the calf lies down and is not seen again during the day. Toward the end of the week the calf may show some interest in other young calves and make short excursions from its mother.

Second week through to sixth week: General pattern much the same as for the first week though calf becomes more active, remaining with the herd for increasingly longer periods in the morning. Still remains concealed during the rest of the day.

Seventh/...

Seventh to ninth week: The young calf is now much more active and follows the herd throughout the day. In most cases young calves "joined" the herd in the seventh week but under certain circumstances (see: relationships between calves) it may only occur in the ninth or tenth week.

(e) Initiation of concealment behaviour:

Lying up behaviour has obviously evolved to afford the maximum amount of protection for young calves which are unable to follow their mothers from the time of birth. The inclination of young calves to conceal themselves is probably an innate behavioural pattern. However, just as fleeing from danger of the more active calves (followers) is in response to the guidance of the mother, there may be some evidence to suggest that roan mothers 'imprint' on their calves in the first day or two following birth the necessity of 'lying low' in the face of danger and thereby gaining maximum protection from this type of danger evasion mechanism. The following observations may be of some significance: while observing a young calf and its mother on 2.12.68 the mother appeared particularly nervous due to the proximity of the author's vehicle. After very briefly nursing her calf she lowered her head, ears extended laterally and brought her nose down towards the calf. The calf dropped down and lay still. Under "Communication" further examples are given. The

impression/...

impression gained from such observations is that the cow could release lying up behaviour in the calf by means of signs whenever danger threatened and that this initiated - if not endorsed - the tendency of the calf to conceal itself. Also, if the mother of a young calf is disturbed while nursing her calf she may lead the calf away to safety - once again reflecting the influence of the mother on the calf in contrast to the lying low reaction.

(f) Emergence of calf from place of concealment:

The emergence from the lying-up site and contact between mother and calf has already been referred to (Mother/Calf relationships, and later under Communication) but may be summarized as follows: during the late afternoon the mother - either alone or in company of the herd - gradually approaches the area where the calf is known to be concealed. Contact between mother and calf has, however, not been observed in the late afternoon. When the mother is about 10-20 metres from the calf she raises her head and gazes intently in all directions. She then settles her gaze on one particular spot, and not long afterwards the young calf makes its appearance and without any further ado it hastens towards its mother. Nursing then takes place.

Playing:

Roan antelope, though superficially creating the impression of quiet docile animals, indulge to a greater or

lesser/...

lesser degree, in a wide variety of activities other than the normal maintenance activities of grazing, drinking and resting. Of the other activities, playing - either in the form of play-fighting or a jubilant outburst of running, kicking and stotting - is one of the most important, especially among the younger individuals of the herd.

Play-fighting, as implied above, may be a misnomer, and is one of the most frequent forms of activity involving 2 or more members of the herd. Depending on the individuals participating, this form of activity may range from light-hearted playfulness - as in young calves - to more serious bouts of sparring in the adult animals and plays an important - if not the deciding - role in establishing the social standing or hierarchy of the various individuals in the herd. As such, this form of activity has been described in more detail in referring to the social ranking order of the members of a herd and is only relevant here where it forms a part in the playing of young calves.

Though the older members of the herd may participate in exuberant playing, it is of rather infrequent occurrence and the main participants are the young calves.

In an analysis of the situations or conditions which have given rise to playing, it would appear that the following factors constitute the most important stimulants for this form of activity:

(i) overcast, cool weather conditions and

(ii) the presence of young calves. Most notable is the impact a newborn calf has in stimulating playfulness in the other young calves in the herd. This seems to be due to the fact that the calves

form/...

form a very close liaison amongst themselves at an early age (see: Relationships among calves) and the addition of a 'new member' to the group invariably arouses great excitement - the degree or level of excitement being the greatest in the youngest of the group and gradually declining in intensity in the older calves.

Of the 15 observations of jubilant playfulness 4 were initiated by the presence of a young calf while cool, overcast weather - mostly accompanied by light showers of rain, was responsible for 8. On the remaining 3 occasions no obvious factor played a role.

On 2 of the 15 occasions only animals over 2 years of age took part; on a further 2 occasions both adults and juveniles participated while playing by young calves only took place on the remaining occasions.

Playing varies in length of time from less than 1 minute to about 10 minutes but seldom much longer. It is difficult to measure the exact time as all members participating are not equally active. Playing is normally confined - as could be expected - to the early morning and late afternoon as this coincides with the general activity rhythm of the herd. Playing is mainly comprised of the following activities:

(a) Running:

Running or galloping at full speed in wide circles around the herd and frequently darting in zig-zag fashion through the herd is one of the most conspicuous features of playing. Every so often

the/...

the animal will stop, suddenly burst into another gallop; abruptly stop, veer around and dart off in another direction. At times they attempt to cut their corners so sharply that they momentarily loose their balance but soon regain control and dart off in another direction. More often than not their mouths are wide open while running about and this appears to be not as much due to exhaustion but from mere appeasement.

In the majority of cases it is this wild, uninhibited and uncontrolled running about that has a contagious effect on the other members and soon one or more of the others join in the gimmicking. The start of a "follow-the-leader" run may also be caused by the playful animal falling on its knees in rather challenging attitude before another and then quickly jumping up and running away again.

(b) Stotting and prancing:

This form of display is closely associated with the running and usually just before coming to a halt after a round of running the animals slow down either into a slow, stiff legged gallop (stotting) which again goes over into a stiff-legged trot (prancing). While stotting and prancing the ears are extended perpendicularly above the head - which is held high in a rather proud manner - while the tail is lifted vertically above the body and continually switches from side to side. This, no doubt, is certainly the most

attractive/...

attractive display while playing. In the young animals both stotting and prancing are solely associated with playfulness. Cows with young calves may sometimes lead their calves away from a disturbance by trotting out before them in the stiff-legged gait (prancing), which suggests that this form of locomotion may have some signal value for the young or may reflect nervousness in the adult. Walther (1958) has also described prancing for the oryx.

Stotting is one of the characteristic displays among the gazelles and in Thomson's gazelle (Walther, 1964) stotting occurs as a transition from one level of excitement to the next, e.g. with the rise or fall in tension and may therefore be regarded as a visual signal for other members of the species (Walther, 1964, 1965; Estes, 1966). In roan antelope stotting does not fulfil any such function and has only been associated with playing.

(c) Play-fighting:

Quite frequently even the very young calves interlude the wild running by confronting one another on their knees and after a few seconds of playful butting with their foreheads and pushing they again jump up and commence running around. These play-fights may be repeated several times between different members during each 'play-session'. This appears to be the earliest

manifestation/...

manifestation of the habit of roan to butt and push one another while on their knees and which in later life develops into the most important form of ascertaining each individual's rank in the social hierarchy and which forms the basis for later ritualized intraspecific fighting.

(d) Weaving:

Rather more infrequently than the above, it has also been observed that at times an individual may fall onto its knees and vigorously shake its head in a clump of long grass while the tail switches from one side to the other.

One young calf has even been observed to butt a heap of ground. Though this display is incorporated in play it also develops into one of the important factors of sociological significance in the adult animals i.e. horning of shrubs, etc. (See fig. 10.)

(e) Kicking up with the hind legs and jumping:

Closely associated with running and galloping is the kicking up of the hind legs. This usually takes place while the animal is running when it suddenly lowers its head and kicks up with its hind legs. This form of play may be repeated several times in a spell of playfulness.

Frequently young calves bolt from a standing position and leap into the air after which they burst into another round of running.

The/...

The following examples will suffice in describing play in Roan antelope:

(i) During the early morning of 1.3.68 Stoffel, a calf of 5 months showed great interest in a young calf of 3 weeks. Suddenly he broke into an uninhibited spell of playfulness, consisting of short spurts of running through the long grass in circles at top speed and occasionally kicking into the air with his hind legs. At times he would fall flat in the grass and vigorously shake his head about, then suddenly jump up, kick into the air and run about again. In passing a young heifer he fell onto his knees in a rather challenging attitude. The heifer responded by going onto her knees but he immediately jumped up again, kicked up and ran away. Shortly afterwards he calmed down and resumed grazing.

(ii) In the late afternoon (1800 hrs.) BG, Nel, Lenie, Fransie, Stoffel and LH became very playful and one after the other as in 'follow-the-leader' they bounded hither and thither through the veld with BG kicking up her hind legs and the others breaking into spells of "prancing" with their ears conspicuously outstretched above their heads.

Communication between cow and calf:

Generally the most accepted form of communication between 2 or more individuals of a species is based upon a

variable/...

variable series of sounds uttered by one or more individuals in a group of animals under a variety of circumstances, with each sound in the "vocabulary" conveying to each member of the group some specific "message" relative to the nature of the prevailing situation, i.e. alarm calls in the presence of danger, distress-calls, etc. Communication may, however, also be attained by visual signals as for example the posture of an individual that may alert the group in times of danger; or by olfactory means such as from urination or the rubbing of the preorbital glands in certain strategic places of the territory or home range.

Such means of communication as mentioned above almost invariably apply to all the individuals of a particular herd or the population of the species as a whole. However, the communication between a cow and her calf presents a problem of its own as the code of communication is directed between a particular adult in the herd to a particular juvenile of the same herd without applying to any other members of the herd.

From observations on the cow-calf relationships in roan antelope it would appear that communication between mother and calf is achieved by both visual (signal) and auditory means.

(a) Visual communication:

This is the general form in which the cow "calls" her calf from its place of concealment to be nursed. When a herd is in the area of a hiding calf the mother normally moves to the one side of the herd and approaches to within a few metres of where her calf is concealed. Anything from

five/...

5 to 20 metres from the calf the cow stops and with head held high and ears extended laterally but turned towards the calf, she will intently gaze in the direction of the calf. Invariably the calf will emerge from its hiding place, approach the cow and start suckling while the cow licks her calf. This form of communication lasts for as long as the calf remains in hiding - for the first 5 to 6 weeks after birth - after which it is apparently no longer required as a form of communication between cow and calf.

In the very early stages - for the first week or so after birth, the cow may also give her calf some signal to lie down if there is any disturbance while the cow is nursing her calf. Usually the cow lowers her head and brings her muzzle close to the calf with ears still extended laterally, on which the calf promptly lies down.

To illustrate this form of visual communication, the following examples may be quoted from field observations:

14.2.68: At 0700 hrs. the herd was located in the vlei in Block 2 but was slowly moving away when the mother of Fransie, LY, turned around and walked back to the vlei. She was extremely wary and after walking a few paces, she first paused and looked round. She approached to within 50 metres of the author's vehicle and gazed intently in a particular direction. Fransie then

suddenly/...

suddenly made her appearance, immediately approached LY and suckled.

20.11.68: During the early morning the herd was grazing in the southern portion of Block 4 but gradually crossed over into Block 2 where André, calf of LYRR, was lying. LYRR suddenly started walking away from the herd and after she meandered 200 metres away from the others she stopped. After she had stood there for a while André emerged from the long grass in which she was lying, approached her mother and commenced drinking.

2.12.68: During the early morning a cow was observed approaching her concealed calf. As she got to a clump of grass she lowered her head close to the ground and Don, her calf, appeared. The cow was extremely nervous with the vehicle so close to her and the calf and after briefly nursing her calf, she brought her nose close to the face of her calf and Don immediately lay down.

It is admitted that these conclusions are derived from field observations under natural conditions and the "signs" given by the mother to their calves may also have been accompanied by some form of auditory communication which was not detectable under the circumstances.

(b) Auditory communication:

No form of auditory communication has been observed on the part of the mother, directed at either her calf or any other individual of the herd. However,

when calling up her hiding calf a cow stands some metres away and gazes in the direction of her calf. On a number of occassions it has been observed that the cow points her nose slightly forward with vague movements of the lips. No sound has actually been heard. Walther (1965) describes the approach of a Grants gazelle mother to her lying young which corresponds almost in detail to that of the roan. He was once able to make out a soft sound uttered by the mother when calling her young (these calls had previously also been heard in Zoological Gardens where he observed different species of gazelle). It is quite possible - even probable - that roan cows also uttered sounds to raise their calves though they could not be detected under the prevailing circumstances.

Actual calling (or sounds) uttered by young calves have frequently been heard. The sounds are short, high-pitched metallic sounds repeated a number of times, not unlike that made by some crickets. When calling the calf rapidly lifts its upperlip with a simultaneous exhalation.

Calling by calves in this fashion is directed at both (a) their mothers and (b) other young calves in the herd. Extraordinary, however, is the fact that only on rare occasions have cows been observed to react quite obviously in response to the calling of the calf. Cows have never been heard to reciprocate a calf's calling - in fact,

no form of auditory communication on the part of the cow in the mother-calf relationship has been noted.

A few examples of field observations will suffice to explain:

(1) Calling of the calf to its mother:

On the morning of 3.1.69 the herd crossed over from Block 4 into Block 2. André and the other young calves were with the herd and after moving some 200 or 300 metres into Block 2 André turned around and started making her way back to Block 4. However, as she was about to cross back into Block 4 the vehicle was parked in her way. She halted, lifted her head and repeatedly called 4-5 times. After waiting for a little while and finding that there was no response from either her mother or any of the other animals, she turned around and rejoined the others.

Cruising through Block 3 on the morning of 10.1.69 by vehicle 2 young calves, André and Nel, were found lying down in a clump of tall grass with their mothers and the herd grazing about $\frac{3}{4}$ kilometers further away. The vehicle was parked 8 to 10 metres from the 2 calves and after a few minutes Nel, the older of the two called softly a few times and then arose while André kept low down with her head on the ground.

After/...

After rising Nel called out again and André stood up. Thereupon the two made their way to the herd. Again there was no obvious response from either of their mothers.

(2) Calling between one calf and another:

On the afternoon of 16.11.68 the herd rested in the area where LYRR had concealed her calf during the morning. When they later resumed grazing activity and crossed from Block 2 into Block 4 Nel and Lenie remained behind where the calf, André, was presumably lying down. After some time they followed the herd into Block 4 but had not reached the herd when Nel turned around and moved back into the firebreak between the 2 blocks. Nel then uttered her shrill call 3 times and, soliciting no reaction from any of the others, returned to the herd. Here she again called 3 or 4 times and moved towards her mother but did not suckle. Without delay Nel again returned to the firebreak and called a number of times. Yet there was no response from the others who continued grazing. Nel then ran back into Block 4 to Lenie; again returned to the firebreak and called. It was now obvious that Nel was directing her calls at Lenie and as she (Lenie) showed no inclination to follow Nel, Nel once more returned to her. The fourth time Nel broke

away/...

away from the herd she hurriedly crossed over into Block 2 and this time Lenie followed close behind her. Stoffel followed suit and one after another the herd animals followed the young ones until the whole herd had eventually crossed back into Block 2.

What actually stimulates young calves to call is not known but it would appear from these observations that calling is most prevalent where there is a certain amount of uncertainty or disturbance involved on the part of the calf i.e. calves most frequently called when the author's vehicle was parked in such a way as to 'cut' them off from their mothers or merely blocked the route they were taking. The deduction could therefore be made that calling is reverted to in times of stress as in the presence of threatening danger.

CHAPTER VI.

SURVIVAL VALUE OF THE MOTHER-CALF RELATIONSHIP.

In the text the relationship between mother and calf has been referred to as rather 'loose', thereby implying a certain degree of neglect on the part of the mother in the care of her young calf. However, the inference is completely subjective and the advantages of such a system cannot be ignored if one considers the wide variety of species adhering to the principles of this system in rearing their young. To obtain an objective picture of the survival value the system provides for roan antelope it may be tested against the following major decimating factors limiting population growth in natural populations of the species:

Predation:

Fully grown roan antelope are, by virtue of their size and pugnacious nature, free from predation by most of the African carnivores with the exception of the lion (Panthera leo) Young calves, however, are weak at birth and their movements poorly co-ordinated. During the period of concealment the defenceless youngsters may fall prey to a large number of predators, including lion, leopard (P. pardus), cheetah (Acinonyx jubatus), wild dog (Lycaon pictus), hyaena (Crocuta crocuta), black-backed jackal (Canis mesomelas), python (Python sebae) and quite possibly even the martial eagle (Polemaëtus bellicosus) and chacma baboon (Papio ursinus). Immatures, from 2 months to 2 years,

remain/...

remain vulnerable to predation by hyaena and the larger predators.

As could reasonably be expected, the effectiveness of the mother-calf relationship against such a wide array of predators would most likely be influenced by the following factors: (i) degree of concealment of the young calf and (ii) the pattern of calving in relation to time (seasons).

(a) Degree of concealment of the young calf:

(i) The role of cover:

In discussing the various phenomena associated with the concealment of the calf, it was pointed out that the area in which the calf seeks refuge is in the rule well provided with shrubs and tall grass in which the calf may effectively "almost disappear from the face of the earth" (Walther, 1969). The habit of "Ablieger" type calves to seek cover alongside vertical objects or in depressions further enhances their success in eluding visual detection. Cover may, however, have a seasonal aspect and will be referred to again under the appropriate heading.

Contributary to the successful evasion of predators by concealment are the elaborate precautions taken to eliminate any possible scent which may betray the position of the calf. The inactivity of some of the important skin glands (preorbital, interdigital, etc.) appears to be a further evolutionary adaptation to this end (see text).

(ii) Tendency/...

(ii) Tendency to "freeze" in the face of danger:

In common with the young of other species in which the infants lie up or remain concealed for the first few days or weeks of life, newly born roan calves are weak and poorly co-ordinated and for the first few days amble about in a slow and unsteady fashion. The habit of lying-up in this species is therefore quite clearly an adaptation to bridge the gap between birth and the time that the calf can assume the normal activities of the herd. Not being able to elude its aggressor by fleeing during this time the only alternative left to the young calf is to depend entirely upon concealment and, even if detected, to "freeze" i.e. to lie motionless, thereby avoiding the attraction of any unnecessary attention upon itself. In calves up to a few days old the tendency to 'freeze' is especially well developed and if encountered in the field they are quite easily approached and handled without making any attempt to run away. On 16.5.69 a calf of 5-6 days old was found lying in a stand of short (about 15 cm tall) Schmidtia bulbosa grass. As the author approached the calf lay 'dead' still but followed his movements with its eyes. The author was able to touch and handle the calf and though its accelerated rate of respiration indicated its fear it did not

attempt/...

attempt to run away. Gosling(1969) also found no difficulty in catching and marking Coke's hartebeest calves shortly after birth. The avoidance of detection through cover and the 'motionlessness' of the calf is the major - if not the sole - behavioural adaptation of the roan antelope calf against predators. The reliance of the young calf on concealment for its survival is clearly illustrated by the fact that the mother frequently leaves the calf entirely on its own while she wanders away to graze and drink with the herd. In the Serengeti National Park, Estes,(1967) and Walther (1969) found that Thomson gazelle mothers remained close enough to their concealed fawns to actively defend them against approaching jackal and hyaenas. If a roan mother is with, or in the proximity, of her calf and it should be threatened by danger - especially a predator - there is no doubt that she will retaliate and lodge a counter attack. During August, 1969, Mr. and Mrs. H. Braack of Skukuza reported a badly wounded roan calf with a herd near the Tsendi river. When they tried to investigate, the calf dropped down beside a shrub while the agitated mother moved off about 10 metres. As they approached the place where the calf lay the mother became quite aggressive and despite a

rifle-shot/...

rifle-shot overhead she would not budge. This seems sufficient proof that a roan cow will in fact actively defend her calf against threatening danger.

After the first few days calves are more prone to jump up; run away a few metres and then drop down in a patch of long grass or other form of cover when threatened by danger. Walther (1969) found this form of 'predator deception' effective even among adult territorial Thomson's gazelle and relates 2 cases in which males managed to escape pursuing wild dogs merely by lying down. In flight young fawns also have the habit of falling to the ground at full pace while the mother continues on her course.

Ansell (1963) records an instance when a young roan calf was cut off from its herd by Land Rover and then immediately lay down. After capture it was handled freely and subsequently released on the same spot. It again lay down and remained in this position until the observer left the area. While searching for a concealed calf during May, 1969, the author almost trod on the calf before it jumped up, ran approximately 20-30 metres and fell down again. The view was somewhat obscured by some shrubs but a search for the calf immediately ensued in the area where

it was thought to have taken refuge. After some time the search was abondoned - without success!

A phenomenon in the relationship between roan calves (see text), which is apparently absent in other "Ablieger" types, is the bond which exists under certain situations between a calf which has already 'joined' the herd and a younger calf still lying out. It has been observed that the older calf may lie down close to the younger one when the herd moves off. During the late afternoon the older calf may emerge from its resting place and start grazing in the area of the concealed youngster while the rest of the herd is nowhere in sight. The result of such a relationship certainly appears to endanger the safety of one or both the calves, i.e. the older calf may attract the attention of a predator on itself and though it may be in a position to escape the onslaughts of the predator, it may nevertheless endanger the life of its younger companion.

However, it is extremely difficult to evaluate the exact survival value of the concealment adaptation in the young and can only be attempted after the following considerations have been made:

(b) Calving pattern in relation to time (seasons):

Though information on the breeding of roan antelope appears to be rather inconclusive for most areas, the majority of authors indicate no peak, or confined breeding season (cf. Blower, 1961, for East Africa; Smithers,(1966) for Central Southern Africa; Fairall (1968) for Kruger National Park). Ansell (1960) reported an apparent peak between April and August for Zambia though records for the period December to April were insufficient to draw any definite conclusions. The lack of a breeding season in the Kruger Park is further substantiated by the births recorded in the roan enclosure, viz. January, 1; February, 1; March, 0; April, 0; May, 4; June, 0; July, 2; August, 1; September, 3; October, 1; November, 2; December, 0. From the available data it may therefore be concluded that there is no seasonal peak in the birth of calves.

The occurrence of births at random throughout the year is in itself of significant ecological importance with regard to the rearing of the young. In his study of wildebeest Estes (1966) found that predation by hyaena is severe on the very young calves and that calves more than a few days old are generally ignored by these predators. He further noted that calves born outside the restricted calving period are more susceptible to predation due to the absence of the buffer of

older/...

older calves which tend to frustrate the onslaughts of hyaena on the younger calves. It is therefore conceivable that the evolutionary processes would have selected for a restricted peak in calving in the wildebeest. As an adaptation to meet these requirements. Estes (1966) found that "peak calving begins abruptly, continues at a fairly constant rate for 2-3 weeks, then declines more gradually, with up to 20 per cent of births spread over the following 4-5 months". Gosling (1969) has further pointed out that the restricted calving peak has the advantage of providing predators with a super-abundance of prey which enables a substantial percentage of the young to survive the critical first few days of life and thereby maintain the population. This example of the wildebeest, a typical "Nachfolge" - species, i.e. a species in which the young calf remains with and follows its mother almost from the time of birth, is quoted to illustrate the alternative to the "Ablieger"-type calves found in the roan antelope. For the wildebeest, Estes (1966) draws attention to the following important factors: mothers do not normally defend their calves, but may do so once the calf has been overtaken in flight; calves are not concealed after birth. In this species it appears, ironically, that the death of one calf has a distinctive survival value for its companions.

On the other extreme is the roan antelope with no particular calving peak, an adaptation unquestionably

evolved/...

evolved to ensure the survival of the young for the propagation of the species. It is the author's contention that the random births of calves is a definite anti-predator adaptation which has in itself great survival value for the species and which further tends to increase the efficiency of the lying-out behaviour pattern in the bridging of the most vulnerable period in the life of the calf.

Gosling (1969) has postulated that "cryptic prey suffer less mortality from predation if their inter-individual distance is greater than the 'direct detection distance' of them by their predators". This statement may certainly be accepted, almost as axiomatic, and the distribution of parturition in roan is clearly aimed at complying with this basic principle. The possibility of detecting concealed calves increases with the number of calves in a given area and also with the corresponding decrease in distance between the calves. Conversely, the chances of flushing a calf become more remote with a decrease in their number and an increase in their inter-individual distance. The lack of a calving peak and the sporadic births have ostensibly evolved to draw maximum benefit from this rule.

(c) Seasonal aspects which may influence calf mortality:

(i) Seasonal aspects of cover:

Under section (a) the importance and role of cover for the survival of the young calf is

emphasised/...

emphasised. However, attention must be drawn to the fact that the quantity and quality of cover varies considerably in accordance with the different seasons of the year. During the wet season there is an abundance of cover in the form of long, rank grass, dense shrubs, etc. which is more than sufficient to suit the needs of the calf.

During the long dry season the deciduous trees and shrubs shed their leaves and the cured grasses are gradually trampled and grazed to the ground as the season progresses. Though these conditions may place an additional stress upon the young roan calf the species once again exhibits a remarkable adaption to these conditions in the cryptic colouration of the calf (rufous-brown at birth) which blends perfectly with the drab background to render the calf almost invisible. Though there is a vast difference in the type of cover available during the different seasons it is probably only in exceptional cases that cover may prove to be insufficient to provide the necessary protection for the young in suitable roan habitat.

A further point of interest merits mention in this respect and that is the habitat preferences of roan antelope. Selection of habitat by roan and the description of the

various components of their habitat will be the subject of a later paper but the following characteristics may be mentioned in brief: roan antelope avoid over-grazed areas and are unable to 'compete', or probably even to hold their own, with other herbivores under such conditions; rank grass stands being an important component in their habitat.

From these two statements it may thus be deduced that roan naturally select areas with sufficient cover for their young and on the other hand that a lack of suitable habitat may place a serious limitation on the natural recruitment to the population. This could possibly imply a higher death rate among the young calves. It seems to be quite conceivable and logical that the mortality among young calves would be increased in areas denuded by over-grazing and trampled daily by hordes of competing ungulates. This point emphasises the fact that competition between herbivores is not only restricted to food plants but also includes the physical aspects of the environment which are required to make a particular area "livable" for a particular species. These physical requirements of the habitat naturally differ from one species to the next.

(ii) Food availability:

The fact that different seasons may be identified in the Kruger Park on the basis of presence or absence of rain also indicates that the availability, palatability and nutritional value of food plants vary accordingly. Fairall (1968) has attempted to correlate the timing of the calving seasons of various ungulates in the Kruger Park to the most favourable time of the year but found that most were off the mark, i.e. either too early for the first rains or toward the end of summer. Most species, however, have their calving peaks close enough to the rainy season to draw benefit from the nutritious young shoots which are normally readily available at this time of the year.

If roan births occur at random throughout the year it could be expected that approximately fifty percent would be born in the period April to September, i.e. the most trying (hazardous) period from the environmental point of view. Roan calves commence nibbling and grazing at 3-4 weeks of age and though they may still subsist on their mothers' milk at that age they gradually become more and more dependent on solids for their nutrition. Most of the Kruger Park falls within the 'sweet-veld' zone of South Africa, which implies that the

cured/...

cured grasses retain much of their nutritional value though one wonders to what extent the young calves are handicapped at an early age by the inevitably less nutritious grazing and the coarseness (unpalatability) of the cured grasses. It would furthermore also be expected, theoretically, that roan would be more dependent on climax grassland, with abundant cover during this period, as competition for the more palatable and nutritious grass species becomes more severe as the availability of such species decreases in the course of the winter. A shortage of favoured species may have a detrimental effect upon a young calf adapting itself to grazing while an animal suffering from malnutrition is generally more susceptible to disease, parasites, predation, etc.

(iii) Water requirements:

It is a well known phenomenon that the plains animals which concentrate around the few available watering points during the dry season immediately disperse into the adjoining country with the first substantial summer rains. The whereabouts of the various species during the summer months (wet period) is a characteristic of each species, viz. some species show migratory tendencies, others again move further from their winter quarters

than/...

than the more localised species. The important fact is that animals are more evenly distributed throughout their available habitat and that inter-specific and even intra-specific competition is greatly relieved. Of the many advantages experienced during the wet season, the following are noteworthy from a survival point of view:

The inter-individual distance between individuals of the same and different species is increased which makes them less prone to predation; water is freely available which avoids unnecessary aggregations and concentrations of animals; food of high nutritional value renders the animals less susceptible to disease, parasites, and malnutritive states.

It is not difficult to visualise the advantages that these conditions hold for the young roan calves and the expectation of survival is also expected to reach its peak during this period.

On the other extreme, conditions are reversed during the dry winter months. As the depressions and other natural waterholes gradually dry up during this period animals are compelled to concentrate in large numbers around the few remaining watering points at the height of the dry season. These conditions harbour additional perils to the roan mother and her calf of which the

following/...

following may be of importance:

To avoid competition and also the carnivore pressure which builds up around high concentrations of herbivores, the roan cow has to withdraw an appreciable distance from the water (2-3 kilometers or more) where she can give birth to her calf in isolation; being dependent on water the mother probably leaves her recumbent calf alone for longer periods than would normally have been the case; pregnancy and the subsequent nursing of a calf may place a stress upon the cow which could be detrimental to both mother and calf; the danger of predation increases.

The life expectancy could therefore quite feasibly be expected to differ between the two seasons.

(d) Other mortality factors among young calves:

(i) Veld fires:

Veld fires are normally restricted to the dry months. Accidental fires, caused by agents such as lightning, poachers, etc., are largely contained by an extensive network of fire-break roads which aid in the effective control of such fires. Veld burning is also applied for pasture management in the Kruger Park on a basis of tri-annual rotational burning (Brynard, 1964). Most of the roan habitat is

therefore/...

therefore burnt at least once in 3 years.

Needless to say that these bush fires could cause havoc among calves under the age of six weeks though older calves are believed to be as efficient in their attempts to escape as any of the other animals faced by these fires. Under normal controlled burning the mortalities suffered by the larger game species are believed to be negligible. Once again, the absence of a calving peak proves to be an advantage in the roan and though young calves may succumb to the heat and flames of a veld fire the losses suffered in this way cannot exceed a small percentage of the annual calf crop.

(ii) Disease:

Roan are known to be highly susceptible to anthrax (Pienaar, 1960; 1961). What effect this, and other diseases, may have on calf mortality remains unknown.

During a recent anthrax epidemic (September to November, 1970) a young calf of 6 weeks died from the disease. Although a number of immatures succumbed to anthrax in the roan enclosure, and also among free-roaming herds, the general impression gained from the distribution of deaths among the various age classes tended to indicate that juveniles

were/...

were less susceptible to the disease. However, the susceptibility of the mature cows directly affects young calves in hiding as the loss of the mother will inevitably also lead to the death of her calf.

What effect other diseases may have on calf mortality has yet to be determined.

(iii) Accidental deaths:

Various other factors may also play a role in calf mortality though their effect may be regarded as accidental e.g. a sudden drop in temperature accompanied by cold winds and rain, a bite from a poisonous snake, starvation due to the loss of the mother, physical injuries such as a broken limb, etc.

Conclusions and discussion:

All the factors mentioned above, - with the exception of veld fires and other accidental forms of death, and diseases - influence the extent of predation on roan calves either directly or indirectly. However, to evaluate the role of each individual factor in terms of its importance as a decimating factor is virtually an impossibility due to the following reasons: (i) death may be due to a combination of two or more of the factors; and (ii) even more important is the fact that no direct calculation of the extent of mortality amongst young calves can be made. In the first place the observer is seldom even aware of the existence of a young calf which is lying up and, secondly, should the calf fall prey to one of its usual predators it is soon devoured

without/...

without leaving as much as a trace. In this case the observer is totally unaware that there had even been a calf at all. In actual fact, the author knows of not a single instance where mortality has been recorded for a calf under the age of 1 month under natural conditions.

It is therefore understandable that the only feasible means by which to determine the loss of young calves at this early age is by means of indirect methods, i.e. by determining the reproductive potential of the species (percentage of calves which could be expected to be born annually) and by determining the percentage of two-month-olds (i.e. those which have successfully emerged from the 'lying-out phase'). By subtracting the latter from the former an indication of the extent of mortality in the first 6 weeks may be arrived at. This method will be applied in a later paper on the population dynamics of this species while it will suffice here to apply an alternative method which does not indicate the actual mortality but provides a useful assessment of the position in one population in relation to another. During June and July, 1969, the author had the opportunity of visiting two areas in Angola where roan are particularly numerous, viz. the Quicama National Park near Luanda in the north of Angola and the Bicuar National Park in the south.

The Quicama population represents a stable population which has probably reached its asymptote for the area while the Bicuar population was heavily hunted until only 4 years ago and therefore represents a 'growing' or expanding population. In both areas carnivora have been almost eliminated by hunting and therefore play no part as a

limiting factor in either population.

Data was collected in each area of the number of animals in the 2 month to 1 year; 1 year to 3 year age classes and those over 3 years classified as adults. These figures were transformed to a percentage of the population and compared with similar figures for the Kruger National Park. The results are given in the following table:

TABLE III:

AGE-STRUCTURE OF THREE DIFFERENT POPULATIONS OF ROAN ANTELOPE.

National Park	No. of animals in sample	% of population	% 2 mths-1 yr.	% 1-3 yrs.	% Adults	% ♀♀ with calves 2 mths-1 year
Quicama	243	12.15(2000)	24.27	25.1	50.61	52.67
Bicuar	117	19.49(600)	27.35	29.91	42.73	74.41
Kruger	47	13.43(350)	21.27	23.4	55.31	47.61

Though the samples differ numerically, the percentage of the total population represented by each sample for the three different populations is of the same order and is also considered large enough for definite conclusions to be made.

It is quite obvious that the Bicuar population is still a "young" population in which growth and expansion is as yet unlimited. The apparently logical conclusion to be drawn from the high reproductive rate amongst these animals is their response to the hunting pressure to which they had been

subjected/...

subjected, resulting in the evacuation of much of their favoured habitat. The probibition of hunting, the scarcity of predators and the availability of habitat are all factors which have obviously favoured reproduction and the survival rate of young calves.

The close correlation between the figures for Quicama and the Kruger Park are of extreme importance and interest as the only factor which these two areas have in common is that they both contain roan antelope populations which have apparently reached their asymptote and may therefore be considered as stable populations. It is also interesting to note that these two populations have reached their optimum density at vastly different levels, a fact directly attributable to different environmental (habitat) conditions.

The limiting effect which predators may have on young calves is almost absent in Quicama due to the rarity of such carnivora in the Park. The only other sources of direct mortality may come from poaching and veld fires which are not considered important factors for roan calves. Whatever the cause(s) of death it is clear that losses in Quicama are appreciably higher than in Bicuar.

The impressive list of predators in the Kruger Park which are capable of killing and devouring young roan calves has been given at the beginning of this section. Comparing the survivorship figures for this area and Quicama one is astounded to find that the difference is a mere 3%! If any conclusions may be derived from these figures the author is prepared to state quite confidently that the role of predation as a factor influencing the normal growth of the

Kruger Park's roan antelope population is small and with no adverse consequences. The author therefore does not believe that predation as such, under present conditions, is in any way endangering the roan antelope population of the Kruger National Park. A further interesting feature emerging from these figures is the stability of the 1-3 year old age class. The apparent decline in the percentage of 2 mnth.-1 year class to the 1-3 year class may be explained by taking into consideration the social behaviour of this species, i.e. it is in the 1-3 year stage that young males are evicted from the herds (see: chapter 3). If the sex-ratio at birth is accepted as 1:1 (from 12 births recorded in the roan enclosure 6 were males and 6 females) then the percentage of 1-3 year olds represents young heifers and a small minority of young male calves. Thus it appears that mortality in all three the areas is virtually nil (or very low) after the initial first 6 weeks of life.

Once again the statement above is endorsed and it becomes quite evident that factors regulating population size must be sought in other spheres than predation or even mortality as such - if serious epizootics may be excluded.

The effect of season on the life expectancy of a newly born calf may be calculated if the age of surviving calves can be determined and in this way reverted back to their date or season of birth. In applying this method it is assumed that births occur evenly in all seasons of the year. A formula by which the age of a calf may be determined in the field to the nearest 6 weeks either way has been established and employed in this study to determine the age of immature animals. The method of age-determination will be incorporated in the paper on population dynamics.

From/...

From a sample of 41 immatures, ranging in age from approximately 2 months to 8 years, the distribution of births occurred as follows in the different seasons:

TABLE IV.

ANNUAL DISPERSION OF BIRTHS OF FORTY-ONE ROAN ANTELOPE CALVES IN THE KRUGER NATIONAL PARK.

January to March.	April to June.	July to September.	October to December.
11	10	12	8

Not only does this table confirm the even distribution of births during the different seasons of the year but also dismisses any possibility of a differential mortality rate based on the season of the year. If the seasons are further reduced to two - to give a much more reliable and realistic picture - based upon the normal weather conditions of the area the following figures are arrived at:

TABLE V.

CONDENSED TABLE OF ROAN ANTELOPE BIRTHS IN WET AND DRY SEASONS IN THE KRUGER NATIONAL PARK.

October to March Wet season	April to September Dry season
19	22

These figures prove that the seasonal factors, mentioned earlier in this section, which may influence mortality directly or indirectly have little bearing on the life expectancy of the newly born roan calf.

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APPENDIX:

TWO DETAILED ACCOUNTS OF MOTHER/CALF AND CALF TO CALF RELATIONSHIPS DURING THE FIRST SIX WEEKS OF LIFE.

BG - NEL.

BG was seen on the 11th September 1968 and had obviously not given birth to her calf though she appeared to be in the final stages of pregnancy.

16.9.68: When the herd was located during the afternoon BG was with the other animals and it was clear that she had already given birth. At 1620 hrs. the herd was in the N.W. corner of Block 1. BG then started moving off towards the water and was followed by the rest of the herd. After drinking they moved away to the north along the eastern fence with BG once again in the lead. For no apparent reason, BG suddenly broke away from the herd and ran ahead for approx. 300 m before stopping and grazing in a patch of thick shrubbery. She appeared to be very nervous and wary and while grazing would jerk her head up at short intervals and gaze intently in all directions but especially in a north-westerly direction. Until now no sign of the young calf was detected and at dusk when BG crossed from Block 1 to Block 3 she had not yet attended her calf.

17.9.68: At 0610 hrs. BG and her calf were found in the center of Block 1. BG was standing 5 m away from her calf while Stoffel, an older calf, was with the young calf and smelling her tail. Stoffel then tried to "mount" Nel but BG made no attempt to drive him away. After a few minutes two of the other calves, Fransie and Lenie, also joined Nel and showed great interest in the young calf. BG then approached Fransie and after smelling the base of her tail she performed flehmen. Both Fransie and Stoffel were then chased away from Nel and each time they approached the calf after that, BG would drive them off again.

BG/...

BG then started licking Nel's back and as they moved in behind a shrub it also appeared if she was licking her calf's anal region. The calf then possibly suckled its mother.

After attending Nel, mother and calf started off in the direction of Block 4 with the calf following close to BG. As they moved off the other calves once again joined Nel and showed great interest in her by remaining close to her and walking round her in tight circles. At this stage LG also joined them and after smelling Nel he twice attempted to "mount" her.

After crossing to Block 4 BG twice licked her calf's back and then smelled Lenie's tail and again had flehmen.

By 0715 hrs. the calf had concealed itself and its mother grazed, together with the rest of the herd, in the vicinity where the calf lay. While grazing Fransie and Lenie remained close to BG while the latter remained on the perimeter of the herd.

During the afternoon the herd had moved down the firebreak between Blocks 1 and 3. Nel was not with the herd and presumably remained concealed in Block 4. At 1755 hrs. BG was still grazing with the herd and showing not the least inclination to raise her calf.

18.9.68: At 0630 hrs. the herd was found close to where they were last seen the previous afternoon. However, it was noticed that BG and LYRR were not with the herd and were subsequently found in the southern portion of Block 4 - close to where Nel had concealed herself the morning before. Nel was not with BG and it appeared as if the cow had already nursed her calf and that Nel was once again in hiding. BG and LYRR were slowly moving in the direction of the herd. BG again appeared to be nervous and wary and frequently paused to gaze in all directions.

In the meantime the herd had also moved up towards the 2 cows and by 0720 hrs. the 2 groups had joined again and the herd was complete.

23.9.68/...

23.9.68: During the afternoon, at 1600 hrs., the herd was found divided into 2 groups: the first consisting of BG, LYRR, RY, LG, BH and Stoffel and the second of the herd bull, LY, LH, BY and Fransie. Lenie was with neither of the 2 groups. The 2 groups were only 200-300 m apart and when BG moved off in the direction of the water the groups were rejoined.

After drinking the animals moved off in a north-western direction with BG in the lead. The herd was moving slowly forward while grazing and BG mixed freely with the others. By dusk they had crossed over into Block 3 and once again BG gave not the slightest indication that she had a calf. Neither Nel nor Lenie were seen during the afternoon.

24.9.68: 0615 hrs. BG and Nel located in south-western corner of Block 3. LG was also with the mother and her calf. Shortly after being found BG, Nel and LG crossed over to Block 4 and were soon followed by the rest of the herd. BG then nursed her calf by thoroughly licking Nel's anal region while she was suckling her mother. After drinking the calf meandered about amongst the other animals that were grazing in the area. The other roan took no more notice of Nel than a casual smell and then continued grazing. At times Nel had drifted up to 50 m away from her mother who stood gazing warily in all directions.

At 0700 hrs. Nel again suckled her mother after which she ran 15 m to some of the other animals (LG, BY, Stoffel). Though Fransie and Lenie were also with the calf, they payed no particular attention to her.

After some 20 minutes BG suddenly broke away at a fast trot, followed by Nel. BG was running toward the eastern side of Block 4 and after running some way, she broke into an easy stiff-legged trot. LG and LYRR followed immediately while the rest of the herd continued grazing, but soon followed slowly.

In the north-eastern corner of Block 4 BG again licked her calf's anal area after which the calf suckled for

a/...

a few seconds. At this stage, 0725 hrs., it appeared as if BG was anxious for the calf to hide itself and chased Stoffel away from Nel. Shortly afterwards Nel lay down and hid herself. During the afternoon Nel again appeared with the herd and escorted her mother into the firebreak between Blocks 3 and 4. BG gave Nel a hurried lick over the anal area after which LG smelled Nel's tail and attempted to "mount" her.

BG and the herd then moved south down the firebreak while Nel and Lenie crossed over into Block 3. After moving away approx. 60 m Nel lay down and Lenie ran back to the herd. The herd eventually crossed over into Block 1 and were heading for the water. Nel was not seen again.

25.9.68: On the morning (0630 hrs.) of 25.9.68 the herd was again split up into 2 groups viz. one group consisting of the herd bull, BG, LYRR, RY and Stoffel and the second of LY, BH, LH, BY, LG and Fransie. Once again there was no sign of either Lenie or Nel. Group 1 was in the area where the calf concealed itself the previous afternoon while the second was on the western side of Block 1. At 0710 Lenie suddenly made her appearance and suckled her mother. At 0740 hrs. Lenie broke away from her group and ran 50 m from the adult animals. After pausing for a while, she ran forward into the firebreak between Blocks 3 and 4 and then crossed over into Block 4 and lay down in the burnt veld. Stoffel at first followed her but soon turned back to the group. Lenie was now completely on her own away from any of the other roan and presumably Nel was lying-up close to where she lay down.

During the day group 1 was disturbed by a bantoe and after running through Block 3 they settled down in the north-eastern corner of Block 4 and rested there until 1700 hrs. Lenie once again joined the group.

After commencing grazing at 1700 hrs. this group crossed over to Block 3 where Lenie again broke away from the group and drifted away on her own towards the north-eastern corner. When she was last seen, she was about 300-350 m from her group and completely on her own. No sign of Nel was seen during the day.

26.9.68: 0620 hrs. The 2 groups had again joined and were found grazing in a long dispersed line from Block 3 and extending into Block 4.

BG, LG and Nel were together in Block 4 with LG obviously taking a great interest in Nel and repeatedly smelled her. BG then approached her calf and started licking her around the head. Nel then turned around and started suckling her mother while BG licked the anal region very thoroughly. After drinking BG again licked Nel's anal area and after a pause of 5 minutes she licked her calf's anal region for the third time. LG then approached Nel and held his nose close to the base of her tail. Nel then suddenly broke out into a spel of playfulness and ran about in circles.

In the meantime LYRR joined BG and LG and they made off in a southerly direction with Nel bounding around them in high spirits.

At 0655 hrs. Nel again suckled her mother while her anal region was being licked. At 0705 hrs. BG and her calf crossed into Block 2 and Nel immediately concealed herself while BG continued grazing with the other herd animals. At this stage the herd bull also joined them and started courting BG.

27.9.68: At 1630 hrs. the herd was located in the north-eastern corner of Block 1. The herd was complete with the exception of Nel. The herd slowly crossed over into Block 3 and grazed in this area until dark.

28.9.68: During the early morning (0620 hrs.) the herd was grazing in Blocks 3 and 4. BG, LYRR, LG and Nel crossed over to Block 4 with the herd bull lagging close to BG who was in her first post-natal oestrus. At 0630 hrs. Nel approached her mother and started drinking while her back was being licked by BG. BG did not lick the anal area. By 0640 hrs. Nel had again concealed herself and did not run off with the herd when it was disturbed by a fence patrol. At one stage it appeared as if the bull was "herding" Nel towards her mother.

After/...

After running away from the fence disturbance for a few hundred metres BG and the rest of the herd slowly returned to within approx. 200 m of where Nel had layed down.

30.9.68: At 1410 hrs. the herd was moving away from the water. Lenie was with the herd but not Nel. The herd moved slowly along the southern fence and settled in the south-western area of Block 1 for the afternoon rest. After grazing had commenced in the late afternoon the herd moved across to the north-eastern corner of Block 2 where Nel suddenly made her appearance at 1730 hrs. RY smelled the calf briefly and then butted Nel away while BG approached her calf. As Nel and BG met, Nel immediately suckled her mother. BG smelled Nel's anal region three times but did not lick it. After Nel had suckled BG, BG licked the calf's ear, eyes, forehead and neck before Nel turned around, lifted her tail and allowed her mother to lick her anal area. After licking the anal area thoroughly for 5 minutes Nel again drank from her mother while her tail was continuously being licked.

While BG was nursing her calf, LG approached BG from the rear and after briefly smelling at the base of her tail, lifted one of his front legs in an action indicating his intention to mount her.

After drinking Nel veered around and made off into Block 1 at a fast gallop. BG instantly followed her calf. They crossed through the tip of Block 1 and were not seen again.

1.10.68: 0615 hrs. Nel and LG together in firebreak between Blocks 3 and 4 with the rest of the herd grazing on either side of the road. At 0630 hrs. BG and Nel approached each other and Nel started drinking while BG licked her anal area. BG licked the base of Nel's tail for 4 to 5 minutes during which time Nel was suckling BG.

Stoffel and LG payed particular attention to Nel and were constantly around her. When Nel had stopped drinking she and BG parted in different directions. At 0650 hrs. BG walked away from the herd for about 150-200 m with Nel walking out in front of her. Nel then turned into

Block 3 and after going a short distance she lay down. BG then returned to the herd. Shortly after Nel had concealed herself, Lenie moved closer to the area where Nel was lying down. Nel was not seen again during the rest of the day though BG remained in the "general area" until dusk.

5.10.68: During the late afternoon, 1720 hrs. the herd was found grazing in the north-western portion of Block 1 from where they moved down to the water at 1730 hrs. The herd was complete with the exception of Lenie and Nel. Neither of the young calves were seen and it is probable that they were hiding together.

6.10.68: 0600 hrs. The herd, together with both young calves, found along eastern section of Block 2. At 0620 hrs. Nel suckled her mother while BG licked her anal region. At 0635 hrs. Nel approached BG and after BG had licked Nel's back and head the calf again drank. After suckling mother and calf stood together for a few minutes with BG appearing quite nervous. When Nel approached BG at 0645 hrs. BG briefly licked the calf's back for 5 seconds but as Nel was going to drink, BG moved away. Nel then moved away 3 m from her mother and at 0650 hrs. BG started licking Nel's back and then the anal area for 3 to 4 minutes before licking the back again for 5 seconds. Nel then drank and while she was suckling BG briefly licked her tail.

At 0745 BG and Nel crossed into Block 4 and were closely followed by Lenie.

8.10.68: At 1410 hrs. the herd, with the exception of RY, Lenie and Nel, came down to drink. After drinking the herd moved away 300 m to the west of the water and settled down for their afternoon rest.

At 1645 hrs. the herd again commenced grazing and with BG in the lead, slowly moved away in a north-western direction. They crossed over into Block 4 and moved up the southern portion into the south-western corner of Block 4. Nel and Lenie were located in the north-western corner of

Block 2 at 1800 hrs. amongst thick shrubbery. RY was close to the 2 young calves and when Stoffel and Fransie saw RY they moved over to her. Fransie joined the 2 young calves. When they were first spotted, Lenie was grazing with Nel standing close to her.

BG and the rest of the herd passed approx. 200-250 m from the 2 young calves on their way to the western side of the camp but made no attempt to join the calves. At 1820 hrs. BG was still along the western fence in Block 4 and gave no indication that she was going to her calf.

9.10.68: 0600 hrs. Nel and Lenie together with the herd on the northern side of the vlei in Block 2 - only 100-200 m from where Lenie and Nel were seen in late afternoon of 8.10.68. At 0610 hrs. Nel approached BG and suckled her mother while BG casually licked the base of Nel's tail. BG then moved out of Block 2 into Block 4 and was followed by her calf. At 0700 hrs. BG once more licked Nel's anal area and at 0710 hrs. Nel lay down amongst some low shrubs some 5 m from her mother. Some of the other animals also followed them and when most of the animals had layed down at 0730 hrs. BG, RY, LG, Fransie, Lenie and Nel were all lying close to one another under a leadwood tree.

18.10.68: During the afternoon the herd was located approx. 300 m to the north-west of the water. At 1645 hrs. the herd, under leadership of LY, started moving northwards and eventually crossed into Block 4. When first seen, Nel was not with the herd. As the herd moved forward, Lenie broke away to the south-west and was ignored by the others. Lenie was last seen when she was 300 m from the herd and it appeared as if she was making her way to Nel. As she disappeared out of sight an effort was made to relocate her but without any success.

19.10.68: During the afternoon (1710 hrs.) the herd was found resting and grazing on the eastern side of Block 2. At first the calves could not be found but soon Stoffel and Fransie became active and commenced grazing with the others.

However/...

However, no sign of either Lenie or Nel was apparent and by dusk (1820 hrs.) they had not yet made their appearance.

The fact that the herd was found on the western side of Block 2 on 19.10.68 certainly indicates that the 2 young calves were in that area and it would seem most likely that Lenie was in fact seeking Nel when she drifted away from the herd on 18.10.68.

20.10.68: 0600 hrs. Herd complete, with both Lenie and Nel present, on the northern side of the vlei in Block 2. Lenie and Nel very attached to each other and constantly remain in one anothers company.

At 0610 hrs. Nel approached BG and suckled for 90 sec. while BG licked her anal region for 75 seconds. At 0640 Nel again suckled BG (25 seconds).

After being nursed, Nel parted from her mother and meandered among the other animals of the herd. It appeared if she attempted to nibble at some grass but she did not actually graze.

21.10.68: At 1000 hrs. the herd was found resting on the western side of the vlei in Block 2. Both Nel and Lenie were also present and were lying only a few metres from the herd bull.

When the herd commenced grazing, it was seen that Nel actually had started grazing young shoots.

Stoffel approached Nel and after smelling at the base of her tail, attempted to "mount" her. At 1015 hrs. Nel approached BG and while Nel was suckling BG licked her anal area.

In the meantime the herd slowly started moving east towards the water. Nel accompanied her mother - or rather the herd - to the water as Nel generally reacted quite independently of her mother. Two hundred and fifty metres from the water Nel stopped and stood and watched the others as they went down to drink. When BG had moved 150-200 m away from the water Nel approached her and suckled for 35 seconds while BG smelled the base of her tail but did not lick it.

After/...

After the herd left they grazed along the eastern fence into the south-eastern corner of Block 3 where they rested during the afternoon. Lenie and Nel were not with the herd any more and had apparently broken away soon after the herd left the water and hid themselves. The 2 calves were not seen again for the rest of the day.

22.10.68: At 0600 hrs. the herd, complete with calves, was grazing in the north-western corner of Block 1. Stoffel approached Nel and sniffed at her tail after which he attempted to mount her. Nel ran away a few metres but Stoffel followed her and again tried to mount her.

At 0710 Nel went up to her mother and suckled. BG did not lick Nel's anal region. After drinking Nel and Lenie ran about in a playful manner with Nel taking the lead and Lenie following her. Nel was already, to a very large extent, independent of her mother and had formed a close association with Lenie, while the only apparent bond between cow and calf was that Nel still frequently suckled BG.

By now Nel was much more active and remained with the herd throughout the day.

After their rest Nel arose (1530 hrs.), approached her mother and suckled. After drinking Nel walked a few paces away from BG but BG followed her and licked her anal area for approx. 5 minutes. Both then commenced grazing.

While resting Nel and Lenie were lying close to one another with Fransie and Stoffel only a few metres off.

Soon after resuming their grazing and other activities after their midday rest, the herd crossed from Block 4 to Block 3. Nel and Lenie broke away on their own and hid themselves and were not seen again.

While the herd was moving down the northern fence BG and LYRR drifted away from the herd and remained behind while the others went on into the south-eastern corner of Block 3. It is possible that BG broke away from the herd to remain in the area in which Nel and Lenie hid themselves.

23.10.68: During the early morning (0550 hrs.) the herd was divided into 2 groups viz. (1) BG, LYRR, Nel and Lenie and (2) the rest of the herd.

Group 1 was in Block 3 and group 2 in Block 1. At 0600 hrs. groups 1 and 2 joined in Block 3. Together the herd crossed through Block 4 and entered Block 2. Though RY, mother of Lenie, was with group 2, Lenie remained with Nel in group 1. At 1600 hrs. the herd was grazing in the vlei, Block 2, but there was no sign of either Nel or Lenie and the two had again concealed themselves.

24.10.68: The herd came down to drink between 1300 and 1400 hrs. and though Nel was with the herd, she did not drink. After leaving the water, Nel drifted away from the others and lay down while Lenie remained with the herd. At 1700 hrs., while the herd was grazing along the eastern side of Block 3, Lenie started off in a north-western direction and eventually lay down in the NW-corner of Block 3. Neither Lenie's mother, RY, or any of the other herd animals took any apparent notice as she wandered off.

At 1715 hrs. BG walked straight in line to where Lenie had disappeared and when she was about 50 m from where Lenie lay down, Lenie arose and immediately walked back to the herd. BG veered to the south and at sunset there was still no sign of Nel.

25.10.68: During the early part of the morning the herd was again split up in 2 groups comprising (1) BG, LYRR, Nel and Lenie and (2) rest of the herd.

Group 1 was found in the firebreak between Blocks 1 and 3 at 0545 hrs. (note the movements of Lenie and BG late the previous afternoon). At 0545 hrs. BG was nursing Nel and after Nel had suckled she left BG and went on grazing with Lenie. At 0600 hrs. the 2 groups rejoined in the north-western corner of Block 1 where they settled down to rest.

26.10.68: Herd at the water between 1315 and 1330 hrs. Neither Nel nor Lenie with the herd. The 2 calves did not make their appearance for the rest of the afternoon and while

the/...

the herd was grazing in the north-eastern corner of Block 3, BG, accompanied by LYRR, diverted from the herd and moved away to the south. This was possibly done by BG to be close to her calf during the night and is undoubtedly the reason for the splitting of the herd. (viz. 23.10.68, etc.)

27.10.68: The herd, with all individuals present, in the north-western corner of Block 1 at 0545 hrs. The herd grazed widely dispersed with Nel and Lenie together 50 m from BG. Nel quite independent of BG and associates closely with Lenie. As the herd quietly grazed, moving forward towards Block 4, BG passed behind the Land Rover while Nel, Lenie, and Fransie came up the firebreak toward the vehicle. When she was 8 m from the Land Rover, Nel looked up and appeared to be somewhat unsettled. Lifting her upper lip rapidly she uttered 3 short, sharp, metallic sounds. Calves apparently communicate both with their mothers and with other young calves in this fashion but rarely has any reaction been noted as a result of their calls. On this occasion BG paid no obvious attention to her calf's calling. By 0720 hrs. activity had declined considerably and the herd rested in Block 4.

Later during the morning the herd moved down to the water (1130 hrs.) but Nel and Lenie did not accompany the others and were not seen again.

28.10.68: 0700 hrs. Complete herd in south-western corner of Block 3. BG crossed into Block 4 and was followed by Nel, Lenie and Fransie. Nel was particularly playful and ran around in circles. At 0720 hrs. BG licked the anal area of Nel and by 0800 hrs. activity had ceased and the animals lay down for their rest.

6.11.68: When located at 1655 hrs. the complete herd was grazing in the burnt veld of Block 4. Nel and Lenie together and also Fransie. Though Fransie frequently associated with the 2 younger calves, the bond between her and Nel and Lenie was of a much looser nature than that between Nel and Lenie. At 1700 hrs. Nel approached BG and suckled for

75 seconds without any nursing from BG. Nel again approached BG at 1750 hrs. and drank for 35 seconds. BG briefly sniffed at her tail but when Nel lifted her tail vertically in the air, BG did not lick the anal area. At 1805 hrs. Nel and Lenie left the herd and wandered off 75-100 m away with Fransie soon following them.

7.11.68: 0545 hrs. Herd found grazing in south-eastern corner of Block 4. Nel had 'joined' the herd and though she followed the same activity cycle as the adults, she still rested for longer periods than the others. Nel lay down at 0600 hrs. but soon rose again and commenced grazing with the herd. The herd came down to drink twice during the day, viz. at 1300 hrs. and again at 1600 hrs. Nel drank with the herd at 1300 hrs. but did not come down to the water the second time.

8.11.68: 1600 hrs. The herd was found resting in the south-western area of Block 4 with Nel and Lenie lying together in the shade of a shrub. When they arose at 1655 hrs. each calf immediately made for its respective mother. RY was resting some 150 m from Lenie and as Lenie wanted to suckle her, RY just shook her off and Lenie followed Nel to BG - 300-350 m away. When Nel reached BG she suckled for 65 seconds, without any preliminaries. BG smelled at the base of Nel's tail, did not lick her anal parts, but flicked her tongue into her nostrils a few times and then allowed Nel to drink. After suckling, Nel parted from BG and she and Lenie went off grazing together.

1716 hrs. BG, RY, Fransie, Lenie and Nel slowly moved slightly to the south. Later Nel moved off on her own and crossed into Block 2, closely followed by Lenie, to an area of thick shrub. The rest of the herd moved further on into Block 1 and the 2 calves remained behind alone in Block 2. The herd went on to drink in Block 1.

9.11.68: Nel and Lenie together with the herd in morning.

LYRR-ANDRÉ.

14.11.68: At 1430 hrs. the herd was grazing in the northern section of Block 4. All the young calves were present but LYRR, who was expected to have given birth, was not with the herd. A search throughout the camp for LYRR revealed nothing.

When grazing activity was resumed after their afternoon rest at 1600 hrs. the herd moved down Block 4 and turned south along the firebreak between Blocks 3 and 4. Some time later Nel turned off into Block 3 and was followed by Lenie. They moved 100 m away from the herd while Fransie and Stoffel also followed them. For no apparent reason the 4 youngsters suddenly charged back to the herd.

At 1720 hrs. Nel again left the herd, with Lenie following her. As they wandered away Fransie and Stoffel went after them. With Nel leading the way they moved further and further into Block 3 and by 1735 hrs. they were 400 m from the herd. A little while later RY started moving in their direction. Nel lay down in a clump of mopani shrubs with Lenie by her side (1745 hrs.) while Fransie, Stoffel and RY grazed 30-40 m away.

By 1805 hrs. the herd had progressed to the south-western corner of Block 3 where LYRR joined them. It was quite obvious that she had already given birth to her calf.

15.11.68: 0520 hrs. LYRR and her calf, André, found alone in the north-eastern corner of Block 2. As the vehicle approached, André immediately lay down and LYRR walked away 20-30 m before lying down in the long grass. (Note: LYRR and André were found in the same area where LYRR joined the herd the previous evening.) At 0535 hrs. LYRR arose - possibly due to disturbance from the vehicle - and started off to the north. She appeared to be extremely cautious and nervous while grazing activity was limited to the minimum. The rest of the herd was grazing some 800 m away in the north-eastern corner of Block 4. In the meantime LYRR moved steadily in the direction of the herd and after pausing for some time 300 m away from the herd she approached to within 30 m of BG (0735 hrs.).

By/...

By 0915 hrs. LYRR was back with her calf in Block 2. As LYRR brought her nose to the base of André's tail, the calf lifted her tail up vertically and the cow licked her calf's anal area for 2 minutes. André moved forward 5 m and LYRR followed and licked her back and head. After the calf had again moved away a few paces she lay down and concealed herself. LYRR then resumed grazing and drifted away from her calf into the southern portion of Block 4 (200 m away from calf).

At 1630 hrs. LYRR was again in the area where the calf lay down and could possibly have nursed her calf though this was not observed. LYRR gradually crossed over into Block 4 but remained on her own and did not join the herd.

Lenie, and probably also Nel, entered Block 2 from Block 4 and made for the northern extreme of the vlei. Fransie and Stoffel initially followed the 2 younger calves but eventually turned back to the herd. Lenie disappeared out of sight - Nel was not seen but it is more than probable that she was ahead of Lenie. These 2 calves were not seen again.

During the late afternoon the herd grazed from the south-western corner of Block 4 eastwards and by 1800 hrs. they joined LYRR in the opposite corner of the block where the herd grazed until sunset.

16.11.68: At 0605 hrs. André and her mother were observed on their own in the north-eastern corner of Block 2 where André had remained since birth. LYRR approached André from 5 m and the calf immediately suckled while LYRR licked her anal region. André suckled for 5 minutes. After the calf had suckled, LYRR continued licking her anal area, back, flanks, ears and eyes. The two then crossed into Block 4 where LYRR continuously licked André, with the exception of short intermittent periods, in all the above areas but particularly the anal region. At 0640 hrs. André again suckled for 1 minute and at 0705 hrs. for a few seconds. Apart from grazing occasionally, LYRR nursed André through to 0710 hrs.

As/...

As LYRR and André crossed into Block 4 they joined the herd which was grazing in that area. Especially Nel, but also Lenie, showed great interest in André and Nel broke into a spell of high-spirited playfulness, i.e. running around in large circles and from time to time breaking into a stiff-legged gallop and then again into stiff-legged trotting. Lenie also galloped about and kicked her hind legs high up into the air. Fransie, Stoffel, and LG also concentrated around Nel but with much less enthusiasm than the 2 younger calves. When the other calves approached too closely to André LYRR dropped her head and they would jump clear 2 or 3 m and again come closer. Once LYRR smelled Lenie's tail and performed flehmen.

At 1515 hrs. the herd was still in the north-eastern corner of Block 2 where André had concealed herself in the morning. After the herd had moved into Block 4 Nel and Lenie remained behind in Block 2 where André was presumably hidden. After some time they followed the rest but Nel soon turned back and moved into the firebreak between Blocks 2 and 4. However, after calling 3 times, she returned to the herd and called another 3 or 4 times and walked over to her mother. Nel then moved back to the firebreak, called and ran back to Lenie, who did not follow Nel. Once more Nel went back to the firebreak and called back to Lenie as she remained with the herd. Nel ran back to her. The fourth time Nel ran away from the herd into Block 2 and Lenie soon followed her.

Gradually Stoffel also moved after Nel and Lenie and eventually the herd also followed the calves. After crossing into Block 2 Nel and Lenie were not seen again and presumably lay down near to André.

17.11.68: 0545 hrs. The herd, with the exception of the bull, André, Nel and Lenie, was found grazing in the southern section of Block 4. There was no sign of the 3 young calves as the herd grazed further into Block 4 to about 200-250 m from the firebreak. Suddenly, and for no apparent reason, the herd looked up and gazed in the direction of Block 2, before BG, LYRR and RY started walking straight to

Block 2 with the others following in the rear. After moving 50 m into Block 2 André emerged from where she was lying and while André was suckling LYRR licked her very thoroughly (0615 hrs.). Shortly afterwards BG, who had moved further into Block 2 ahead of LYRR, returned, accompanied by Nel and Lenie. They passed LYRR and her calf and crossed back into Block 4. LYRR remained behind and nursed her calf before following BG at 0635 hrs. André followed her mother.

Though no calf was heard calling, the sudden reaction of the cows and in particular the 3 mothers: BG, LYRR and RY, would suggest that they reacted in response to one of the calves calling.

19.11.68: At 1720 hrs. the herd was grazing in the north-western corner of Block 1. Nel and Lenie were with the adults but André was not seen.

By 1730 hrs. Nel had broken away from the herd and ran to the east, followed by Lenie. The 2 calves disappeared in the distance and were not seen again.

20.11.68: 0600 hrs. Complete herd, with the exception of André, was found together in the south-eastern corner of Block 4. Gradually they crossed over into Block 2 and by 0625 hrs. LYRR slowly drifted away from the others to a distance of 200 m before she stopped and paused for a while. Suddenly André made her appearance 5-8 m from her mother (0635 hrs.). Without hesitating the calf walked to LYRR and commenced drinking - André suckled without a break for 5-5½ minutes while LYRR intermittently licked the calf's anal region. After suckling André stood in front of her mother while LYRR licked her anal area and also the rest of the body continuously for 20 minutes. After being nursed, André playfully ran around her mother in circles before LYRR again licked her calf for a few minutes. LYRR then moved forward to an area of fairly thick shrub where the calf lay down and LYRR returned to the herd (0710 hrs.). While LYRR was nursing André she was 200-300 m from the herd and was not followed by Nel or Lenie.

21.11.68/...

21.11.68: During the afternoon the herd rested and grazed in Block 4. At 1630 hrs. Nel - followed by Lenie - broke away from the herd and moved 150 m into Block 3 before lying down. André was not seen at all and the 2 other calves did not rejoin the herd during the afternoon.

22.11.68: At 1700 hrs. the herd was grazing in the south-western corner of Block 4. The herd bull was not with the herd and neither of the 3 young calves. Nel and Lenie were lying together in Block 2 and after commencing grazing at 1720 hrs. they made no attempt to join their "elders" but rather moved deeper into Block 2. Presumably the 2 were in the area where André was concealed. At 1800 hrs. BG diverted from the herd and walked across to Block 2, where Nel and Lenie were grazing. Nel suckled BG and in the meantime some of the other herd animals followed them into Block 2.

23.11.68: The complete herd, together with LYRR and André, were grazing in the southern section of Block 4 at 0540 hrs. LYRR kept licking André's anal area at short intervals to 0600 hrs. Nel showed great interest in André and remained close to her. At 0610 hrs. André crossed over into Block 2 - alone - and concealed herself while the rest remained in Block 4. Though Nel and Lenie remained with the herd, André was not seen again for the rest of the day.

26.11.68: During the early morning (0545 hrs.) the herd was found split up into 2 groups viz. (1) the largest group including the 3 young calves: André, Nel and Lenie and (2) consisting of LH, BH, LG and LY. LY remained behind on her own in Block 4 while the 3 other members of the herd crossed over into Block 2 and joined group 1 in the vlei (note: LY was due to calve and was isolating herself from the herd).

LYRR nursed her calf at short intervals until 0630 hrs. while Nel, Lenie and Fransie were constantly keeping to André and showing their interest in the young calf. The 3 older calves periodically also broke into

spells/...

spells of cavorting: running around in circles, kicking up their hind legs and playfully challenging one another to a duel.

By 0630 hrs. the herd had moved to the eastern side of Block 2 and after LYRR licked André's anal area for a few minutes, André left the herd, crossed into Block 1 and 200 m further she lay down. LYRR did not follow her calf but stood with the rest and kept a watchful eye over her calf as she disappeared into the bush. Neither Nel nor Lenie showed any inclination to follow André and they remained behind with the herd.

After André had concealed herself the herd moved away in a northerly direction and crossed into Block 4. Here LY again joined the herd and together they grazed across into the north-eastern corner of Block 3 where they rested until late afternoon. At 1700 hrs. Nel broke away from the herd and was soon followed by Lenie. BG and Fransie initially also followed the two calves but by 1745 hrs. the latter two had rejoined the herd again with no sign of the other two calves for the rest of the day.