THE BEHAVIOUR OF THE BONTEBOK DAMALISCUS DORCAS DORCAS WITH SPECIAL REFERENCE TO TERRITORIAL BEHAVIOUR

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FIGURE 1. An adult bontebok ram on his territory.

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I. INTRODUCTION

A. Distribution and History of the Population

The bontebok, (Damaliscus dorcas dorcas (Pallas, 1766)), is one of the rarest antelopes (Artiodactyla) in Africa and probably the rarest in Southern Africa. There is a paucity of historical references to the bontebok and also considerable confusion of nomenclature due to different systematists of the era giving the animal different names. The discovery of the closely allied blesbok, (D. d. phillipsi Harper, 1939), on the inland plains of what is now the Orange Free State, approximately 100 years later than the bontebok, confused the travellers of the time to such an extent that it is now difficult to be certain just where the bontebok was or was not seen. Bigalke (1955) and Skead (1958) have examined the existing historical references to both races and their evidence is accepted by Ansell (1968) who has revised the classification of African mammals for the Smithsonian Institute.

It appears that the bontebok was always restricted in range to the coastal plain of the South Western Cape and in particular its range was bounded by the Bot river (just west of Caledon) in the west, Mossel Bay in the east, the Langeberg mountains in the north and the sea in the south. The range of the blesbok covered the inland plains of the Orange Free State, Southern Botswana and the Southern Transvaal. At its most southern point it was separated by a belt at least 200 miles (320 km) wide at its narrowest from the range of the bontebok (Skead). This distribution covers practically the same area as the Coastal Rhenosterbos veld and the Coastal Macchia veld types of Acocks (1953).

Indiscriminate hunting and the enclosure of land for farms by the early settlers seriously reduced the numbers of the bontebok so that as early as 1830 the species was in real danger of extinction and the few remaining herds eked out an existence on the sour strandveld. Fortunately, enlightened landowners in the Bredasdorp area, notably the Van Breda, Van der Byl and Albertyn families, preserved the animal by enclosing as many as they could on their land. The situation was not greatly improved, however, by 1931 when the first Bontebok National Park was proclaimed. Its area was only 843.1 morgen (722.5 ha) and it was situated in the strandveld or Coastal Macchia of Acocks, about 17 miles south of Bredasdorp.

According to Barnard & Van der Walt (1961) and Van der Merwe (1968) the Park started with 17 animals, though Bigalke states that there were 22. At first these animals reproduced rapidly and to prevent overstocking the National Parks Board of Trustees decided to distribute specimens to local farmers, in an attempt to establish alternative breeding nuclei. The result, however, was not satisfactory. The herd never numbered much more than 100, and it appeared that the Park was too small to support more. The Board therefore next turned its attention to improving the carrying capacity of the Park by establishing artificial pastures. This, however, seemed to provide an ideal breeding ground for parasites and many animals were lost due to parasite infestations (Van der Merwe). Post mortems showed the presence of conical fluke (<u>Paramphistomum</u> sp.), wireworm (<u>Haemonchus</u> sp.), brown stomachworm (<u>Ostertagia</u>) and bankruptworm (<u>Trichostrongylus</u> sp.) in great numbers. Signs of weakness and ataxia in a number of animals which otherwise appeared to be in reasonable condition led to a diagnosis of 'swayback', a copper deficiency; (Barnard & Van der Walt). It was known that the South Western coastal belt was lacking in the copper-cobalt group of trace elements, and that severe worm infestations aggravated the condition.

The Board next attempted to obtain more land in order to enlarge the Park, but since none of the neighbouring farmers could be induced to sell, the decision was taken to search for a wholly new Park with better grazing conditions. After a long search, a suitable tract of land was eventually found near the town of Swellendam, and a total area of 1,706 morgen (1461.4 ha) was purchased by the State and proclaimed as the new Bontebok National Park on 24 March 1961 (Van der Merwe). During March 1960, a year before proclamation, 84 of the 95 animals in the old Park were captured in crush pens and transferred the 60 odd miles (100 km) from Bredasdorp by truck. They were sedated with a 5% solution of chlorpromazine hydrochloride ('Largactil'), injected intravenously, and of the 84 transferred 61 survived the critical first three days in the new Park (Barnard & Van der Walt). During December 1965 a further 1,576 morgen (1350.0 ha) were added to the Park, bringing it to its present size of 3282 morgen (2811.4 ha).

B. Present Status

The introduced bontebok thrived in their new environment and quickly began to improve in condition and to increase in number. In April 1970 the number in the Park stood at approximately 260, having increased at an average net annual rate of about 18% since 1960. Nevertheless, the overall situation is not quite as good as it might be, since a census conducted by the Cape Department of Nature Conservation showed there to be about 780 bontebok in the whole of the Southern Cape, including all those in other reserves and on private farms etc., as at July 1969. Since this figure does not include the 1969 calving season the number is now doubtless over 800. However, the Red Data Book, quoted by Ansell (op. cit.), gave the 1965 figure as ± 750, so that increase since then seems to have been slow.

C. Description and Studies on Related Species

The bontebok belongs to the alcelaphine tribe of African antelopes which is characterised by the presence of horns in both sexes, face glands, pedal glands on forefeet only and lack of inguinal glands. There is one pair of mammae and no preorbital fossa or ethmoid fissure, (Ansell). To the observer in the field the long face, high withers and sloping hindquarters are characteristic. The tribe Alcelaphini contains two hartebeest species (genus Alcelaphus), two wildebeest species (genus Connochaetes) and three "bastard" hartebeest species (genus Damaliscus).

According to Roberts (1951), the description of the bontebok is as follows: "General colour rich brown on head, neck, body and outer side of upper part of legs; but with a broad "saddle-mark" of a much lighter colour from the top of shoulders to forepart of rump; the ears are whitish, as also the external base; a white blaze extends from the base of horns to the nose, the part above the level of the eyes narrower, and narrowest just above the level of the eyes, where it broadens out over the muzzle; the hinder part of the rump, around and over the base of the tail, pure white and connecting up with the pure white of the underparts of body as far forward as a line between the forelegs; this white of the underparts extends downwards inside the fore and hind legs on the upper part; the lower part of legs pure white, except for a brownish stripe down the front of the forelegs and a shorter mark on the front of the hindlegs, above the hooves."

From the foregoing it would seem that Roberts had never seen a live specimen. In particular, the ears are not whitish, but brown, though lighter than the general body colour, and the external base is darker brown. Adult males are very dark brown and present a generally blackish appearance. The hindquarters, especially are nearly black, which contrasts well with the snow white hinder part of the rump. He also does not mention the lovely purplish bloom to be seen in certain lights on the light brown 'saddle' of animals in good condition.

The horns of both sexes are ringed almost to the tip. Adult males weigh around 150-190 lbs. (68-86 kg). Data on weights of females is scarce but they are considerably lighter. An adult female in good condition, carrying a full term foetus weighing 15 lbs. (7 kg), weighed 124 lbs. (56.4 kg) including foetus.

The closely related blesbok is very similar in appearance, but lacks the white rump. It is merely a lighter brown on the hind part of the rump and around the base of the tail. In addition, the narrowest part of the white face blaze, just above the eyes is constricted completely so as to form a brown bar of varying width across the face. In the bontebok, the blaze is not normally so constricted as to form this bar (see Fig. 1.). Interestingly enough, in view of the close zoological relationship between these two animals, this bar is present in some bontebok. In order to determine the frequency of occurrence of this bar in bontebok, I conducted a census on a sample of 115 adults (68 female and 47 male). In both sexes 19% were found having this brown bar across the face.

To my knowledge no previous work has been done on the bontebok, but du Plessis (1968) has worked on productivity of blesbok with some incidental observations on behaviour and C. Lynch is currently studying behaviour of this species at Rietvlei near Pretoria. Backhaus (1959) has studied the behaviour of Lelwel's hartebeest, Alcelaphus buselaphus lelwel, and Dowsett (1966) the behaviour of Lichtenstein's hartebeest, A. lichtensteini. Walther (1966) has made some observations on captive black wildebeest, Connochaetes gnou, and W. von Richter is currently studying the behaviour of this species in the Willem Pretorius game reserve, Orange Free State. Gnu, C. taurinus, ecology has been studied by Talbot & Talbot (1963) and gnu behaviour by Estes (1969), which will be cited hereafter simply as "Estes".

D. Habitat and Study Area

The bontebok is exclusively a short grass eater and though no grazing study was attempted during this work, casual examination of the veld at various times during the year showed that common quick grass, Cynodon dactylon, and red grass, Themeda triandra, seemed to make up the bulk of the animal's diet. From what is known of the historical distribution of the animal it appears that the open coastal plains were its preferred habitat. However, due to the climatic conditions of the South Western Cape, being a winter rainfall area with warm dry summers, the vegetation is dominated by hardy, low shrubs with a xerophytic character, so that to the eye the landscape does not present a grassy aspect. The dominance of mostly inedible shrubs must mean a reduced carrying capacity for short-grass eaters.

The study was conducted in the Bontebok National Park situated about four miles south of Swellendam at 20°30'E and 34°3' 45"S. The area of the Park is about 10.8 square miles (28.1 sq. km). As the crow flies the sea lies only about 30 miles (48 km) to the south and the Langeberg mountains, running east to west are about 5 miles (8 km) to the north. The height of the Park varies between about 200 feet (60.9 m) and 650 feet (198.0 m) above sea level. The Breede river, which normally flows strongly throughout the year, forms the southwestern boundary of the Park. According to Theron (1967) 90% of the Park is occupied by alluvium and gravel terraces. In general, a flat, sandy, alluvial plain is situated in the western side of the Park which is enclosed by sloping, stony ridges, which rise to the level of the gravel terrace occupying the major part of the remainder of the Park. The gravel terrace consists of well-rounded white and brown sandstone boulders, with much smaller pebbles and large stones also present in the sandy gravel.

This area falls into the winter rainfall region but according to Grobler & Marais (1967) the local rainfall figures show that Swellendam receives rain throughout the year with a spring maximum. Of the annual precipitation, 21% falls in summer (December to February), 26% in autumn (March to May), 22% in winter (June to August) and 31% in spring (September to November). In the Park itself rainfall figures have been kept since 1961 and the annual average is 544.6 mm (21.4"), (Grobler & Marais). The Park is drained into the Breede river by a single watercourse which is dry except after heavy rain. The animals have access to the river at certain points and there are a number of small artificial water holes distributed through the Park. In summer the temperature may rise above 95°F and in the winter of 1969 the lowest temperature I recorded was 36°F.

In addition to the 260 bontebok in the Park there are, besides, 16 buffalo, 6 red hartebeest, 24 eland (Taurotragus oryx), c. 150 springbok (Antidorcas marsupialis), c. 170 grey rhebuck (Pelea capreolus), a few bushbuck and unknown numbers of steinbok (Raphicerus campestris) and Cape grysbok (R. melanotis). There are no large mammalian predators but silver jackal (Vulpes chama), and aardwolf (Proteles cristatus) are present in small numbers. The yellow mongoose, Cynictis penicillata, is present in considerable numbers. As to birds, 144 species have been recorded in the Park, (Winterbottom 1967).

The vegetation of the area has for centuries past been influenced by the activities of man. Before the coming of the white man the Hottentots' cattle grazed here and later on the European settlers' cattle. The use of fire to provide grazing was widespread and during the 19th century a racecourse occupied what is now the western half of the Park. With regard to present veld management in the Park, the use of fire is excluded and a bush cutter, towed behind a tractor, is at present being used experimentally to cut all shrubs to near ground level in an effort to promote the growth of grass.

The vegetation in the Park is mainly low shrubs varying in height from about 30 cm on the flats to 70 cm on the moister parts of the ridges, (Grobler & Marais). These can be divided into a number of communities but the most important in terms of area are the renosterbos, Elytropappus rhinocerotis, communities on the sandy soil of the flats where stones are mostly absent, and the Leucadendron communities on the ridges and gravel terraces. Here the soil is also sandy and characterised by the presence of great quantities of stones ranging from pebble-size to small boulders. On the flats, renosterbos is dominant and some other shrubs present are Aspalathus spinosa, Montinia caryophyllacea, Eroeda imbricata, Berkheya armata and Corymbium scabrum. The most important grasses here are Eragrostis curvula, Themeda triandra and Ehrharta longiflora. The Leucadendron communities are dominated by L. adscendens and Pelargonium ovale. Also present are Cliffortia ruscifolia, Metalasia muricata, Elytropappus rhinocerotis, Serruria fucifolia, Stoebe plumosa and Berkheya armata. On the banks of the Breede river, thickets of Acacia karroo are an important source of shade and cover.

E. Methods

Fieldwork for this study was commenced during the end of January 1969 and terminated in mid-April 1970. It was conducted on a full time basis and follow-up visits were made to the Park at intervals during the remainder of 1970. The study was carried on exclusively in the Bontebok National Park which contains by far the largest herd of bontebok in the country. Visibility in the Park is good and all observations were made from a vehicle with the aid of binoculars at distances ranging from about 30 m to over 400 m. Most animals were tolerant of a motor vehicle but there were one or two exceptions, particularly territorial males whose territories were situated away from the roads and who were therefore unused to being approached closely by vehicles. Females were on the whole more nervous than males and especially females with new born lambs were very nervous and would run from a vehicle at 100 m or more.

As many aspects of bontebok behaviour as possible were tackled including social, reproductive and territorial behaviour. When it became clear that bontebok were strongly territorial this aspect was singled out for particular attention as being the most rewarding during a relatively short field study. This necessitated the ability to identify individuals positively. There were only one or two animals in the Park with deformed or broken horns or any other physical distinguishing feature, and so the search for natural marks proved abortive. It was then noticed that the shape of the white forehead blaze above the eyes varied from animal to animal. An attempt was therefore made to photograph head-on as many animals as possible and so to build up a system of photographic identification. This worked well for some individuals with particularly characteristic forehead blazes, either as to shape or size, but others had very similar blazes which proved hopelessly difficult to distinguish. Sometimes an animal could be identified as long as it stayed in a particular area or with a particular group, but as soon as it moved away it became impossible to identify it again positively. The only alternative therefore was to capture animals by darting and to mark them with collars. Accordingly, in May 1969, five territorial males were successfully darted using a gas-powered 'Cap-Chur' rifle and drug-filled projectile syringes. During November and the beginning of December 1969, a further ten adult males were captured, making 15 in all, of which 14 were territorial.

The drugs used were the neuroleptic-analgesic combination of Azaperone and Fentanyl. These drugs worked extremely well, (Barkhuizen, in press) and the animal could normally be handled about eight minutes after darting. No fatalities were experienced and there was a remarkable absence of adverse side effects often accompanying the narcotic action of the drugs. The animals were normally on their feet again in a matter of seconds after the administration of the antidote, Lethidrone. The weights and measurements of all but one or two animals were recorded in the field. Collars of blue heavy-duty 'Sterkolite' were cut from large sheets and fastened round the animal's neck using a pop-riveter. This was both quick and efficient and permitted tailoring of the collars to suit individual animals.

'Sterkolite' is an industrial nylon material covered with polyvynil plastic and is both very strong and weatherproof. Collars were cut 27½" x 4½" (68.7 cm x 11.2 cm) and each carried a two digit number cut from white 'Sterkolite' sheets which was both glued and riveted to the blue collar. The number could be read at over 250 m with the aid of binoculars.

All the marked animals were in the 'old' or western side of the Park comprising the original area of 1706 morgen, and this is where observations were mainly concentrated. This was because it contained the greatest concentration of territorial males (see Map 1), and also because the veld here was relatively free from stones making it possible to drive over it in an ordinary car, which was frequently necessary for making observations. Monthly counts throughout the year showed there to be between 25 and 30 territorial males in the whole Park at any given time, so that my sample of 14 represented 50% or better of the number of territory holders.

Territories of all males in the western section of the Park were visited on an almost daily basis. Position, association and activity of the males were noted as also that of any animals (e.g. females) with which the male was associating. At the beginning of January 1970, fixed markers were put out on selected territories and the distance the male was found from his marker was subsequently recorded during spot checks. The whole Park was censused at least once a month and the number, position, age and sex of all bontebok seen was recorded, thus yielding distribution and association patterns of different sexes and age groups for the whole year. Particular attention was paid to aspects of territorial behaviour such as defence and advertisement of territory and also courtship and mating behaviour. During the rut of 1970 a sample of 100 ritualized encounters between territorial males was recorded on tape for analysis of the Challenge Ritual (Section VII) and for comparison with that of the wildebeest (Estes). A 35mm single lens reflex camera with 400mm telephoto lens was used to photograph all displays and all aspects of the Challenge Ritual. This was also documented on 800 feet of 16mm cine film. The diurnal activity patterns of selected territorial males and associated females were recorded on printed activity sheets during 12 hour shifts at intervals throughout the year. Parturition and behaviour of females during the calving season was observed and an attempt was made to establish something on the gestation period, as the scant information available on this is open to question. Some observations on the duration and frequency of suckling by young lambs were also made. Observations of known animals yielded some information on home range size of females.

II. THE SOCIAL SYSTEM

A. Sexing and Ageing

As du Plessis (1968) remarks: "Because both sexes have horns and are also rather similar in other respects only the experienced observer can sex a herd of blesbok on open range." The same is true of bontebok. In general, the females have more slender horns which hardly thicken towards the base, whereas the horns of males are more prominently ridged and the base circumference is about one inch (2.5 cm) greater than in females. The penis sheath of males is visible but not conspicuous from the side, and in adult males the large, white scrotum is clearly visible from behind. The udders of lactating ewes are also visible from behind. In addition, mature males are darker in colour, particularly on the neck, and are larger.

Unfortunately, no series of bontebok skulls exists for ageing by tooth replacement and wear. In the field, on the basis of observation alone, I recognised four age classes:

1) Lambs in their first season.
2) Juveniles in their second season (yearlings).
3) Males in their third season (two year olds).
4) Adult males and females.

Lambs are easily distinguishable in their first year on the basis of body size and horn development. Yearling males can be aged on the basis of body size, horn development and coat colour but the most reliable guide is the very small size of the testes. The scrotum is also the best character for distinguishing two year old males. It is greyish and somewhat smaller than the large, pure white scrotum of adult males. At three years they are indistinguishable in the field from adults. Young females can only be certainly aged up to the end of their second year on the basis of body size, horn development and their shaggier and lighter coat. At two years of age females become indistinguishable in the field from adults.

B. Breeding Age of Females

No yearling female during the study was seen either pregnant or with a lamb. Only some yearling females join territorial males, the rest remain with the bachelors. Although adult males did sometimes display to and sniff the vulvas of yearling females, they normally ignore them in the presence of adult females. However, adult males were occasionally seen attempting to copulate with yearlings but no successful copulations were seen due to the evasive action taken by these yearling females. On these grounds, then, it is the view of this author that females do not come into oestrus before the rut following their second birthday, when they are about $2\frac{1}{4}$ years old. They would therefore not produce their first lamb before 3 years of age. This contrasts strongly with the breeding age of 15 months for 75% of wildebeest females given by Estes (1966).

C. The Tendency to Aggregate

The bontebok is a gregarious antelope. Unfortunately, reference to it in the records of the early travellers are sparse and what there are give very little information. We know little beyond the fact that it did occur in large numbers. We do not know how many there were, nor anything about the size of the herds. Its close relative, the blesbok, was evidently very gregarious. Gordon Cumming (1909), quoted by Skead (1958), travelled in the Western Free State and in 1848 saw "... one purple mass of blesboks ..." and again " ... a continued stream of blesboks may often be seen ... covering the landscape as far as the eye can see".

The bontebok is an extremely conspicuous animal. With its generally blackish appearance at a distance and the strongly contrasting white rump and face, it can easily be picked out from afar with the unaided eye or with binoculars even when it is standing motionless. The springbok falls into a similar category; though of a much lighter brown it has a black stripe along its flank and also a shining white rump. This is in marked contrast to the grey rhebuck, for example, which is cryptically coloured and when standing motionless on a hillside is practically invisible. Only when it runs and lifts its tail to reveal the white underside is it easily seen. Noting the gregarious nature and conspicuous colouring of wildebeest, as well as such highly gregarious species as caribou, (<u>Rangifer tarandus</u>) and bison, (Bison bison), Estes makes the interesting observation that "revealing coloration and/or markings seem to be typical of the most gregarious ungulates, suggesting that in their case selection in favour of species-specific recognition and social-facilitation signals outweighs predator-selection against conspicuousness".

The population explosion and resultant treks of millions of springbok in one vast army (Cronwright Schreiner 1925), represents perhaps the zenith of ungulate gregariousness. At Rietvlei, Lynch (pers. comm.) reports that blesbok ewes form large nursery herds of over 100 females before the rut and that after the rut large aggregations of blesbok form herds of over 650 animals of all sexes and ages. In view of its close relationship one would perhaps expect bontebok also to form large herds. It is impossible to come to firm conclusions when working with a small population of only c.250 animals but in the case of bontebok at Swellendam the bachelor males show the strongest tendency to aggregate and I have seen up to 75 males together including yearlings of both sexes. The females distribute themselves through the territorial network (Section II.E) and do not seem to show such a gregarious nature, as the largest number of females I have seen together on the territory of one males is only nine. It is possible that as the population grows at Swellendam a greater tendency for females to aggregate will manifest itself.

However, it is noteworthy that the situation at Swellendam the year round resembles that at Rietvlei during the rut and amongst the sedentary portion of the Ngorongoro wildebeest population (Estes). During the rut at Rietvlei the large nursery herds split up to form small harem herds seldom consisting of more than 15 females plus their calves. Each of these harem herds is attended by one adult male (Lynch pers. comm.). In the Ngorongoro Crater, Estes was studying a population of around 14,000 wildebeest, which showed considerable seasonal fluctuation in numbers. However, 70% - 80% of this population never left the Crater, yet the majority exhibited grouping and movement patterns typical of migratory rather than sedentary populations. They remained the whole year in aggregations of from 100 to over 1000 females and young, which moved from one part of the Crater to another according to grazing conditions. On the other hand, the grouping pattern typical of a sedentary population was displayed by anything from 10%-45% of the Crater's wildebeest, depending on the season. A permanently established network of territorial males and separate small nursery herds averaging about 10 females, calves and yearlings, each with only one adult male was diagnostic. Thus it would appear that even in highly gregarious species the females do not necessarily congregate in large herds.

D. Population Structure

The gregarious African antelopes group themselves into two broad social classes based on sex and age: nursery herds consisting of females and young and bachelor herds of males of all ages. Among territorial species must be added the extra class of territorial males, often solitary. Brooks (1961) was one of the pioneer workers on African ungulates and in his study of the Thomson's gazelle, Gazella thomsoni, he recognized four kinds of social group:

1) Harem herds consisting of a variable number of females and young accompanied by a single adult male.
2) Scattered females.
3) Bachelor or male herds consisting of males of all ages.
4) Solitary males.

This arrangement describes the social system of the bontebok quite well, and it is evident that the harem herds are merely nursery herds under another name. In the presence of territorial males the large nursery herds break down into smaller units. The resulting small groups of females distribute themselves through the territorial network and are tended by single adult males.

E. Herd Composition

At Swellendam much of the Park is divided up into a mosaic of territories, each one defended by a single adult male (see Map 1). Within this mosaic small groups of females and young wander at will. Each group of females normally grazes on the territory of a male who closely attends and herds all females on his territory. Any stray female wandering on to the territory will be greeted by the male with his sexual display (Fig. 2).

Some territorial males were always with females while others were often alone. The mean number of females per group was 3.0 during the rut months of January, February and March and 2.5 for the remainder of the year. The range in group size was from 1 to 8 females per group for a sample varying between 41 and 85 females. The latter figure is close to the total number of adult females in the Park at the present time. The female groups were accompanied by a mean number of 1.5 lambs per group.

The non-territorial males congregate in a single bachelor herd of 60-70 animals of all ages. These are the young, subadult males from yearling age upward; the very old and decrepit males; and also a number of perfectly fit-looking adult males. Yearling females, after leaving their dams, also join the bachelors at least for a while.

F. Lambing and Rutting Seasons; Gestation Period

The bontebok is a strongly seasonal breeder and lambs are born in the spring. The peak months for births are September through October and 80% of the annual lamb crop has normally arrived by the end of October (Table 1). A few continue to arrive right up to the end of February.

The peak rutting months are January to mid-March (based on my own observations). Copulation was observed as late as 8 April in 1969. These dates more or less agree with a gestation period of about 8 months (240 days). Brand (1963) gives a gestation of 288-308 days, but it seems unlikely that this can be correct, since it is longer than for any bovid except the buffalo. The comparative figure for the blesbok is only 235 days (Kenneth 1943). Kenneth, in the same work, gives the figure for the bontebok as 230 days. The only evidence obtained by the present author is in respect of two females whose dates of mating and calving were known. One female calved 237 or 238 days after mating and the other 254 days after mating. These figures may not be reliable since, assuming the bontebok to be seasonally polyoestrus, if a female is not fertilised at any given mating she may come into oestrus a second time and mate again. This would have the effect of making the true gestation shorter than the observed period between the first mating and parturition.

The Table below summarises births in the Park for the last 5 years. The figures were taken from somewhat incomplete monthly reports.

TABLE 1

Cumulative Bontebok Births at Swellendam 1964-69

1964-5		1965-6		1966-7		1967-8		1968-9	
27 Aug.	1	End Aug.	0	End Aug.	1	End Aug.	?	22 Aug.	2
Mid Sept.	5	8 Sept.	1	End Sept.	13	End Sept.	?	End Sept.	25
End Sept.	9	End Sept.	12	End Oct.	?	End Oct.	38	End Oct.	44
Mid Oct.	19	End Oct.	25	End Nov.	?	End Nov.	40	End Nov.	46
End Oct.	29	End Nov.	25*	End.Dec.	27	End Dec.	?	End Dec.	49
End Nov.	29x	End Dec.	26	End Jan.	30	9 Jan.	45	End Jan.	51
Mid Dec.	30	End Jan.	23			20 Feb.	47	End Feb.	53
End Dec.	31								

x = 2 dead   * = 4 dead

Therefore, the figures given must at least be maxima, since if a female is fertilised at a given mating she will not come into oestrus and therefore will not be served again.

G. Overall Sex Ratio

Despite frequent attempts it was always found extremely difficult to accurately sex and age all the bontebok in the Park. Even with a population as small as 250 animals some were inevitably wrongly sexed due to their being too far away or mixed up in a large group; or, due to the uneven nature of the topography, the presence of many small kloofs, thickets of bush and trees etc. some were not seen at all. My final estimate was that in approximately 215 animals above the age of one year (including yearlings) there were 100 females and 115 males. This gives an overall sex ratio, excluding lambs, of 87 females : 100 males.

During October 1969, I sexed the calf crop from the 1968-9 calving season, by which time the calves were mostly a year old and relatively easy to sex. Of 49 calves sexed, including one still-born female, there were 26 males and 23 females. This gives a sex ratio of 88 females : 100 males.

III. THE BACHELOR HERD

A. Formation

Bontebok of both sexes leave their dams as yearlings. This is accomplished quite peaceably and the yearlings seem to leave their mothers of their own accord during the lambing season when the new lambs are being born. However, it is not unusual for a few yearlings of either sex to remain with their mothers well into their second year. There is some reason to suppose that if a female does not produce a new lamb in the breeding season, then that female will continue to tolerate her yearling offspring. For instance, in May 1969, six months after the lambing season, it was verified in the case of a yearling male and a yearling female continuing to accompany their mothers that these two females were not accompanied by lambs of the current season. Table 2 illustrates the gradual way in which the yearlings leave their mothers.

I have seen very little evidence that the yearlings are forced out of the nursery herds by the intolerance of the territorial male on whose territory the group happens to be grazing. Schenkel (1966) reports that dominant male impala are responsible for chasing the young males out of the female herds at the age of 10-12 months. Estes reports the same in wildebeest but adds that the old calf initiates its own rejection by awakening the hostility of its own mother first, thus directing the attention of the territorial male towards it. In the course of 15 months work at Swellendam I have only six instances recorded in my field notes where a territorial male was seen to chase or threaten an older lamb, none of these, apart from the case related below, serious or prolonged. Females were occasionally seen to threaten any animal that came too close to her new lamb. On May 14 1969, a territorial male was seen vigorously chasing a yearling male which was grazing with its mother on his territory. He chased him several times in tight circles, the yearling trying all the time to keep close to its mother. Eventually the territorial male succeeded in separating them and while he chased the yearling the female ran behind them, bringing up the rear. Later in the same day the female was seen without the yearling. A factor of rele-

TABLE 2

Number of Yearlings remaining with their Mothers

Date	No. of nursery groups containing yearlings.
Sept. - Oct. '69 (calving)	18
Nov. '69	11
Jan. '70 (post-calving)	6
Mar. '70 " "	5
April '70 " "	4

vance here, though, was the fact that immediately prior to the above episode the territorial male had engaged in a Challenge Ritual (Section VII) with a territorial neighbour. It is not uncommon for the male to show aggressive behaviour at the termination of these ceremonies, and he may chase any males which happen to be in the vicinity.

The old lambs start to leave their mothers during the height of the calving season, when they are approximately 12 months old. From this age they are called yearlings for the next year of their lives. In October it was quite common to see small groups of from four to about ten yearlings of both sexes wandering through the Park together, away from their mothers. Lone yearlings could also be found scattered about at this time. The groups of yearlings were seen alone; or temporarily attached to some wandering female; or already having joined groups of bachelor males. In the calving season (Sept. - Oct.), it was still common to see females accompanied by both a new calf and by the yearling of the previous season, but by the end of December most of these yearlings of both sexes had joined the bachelor herd.

It is noteworthy that yearling females also join the bachelors and while some may leave to join a territorial male as early as 18 months of age, others stay with the bachelors for the duration of their second year. Indeed, it was noticed that throughout the study period there were always from two to five adult females to be found with the bachelors and sharing their daily routine. Even during the calving season these females did not leave and females with very young calves could be seen grazing in the midst of an aggregation of males.

B. Movements

At Swellendam there is only one bachelor herd consisting of up to about 75 males of all ages and including yearling and other females already referred to. This is a loose association of animals which follow the same general daily routine. They wander at will more or less anywhere in the Park though they show a definite preference for certain areas, notably a kloof next to the railway line where they spent most of the winter of 1969.

The herd does not stay rigidly together all the time, however, and it is not uncommon to find small groups of from two to twenty animals anywhere in the Park. Lone bachelors, too are not unusual but the probability is that these will sooner or later join up with one or other of the small groups.

The bachelor herd seemed to shift its centre of activity at will and grazed anywhere in the Park including on occupied territories of males with their harems of females. Fig. 3 shows a group of bachelors grazing together. If a territorial male should suffer an invasion of bachelors there is generally nothing he can do about it. He may chase them at intervals all day and may stand in their midst in 'proud' posture, with head held high and ears forward (Fig. 4) looking at the offending animals, which is interpreted as threat; but he can only chase one at a time, which then normally just runs in a circle until it returns again to the bachelor group. Chasing is usually at a gentle canter and over a distance of only 30-40 metres or less. This is interspersed with bouts of more vigorous chasing at a gallop, but still the territory holder normally fails to clear his territory of the invaders. It is evident that he cannot afford to spend too much time and energy in such aggressive activities since he must also have time to feed and rest and to attend to his females. The best that the territory holder can do in these circumstances is to segregate himself and his harem at one end of his territory and leave the rest to the bachelors. Estes noted that in the midst of large aggregations in the Ngorongoro Crater the best that a territorial male wildebeest could do would be to clear a space round himself by repeatedly charging into the mass. Bachelor male bontebok are quite docile and always give way before the owner of the property. They have never been seen to challenge nor to fight him. On the other hand, nor has a territorial male been seen to make physical contact with nor to hurt a bachelor when chasing him.

C. Functions of the Bachelor Herd

The bachelor herd is the outcome of the gregarious drive of the young males and presumably serves the same function for all males without property as nursery herds do for females and young.

FIGURE 2. High intensity sexual display by the male (right) as he approaches the female (left) prior to sniffing her vulva. Note tail curled over back, muzzle outthrust and head held low.

FIGURE 3. A group of bachelor males grazing and resting together. Note two males standing in reverse parallel position (Challenge Ritual) at top right.

Only territorial males eschew the communal life and choose a solitary existence. The bachelor herd provides the necessary security and social contact for the remainder. It provides a haven where the young male can mature in his own good time and without interference from or molestation by other males. It is not known how long a male may spend with the bachelor herd, but since he is not mature before 3 years of age, it must be a minimum of two years and is in all probability a lot longer (Section V.G.). It may well be that, indeed, those males lacking sufficient self-assurance to leave and establish their own territories, spend their whole lives with the bachelors, though evidence to support this contention is lacking.

A number of very old and decrepit looking males have been seen grazing peaceably with the bachelors, so that the herd affords a retreat for the aged as well. In addition, at least three collared males which had abandoned their territories at various times during the study period were seen grazing with the bachelors and not showing any aggression towards them. Thus a male when not on territory is presumably as subject to the normal gregarious behaviour as any other animal of the species.

A percentage of the herd consists of adult males in prime condition and it is from among these that males will leave to establish their own territory in a vacant area or to challenge an existing territory holder for the right to his territory. The bachelor herd therefore acts as a reservoir of young adults before they become territorial. This is an important function for it is obviously vital to the breeding success of any population that the territorial males, which are responsible for all mating, should be the most dominant and the fittest available in that population. Hence, the numbers of 'aspiring' adult bachelors provide competition for the established territory holders and ensure that no territory holder who is past his prime will remain unchallenged - that at least is the theoretical viewpoint. As explained in Section V.H. there is no evidence of strong competition for territories at Swellendam.

According to Estes, "The intolerance of territorial males forces bachelor herds to the fringes of wildebeest habitat, where territorial spacing is wider and harassment is correspondingly reduced. In this way bachelor males are largely removed from food competition with nursery herds and obliged to subsist in the least suitable parts of the habitat." He further reports that locations in the Crater most commonly occupied by bachelor herds were in areas of long grass normally avoided by other wildebeest. At Swellendam the habitat is very uniform and the study area is far too small to allow of valid comparison of bontebok bachelor behaviour with that of wildebeest; nonetheless, it was interesting to see up to 60 or so bachelors grazing on a male's territory. Thus, at Swellendam, the bachelors undoubtedly compete directly with territorial males and nursery herds for grazing.

D. Age Composition

Males of all ages from yearling upward are found in bachelor groups and due to the restricted calving season age classes can be distinguished up to the age of three years, as detailed in II.A. There is some tendency, particularly among the yearlings, for them to group themselves into age classes, but on the whole this tendency is rather weak, so that it is most common to find groups containing all age classes. This tendency resulted in the formation of subgroups which might contain, say, 6 yearlings and one adult male, which might split away from the main herd for part of the day. Schenkel (1966) reports that in impala bachelor herds the yearlings may form temporary subgroups, whereas Estes discerned only a weak tendency to age-grouping in bachelor wildebeest. It was noticeable that the handful of yearling female bontebok with the bachelors would stay together. Table 3 gives an idea of the sort of bachelor groups which may be encountered at random through the Park. It also illustrates the previously mentioned fact that the bachelors do not stay together in one herd all the time.

E. Spacing

Both Schenkel (1966) and Estes remark on the apparently greater 'individual distance' required by bachelors of impala and wildebeest respectively, which results in a wider spacing between members of the herd than is the case with females which

TABLE 3

Bachelor Groupings

Date	No. in group	Adult Male	2 year old male	Yearling Male	Yearling Female
20.2.70	5		3	2	
	5	1	2	2	
	3	1	2		
23.2.70	6	1	1	4	
	6	1	3	2	
	2	1	1		
26.2.70	6	2	4		
	2	1		1	
	3	1	1	1	
	2	1		1	
	2	1		1	
	4		2	2	
	10	1	1	8	
	5	3		2	
	4	1		3	
	5	2		3	
2.3.70	19	5	5	9	
5.3.70	24	1	10	13	
9.3.70	4	1	3		
10.3.70	23	6	7	10	
	12	3	3	6	
	11	4	1	1	5

have a more irregular, clumped distribution. The same is probably true of bontebok, but in a rather imprecise way, difficult to define. The difference was not obvious to me in the field, perhaps because bontebok harems are so small. Nursery groups of females and young certainly show the clumped pattern of distribution and tend to remain as a more compact unit. The bachelors are rather more widely spaced when grazing and yet within the herd there may be small knots of animals feeding close together. When resting, either lying or standing, some animals form very compact groups with only a few feet between individuals, while others are scattered about in between. In general, I would not describe the spacing among bachelors as regular. A field note of 16.4.70, while watching the herd of 75 bachelors illustrates: "spacing is irregular - some animals are lying in clumps or feeding in groups, while others are scattered about, feeding or standing more or less alone and 50 or more yards from the nearest animal. Those in groups are from less than 5 to approximately 25 yards apart." Nursery groups of females, though usually more compact, particularly when resting, may at times become quite scattered when grazing. See Figs. 3, 5 and 6.

F. Activities within the Bachelor Herd

There does not seem to be any rank or social hierarchy within the herd and it is very seldom that one sees a bachelor chasing or threatening another of whatever age. Amicability is the order of the day and animals of all ages graze or rest close together. Even ex-territorial males who have abandoned their territories and come to join the bachelors are as amiable as the rest. The members of the herd follow the same general daily routine as illustrated by Fig. 7, which is based on one full day's observations only. The observation hours were dictated by the time at which the animals congregated in the morning, and left the observation area again in the evening, as was their custom.

In general, there is very little activity or excitement among the bachelors over and above the normal daily activities of grazing and resting. The only play activity to be regularly witnessed is the play-fighting of the yearlings. This occurs (Fig.55)

FIGURE 4. The 'proud' posture of the adult male. Head held high and ears out.

FIGURE 5. A territorial male (left) and his harem of females and young stand in a compact bunch.

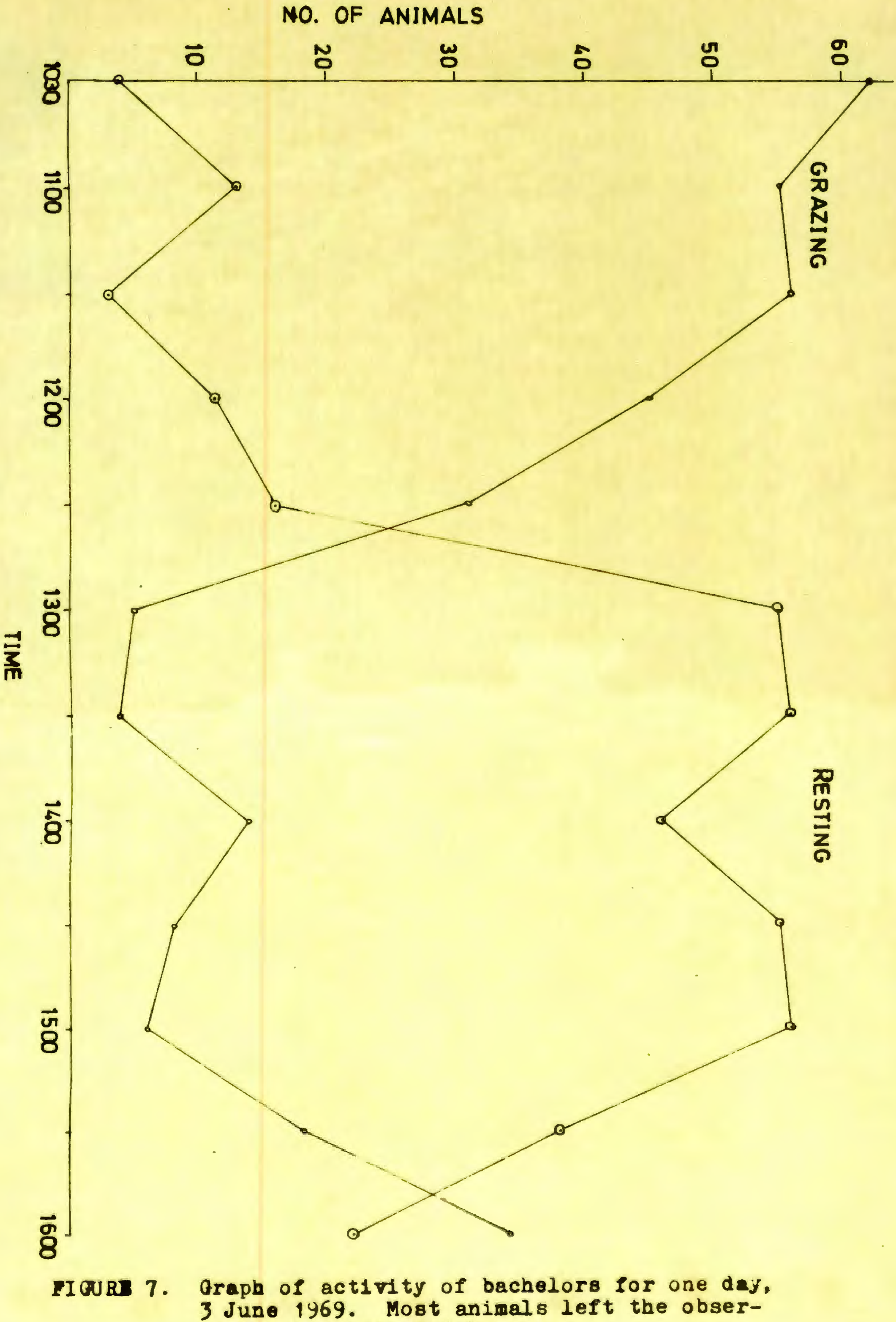

FIGURE 7. Graph of activity of bachelors for one day, 3 June 1969. Most animals left the observation area at 1615 hours.

sporadically throughout the day and sometimes several pairs of yearlings may be engaged simultaneously. The fights are of very low intensity and may last for five minutes or so. The two yearlings usually just stand facing each other with lowered heads and alternately engage and disengage horns, twisting heads left and right and lightly pushing against each other. Sometimes they will drop to their knees in the proper fighting stance of the adult and push more vigorously. The older classes of male do not seem to indulge in this play-fighting.

Both von Richter (pers. comm.) for C. gnou and Estes for C. taurinus remark on the evident dormancy of the sexual and territorial drives among the bachelors, nonetheless the older age classes of bontebok bachelors show both sexual and territorial behaviour sequences. Both adult and yearling females, habitually to be found with the bachelors, may from time to time be approached by adult males. The male will perform the characteristic sexual display (Fig. 2), and sniff under the female's tail. The female normally allows the male to sniff but avoids any further attentions by running round him, flank to flank, in tight circles. An adult bachelor has been seen trying to mount a yearling female with full erection. He continually displayed to her and ejaculated spontaneously on the ground. Other males do not seem to notice or pay any attention to a male displaying to females near them. One exception was a case where four adult males, one two year male, one yearling male and five yearling females were seen together. An adult male tried to mount one of the yearling females several times, grunting and with erection. The young female seemed bewildered and did not take any evasive action. Another adult male then attacked the molesting male without warning, and struck him with a horn thrust in the flank. The molesting male bellowed loudly and ran off, but no visible damage resulted. The other male did not pursue him. These young females are not in oestrus and no successful copulation was witnessed by bachelors.

In the context of territorial behaviour all the main steps in the Challenge Ritual (Section VII) have been seen performed by the older age classes of bachelors, from two years old upwards. All actions are performed at low intensity and bachelors were never seen to perform a complete ritual. They just walk up together and seemingly perform some of the steps at random. Even so, the high intensity actions such as fighting and cavorting have been seen at low intensity. The most commonly performed steps are reverse parallel standing accompanied by mutual anus sniffing and head shaking.

IV. THE CONCEPT OF TERRITORY

A. General

It seems that the concept of territoriality and the realisation of its significance in the lives of many species of animal has been slow to diffuse into modern biological thought. Perhaps man is psychologically unwilling to recognise that the behavioural trait manifested by a display of property ownership is not peculiar to man, but is a fundamental characteristic of animals in general. It may not be found in all animals nor developed to the same extent in those where it is (Burt 1943). According to Burt, the best definition of territory is that of Noble (1939) who defines it as 'any defended area'. Smith (1966) seems to concur when he says (p.372) "Territoriality exists when an individual animal claims a certain area and defends it against others of the same species ...". Nice (1941) says: "It is based primarily on a positive reaction to a particular place and a negative reaction to other individuals." Territory should not be confused with 'home range' which is merely the area habitually covered by an animal in the course of its daily activities. Home ranges of animals may frequently overlap, but in terms of the above definition one does not expect territories to overlap, since the territory is the protected part of the home range.

The study of territoriality began with the pioneering work of Altum, Moffat, Brewster, Herrick and Eliot Howard, during the early years of this century, on various species of birds (Nice 1941). The concept of territoriality as developed with regard to birds was gradually expanded until it came to be realised that the concept could have application to all species of higher animals, and even some lower ones. Even so the acceptance of the concept for mammals was rather slow and it is only during the last dozen years or so that field research into the biology of a number of species of ruminants has revealed the presence of a class of territorial males in almost all species studied to date.

Territorial behaviour has great variations which are related to differences between species and their habitats to seasons and climates, to population pressures, to social organization, to fluctuations of food supply, to predation and so on. It is complex behaviour of high order and includes many elements of selective and discriminatory response, for instance: attack, encroachment, defence, challenge, vocalization, feeding and security-seeking; all of which are expressed with reference to topography as well as to other organisms.

Carpenter (1958) agrees with the fundamental point made by Darling (1952) that territory is a social phenomenon, involving flocks, pairs, groups and herds. It is a form of intraspecific competition which concerns the degree of tolerance and intolerance between individuals. Wynne-Edwards (1965) says that social behaviour, as expressed in territoriality has two main purposes: firstly, a territorial system is a population regulating mechanism in that it limits the number of adults permitted to breed, and secondly, it prevents overuse of the habitat. Territoriality is a system which results in the parcelling out of the habitat into a mosaic of breeding and feeding lots. Individuals with no territory cannot breed, and the system might therefore have evolved for the exact purpose of imposing a ceiling density on the habitat and for efficiently disposing of any surplus individuals, which are normally forced into poor habitat and form a sort of floating population reserve. The rate of exploitation of the food resources of a habitat will automatically be prevented from exceeding a certain critical threshold. Nice (1941) takes the view that, in relation to birds: "The chief function of territory is defence - defence of the individual, the pair, the nest and young."

According to Smith (1966), territorial behaviour controls both under- and overpopulation. Since excess animals are forced into less suitable habitat to form a floating reserve, overpopulation of better habitat is avoided. When mortality creates openings, the vacated territories are re-occupied by individuals moving in from marginal areas. In addition to stabilizing the population, territorial behaviour also assures resident animals of isolation. The territory provides a place for courtship and mating without interference from others of

V. THE TERRITORIAL MALE

A. The Territorial Network

The presence of a single adult male with a group of females repeatedly to be seen in the same area over a period of time is diagnostic of territorial behaviour. Even before the commencement of the marking programme, the sighting of male bontebok day after day in the same place, either alone or with females, made it clear that they were territorial. After marking the sample of males with collars it could be verified that it was in fact the same male seen in the same place from day to day. All doubt on the issue was removed when these males were seen to chase away from their areas any would-be intruders.

The territorial males are scattered round the Park in a somewhat irregular fashion (Map 1) with, in most cases, plenty of space between neighbours. Some males have to walk more than $\frac{1}{4}$ of a mile ($\frac{1}{2}$ km), if they wish to interact with a territorial neighbour. The fact that a few territories are small and clustered and in this area frequent interactions between territorial neighbours occur, makes it appear that other portions of the Park are under-utilized - the overall habitat being very uniform. As already pointed out, the bachelor herd contains a number of perfectly fit-looking adult males. The reasons why some, at least, of these do not leave to take up a territorial existence are not clear. It may be that they lack the necessary self-confidence and drive. One factor of obvious importance is the age of the males. Many of the bachelors are unquestionably subadult. Unfortunately, it is impossible to guess at the age of adults without capturing and inspecting every individual, but many that looked adult were quite possibly only 3-5 years old. In accordance with what is said in Section V.G. these animals are probably not sufficiently mature to hold a territory. As far as I could tell, the onset of the rutting season did not affect the behaviour of the bachelors, and it did not seem to me that more territories were being established during the rut of 1970. Indeed, one or two that had been occupied for the previous year were conspicuously vacant at this time (see V.I.).

MAP I Diagram of territories for 1969 in the Bontebok National Park. Territories in the western section of the Park are numbered (= group nos.). Each territory or group contains one adult male. The prefix "C" denotes the collar number of marked males territory defended at any given time.

Estes remarks: "As there are no visible boundaries to show where one territory ends and the next begins, it is far easier to measure the spacing between males than it is to delineate a single territory." Accordingly, Estes placed fixed markers on the stamping ground of each territorial bull and estimated the distance of the bull from the marker. The stamp proved to be where the bull spent most of his time. It is a bare area of soil where the bull drops most of his dung and where he lies, paws, rolls and rubs his face and horns.

Territorial bontebok do not have a stamp, in the sense of one particular spot more used than the rest, though there are fairly conspicuous dung sites scattered about each territory. Most males, however, spent more time in one area of their territory than in any other - for instance, under a convenient shady tree. I therefore placed whitewashed stones in the most frequented portion of each territory and recorded the distance of each male from his marker during spot checks. Distances were at first paced, but being alone this proved too time-consuming and disturbed the animals too much. Subsequently, distances less than 50 metres were estimated by eye, while all others were measured by means of the odometer of a vehicle. This method permitted the plotting of the movements of individual males and also, by measuring the distance between adjacent markers, an estimation of the spacing of the males.

The average year round figure of approximately 25 territorial males in the 10.8 square miles of the Park (28.1 km^2) gives a density of less than 2.5 males per square mile (1.1 males per km^2). Table 4 summarises the mean spacing and density of territorial males of a few species of African ungulates. The figures for the bontebok were arrived at by measuring the distance between adjacent markers for two groups, one of 6 and the other of 4 territorial males. The calculated density of 25-30 males/sq. mile (10-12 males/km^2), is based on the assumption that this mean spacing is uniform throughout the habitat. This is not the case, however, since these two groups are the most closely spaced in the Park, which is not uniformly inhabited by territorial

Table 4. Spacing and Density of Territorial ♂♂ of Different Species

Species	Season	No. ♂♂ in sample	Mean yards	spacing Metres	Calculated density ♂♂/sq.mile	Actual Density ♂♂/sq. mile	Author
Bontebok	All year	6	323		30	4	
"	" "	4	349		25	4	
Wildebeest	Pre-rut	249	120-160		123-183		Estes (1969)
"	rut	300	120-145		147-221		" "
Waterbuck	All year	8				4.7	Spinage (1969)
"	" "	8				1.5	" "
Uganda kob TG	" "			15-30			Leuthold (1966)
" " ST	" "			100-200			" "
Thomson's gazelle	" "		200-300				Estes (1967)
Grant's gazelle	" "		800				" "

TG = Territorial Ground ST = Single Territory males. All other males are more widely spaced than these, with many around ½ a mile (0.8 km) from their nearest neighbour and in the eastern section of the Park this may be as much as a mile (1.6 km). In the western or old section of the Park, where territorial activity was greatest, there was a maximum of up to 20 territorial males in an area of about 5 sq. miles (12.8 km^2), yielding a true density of about 4 territorial males per sq. mile (1.5 males per km^2).

This density is seen to be extremely low when compared with that of wildebeest (Table 4). However, it should be borne in mind that when calculating his densities, Estes presumably assumed a uniform distribution of territorial males through the habitat, which may not have been realistic. Waterbuck and the gazelles have densities comparable with what I found for bontebok. All species in the Table, with the exception of waterbuck, are animals of the open plains.

Territorial male bontebok range fairly widely and may occasionally be found up to ½ a mile (0.8 km) from their markers. The average figure is, however, much less. In 522 observations of 14 known territorial males, with a minimum of 25 observations per male, they were found within 200 yards (183 m) of their markers in 60.1% of cases and more than this distance in 39.9% of cases. The actual mean distance males were found from their markers for these 522 observations was 191 yards (175 m). Estes sample of territorial male wildebeest were found within 100 yards of their markers in 88.7% of 1291 observations, whereas for the above sample, territorial bontebok were within 100 yards in only 33.3% of observations.

The low density of territorial bontebok in the Park coupled with the mean radius of movement of only 191 yards (175 m) around the marker, means that in fact most territories are separated by larger or smaller areas of no-man's land. The marker stones were not necessarily in the geographical centre of the territory, and were in some cases close to artificial boundaries such as fences or roads. This radius of movement is in some cases, therefore, not a true radius. That is to say, a male might be found much more frequently on one side of his marker than on another. If the stone was close to a territorial boundary then his range of movement on the side nearest his territorial neighbour would be restricted.

In the most densely inhabited part of the Park a male may have up to 5 territorial neighbours; but others may have only one, so that large sections of their boundaries do not abutt on to the territory of any other male. In such cases the boundaries of the territory are ill-defined; but even where territories abutt each other the neighbouring males do not necessarily seem to recognize fixed boundaries - there usually being some shadowy sort of no-man's land in between. This might be expected, perhaps, in view of what Lorenz (1966) has said about the declining self-confidence of each male the further he is from the centre of his territory. Thus, boundaries are decided by exactly matching the self-confidence of two territorial rivals at some geographical point, where each is a certain distance from his focus of activity. These boundaries, then, might shift within narrow limits from day to day, following daily changes in the health of the males and such things as hormone levels which Estes suggests 'fuel' the sexual-territorial drive. In some cases a fence provided a definite artificial boundary and sometimes a road or a hill slope seemed to be recognised as a boundary by the animals.

C. Activities of the Territorial Male

1. Association

Most territorial males were found both with nursery herds and alone during the course of fieldwork. Only 4 out of 18 known territorial males were never seen alone in a total (for those 4 males) of 235 observations. Of the other 14 males some were often alone and some only occasionally. In a total of 620 observations for those 14, with a minimum of 30 observations per male, they were alone on 127 occasions (20.5%). Most of the territorial males in fact are with females most of the time, so that a truly solitary existence is not a characteristic feature of bontebok territoriality. This is in contrast to wildebeest, where Estes reports that in 1122 observations of known territorial males they were found alone 74.2%, with another bull 6.3%, and with a herd only 19.5% of the time.

2. Courtship

There is considerable mutual interest shown in each other's activities by the territorial male and the group of females and young on his territory. They normally graze and move as a group throughout the day and the male herds and courts the females at intervals. Though, strictly speaking, they are not his 'property', and are free to come and go as they like, he will normally try to prevent any female from leaving the harem and will greet any female wandering on to his territory with prancing courtship display.

In contrast, for example, to impala which has several courtship displays (Schenkel 1966), the bontebok has only one sexual display, which with high and low intensity forms, is used in several situations. In the high intensity form of the display the tail is lifted and curled over the back; the head is carried low with neck and muzzle outstretched and the horns laid back (Fig.2). The ears are held out sideways from the head and somewhat drooping, (Fig.18). In low intensity form (Fig.8), the tail is lifted only to the horizontal or less, and the carriage of the head is more erect. Intermediate gradations are often seen. The almost identical display in blesbok is described by du Plessis (1968) as a mating approach, but in bontebok it is much more than this and has been seen in at least the following seven situations:

a) In the general situation of courting females. A male will approach a female in display attitude and will sniff her vulva once or a number of times. The female normally allows him to sniff and will wait for him with tail held away from her body and hindlegs slightly bent (Fig.9). The male often sniffs along the underside of the female's raised tail. 'Flehmen' on the part of the male was never observed in bontebok. The urination-Flehmen ceremony, in which a displaying male solicits urination from a female, samples her urine by taking some into his mouth and then shows Flehmen (Schneider 1934), does not occur in bontebok. Flehmen by the male is assumed to be for the purpose of olfactory testing of the female's urine, in order to determine her state of oestrus. In bontebok, no male was ever seen to show any interest in a female's urine. The urination-Flehmen ceremony is characteristic of the sexual behaviour of many ungulates, e.g. Uganda kob (Buechner & Schloeth 1965), impala (Schenkel 1966), springbok and eland (personal observation).

Characteristically, after the male has sniffed for a few seconds, the female swishes her tail rapidly from side to side and darts a few feet away from the male. Sometimes the male will follow and sniff again or a number of times. The female may stand with tail lifted and invite the male to sniff again. If not he may simply continue grazing. If, however, the male becomes too persistent or if he tries to mount an unreceptive female, she will run round him in very tight circles, flank to flank, keeping her nose very close to his rump, thus thwarting his efforts to mount. Should the male persist in trying to mount, they may complete several small circles in this manner, nose to tail, virtually on the spot. During this "mating circling", (Paarungskreisen, Walther 1958), the female normally holds her head low in the submissive posture (Fig.10). In between bouts of circling the male and female stand together with heads up. At intervals during the day the male may go round and sniff every female in his harem. If a female is lying down he will go over and stand by her in display attitude or nose her rump, when she will get up and allow him to sniff. Quite often he will also sniff the spot where she was lying. In contrast to the sideways-hold ears of the display, the male holds his ears back while sniffing and the female does the same while being sniffed.

I have not been able to detect any relation between the intensity of the sexual display and the oestrus state of the female. The high intensity form of the display is the normal form and this is performed to any female at all seasons of the year. Males have occasionally been seen to perform the high intensity display to yearling females, which are definitely anoestrus. Although a male may try to mount a female after displaying to her, copulation is not the usual outcome. Copulation

FIGURE 9. A territorial male sniffs the vulva of one of his ewes, in order to test her state of oestrus. Note ears of both animals held back.

FIGURE 10. "Mating circling" or Paarungskreisen. An unreceptive female (nearest camera) runs, flank to flank, round a male who is trying to mount her, in order to avoid his attentions. Note the head-low appeasement posture of the female.

was, in fact, witnessed on only nine occasions whereas males were seen displaying to females many hundreds of times. On a few occasions outside the rut, males were seen, after repeatedly displaying to a female, to erect the penis while standing next to her, and to ejaculate spontaneously.

The frequency of the sexual display was worked out while engaged in 12 hour activity studies of selected territorial males. For 12 whole days (144 hours) during the rut, involving six different males, the mean frequency of the sexual display was 0.97 displays per female per hour. For 15 whole days (160 hours) during the non-rut period mid-June to mid-September, also involving six different males, the mean frequency of display was 0.36 displays per female per hour. Working on the total number of displays per female for the two periods (rut and non-rut), and testing figures by means of Chi^2, the difference between them is just statistically significant ($Chi^2 = 3.95$, $p < .05 > .02$).

From the frequency of its occurrence, I have formed the firm impression that the vulva-sniffing ceremony is not only for informing the male of the oestrus condition of his ewes, but has also a deeper social significance in connection with keeping the group together and dissuading the females from leaving his territory.

b) If a female tries to leave his territory or if one strays too far away from the rest of the group, the male will often run over to her, stand by her in display attitude and sniff her. In most cases she will immediately turn and rejoin the group. If a male notices a female moving away he may just look up at her and display from wherever he happens to be standing. This 'display-at-a-distance' is not a common occurrence but I have about a dozen recorded cases where it caused the female to return to the group. Once or twice a female has been seen to run up to such a displaying male from more than 50 metres away, with head low in the submissive posture, and the male then sniffed her vulva.

Should a female not react to the male's display but continue to move away, he may give chase. Some spectacular chases have been seen in which a female, often accompanied by a young lamb, has tried to escape at full gallop, pursued by the male. The ewe may jink and swerve frantically at full speed, but the male heads her off each time until she submits and he then shepherds her back to the group. Sometimes she is too fast for him and makes good her escape or the male may just give up the chase. On the other hand, it sometimes happens that a male pays no attention to a female leaving his territory, beyond looking at her.

c) If a wandering female appears on the edge of his territory the male will almost invariably run over to her and greet her with prancing courtship display. On such occasions he uses the 'display-run', which is simply the normal sexual display set to a slow canter. It is rather a bouncing gait which enhances the prancing effect (Fig.11). He usually sniffs the new female and tries to shepherd her back to his group if he has one. Such a female may or may not submit to the male's attentions. Sometimes she will settle down at once to grazing on the male's territory, but quite often she merely continues walking on across the territory. She will usually stop and allow the male to sniff her then walk or run on. The male may follow her until she is off his territory but he will not molest her. Figure 12 shows a female running across a male's territory, the male following her with display-run, denoting his sexual interest.

In 26 recorded cases of a strange female entering a male's territory, the male went to greet her with sexual display in 25 of them.

It is interesting that in the large wildebeest population of the Ngorongoro Crater, Estes remarks: "I always found it hard to predict whether a bull would react to the entry of females with indifference, by trying to detain them (sexual interest), or by chasing them out (aggression). The time of year, the bull's temperament and mood, the behaviour and number of females, all seemed to be factors." In the small population of bontebok, sexual interest was the dominant behaviour pattern shown by males to new females and seldom would a male react to the arrival of a new female with indifference and never with aggression.

d) From time to time aggression between females may flare

FIGURE 11. Display-run by a territorial male. The normal sexual display is set to a prancing canter.

FIGURE 12. A territorial male display-running after a female, in an attempt to detain her on his territory.

up within the nursery herd for no apparent reason. This may take the form only of threatening with the horns, but actual horn clashes may occur and occasionally a horn battle of some vigour may ensue. Should this happen, the territorial male will usually run up and stand between the two females displaying strongly for some seconds. He may then sniff one or both of them. Such intervention by the male in female quarrels was seen about half a dozen times, and in every case the females concerned desisted immediately and resumed grazing.

e) During the course of the day, the whole group may make sudden movements from one part of the territory to another, in order to commence grazing or to lie in the shade of trees etc. These movements can be initiated by any member of the group moving in a determined fashion in a given direction, but are most often initiated by the male, who sets off with display-walk (Fig.8). This use of the display by the male to lead his females from place to place was recorded about 20 times in the field. The females and young normally follow in single file. The male may be some way ahead of the others while leading them and he will stop and look back over his shoulder to see if they are following. If they are not, or are tardy, he will stand in high intensity display, looking back at them, apparently to encourage them to hurry up, before he walks on again.

f) After aggressive activity involving chasing foreign males away from his territory, a male will often return to his group with display-run. When he reaches them he may either stand in their midst displaying strongly for some seconds or he may go round and sniff the vulvas of the ewes. In 31 cases where a male was observed to return to his females after absence, including being away to chase intruding males from his territory, he displayed to them on 25 occasions (80.7%).

g) After being away from the group while engaged in the Challenge Ritual (Section VII) with a territorial neighbour, he returns to his group as for f) above. See Table 14 for frequency.

3. Herding

Rather infrequently the territorial male may find it necessary to herd his whole group of females back towards the centre of his territory. This is most likely to be the case where the group has grazed to the very boundary of the territory, which often stimulates the male on the adjoining territory to approach. The home male then herds his females away from the approaching male by running straight at them, at a good pace, from the direction opposite to that in which he wishes them to go, with head carried rather high and ears forward - indicating an element of threat. He seems to lunge at them and drives them before him, with his tail lifted above the horizontal and flourished like a flag. This herding of the whole group by the male, was seen fewer than 20 times during the course of field work.

D. Quantitative Study of Daily Activity

1. Description

The method used by Spinage (1968) during his study of the Uganda defassa waterbuck was adopted. The activities of the bontebok were divided into their most basic daily components as follows: grazing; ruminating, differentiating between lying and standing; resting, differentiating between lying and standing; and other, which includes all other activities such as sexual or aggressive behaviour, moving, drinking etc. A special form was drawn up having a column for each activity and a remarks column for detailed behaviour notes. A four minute interval was used. Every four minutes a tick was entered in the appropriate column for each animal under observation. The activity occupying the major part of each four minute interval was ticked, and not necessarily the activity being performed at the end of each interval.

It was found that due to the rather closely co-ordinated activities of the groups and the open nature of the habitat, up to four animals could be watched simultaneously, though it was not easy in all situations to identify each of the four, and this proved to be the limiting factor. More usually the territorial male and one of his females were chosen for simultaneous study. Sometimes excursions of the male outside his territory rendered simultaneous observation impossible. During the rut of 1970, territorial males were watched exclusively to obtain data on the Challenge Ritual (Section VII). The chosen animals were watched if possible for 12 consecutive daylight hours, from 0600 to 1800 hours, but in mid-winter the short days rendered 10½ hours the maximum possible. In addition, Fahrenheit temperature and relative humidity were recorded at hourly intervals throughout each day. All observations were made from a vehicle using 12 x 50 binoculars and observation distances varied from about 30 metres to over 400 metres. The programme was continued throughout the year in order to show up any seasonal variation in activity.

The validity of this procedure depends upon watching behaviour which is undisturbed by the presence of the observer and is therefore completely normal. Considerable care was therefore taken not to disturb the animals, which are accustomed to tourist traffic. It is believed that the results obtained represent an accurate picture of bontebok daily activity.

2. Results

A summary of the results obtained for different seasons is presented in Table 5. The time spent per day in each activity is expressed as a percentage. Under the headings ruminating and resting, the differentiation into lying and standing has been dropped and both lumped into one figure. All males recorded were territorial.

The activity pattern of any given animal could vary considerably from day to day, so that the amount of time spent per day in each activity was not constant, nor was the time of day when it was performed. Only a summary is presented here. On the whole there was a strongish tendency towards a bipolar pattern of grazing - grazing being most intensive in the early morning and again in the evening, with the middle of the day spent resting and ruminating. In particular, the first two hours after dawn were almost exclusively spent grazing. Fig. 13 represents graphically the amount of time spent grazing by a sample of territorial males in each hour during the day.

The composite results show two significant trends.

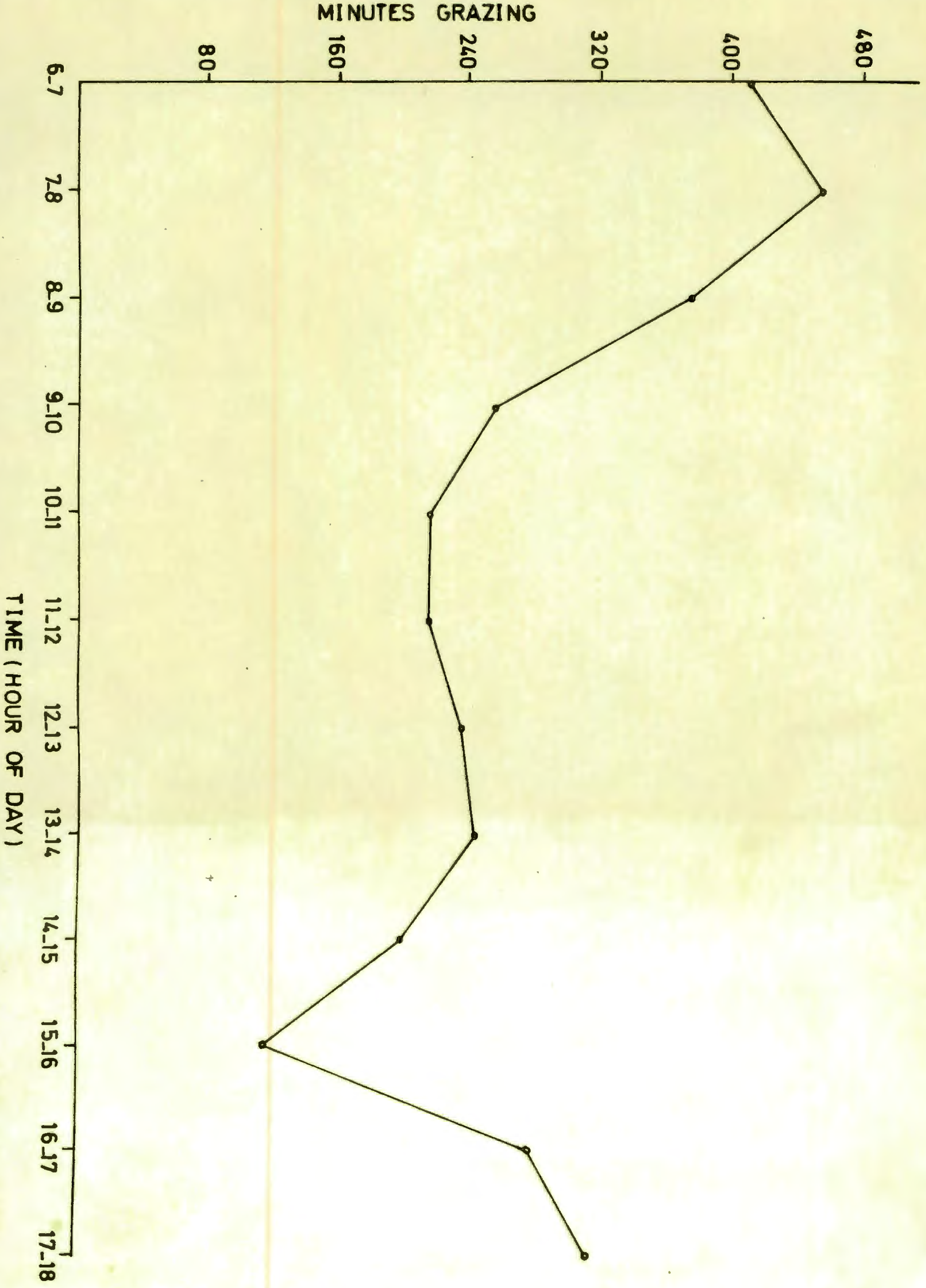

FIGURE 13. Composite graph of grazing activity throughout the day. Based on ten days (120 hours) observations of five territorial males during the rut between 27 Jan. 1970 and 24 Feb. 1970.

Table 5. Summary of mean daily activity

Observations						Mean % Activity			
Season	Period	No. days	No. hours	No. Animals	Sex	Graze	Ruminate	Rest	Other
Late rut	5.3.69 - 16.4.69	15	179	3	♂	48.0	22.4	13.4	16.4
Late rut	5.3.69 - 16.4.69	11	131	2	♀	54.1	19.7	19.7	6.4
Winter	13.6.69 - 17.9.69	13	139	6	♂	66.0	15.4	6.5	11.6
Winter	13.6.69 - 17.9.69	10	107	5	♀	73.0	18.9	4.0	4.1
Calving	9.10.69 - 20.11.69	5	56½	3	♂	58.5	28.9	6.6	6.7
Calving	9.10.69 - 20.11.69	6	68	3	♀	67.7	23.9	4.8	3.6
Rut	27.1.70 - 4.3.70	13	156	6	♂	46.3	24.0	13.4	16.1
	YEAR ROUND MEAN ACTIVITY				♂	54.7	22.7	10.0	12.7
					♀	64.9	20.8	9.5	4.7

The first is a seasonal one. There is a nearly 44% increase in grazing time from 46% to 66% of the day for territorial males between the rut and mid-winter. This result is statistically highly significant: $t=6.55$, $DF=24$, $p<.001$, (Table 6). This is accompanied by a compensatory drop in time spent ruminating and resting and by a smaller drop in 'other' activity. The few results obtained for the calving season, between the middle of September and the end of November, show an intermediate figure for grazing of 58.5%. This period shows an increase over the winter figure of the time spent resting and ruminating, and 'other' activity is at its lowest level for the year. Other activity is highest during and immediately following the rut (Table 5). Statistical analysis of the results by means of the 't' test (Table 6) showed, however, that there was no significant difference between other activity during the rut and during winter. The falling off in other activity during the winter is not the main factor explaining the rise in grazing time. This seems to be much more referable to a decrease in time spent ruminating and resting. This is true of both sexes. Males decrease the amount of ruminating and resting from a late rut combined figure of 35.8% to 21.9% in winter. Females show a decrease from 39.4% to 22.9% (Table 5).

This suggests that perhaps temperature is a factor and that the heat of summer necessitates more time to be spent in resting. The mean maximum temperature for the 16 observation days during March and April 1969 was 82.6°F with a mean relative humidity of 44.3%. For 13 observation days from mid-June to mid-September the mean maximum temperature was 74.0°F and RH 49%. This correlates with the above figures of ruminating and resting. When the temperature starts to rise during early summer, ruminating and resting also show an increase. Thus for 6 observation days from mid-October to end of November, the mean maximum temperature was 81.2°F and RH 49.5%. Males spent 35.5% resting and ruminating during this time and females 28.7%. Unfortunately, a broken thermometer prevented me from recording temperatures in the rut of 1970.

Concerning the effect of temperature, Harker _et al_ 1954, have this to say: "In the tropics day temperatures are

TABLE 6

Statistical Analysis of Activity

Sex	Period	Activity	%	SD	t	DF	p
M	rut	graze	46.3	7.76)	6.55	24	$<.001$
M	winter	graze	66.0	3.87)			
F	rut	graze	54.1	8.13)	5.37	19	$<.001$
F	winter	graze	73.0	4.57)			
M	year round	graze	54.7	7.67)	4.77	71	$<.001$
F	year round	graze	64.9	7.87)			
M	rut	other	16.1	5.59)	1.94	26	$<0.1> .05$
M	winter	other	11.6	3.94)			
M	year round	other	12.7	5.30)	11.95	71	$<.001$
F	year round	other	4.7	3.79)			

much higher than in temperate zones. Consequently, the efficiency of the heat-regulating mechanism is an important factor influencing the adaptability of animals to the tropics. It is to be expected that different species ... vary in this respect". Studies on different breeds of cattle by Hennings & Miller (1952), Bonsma, Scholtz & Badenhorst (1940), Rhoad (1938), Seath & Miller (1946) and Paine, Laing & Raivoka (1951) all quoted by Harker et al (op. cit.) have shown that high temperatures affect their grazing habits and, in particular, grazing time tended to fall during the hot months. Clear cut differences were shown between breeds adapted to tropical climes and European breeds under the same conditions. The adapted tropical breeds grazed longer in hot weather. It was concluded that the more efficient an animal was in disposing of excess body heat, the longer it would spend in grazing during daylight. Since temperature does affect grazing time it is presumably fair to conclude that it has some effect even on an indigenous wild animal and that therefore bontebok will graze longer when the weather is cooler.

The second trend emerging from the results is the rather clear cut difference between male and female activity patterns. Statistical analysis of year round grazing and 'other' activity for male and female show highly significant differences between the sexes; see Table 6. On a year round average the female grazes 10% more than the male and performs 8% less other activity (Table 5). The time spent ruminating and resting is very much the same for both sexes. The smaller amount of other activity for the female is perhaps fully expected in view of the fact that the male must spend time mating with all oestrus females on his territory, must defend his territory against interlopers and also engages in Challenge Rituals with neighbouring territorial males. It is not so clear how the male can maintain his condition, while expending considerably more energy than the female while engaged in the above pursuits and yet spend 10% less time in feeding than she does. As far as can be observed the intensity of feeding is the same in the two sexes. On the other hand, the majority of adult females have either a calf at heel, requiring milk, or one 'in utero' the whole year round and it may be that the energy expended on this account more than offsets the greater activity of the male. No systematic nocturnal observations were attempted and it is also conceivable that males make up their feeding deficit at night. This seems unlikely, however, in view of the evidence obtained by Spinage (1968) during his study of the defassa waterbuck in Uganda, where seasonal changes are not pronounced. Including nocturnal observations, (on males only) he found an even greater discrepancy between male and female waterbuck daily activity than I found for bontebok. Territorial male waterbuck averaged 44% of the day feeding and 21% in other activities, while females averaged 62% feeding and 7% other. His small sample of nocturnal observations shows a drop in feeding time at night.

It is also interesting that all seasonal changes in activity by the male, whether increase or decrease, are reflected by similar changes in the same activity of the female. This demonstrates the rather closely co-ordinated activities of the group, so that even on a day to day basis an increase in the amount of time spent, say, grazing or ruminating by the male is almost certain to be reflected by a proportional change in those activities by the females. This is due to the fact that the male is the initiator, in most cases, of all activities in the group.

The 'other' activity of the male is referable mainly to moving about, to sexual activity, to defence of territory and th Challenge Rituals (Section VII) with other territorial males. In the winter sample of daily activities (13 days) and in the sample covering the rut (13 days), there is very little difference in the total percentage time spent in these activities. Thus, in the winter, approximately 60.6% of the total other activity is spent in Challenge Rituals, defence of territory and sexual activity - 592 minutes out of 976 minutes. In the rut, this figure for the same activities falls to 55% - 800 minutes out of 1512 minutes. This in turn means that the majority of other activity throughout the year is simply moving about or otherwise unclassifiable activity.

Of the activities mentioned, the Challenge Ritual is the most important throughout the year. The time spent in this pursuit is about 27.6% of all other activity in the winter, rising to about 30% of other activity during the rut. Testing the raw data by means of a 2x2 contingency table yields a value of $Chi^2 = 1.62$ for 1 DF, $p = 0.2$. The difference in this activity is not, therefore, statistically significant. This is a somewhat surprising result since, subjectively it appears that there is much more interaction between territorial neighbours as one drives round the Park during the rut.

Sexual activity, on the other hand, does show a significant difference. It rises from 10.6% of all other activity in the winter to 13.6% during the rut. Testing the raw data by means of a 2x2 contingency table yields a value of $Chi^2 = 4.9$ for 1 DF, $p < .05 > .02$, which is just significant. This result tallies with that given for the frequency of sexual display (Section V.C.2.a).

The results presented in Table 6 were obtained by analysing the raw data - day by day percentages of the activities for each animal - and all percentages were transformed before calculation using the arcsin transformation (Bishop 1966).

E. Home Range of Females

Concerning the home range in mammals, Jewell (1966) says: "The home range is an arena for activity with spatial qualities that vary throughout its extent, and that is subject to great irregularity in intensity of use." Again: "Fundamentally the home range is an area with a certain productivity that meets the energy requirements of the individual, or group, that occupies it." He defines it thus: "home range is the area over which an animal normally travels in pursuit of its routine activities".

As explained already the females wander at will within the territorial mosaic. They come and go as they please so that they are by no means the 'property' of the male on whose territory they happen to be grazing. Nonetheless, most small groups of females seem to form associations between their members which are of an enduring nature and semi-exclusive in character. This trait, combined with the restricted home range of most females, which may coincide with the extent of two adjacent territories only or even only one of them, imparts considerable stability to

TABLE 7

Periods Spent by Known Females in a Home Range to 30 June 1970

Female	Date identified	Date left home range or last seen	Period (months)	Comments
G11/1	31.1.69	19.6.69	4½	Moved to neighbouring male
G11/2	2.6.69	27.6.70	12+	
G11/3	2.6.69	27.6.70	12+	
G11/4	14.10.69	27.6.70	8+	
1/A	25.1.69	7.11.69	9½)	These 3 females seen only on one or other of 2 adjoining territories.
1/B	25.1.69	7.11.69	9½)	
1/E	25.1.69	7.11.69	9½)	
G12	7.2.69	11.6.69	4	On territory 12.
G12	11.6.69	8.8.69	2	Moved to territory 2.
G12	8.8.69	5.1.70	5	Returned to territory 12 - then disappeared.
2/1	27.3.69	29.9.69	6	On territory 2.
2/1	29.9.69	31.3.70	6	Moved to territory 20.
2/1	1.4.70	26.6.70	3+	Returned to territory 2.
04/1	8.8.69	14.4.70	8+	
04/2	8.8.69	14.4.70	8+	
15/1	12.8.69	18.12.69	4	Died
16/1	14.8.69	27.6.70	10½+	
16/2	14.8.69	16.4.70	8+	
14/1	21.11.69	14.4.70	5+	

+ = still in same home range at conclusion of fieldwork.

behaviour of females such as 2/1 and G12 is perhaps of note in that they seemed to possess two home ranges and moved from one to the other without apparently spending time in the intervening area. Female 2/1's two ranges were more than a mile (1.6 km) from each other.

From time to time it seemed that females made excursions outside their accustomed home range, since it was noticed occasionally that a known female might be missing from her usual area on one day but back there the next. A few other known females seemed to be unattached to any particular male's territory and wandered over a much larger home range which might comprise around a $\frac{1}{4}$ of the whole Park. Females, even when attached for an extended period to one male, do not play any part at all in the defence of the territory.

The actual size of the home range of the females listed in Table 7 is difficult to give for the reasons already outlined in connection with estimating the size of territories. For one thing, the boundaries are not clearly defined. Another factor is that the home range is subject to unequal intensity of use. I have attempted to arrive at an estimate of the size of the 'core area' - that is the part of the home range exclusively and most intensively used by the group - by calculating the mean range of movement of the respective territorial male with each group, from the distances he was found from his marker stone. Core area was used by DeVore & Washburn (1965) to describe the part of the home range most intensively used by the baboon troops they were studying. They found that core areas of adjacent troops did not overlap.

The approximate sizes of core areas within a few territories are presented in Table 8. The overall home range of the females involved (coinciding with the full extent of the territory of the respective male), would be considerably larger. For the purposes of calculation the mean distance that each male was found from his marker was assumed to be a radius about the marker. The core areas are therefore assumed to be circular. Core areas calculated by this method vary from about ten to 73.6 acres.

TABLE 8

Core Areas of Females and Territorial Males

Male Territory	Female Identification	CORE AREA		PERIOD
		Acres	Hectares	Months
11	G11/1,2,3,4	15.3	6.2	4½ - 12
1	1/A,B,C	13.0	5.3	9½
2	1/A.B.C.	73.6	29.8	
2	2/1; G12	73.6	29.8	9+; 2
20	2/1; 14/1	28.2	11.4	6; 5+
12	G12	10.3	4.2	9
22	04/1,2	35.1	14.2	8+
23	16/1,2	56.3	22.8	10½+; 8+

F. Time Spent on Territory by Males

The bontebok, though a strongly seasonal breeder, is territorial throughout the year. A number of antelope species which have been found to be territorial the year round, have been in equatorial regions, where there are no marked seasonal changes and where breeding continues the year round, e.g. waterbuck (Spinage 1969) and Uganda kob (Leuthold 1966). Concerning the wildebeest, Estes remarks (1966): "Territorial behaviour throughout the year in the wildebeest is an interesting phenomenon, considering that it is one of the few mammals in equatorial Africa with a strongly seasonal reproductive cycle."

Apart from the 14 territorial males marked with collars during the year there were a few more which were certainly identifiable. The periods of time for which all known males were on territory up to the end of June 1970 are presented in Table 9. Many of the animals listed in the Table were undoubtedly on territory a lot longer than indicated, but in most cases I could not be absolutely sure prior to their being marked. As Estes says (p.352): "And yet there is reason to believe that territorial males of many antelopes, circumstances permitting, might spend their entire adult lives on the same piece of ground."

From Table 9 it can be seen that of the 15 males in the sample, six were known to have remained on territory for more than one year.

In a sample of 26 territorial male wildebeest whose histories were known for at least one year, Estes found that 20 maintained the same territory for this period, and of 13 known for 2 years or more, 7 maintained the same territory for this period.

G. The Age of Territorial Males

Unfortunately, no skulls of bontebok were available at Swellendam for ageing by means of tooth eruption and wear as, for instance, Spinage (1967) was able to do for the defassa waterbuck. Consequently, the best that could be done was a superficial examination of the animal's incisors at the time of capture for marking purposes. Ages arrived at by this method are pure guesswork, but undoubtedly the condition of the incisors

TABLE 9

Periods of Territoriality of Known Males to 30 June 1970.

Male	Date identified or returned	Date marked	Left territory	Still on territory at	Period (months)
01	6.2.69	13.5.69		29.6.70	17
03	11.2.69	17.5.69		26.6.70	16½
02		16.5.69	6.6.69		½
02	31.1.70		15.2.70		½
04		26.5.69		28.6.70	13
05		27.5.69		27.6.70	13
09	25.3.69	5.11.69	31.1.70		10
Gp 11	31.1.69	unmarked		28.6.70	17
11		12.11.69		28.6.70	7½
12		2.12.69	Betw. 4/5-26.6.70		5
13		3.12.69	Died end April 1970		5
14		3.12.69		28.6.70	7
15		3.12.69	28.1.70		2
16	2.6.69	2.12.69		28.6.70	13
06	28.8.69	31.10.69		28.6.70	10
07		4.11.69		28.6.70	8

does give some indication of both relative and absolute age. The small number of skulls collected during the study period was of little help, but provided newly erupted incisors for comparison.

Briefly, the incisors of all males examined were well worn. Not one male could be classed as 'prime'. Though in good physical condition all seemed to be past their prime. Some, indeed, with incisors missing or worn nearly level with the gum were obviously very old. Estimated age 7 - 11 years.

This may help to shed some light on the problem of the age at which males first become territorial. According to Leuthold and Kiley-Worthington, Uganda kob and waterbuck first become territorial at around 3½ years. Exactly this age (40 months) is given by Estes as that at which the majority of wildebeest become territorial for the first time. However, since these authors give no evidence from animals of known age this is presumably guesswork. According to Talbot and Talbot (1963) wildebeest only attain full body weight at 40 months and data presented by Spinage (1967) show that defassa waterbuck only possess their full set of permanent teeth at about 3½ years. Since the animal is evidently still growing, and therefore not fully adult, even though it may be sexually mature, it is most unlikely it could hope to establish a territory before this time. In fact, in his latest publication (1969), Spinage says that waterbuck first establish or attempt to establish a territory in their fifth to sixth year which coincides with the age at which horn length, body and testes weight reach their asymptotic levels.

This seems to me to be a more realistic estimate and, though I have no data on attainment of full body and testes weight for bontebok, my failure to find any young animals in my sample of territorial males suggests that neither do bontebok become territorial before four or five years of age. Estes stresses the profound psychological significance of territory, since an animal's behaviour is one thing inside the territory and quite another outside it. It appears unlikely that an animal barely attaining adulthood will have the necessary self-assurance to be able to compete for a territory. No doubt, for this reason there may be considerable variation in the ages at which individuals leave the bachelor herd. Spinage too, (1969) suggests that the precise age at which an animal becomes territorial depends upon temperament rather than any endocrine factor. By temperament I assume he means individual genetic variation among the males.

H. Territorial Pressure and the Ratio of Bachelor : Territorial Males

As has been pointed out already, the bachelor herd forms a sort of floating reserve from which future territorial males will be drawn, and it always contained a proportion of perfectly healthy adult males. It was always found extremely difficult to satisfactorily age the entire bachelor group of c.70 animals. The scrotum of each had to be clearly seen, since this was the only reliable guide. This was only possible from certain angles and the constant movement of the animals meant that one quickly lost track of those that had been aged and those that had not. As far as I could ascertain there were about 25 males with adult size scrota among the bachelors. Thus the adult male population is divided approximately 50 : 50 into territorial and bachelor animals. Leuthold estimated that about 50% of adult male Uganda kob were territorial at a given time and Estes gives a figure of $\frac{1}{3} - \frac{2}{3}$ of adult male wildebeest.

Estes goes on to say (p.301) that adult males may be relegated to bachelor herds not because they are unfit but because they are supernumerary. The exact ratio will depend on the number of adult males in relation to the area of the habitat. These excess males provide the main source of competition to established territorial males and he suggests that this competition is the basis for the phenomenon of permanently occupied territories.

The low density of territorial males at Swellendam has been mentioned. The situation among a population of 14,000 wildebeest may be very different, but at Swellendam there is no evidence of strong competition for territories from the bachelors. Thus, territorial pressure, which I would define as competition among adult males to hold territories in a limited area, is low. At Swellendam it does not seem to me that this low territorial pressure can be responsible for males holding permanent territories. A few case histories may help to illustrate:

I. Changes of Territory during the Study Period

Male 02 had a large territory from the end of January 1969 when fieldwork was commenced, until June 6 1969, when he abandoned it and went to join the bachelor herd. Some time during March 1969 male 09 established a small territory appropriating the western section of male 02's area, apparently without fighting. At this time male 02 was always with females and male 09 was alone. When 02 abandoned his territory 09 gradually extended his range and within a few days had taken over the whole of 02's old area including his females, which he held up to the end of January 1970. Up to this time no new male had come in to attempt to occupy 09's old area, which remained vacant, though partially included in 09's new area. At the beginning of February 1970, male 02, having been seen in the vicinity for some days previously, returned to his old territory and ousted male 09. It is uncertain whether 09 just left or whether fighting was involved. On January 30 1970 09 was seen to chase 02 furiously right off the territory. Having vacated the territory, 09 was seen nearby apparently in good health with some bachelors on 10 February 1970. This was the last time he was seen. 02 held his old territory for only 2 weeks before he also disappeared and was never seen again. The territory was then taken over by a new unmarked male. But up to end of June 1970, 09's original small territory remained vacant.

Male 15 was not marked until 3 December 1969, though he was known to be on territory for most of the preceding year. He proved to be the oldest of all the marked territorial males having several incisors missing. He abandoned his territory on 28 January 1970 and went to join the bachelors. At the end of June 1970 his territory still remained vacant, though a neighbour male 05, appeared to have appropriated part of it.

An unmarked male, group 9, disappeared at the beginning of April 1970, having been on territory since the beginning of the study, and his territory was still vacant at the end of

June 1970. Male 13, on the other hand, was found dead during the fourth week in April 1970 and his territory was taken over by a new male by 4 May 1970. Male 12 disappeared some time between 4 May and the end of June 1970. On 29 June 1970 his territory was still vacant.

Thus, not only is there space in the Park for aspiring males to stake out new territories, but even vacated territories are not necessarily re-occupied at once. Territorial pressure according to my definition is therefore low.

J. Sex and Aggression in Relation to Territory

If a male is to maintain a permanent territory, he must remain aggressive the whole year. One might expect a rise in aggressive activity during the rut. It has already been shown (Section V.D.2) that there is a significant rise in sexual activity at that time. Analysis of the same sample of daily activities treated there, 13 days in the winter and 13 days covering the rut, shows that in fact the level of aggressive activity falls from a value of 22.6% of all 'other' activity during the winter to only 9.5% of all 'other' activity during the rut. Testing the raw data by means of a 2x2 contingency table gives a value of $Chi^2 = 82$ for 1 DF, $p < .001$ which is highly significant. This is perhaps a surprising result. It is only partially explained by the rise in Challenge Ritual and sexual activity during the rut. It was pointed out in Section V.D.2 that the proportion of time spent in sexual, aggressive and Challenge Ritual activities together worked out to be higher in the winter than during the rut. Since the total 'other' activity is higher during the rut, it would seem that the balance must be made up of unclassifiable activity - mainly moving about. It seems possible that this could be interpreted as appetitive behaviour - the territorial male seeking a releasing situation, which due to the understocked nature of the Park is not forthcoming.

In any event, the evidence does show that males are actively engaged in maintaining their territories throughout the year. It is particularly interesting that sexual activity should apparently outweigh aggression during the rut. (Sexual activity

13.6% of other, aggression 9.5% of other). This observation runs counter to that of Estes who says (p.301) that: "even during the rut and with a female in oestrus on his ground, a bull expends far more time and energy fending off intruding rivals than on mating with the female." One would expect, a priori, that if there is strong competition for territories then aggression would dominate sex, since a male would be preoccupied in maintaining his territory. Perhaps it is the situation at Swellendam with low territorial pressure combined with the bontebok system of semi-permanent females that permits the reverse to occur.

K. The Ambivalence of the Sexual Display

It is recognised by ethologists that conflicting drives operating simultaneously on an animal may result in behaviour that is ambivalent or otherwise hard to explain. In birds and fish this may result in patterns of behaviour being performed in close sequence which belong to conflicting emotions, or in behaviour the postures of which are actually a compromise (Hinde 1966, p.249 et seq.), between, say, threat and courtship. Among mammals less work has been done, but Leyhausen's (1956) series of drawings of the threat posture of the cat, showing how it changes with increasing fear, is well known. In particular, the influence of sex hormones on both aggressive and sexual behaviour of mammals is accepted (Hinde p.166 et seq.).

In the members of the Bovidae that have been studied to date, the basic aggressive posture is 'head high' or 'proud posture' (Schenkel 1966), (Fig.4). In this posture territorial male bontebok inspect any disturbance or approaching buck, with head held as high as possible and ears forward. I have not been able to detect any specific appeasement posture (Demutstellung, Walther 1966) among adult male bontebok. The black wildebeest performs specific and pronounced appeasement behaviour (von Richter pers. comm.), perhaps due to the exceptionally aggressive nature and dangerous horns of this species. When severely harassed a black wildebeest will throw itself on to the ground and roll at once on to its side, thus exposing its belly, emitting the while a loud distress call. Male bontebok and lambs of both sexes up to yearling age use a 'head low' appeasement posture, (Fig.14). In this posture, with muzzle close to the ground, sometimes almost as though grazing, the submissive animal may run up to and past the threatening male. It is noteworthy that threatened animals besides using this posture to escape, may actually run towards the dominant male with head low. I have never seen head low used by females and lambs among themselves but only towards males. The submissive posture of the lamb is usually more pronounced than that of the female, who does not as a rule dip her muzzle quite so low as a lamb may.

Estes reports (p.333) that no stereotyped Demutstellung is displayed by territorial male C. taurinus. The head low posture seen in many bovids (Walther 1966) was not seen in taurinus males and rarely in females, but either sex could resort to agonistic grazing when approached by a belligerent conspecific. Females would sometimes resort to lying down with head and neck on the ground when sexually molested by a male. Even when severely sexually molested by a male, I have never seen a female bontebok lie down or utter any distress call. She continues to run round and round the male, flank to flank, (Paarungskreisen), usually with head low (Fig.15). Less commonly she may simply run away.

Von Richter (pers. comm.) says that head low is to be interpreted as low intensity threat, besides 'unconvincing' appeasement. In black wildebeest, territorial bulls herd and chase nursery groups or non-territorial males with head low. However, I have no evidence at all that it is to be interpreted as threat, at whatever intensity, in bontebok. Lambs running up to the territorial male with head low do not invoke any aggressive response. In any case, it seems unlikely that lambs of less than one year would use a posture implying threat towards an adult male. I have not seen adult males use the posture at all. The closest they come to it is during agonistic grazing in the Challenge Ritual. This is mostly true grazing, whereas Demutstellung is grazing attitude, or nearly so, set to a canter.

The posture of the male during sexual display contains a number of appeasing elements (Fig.2). The head is carried low with muzzle outthrust - below shoulder level in high intensity display. The horns are laid back so as to point away from the

FIGURE 14. A yearling lamb (right), walking behind its mother, shows head-low appeasement when a territorial male (out of picture) approaches.

FIGURE 15. A female (back to camera) shows head-low appeasement when sniffed by a territorial male.

female, and while sniffing the female the ears of both animals are also laid back. This is in entire contrast to the carriage of the head in proud posture. In addition, the tail of the male is lifted and curled over his back. The significance of this was not clear until lambs were occasionally seen to run to a threatening male with head low and with the tail curled up over the back in what was presumably extreme submission. Thus a juvenile submissive behaviour pattern seems to have been incorporated into adult courtship.

The need for the male to adopt an appeasement posture in order to approach the female for the purpose of copulation is self-evident. To find submissive elements in the male's courtship display is therefore to be expected. However, observations of the reaction of members of the nursery herd to the courtship display made it appear that the display was in fact ambivalent and carried elements of aggression not evident to the observer. The evidence for this is as follows:

1) A territorial male often displays to his females on returning from chasing an intruding male off his territory, or after any period of absence. As recorded in Section V.C.2.f males have been seen to display to females in 80.7% of observed cases. It may be supposed that if a male returns to his females immediately after aggressive chasing his aggressive threshold may still be low. Thus unreleased aggression carries over into sexual display.

2) A territorial male often displays to his females on returning from engaging in the Challenge Ritual (Section VII) which is mostly ritualised aggression. In a sample of 100 Challenge Rituals observed from start to finish at least one male was observed to display to his females at the conclusion of the Ritual in 41 cases (41%). The rest of the argument is as for 1) above.

3) As already related in Section V.C.2.b., if a female strays from the nursery herd or if a new female comes on to the territory, the male may display to her from some distance away. Cases have been seen in which a female has run up to such a displaying male from more than 50 metres away, with head low,

muzzle almost touching the ground, in appeasement posture. The male then normally sniffs her vulva. During Paarungskreisen also, the female circles with head low. This also shows therefore the threatening nature of the sexual display.

4) Lambs of yearling age apparently treat the sexual display as wholly threatening. On one occasion a territorial male displayed strongly between 2 lambs nearly one year old which had been having a mock fight. One of the lambs immediately ran up to him in extreme Demutstellung, muzzle on the ground and tail curled over its back. Older lambs will behave in the same fashion when their dam is being displayed to by the male.

5) Conversely, if a male persists in displaying to and sniffing a female, it occasionally happens that, instead of circling, she simply runs away. She may or may not show head low in this case. The female may run only a few yards if she is a resident female and remain grazing on the territory. A female may also run off when approached at a distance by a displaying male.

This seems to me an interesting example of appeasing and threatening elements combined in the male's courtship display.

VI. DEFENCE AND ADVERTISING OF TERRITORY

A. Defence of Territory

The central concept of territorial behaviour is intolerance of conspecifics limited to a certain area - "raumgebundene Intoleranz" Schenkel 1966 b. Male bontebok have been seen actively defending their territories at all seasons of the year. Active defence takes the form of chasing interlopers away from the male's area.

Chasing is not normally vicious, often only at a canter or even at a walk and somewhat ritualised in nature. As du Plessis (1968) noticed in blesbok, the resident male often seems to wait for the intruder to start running before giving chase. Reference to chasing bachelors has been made in Section III.B. The ritualised nature of chasing was made clear on a number of occasions. Once a territorial male ran towards a juvenile male who was grazing on his territory. The juvenile ignored him and carried on grazing. Instead of attacking him, however, the territorial male merely ran past and shook his horns at the juvenile as he did so. He then had to turn and come back again before the juvenile ran. Usually if a territorial male catches up with a bachelor while chasing him the bachelor will speed up frantically in trying to make good his escape. It has been seen a number of times, however, that a territorial male has caught up with a juvenile while chasing him. He does not attack him nor make any intention movements with his horns, but deliberately slows down and allows the juvenile to escape. The juvenile has not been seen to show any appeasement behaviour on these occasions. Sometimes the territorial male will just walk, usually head nodding, towards bachelors grazing on his territory and they give way steadily before him, also at a walk.

Bachelors are invariably docile and have never been seen to challenge or fight a territory holder (Fig.17). They may nevertheless be quite "cheeky" and if a territorial male is trying to clear his territory of bachelors they may just run a few yards out of his way and then continue grazing as before. Because of the necessity of feeding, resting and attending to his females, a territory holder cannot spend all his time chasing intruders, so that if he suffers an invasion, in between bouts of chasing, he simply ignores them and grazes in another part of his territory. The territory holder may also resort to aggressive cavorting in order to induce bachelors to flee. He runs up to a grazing stranger and when close to him he leaps into the air two or three times, all 4 feet off the ground. Landing with his front legs first he then kicks out with his hind legs, as though he were a 'bucking bronco' in a rodeo. This performance is followed by a vigorous headshake and the intruder moves away at once. Though he will never stop to contest the issue, a bachelor may still register his disapproval of being forced to give way by swishing his tail and shaking his head as he starts to run. He may also himself occasionally cavort in front of the superior male before taking to flight.

In the case of adult bachelors the territorial male seldom chases them in as straightforward a manner as he does juveniles. He walks or runs up to the bachelor and stops next to him or in front of him, presenting his side in 'lateral presentation' posture. This is a challenge and precipitates some elements of the Challenge Ritual. Most commonly these are reverse-parallel standing, mutual anus sniffing and headshaking. However, a bachelor was never seen to go through a complete Ritual with a territorial male and after only a few seconds would usually break off and run away. Sometimes a territorial male would run up to the bachelor, stand next to him and then urinate. This too was almost certain to bring about the instant departure of the bachelor.

The most serious chasing by far was seen during the rut and involved territorial males. One territorial male (A) would run into the middle of the territory of one of his neighbours, (B), and would run at full speed into the midst of B's females, scattering them in all directions, with the apparent aim of taking them over. This precipitated a furious chase and male B would chase male A at a full gallop (Fig.16). A was by no means keen to give up and he would run round and round in big circles, coming back at every opportunity to B's females and displaying to them when he got near enough. B was just as intent on getting rid of the interloper and if he could get close enough, lowering his head so that his horns were pointing forward, would

FIGURE 16. Territorial males chasing each other at full speed, in the rut of 1970. The male being chased ran into the territory of the other and tried to take over his females.

FIGURE 17. Territorial male, collar 02, chasing bachelor males off his territory.

make a serious attempt to jab A in the hindquarters, as they raced around. This was the only time that such an attempt to attack was seen. After a full five minutes of galloping round and round, twisting and turning this way and that, A would eventually retire to his own territory and leave B to collect his scattered females. No Challenge Ritual resulted from these encounters which were presumably a test of sheer endurance.

Normally a territorial male would not continue the chase of a bachelor once off his own territory and on many occasions he was seen to stop at his presumed border. This would be in agreement with the concept of territory already defined in which territorial behaviour is seen as the defence of a fixed area of ground. Sometimes though, a territorial male would not stop at his boundary but would chase strange males well off his own area. This depended particularly upon the proximity or otherwise of a neighbouring territory holder. A territorial male was more likely to continue the chase if a neighbour was absent or a long way off. Normally if one territory holder chased a bachelor on to a neighbouring territory the proprietor would come running across to intervene and would chase the bachelor on his own account. When this happened the first male usually retired immediately to his own territory. Some anomalies were witnessed, however.

On 16 October 1969, territorial male G12 chased a yearling male for nearly half a mile, right across the territory of a neighbour, male G8, and well onto the territory of another, G9. All these three were unmarked at that stage. Male G9, who was grazing, looked up and saw the yearling running past, chased by G12. Instead of joining the chase, however, he contented himself with shaking his horns at them as they went by and then went off to chase another juvenile male, which was grazing hearby, on his own account - a nice instance of redirected aggression. G12 eventually returned to his own territory but quite slowly, stopping to graze on G9 territory and unchallenged by G9. When G12 had returned to his own area, however, G9 then walked over and there followed a Challenge Ritual on G12 territory. On another occasion collared male number 01 was seen chasing a male at full speed more than a kilometre from his own territory. On this occasion he ran onto the territory of male G8 who at once ran across to intercept and chased the bachelor on his own account. When this happened 01 turned about and headed straight back towards his own territory at a run. Collared male 04 was also seen chasing bachelors well off his own area and indeed used to conduct lengthy excursions of 2 hours or longer duration well outside his own territory, during which he chased bachelors and was himself chased by other territorial males.

The movement of females from one territory to another was also a factor liable to provoke males to cross territorial borders. Though in most instances a male would not cross his boundary either when trying to attract females or when trying to prevent them from leaving his territory yet sometimes he would be induced to go and display to females on a neighbour's territory. In such a case the defending male would invariably race over and chase the intruder out, who never stopped to contest the issue but retreated at once.

A female in oestrus was particularly liable to create excitement among the territorial males. On 7 February 1970, collared male 13 was seen mating with an oestrus female on his territory. She ran across on to a neighbouring territory (male 12) hotly pursued by 13. 12 intervened and chased off 13 and then mated with the female himself until a third territorial male, collar 11, alerted by all the excitement, came running across from his own territory onto male 12 territory. Male 12 immediately gave vigorous chase to 11 and really tried to jab him with his horns. The female took advantage of the confusion to leave male 12 territory and she ran across onto male 11 territory. Whereat male 11 promptly left male 12 and returned to his territory to mate with the female. Male 12 remained behind on his own territory.

B. Territorial Advertising

Schenkel (1966 b) has rightly criticised the tenuous and undefined relationship between "marking" and "territory" in mammals. This has stemmed from subjective interpretation and too hasty acceptance by some authors of some behaviour patterns in mammals as "marking", when in fact no mark is set, or when there is no evidence that conspecifics take note of the marks set nor avoid the demarçated area. He rejects acoustic and static-optical demarcation as marking, since no mark at all is set and calls in question scent marking by means of dung and urine unless a ritualised posture or pattern of behaviour is followed while performing these excretory functions. Special postures previously referred to as optical-marking (static or dynamic) he suggests should merely be called impressive or threatening displays. In view of these justified criticisms, then, it seems much less objectionable to use the term "territorial advertising" instead of "marking of territory" when speaking of any behaviour pattern which may serve to render the territory owner's presence more conspicuous.

Schenkel also points out that manifestations of presence (Manifestationen der Präsenz) are important in maintenance of territory, and probably under this heading many patterns of so-called marking should really fall. The chasing described above under 'defence of territory' may perhaps serve to pick out the territorial males by their greater activity. This manifestation of presence might be termed 'dynamic-optical advertising'.

1. Static-Optic Advertising

As Estes points out, the most basic advertising action is just being there. "Proud posture" is well known among ungulates and territorial male bontebok normally carry their heads higher than females and bachelors. They stand with their heads as high as possible, ears forward and held out (Fig.4). They inspect the source of any disturbance, the observer, any wandering bontebok or they just stand and look around their territory for a few seconds at intervals throughout the day. There are times, of course, when the head carriage of the male is indistinguishable from that of his females. The proud posture of the male is interpreted as threat, and in this pose he inspects any approaching bontebok. This is always the first step preparatory to chasing off an intruding bachelor, though if the wanderer should turn out to be a female, this will quickly go over into sexual display. A number of cases have been seen where the proud posture of the territory owner inspecting an approaching bachelor has caused the latter to stop and then to change course so as to avoid the territorial male, sometimes at a distance of 200 metres or more.

A male may spend a significant portion of the day just standing or lying on his territory (Table 5). Though he may be doing no more than fulfilling his normal daily needs of resting and ruminating yet the territorial male often manages to make himself conspicuous by choosing short grass to lie on or by lying alone, (Fig.19). Sometimes he will choose a small mound to stand on, if there is one on his territory, and there he may remain for an hour or more at a time (Fig.20). Backhaus (1959) noted the same habit in hartebeest. However, I have occasionally seen adult female bontebok doing exactly the same thing. Hediger (1949) maintains that standing or lying in a conspicuous position is, in Schenkel's terminology, manifesting one's presence and therefore a form of territorial advertising.

Bontebok also have a characteristic mode of standing which they employ particularly on hot days, (Fig.21). This is not confined to territorial males and one may see whole groups standing close together, muzzles very low, sometimes almost touching the ground, chins tucked in and horns pointing forward. In hot weather they may maintain this pose for hours at a time in the middle of the day. They look very sleepy but in fact do not seem to sleep. They continually open and close their eyes, swish their tails, flick their ears and make restless movements of a yard or two this way and that. It is possible this habit has something to do with thermo-regulation. Having their muzzles close to the ground they might be able to take advantage of convection currents bringing in cooler air closer to the ground. Secondly, they stand predominantly facing the sun, thus exposing the smallest possible body area to the radiation, and they move their position so as to follow the sun through the course of the day. I was able to prove this statistically by driving circuits on very hot days. The number of animals seen just standing in the sun was noted, together with the direction of orientation. If groups of animals were encountered the number orientating, their direction of orientation and the number engaged in other activities

FIGURE 18. The sexual display of the male seen from the front to show the drooping ears.

FIGURE 19. Territorial males usually choose a dung site, situated on short grass, to lie on. Here, a female and lamb graze close to the recumbent male.

FIGURE 20. A territorial male stands, head up, on a slight mound. Note the difference in posture of the female (right), standing behind him.

FIGURE 21. A nursery herd of females and young stand in the sun. They stand in the typical 'hot weather position', with heads low, chins tucked in and horns pointing slightly forward.

(grazing, lying etc.) were recorded. The results obtained are presented in Table 10, which is a summary of several circuits driven between the end of October and the end of December 1969. The wind direction did not seem to be an important factor. Even when there was a wind they might stand either facing it or broadside to it while orientating so as to face the sun. Statistical analysis of the figure, for animals just standing in the sun ($260+22+37=319$) gave a value of Chi-square $= 541.6$ for 2 DF, $p < .001$. There is therefore a highly significant difference from a random orientation. From examination of the raw data it is obvious that animals stand so as to orientate towards the sun significantly more than any other direction.

2. Vocal Displays

Unlike the wildebeest (Estes), the bontebok is an extremely silent animal. Vocalisation does not play any part in advertising territory. The only sound regularly heard is the alarm snort - a short, explosive sound produced by expelling air rapidly through the nostrils. Both sexes snort, but it was noticeable that if a territorial male was with females he would stand closest to the source of disturbance and face it while giving the alarm snort. Other sounds I have heard are the grunting sequence emitted by a male when mounting a female prior to copulation, and the staccato bleats of a young lamb looking for its mother.

3. Dung and Urine

Marking the territory with the scent of the owner's own dung and urine is regarded as the oldest form of territory demarcation (Estes). Schenkel, as previously mentioned, rejects marking by means of faeces and urine unless ritualised display is involved in their production. This criterion would be met by the gazelles (Estes 1967) and springbok (personal observation). Territorial male springbok use a linked urination-defaecation sequence in which urination is performed in a wide "rocking horse" stance and followed at once by defaecation in a deep crouch on the same spot, usually an existing dung pile. Pawing the dung pile usually precedes the urination-defaecation sequence. Thus the distinctive and unambiguous movements involved come to have a visual display function.

The position with bontebok is somewhere "inbetween". All bontebok territories have fairly conspicuous dung sites scattered about, situated either on bare earth or where the grass is very short. A number of sample counts were carried out on different male's territories in order to estimate the approximate density of these sites on a territory. All distances were paced. The results are presented in Table 11. The overall density was calculated to be about 1.7 used dungsites per acre (0.7 per hectare). Estes (1967) in 2 small sample counts on Thomson's gazelle territories found an average of about 1 dung site per 100 ft. quadrat. Thus, by comparison, the density of dung sites on bontebok territories is rather low.

The problem is to decide whether they can, in any sense, be regarded as territory markers. Bontebok do not perform the linked urination-defaecation sequence already described and the defaecation posture of the male is relatively unexaggerated (Fig.22), though more distinctive than that of the female, who usually defaecates while walking. The dung sites undoubtedly have significance for the territorial males. They defaecate on them almost exclusively and usually choose one to lie on. They also kneel and horn the soil in these patches of dung (see Section VI.B.5). Males deviate from their path in order to defaecate on a dung site and have often been seen deliberately walking as much as 40 metres to one before defaecating. Actual observations showed that in 202 recorded cases of defaecation by territorial males they chose dung sites in 173 (85.6%) of these. The position with lying down is not quite so clear cut. In 130 recorded cases of males lying on their territory, they lay on a dung site in 69 (53.1%) of these. It is fairly common for a territorial male to sniff the dung site before defaecating. In 98 recorded cases of defaecation the male sniffed the spot first in 34 of them (34.7%). Females do not defaecate on the dung sites and seldom lie on them.

Bachelor males defaecate at random and do not normally pay any attention to dung sites. They certainly do not avoid occupied territories. Territorial males have been seen to sniff and defaecate on dung sites on another male's territory. This

TABLE 10

Orientation of Standing Bontebok

acing Sun	% of Total	Back to Sun	% of Total	Broadside to Sun	% of Total	Other Activity	% of Total	Total
260	55.2	22	4.7	37	7.9	152	32.3	471

TABLE 11

Counts of dung sites on territory sample areas

Ident. No. of Territory	Area of Count (Acres)	(Hectares)	No. of Dungsites In use.	Not in use
1	c.20.0		30	9
11	c.1.25		3	3
11	c.1.2		3	0
8	c.2.33		9	4
9	c.1.4		7	3
2	c.3.0		4	2
1	c.4.0		4	0
KT	3.0		1	5
KB	3.0		5	5
	39.2	15.9	66	31

happens particularly while returning to their own territory at the completion of a Challenge Ritual. Thus it may be that any dung site will stimulate a territorial male to stop and defaecate. The fact that these dung sites are of particular significance only to territorial males makes it tempting to regard them as markers of territory. However, since no behaviour patterns have been seen which might be connected with recognition or avoidance of such marks by conspecifics, it is doubtful whether this is valid. The use of faeces and urine to set scent marks among the Canidae is well known and it appears that conspecifics do in fact inspect and take note of these marks. Lorenz (1954) ascribes the function of territory marking and warding off intruders to the deposition of urine on conspicuous objects by male dogs.

Kleiman (1966) citing Lyall-Watson (1964) offers the interpretation that scent marking in the Canidae serves to maintain the animal's familiarity with its environment and that odour is added to specific visual landmarks both to familiarize the animal with new territory and to refamiliarize it with old terrain. This explanation could very well apply to the dung sites of bontebok. The scent of the male's own dung, concentrated in small areas scattered about his territory, could serve to reinforce the assurance gained from a known home range and so bolster the self-confidence the male requires to maintain his territory. It would seem that more work needs to be done on the precise relationship between territory and marking in mammals.

4. Preorbital Gland

The use of the secretion from the preorbital glands to mark objects such as trees and grass stalks etc. has been noted in a number of ungulate species, Hediger (1949). Bontebok have a fairly conspicuous invaginated preorbital gland situated below the eyes (Fig.23). The orifice is rather small and remains permanently open, so far as I've been able to see. The glands are larger in males than in females and secrete small quantities of a black substance. No deposits of preorbital gland secretion have been found in bontebok territories, such as Estes (1967), for instance, found in Thomson's gazelle territories.

FIGURE 22. A territorial male defaecates on a dungsite.

FIGURE 23. Close up of the head of a drugged male to show the preorbital gland situated in front of the eye.

However, territorial males have been seen waving their muzzles in the grass (glandular weaving) in a characteristic manner, (Fig.24). The male stands and brings the openings of the two glands down alternately on to the end of a suitable grass stalk. The end of the grass stalk or twig is thus inserted into the openings of the glands. The male then waves his muzzle, forehead, and the base of his horns from side to side across the end of the grass stalk. The male then again sticks the stalk into the gland openings and the whole process is repeated. He may stand and continue this performance for a good two minutes at a time. Sometimes the stalk chosen is next to a dungsite and the male may defaecate after weaving.

On about half a dozen occasions I have been able to locate the actual grass stalk used for this glandular weaving. Sometimes there is no trace whatever of secretion on the tip of the stem. Two or three times I have found the tip just perceptibly damp and discoloured by the black secretion. The amount of secretion transferred is thus very small.

The existence of this behaviour pattern and the fact that it is predominantly performed by territorial males - (I have only about half a dozen records of females weaving in 15 months of fieldwork), suggests that it may have a demarcating function. However, it has been infrequently seen - I have less than 50 records of weaving even for territorial males and, as mentioned, no glandular deposits have been found in bontebok territories.

The frequency of weaving among territorial males for 13 whole days during the rut was an average of once per day, with a range from nil to 3 times per day. From mid-June to mid-November the frequency for 19 days fell to only 0.2 times per day per territorial male. These figures are exclusive of weaving occurring in the Challenge Ritual. This evidence, as well as the fact that no behaviour patterns have been seen in bontebok which might be connected with recognition of such scent marks, leads the present author to believe that the preorbital gland does not play any functional role in demarcating territory. It may, perhaps, be a relic pattern which has lost its functional significance.

5. Demonstration-Threat

The importance of distinctive postures serving as visual displays has been pointed out by Hediger (1949) and by Estes. It has been mentioned already in connection with the linked urination-defaecation sequence of springbok and gazelles. If a display implies threat but is not directed at any individual then it is merely social demonstration or advertisement (Estes citing Schloeth 1958). In the case of wildebeest, Estes gives examples of horning the ground, pawing and defaecating, and rolling as aggressive actions serving as advertisement for the territorial bull. Estes follows Hediger in referring to these actions as demonstrative-marking. However, as no mark is set I prefer to follow Schenkel and call them impressive displays or symbolic threat at a distance.

"In the context of foraging, digging for subsurface water, or preparing a resting, wallowing, rolling or marking place, pawing may be seen in probably all hoofed animals" (Estes). I have never seen bontebok paw the ground in any context, either preparatory to kneeling or defaecating; nor have I seen bontebok roll.

Urination in some contexts is undoubtedly aggressive. This is so particularly during the Challenge Ritual where it probably has a threatening function. It has been mentioned that a territorial male will sometimes approach an intruding bachelor on his territory, stand next to him and then urinate. The bachelor usually moves off at once. I have also noticed that if an observer on foot disturbs a harem herd, the territorial male, remaining behind his females to snort at the observer, will sometimes stand broadside on in a wide stance and urinate. This I assume to be symbolic threat. It seems relevant therefore to mention that though urination occurs at random and does not play a part in marking territory, yet it has often been noticed that a territorial male will remain in urination posture (Fig.25) long after the flow of urine has ceased. I have records of males remaining in urination posture as long as 70 seconds. The mean of 25 events timed from the start of urination until the male moved out of the posture was 29.4 seconds. It is thus possible that the posture serves a display function related to advertising

FIGURE 24. Glandular weaving by a territorial male. The male brings the openings of his preorbital glands down on to a convenient grass stalk, thus transferring glandular secretion to the grass.

FIGURE 25. Urination by a territorial male.

the status of the male.

Precisely the same considerations apply to defaecation. It takes a bontebok ram only about 5 seconds to actually drop his dung, but I have several records of territorial males remaining in defaecation posture for around 30 seconds and up to 40 seconds. The mean of 42 events timed from the start of defaecation until the male moved out of the posture was 16.2 seconds. It is again possible, therefore, that the assumption of the excretory posture serves a signal function in connection with advertising the presence of the male.

Unquestionably of display significance is the act of kneeling and horning the soil (Fig.26). This is linked with defaecation and is performed almost exclusively by territorial males. There are two types of horning. The first is 'forward' horning, in which the animal goes on its knees and horns the soil with forward strokes of the head, both horns simultaneously touching the ground. While doing this it sometimes picks up branches and litter which remains attached to the horns when the animal gets to its feet. This behaviour is uncommon but females are usually involved. They often choose a small shrub to horn and either kneel or stand while so-doing.

The usual type of horning is 'sideways' horning. The animal also goes on its knees and turning its head from side to side draws first one horn through the dirt and then the other. This may be performed once only with each horn or several times. Territorial males always horn in a dung patch and after horning they get to their feet, move forward the length of their body and then defaecate on the same spot. This behaviour pattern is prominent during the Challenge Ritual where it is undoubtedly threat. Estes points out that the provocative nature of the sequence of actions is probably due to the fact that kneeling is also the position for fighting in the Alcelaphini. As he says, it probably arose as redirected agression rather than as scent marking. Soil horning is interpreted as threat by Schenkel (1966) for the impala and by Leuthold for the Uganda kob. The latter, however, reports both ground and bush horning and does not distinguish between the two.

FIGURE 26. Linked soil horning followed by defaecation on the same spot by a territorial male.

The distinction between forward and sideways horning may be related to that between bush and ground horning which Schenkel (1966) draws for the impala. He noticed that animals might rub their faces in a shrub or horn a tree and that this activity did not appear to have any display significance, whereas soil horning was threat. Thus, forward horning by bontebok is likely to be a "comfort" activity since a shrub or a branch lying on the ground are normally the objects of the horning. It is an uncommon activity and I have less than a dozen field notes of shrub horning by bontebok.

Sometimes a variation on the theme is employed by males. They go on their knees and horn but instead of getting up and defaecating, they first of all lie down completely on the dung patch before rising again immediately and then defaecating. Sometimes the hindlegs are not fully lowered into the lying position before the animal gets up and defaecates. This act of lying down momentarily is presumably due to the fact that kneeling is also the first step in the normal act of lying, so that once on its knees, the animal "forgets" why it is there and simply completes the usual sequence of actions in becoming recumbent. Another act of possible significance is performed by males while recumbent. They turn the head sideways and rub one horn then the other in the earth (Fig.27). This is nearly the same action, performed while lying, as they perform on their knees in normal horning. Sometimes they perform a muzzle-to-flank movement afterwards. As far as I've been able to see this act brings only the horns into contact with the soil and, unlike wildebeest (Estes), the frontal region and preorbital glands do not touch the earth. Indeed, the configuration of bontebok horns rather prevents this from happening so it is probably not a case of transferring preorbital gland secretion to the ground.

Dowsett (1966) reported that Lichtenstein's hartebeest, which possesses well-developed preorbital glands, horns the soil by going on its knees, turning its head from side to side and digging up earth with its horns. Both sexes do this. It then rubs the sides of its face in the earth, and then the face on the side of the body before getting to its feet. Blackish marks were seen on the flanks of animals due to the transfer of the secretion

FIGURE 27. A territorial male drags his horn through the dirt while lying down.

from the preorbital glands.

Soil horning as an independent display is undirected and may be performed by territorial males while alone or with only females present. It is not a common display and in 117 recorded cases of defaecation by territorial males during the rut only ten undirected hornings were performed (8.5%). As an alternative gauge, during 13 full days in the rut (12 hours observation per day), the frequency of undirected horning was only 0.54 per territorial male per day. For 19 whole days from mid-June to mid-November (non-rut), the frequency dropped to 0.16 per male per day.

It was noticed, however, that a number of different stimuli could excite a male to horn the soil and these were counted as directed displays i.e. directed at a particular individual. For instance, not only is soil horning conspicuous during the Challenge Ritual but also after it. A male will sometimes stop to horn the soil on his way back to his own territory at the completion of a ritual, Table 14. He may use it as a threat display to bachelors, by standing next to an intruder on his territory and then going on his knees and horning the soil. They may also do it as a threat display to the observer, as when disturbed by a vehicle the male may move off a few yards and horn the soil. If forced to give ground at his boundary by a neighbouring territory holder, a male may go off and horn the soil to vent his feelings - redirected aggression. He attacks the ground as he wishes but fears to attack his rival. The frequency of such directed horning displays was almost 1.0 per male per day for 13 whole days (12 hours per day) during the rut, excluding hornings performed during Challenge Rituals. During systematic observations of territorial male Uganda kob, Leuthold reports that soil horning was not seen more than twice in 10 hours observation in each of seven males observed. However, he does not distinguish between directed and undirected displays. Female bontebok were very occasionally seen to go on their knees and sideways horn just like a male (less than half a dozen observations in 15 months). They do not use a dungsite nor do they defaecate afterwards.

Leuthold reports that the most remarkable series of soil hornings he saw occurred when a territorial male was seen to beat the ground or small bushes with his horns six times in 9 hours of observation.

I witnessed a remarkable series of soil hornings by a territorial male bontebok on 4 February 1969. The male horned the soil, on his knees, 11 times in a period of 290 minutes. Three of these were followed by defaecation. The male was very active in between the bouts of horning. He was constantly either chasing off bachelor males or displaying to and herding his females. There had been considerable activity on this particular territory (Group 1) for the previous few days, due to an invasion of bachelor males.

VII. THE CHALLENGE RITUAL BETWEEN TERRITORIAL MALES

A. Outline

At the beginning of the study frequent ritualised encounters between neighbouring territorial males were seen in which the two males would stand head-to-tail and sniff each other's anus. This ceremony was preceded by a long slow approach and took place either at the presumed border of the two territories or well inside the territory of one male. At the conclusion of the ritual the males would return to their respective territories without fighting. This was called the mutual anus sniffing ceremony. On reading Estes outstanding piece of work on wildebeest, however, it became quite obvious that I was witnessing behaviour very similar to that of wildebeest which Estes called the Challenge Ritual. I have therefore adopted his terminology which will henceforth, for the sake of conciseness, be abbreviated simply to "CR". It was decided to go ahead with a comparison of bontebok and wildebeest CR behaviour and accordingly, during the rut of 1970 I collected a sample of 100 CR's, tape-recorded in the field and then transcribed for analysis.

Reference has already been made (Section V.D.) to the proportion of the day spent in this activity by territorial males. In any event, once one has seen it in the field it is obvious that it is an activity of considerable importance to the animals. In absolute terms, for 13 whole days during the rut, an average of 35 minutes per day was spent engaged in the CR with a range from nothing to 80 minutes per day. During mid-June to mid-September this fell to an average of 20½ minutes per day, with a range from nothing to 46 minutes. One might say that, in general, a male goes through the CR with each of his territorial neighbours once a day. However, it is equally common for a male to have several encounters in a day or none with any particular neighbour. The fairly marked difference, incidentally, in the daily time spent in CR activity between winter and the rut bears out my own subjective impression of the general level of activity, which was not borne out statistically (Section V.D.) where CR activity was expressed as a proportion of total 'other' activity.

Curiously enough, my sample of 100 rituals, timed from start to finish, had a mean duration precisely the same as Estes sample of 71 rituals - namely 6.5 minutes. The shortest ritual I recorded was about one minute and the longest 23 minutes.

Territorial males show definite appetitive behaviour for these encounters and many times have been seen walking $\frac{1}{2}$ km (more than $\frac{1}{4}$ mile) or so into the middle of a neighbour's territory in order to interact with him. No particular stimulus has been observed to trigger off such episodes. The male apparently just "decides" to go. On the other hand, it has been noticed that any external stimulus can precipitate a CR. For instance, a bachelor being chased across his territory by a neighbour will lead to the home male intervening and may often result in a CR between the 2 territorial males. Any other disturbance, for example by the observer, can lead to a male going off for a session with his neighbour. This is presumably due to him requiring an outlet for the aggression aroused in him by seeing other males being chased, or by himself being forced to move.

When I first saw the mutual anus sniffing encounters I thought they must be something to do with defence of territorial boundaries, and that if one male overstepped his border the defending male would come across to "see him off", but in a ritualised fashion. This may have been true of a percentage of the rituals which did take place at presumed territorial boundaries, but the above observations of males deliberately walking long distances in order to interact made it abundantly plain that by and large it was not so. Having seen it many times, it often gave the impression of being merely social stimulation sought for its own sake. In all probability, however, it was not so - see Discussion. I recorded 24 rituals (24%) which took place at what I considered to be territorial borders; 76% were therefore within the domain of the defending male.

As Estes noted for wildebeest no two CR's are exactly the same. To give an idea of the variability and of precisely what happens during these ritualised encounters, I cannot do better than follow Estes and relate three complete rituals. The male initiating the action is called I, for invader, and the other male is D, for defender.

B. Three Protocols

1) 7 January 1970, 10.28. I, who has been drinking at a fountain is returning to his own territory and is crossing D's territory. I walks steadily, head normal height, just above shoulder level. D stands and then walks towards I who continues to walk on. When I is almost past D runs towards him, head up and shakes his head at I. D stops squarely in I's path, presenting his side (lateral presentation) and defaecates. D shakes his head. I walks behind D and stands. Then with a small prance and a leap, I turns swiftly towards D, shakes his head and swishes his tail. D then comes round behind I and sniffs his anus. Then D shakes his head and I turns and leaps into the air (cavorts) and starts to run back towards his own territory. D gives an answering cavort and pursues I at a fair gallop. I reaches his own territory and D stops at the border. Duration 1½ minutes.

2) 25 January 1970, 19.23. I has crossed on to D's territory. The males stand close together in 'reverse parallel' position (head-to-tail). D shakes his head, then sniffs I. Mutual anus sniffing with tail swishing follows, lasting about 2 seconds. A short pause, then two more bouts of mutual anus sniffing with tail swishing each lasting about 2 seconds. The males remain in the reverse parallel position. D shakes his head. I puts his head down to the ground and up again almost at once ('head dip'). I walks round behind D and comes round so that they face the same way. I sniffs D's anus, who turns his head round towards I and then shakes his head. D walks away, puts his muzzle down to sniff the ground and then defaecates. I stands looking away ('head flagging'), head held high. D scratches his ear with his left hindfoot for 8 seconds. I stands behind him still head flagging. D is standing in front of I, presenting his side. D turns round and I sniffs his anus. Then they face each other and touch noses and then both shake their heads at once. Then they turn apart a little and D comes forward so that they return to reverse parallel standing. More mutual anus sniffing with tail swishing follows. Ears are laid back

during anus sniffing. I moves so that he stands behind D looking away in the other direction. D scratches his neck with his left hindfoot. I puts his muzzle down to the ground. D puts his head down in grazing attitude and begins to walk away. I simultaneously begins to walk away back to his own territory. Duration 5 minutes.

3) 5 February 1970, 17.18. I walks into the heart of D's territory from where he was grazing 200 metres away. D stands waiting, head up and ears back. I walks behind D, shakes his, head, shakes it again, then cavorts, just lifting his forefeet off the ground. D just stands and headflags. The 2 males stand about 6 metres apart, looking in opposite directions. D walks round behind I who shakes his head. D stands at right angles, presenting his side to I's rear and then sniffs I's anus. I shakes his head and then comes round into reverse parallel position and sniffs D's anus. D shakes his head and swishes his tail. They just stand reverse parallel. I cavorts, lifting just his forefeet off the ground, then shakes his head and puts his muzzle down. D shakes his head. I leaps into the air again. Both males cavort, but only their front legs leave the ground. Both shake their heads. They were standing reverse parallel but when I cavorted D turned to face him, and then turned away again. I puts muzzle low, D follows suit and walks away. I follows and and they graze close together. Now D trots away and I follows. D is in the heart of his own territory. D breaks into a canter and still I follows. Then D stops with head up and I comes up with muzzle low and walks on. Both graze close together, I behind D. I then stands headup, while D grazes close to him. Then I glandular weaves in the grass for a few seconds, then walks after D who walks on. D goes on his knees and sideways horns the soil, first one horn then the other being rubbed in the dirt. He gets to his feet and defaecates on the same spot in exaggerated low crouch position, then shakes his head vigorously. I comes up and stands behind him while he defaecates, and gives a small headshake. They stand more or less reverse parallel. I puts his muzzle down and starts glandular weaving D turns so that they face the same way, then scratches his muzzle with his right hindfoot for 2 seconds on the side nearest to I. D then

defaecates and walks behind I, who shakes his head. They stand reverse parallel. I performs head dip. D stops behind I. I turns to sniff D's anus. Mutual anus sniffing follows. Both males cavort slightly, front legs leaving the ground, and both shake their heads. I again cavorts and shakes his head. D shakes his head and defaecates. I stands behind him facing the opposite way. They move into reverse parallel. I turns his head towards D, then performs head dip (muzzle down to ground then up), then shakes his head and D walks away. I just touches his flank with his muzzle ('head-to-flank') on the side away from D. I walks with muzzle low towards D who is grazing. I stands and waves his muzzle in the grass (glandular weaving), while D grazes close by. The males more or less face each other. I continues weaving and D turns away. I performs head-to-flank then grooms his shoulder with one stroke of his incisors. Then continues glandular weaving. D has moved a few yards away. I again performs head-to-flank, then turns and walks away from D who is grazing. I walks back to his own territory. Duration 8 minutes.

C. The Basic Ritual

When one has watched a number of CR's in the field the basic components of the behaviour emerge quite clearly. There are a number of simple steps occurring roughly in the following sequence:

1) The invading male walks deliberately into the defending male's territory. He usually pauses frequently to 'head flag' - that is to stand with head high looking away from the defending male, who himself usually stands head flagging (Fig.28), while the other male approaches.

2) The 2 males walk up close together and move into the 'reverse parallel' position. They may stand motionless in this position for some appreciable time. (Fig.29).

3) Mutual or unilateral anus sniffing follows, accompanied by tail swishing. (Fig.30). There are usually several bouts of this.

4) Head shaking by one or both males usually follows anus sniffing. (Fig.31).

5) The males may continue simply standing together with heads up for a significant period. They look around, but not at each other.

6) While standing in reverse parallel with heads up, one or both males perform 'head dip' (Fig.32).

7) The males move a few yards apart and perform any or all of the following actions: urination, defaecation, soil horning, cavorting and glandular weaving. (Figs.33-37)

8) Movement: one male may walk or canter some distance during the CR, followed by the other.

9) The 2 males move apart slowly, sometimes grazing, and the invader returns to his own territory. (Fig.38)

The above is an entirely idealized version and in fact any of the actions can occur in any sequence or be omitted entirely. At a low level of intensity the 2 males may just walk up and stand together for a few minutes and then move apart grazing and that's all. Sometimes even long rituals conducted at quite a high intensity and containing at least 15 different action patterns will not contain any anus sniffing at all, the 'central' action of the CR. Thus the sequence of events in any given CR is quite impossible to predict. The seemingly straightforward chain of releaser-response-releaser actions making up the ritual is largely illusory. The CR is in fact characterised by its variability both in terms of the sequence and inclusion or omission of actions performed and in the intensity of performance of different actions.

Estes (p.316) points out that this variability should not obscure the fact that the actions which are performed are still species-typical behaviour patterns. The repertoire of responses with which each animal can express gradations of feeling, though considerable, is still limited to a definite number of fixed action patterns. This is perhaps not saying very much since it is evident that the behaviour repertoire of every species is finite and limited in extent. In the CR there is scarcely one action which is peculiar to the CR and I think that all are actions which have been seen performed in ordinary contexts out-

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STEPS IN THE CHALLENGE RITUAL

FIGURE 28. Head flagging by both males during the approach. The males look away from each other all the time.

FIGURE 29. Reverse parallel position. Both males stand head high.

FIGURE 30. Mutual anus sniffing while in reverse parallel position.

FIGURE 31. Aggressive head shaking. The male on the left keeps his head low in grazing attitude.

FIGURE 32. Head dip. The male on the left dips his muzzle suddenly to the ground, as though about to graze, but raises it again at once.

FIGURE 33. Urination by the male on the left. The other male faces away.

FIGURE 34. Defaecation by the male on the right. The other male comes to sniff him.

FIGURE 35. Soil horning. The other male looks away.

FIGURE 36. Glandular weaving by the male on the left during the Challenge Ritual.

FIGURE 37. Cavorting. The other male horns the soil.

FIGURE 38. The males graze together before moving apart at the end of a ritual.

FIGURE 39. Unilateral anus sniffing in the reverse parallel position.

TABLE 12

Challenge Ritual Activities
Frequency* and Percentage of Activity in 100 Rituals

Activity		Frequency		%	
Walk or run during CR led by	I**	0.25	0.86	22	61
	D	0.61		42	
Head Flag		-		86	
Reverse parallel position		1.90		88	
Stand, walk or graze parallel (head-to-head)		0.37		26	
Unilateral anus sniff	I	1.36	2.12	67	80
	D	0.76		39	
Mutual anus sniff		2.19		65	
Jump away from sniff with or without horn contact		0.30		28	
Head turning	- without nose contact	0.56	0.75	42	45
	with nose contact	0.19		16	
Pivot		0.02		2	
Angle horn		0.07		7	
Head dip	I	1.90	3.67	74	84
	D	1.77		69	
Grazing		1.40		70	
Mutual circling		0.10		9	
Circling in front		0.08		6	
Circling behind		0.22		19	
Lateral presentation	I	0.20	0.44	16	35
	D	0.24		24	
Lateral presentation to hindquarters	I	0.13	0.51	11	36
	D	0.38		26	
Head shake	I	4.69	9.16	94	98
	D	4.47		94	
Tail swish		0.38		21	
Glandular weaving		0.55		28	
Urination	I	0.32	0.61	32	47
	D	0.29		24	
Defaecation	Ordinary	0.74	1.19	44	61
	Low crouch	0.45		28	
Cavorting	I	0.39	0.82	22	38
	D	0.43		27	
Soil horning	Not facing I	0.24	0.65	18	34
	D	0.35		25	
	Lying	0.01		1	
	Facing	0.05		5	
High speed chase		0.03		3	
Combat Position		0.02		2	
Combat		0.03		3	
Alarm snort		0.32		6	
Foot stamp		0.05		2	
Ruminate		0.02		2	
Shake coat		0.03		2	
Head-to-flank		0.78		37	
Grooming (with muzzle)		1.20		56	
Scratching (with hindfoot)		0.90		44	
Head nodding		0.27		12	
Hot weather position (standing)		0.08		5	
Herds female		0.02		2	

* Frequency= No. of times event occurs per ritual.

** I = Invader D = Defender

in what percentage of the sample of 100 rituals each action was performed. For instance, head shaking occurred in 98 out of 100 rituals and was seen an average of 9.16 times per ritual.

1. Approach and Withdrawal; Head Flagging

One male typically initiates the encounter by walking into the neighbour's territory. He is going to challenge him to a duel - a ritualised duel in which neither side will emerge as the victor. He walks steadily with head at normal height until, in most cases, he arrives within about 50 metres of the other, when he stops to head flag and, often, to groom or scratch himself. Sometimes he may stop more than 100 metres away to head flag before walking on again. The defending male usually spots the invader at a distance and signals his acceptance of the challenge by standing motionless with his head held high and looks away from the invader. When the invader stops to head flag it is common for the defender to complete the approach by walking up to the invader - this happened in 56 out of 91 rituals (62%). The last stages of the approach are sometimes slow and protracted, the males moving together gradually and averting their heads from each other all the time (Fig.28).

Head flagging is presumably appeasement behaviour analogous to the averting of the head in gulls (Tinbergen & Moynihan 1952), which has the function of directing the weapons of the enemy (the horns and beak respectively) away from the opponent. It also serves to counteract the menace implicit in the 'head-up' posture, for while head flagging the gaze is never directed at the opponent. If a territorial male wishes to threaten an intruding bachelor he looks straight at him with head held high. Head flagging is conspicuous in the CR and was recorded in 86% of rituals.

It is noteworthy that bontebok seldom approach for a CR in grazing attitude, in contrast to wildebeest (Estes), and I only recorded grazing during the approach in 7% of rituals. Even then the final approach was made with head at normal shoulder height and never in grazing attitude. Since head low in the grazing attitude is as far removed as possible from the threat implicit in head high 'proud' posture the approach of bontebok is presumably more challenging than that of wildebeest. Hence the pauses to headflag, to offset the challenge and so to prevent possible attack.

Another feature of importance is that the incursion of the invader carries him into the heart of enemy country. This both without incurring attack and without affecting the outcome of the CR, for rituals whether conducted at a border or in the middle of one male's territory ended the same way. As previously mentioned, 76% of rituals took place inside the defending male's territory. This would seem to be at variance with one of the principles of territorial behaviour which holds that a male is more aggressive and self-confident the nearer he is to the centre of his territory. Thus one must presume that there is a powerful combination of drives inducing a male to leave the sanctuary of his own area in order to play an "away match".

Whereas it is well known that a football team is much more likely to lose when playing away from home, the result of these CR's is not so simple to decide. There does not seem to be a winner or loser, which is in accord with the idea that all territory holders are truly equal. At the conclusion of the ritual the invader simply walks back to his own territory again with his head at normal height. The withdrawal by the invader was not normally made in grazing attitude, though it is surely significant that grazing was recorded in a high proportion (50%) of rituals by at least one male, at the <u>end</u> of the encounter, just before the 2 males separated. Furthermore, the invader is by no means coerced into returning to his own territory, for in 55% of rituals it was the defender who signalled the end by moving away from the invader, often grazing. The invader, as though at a given signal, would then usually turn and walk away. The defender pays him no further attention, but stands or grazes where he is.

Thus, as far as I could see, there was no question of a defeat for the invader implicit in his act of moving away from the defender and Estes (p.335) suggestion that the grazing attitude is employed by wildebeest during the stage of withdrawal in order to minimize the releasing value for attack, does not seem to apply very clearly to bontebok. There seems, in fact, to be virtually no tendency for the defender to attack during the approach and withdrawal phases. The invader sometimes departed at a run from close to the defender without provoking any attack. Besides, if it were a question of the defender being victorious he would hardly be the one to move away so often, leaving the invader still in the middle of his territory.

2. Movement: Walking or Running (F=0.86; %=61)

Challenge Rituals are not necessarily conducted on one spot. In a surprisingly high percentage of rituals (61%) the males walked (Fig.43) or ran during the encounter distances ranging from about 30 metres to more than ½ km. In 42 rituals this movement was led by the defender and in 22 by the invader. Sometimes the males would only run to a dungsite where they would perform defaecation or horning, but on other occasions a defender would canter or walk right across his territory, followed by the invader. If the defender stopped so would the invader and if the defender ran on the invader would follow. Sometimes the males would come together each time in between bouts of movement but if the defender persisted in moving away from the invader the latter would usually give up and return to his own territory.

On some occasions when the defender ran from the invader at high speed it looked for all the world as though he were fleeing. This impression was belied by the fact that he would often cavort and stop to horn the soil and defaecate - thus demonstrating his basically aggressive feelings. The invader never attacked him in these situations and would follow along behind and then stop at a respectful distance while the defender horned the soil. The reason for these bouts of movement was not clear, especially when conducted merely at a walk.

During three out of 100 rituals a fullscale chase developed. On two occasions it was the invader and once the defender who broke away and ran at full speed across the other male's territory. This provoked the other male to give chase and the 2 males ran round in large circles, twisting and turning this way and that at full gallop. This continued for two or three minutes, the distance between the two males seeming always to remain the same. No attempt on the part of the chasing male to jab the male in front with his horns was seen on these three occasions and when the male in front stopped the male behind also stopped, without any attempt to attack him. It appeared therefore that this was just an 'exercise' and perhaps served to provide extra stimulation for the males or to work off their excitement. On the other hand no particular stimulus preceded these chases - one male suddenly started to run for no apparent reason. These chases were very similar in character to those described in Section VI.A., (Fig.16), except that these occurred in the middle of a CR.

3. Reverse Parallel (F=1.90; %=88) and Parallel (F=0.37; %=26) Positions

Reverse parallel position is highly preferred (Fig.29) and was recorded in 88% of rituals. When the two males come together at the beginning of the ritual they nearly always move straight into reverse parallel. They stand head-to-tail, heads up and with their flanks usually less than a metre apart. There is no doubt in my mind that it is an appeasing position or at any rate a position of safety, nor that the males move purposefully into this position. The weapons, the head and horns of each male are removed from view of the other and the rump is presented for the ensuing anus sniffing. What further leads me to suppose that it is a position of safety, is that it is the identical position adopted by a female during "Paarungskreisen", when she is being sexually molested by a male, (Fig.10). She runs round him flank to flank, in small circles virtually on the spot, but in between the efforts of the male to mount the female they stand motionless in reverse parallel with heads up, very similar to the position adopted during the CR. When the female actually runs round the male she puts her head low.

Territorial males may stand motionless in reverse parallel for significant periods of the CR. It seems, as Estes says, to be like a "neutral corner" - a position which the males were anxious to reach. It does superficially resemble a position of "lateral presentation" given simultaneously by both males, but as far as I could see reverse parallel did not contain any of the threatening elements of lateral presentation and was not in any way related to it.

The parallel position, head-to-head, was observed much less frequently, in only 26% of rituals (F=0.37 against F=1.90), and for only brief periods of time - usually only a few seconds. I counted it if the males stood, walked or grazed side by side and facing the same way. The parallel position is evidently much more provocative than reverse parallel and it was noticeable that if, as sometimes happened, a male turned out of reverse parallel so that the 2 males faced the same way the other male would usually turn at once into reverse parallel again. Only when grazing would the 2 males remain side by side for any length of time, presumably because the head-low grazing attitude has the minimum releasing value for attack.

Walther (1965) quoted by Estes says that the reverse parallel position adopted by displaying Grant's gazelles allows the loser to withdraw "not too hastily", whereas a fight might be an unavoidable result of a direct confrontation. In the case of reverse parallel in bontebok, I would not say that it facilitates in particular withdrawal. As already explained this does not seem to be much of a problem, but what it does do is to permit the animals freedom of movement. They can walk forward quite naturally out of reverse parallel in order to graze, move away, defaecate, horn the soil or perform any of the other activities associated with the CR. This is perhaps its special significance.

4. <u>Anus Sniffing</u> (<u>Mutual</u> F=2.19; %=65, <u>Unilateral</u> F=2.12; %=80)

Anus sniffing is conspicuous and common during the CR and is most often performed, whether mutual or unilateral, from the reverse parallel position. Several bouts of mutual anus sniffing (Fig.30) may occur during a ritual, each one lasting about 2-3 seconds. The 2 males stretch their muzzles to sniff each other, with lowered heads and horns and ears laid back. Vigorous tail swishing with tail lifted invariably occurs on the part of the animal being sniffed. In between bouts of anus sniffing the males continue to stand, heads up, in reverse parallel. Unilateral anus sniffing may be performed when standing reverse parallel, if one male sniffs the other without reply (Fig.39), or when the males have moved a few yards apart, one may approach to sniff the other, usually standing behind him and not in reverse parallel (Fig.40). Quite often, if one male defaecates during the ritual the other goes to sniff him, putting his nose in the path of the pellets of falling dung, (Fig.34).

The fact that a territorial male will tolerate such close approach by another and even physical contact which does not seem to be in a context of social grooming, is interesting. The actual anus sniffing is very similar to the vulva-smelling of a female by a male, the main difference being that during the CR the males lift and swish their tails while being sniffed. The horns and ears of a male sniffing a female are laid back in the same way as for anus sniffing. This posture is assumed to be appeasing as related in Section V. for otherwise the other animal might be inclined to attack. Furthermore, since, while actually sniffing a female, the male may drop his tail from its position lifted over his back, which is peculiar to the sexual display, vulva-smelling then becomes rather similar, as far as the posture of the male is concerned, to his stance during unilateral anus sniffing. (Compare Figs.9 and 40).

This suggests the possibility that this action is derived from sexual behaviour. If one considers that the sexual and territorial drives in the male are closely linked this seems feasible. Since bontebok are territorial throughout the year and there are often periods when there are no females on their territory, it is possible that unreleased sex drive could have appeared and become ritualised in the CR.

A possibly more likely explanation is related to the importance of scent among most mammals, and in particular the scent of the excretory products. The importance of the dung sites either as territory markers or as reinforcers of the male's self-assurance has been described. The anus sniffing, therefore, and the sniffing of the other male's dung may be related to mutual recognition and identification of the two males. One must presume that two territorial males living for months or years on adjoining territories come to know each other as individuals. Perhaps there is some assurance to be gained from recognising the other male by his scent since the same two males perform the CR together probably many hundreds of times. It is possible too that the anus sniffing fulfills mainly a greeting function (while at the same time identifying each other by their scent), though presumably not a friendly one, and that each male demonstrates his self-confidence by permitting himself to be sniffed.

It is most interesting that Lorenz (1954) observed precisely the same behaviour between male dogs in a situation of challenge; and only between dogs that were equal rivals. The dogs, on meeting, moved into reverse parallel position and mutual anus sniffing followed. This was accompanied also by circling in the reverse parallel position as seen by Estes for wildebeest. According to Lorenz, the proffering of the hindquarters for sniffing demonstrates the self-assurance of the male. It thus amounts to a face-saving device which permits the males to meet, to act unafraid and yet to avoid a fight. After mutual anus sniffing the two dogs move apart and simultaneously perform agonistic urination against suitable nearby objects - just as male bontebok may defaecate, urinate, horn the soil etc. after anus sniffing. It seems that it must be more than mere coincidence that has produced two so similar behaviour patterns in similar situations in two groups as unrelated as the Canidae and Bovidae.

As with dogs, then, the submission on the part of male bontebok to being sniffed by a territorial rival may be a proof of his self-assurance. Sniffing undoubtedly arouses aggressive responses in him, however, and these will be discussed hereunder.

<u>5. Responses to Anus Sniffing</u>: <u>Head Shaking</u> (F=9.16; %=98);
<u>Head Turning</u> (F=0.75; %=45); <u>Jump Away</u> (F=0.30; %=28);
<u>Angle Horn</u> (F=0.07; % = 7); <u>Pivot</u> (F=0.02; % = 2)

Head shaking is the most frequently performed act in the whole repertoire of the CR (F 9.16). It is the movement equivalent to signalling 'no' in man and is performed with varying degrees of vigour, from a barely perceptible movement of the head to a really vicious shaking of the horns, but always with the head held high, which gives the motion its maximum effect (Fig.31). It is associated with aggression or defiance and occurs at all stages through the CR. It is particularly common as a response to anus sniffing, after soil-horning or defaecation, or when one male comes close to the other. Outside the context of the CR it is seen mainly in adults of either sex. Territorial males shake their heads at bachelors encroaching on their territory, and bachelors may shake their heads in defiance when forced to give ground by a territorial male. Females occasionally shake their heads at each other during brief squabbles and a female may even defiantly shake her head when an adult male comes to try and sniff her. When standing during heavy rain animals of both sexes shake their heads and horns in a similar way.

As mentioned above, the male is constrained in most cases to suffer being sniffed by the other male. However, there are a number of indications that he would actually like to move away or to turn and face his opponent. The first of these is 'pivoting', which was only observed in 2 rituals. The male being sniffed slides his hindquarters away from the other male, thus preventing sniffing. Estes observed this in 7% of wildebeest CR's. Secondly, there is 'angle horn' which is also uncommon in bontebok, having a frequency of only .07. This is much less than the frequency of .57 for this action in wildebeest found by Estes. In this action the male being sniffed cocks his head at an angle over his shoulder towards his opponent so that his near horn is "aimed" at him. It is performed with the head held as high as possible. In bontebok it is not a very clear or conspicuous action and it is quite possible that it is in fact more common than my results show and that I missed it during the recording of early rituals, especially as in some cases the intention to turn the head is merely "suggested". Estes say that this act may express the inhibited desire to turn and face the opponent. I would confirm this interpretation from what I have seen in bontebok and further evidence is supplied by the fact that bontebok sometimes actually do turn to face the opponent who is doing the sniffing.

This may happen in two different ways. Firstly, the male being sniffed may, without moving his hindquarters away, turn his muzzle right round towards the other animal (Fig.40). Approximately 25% of these occasions resulted in the 2 males touching noses (F=0.56 without nose contact; F=0.19 with nose contact). Head shaking may follow nose touching. Nose touching (Fig.41) is not a prelude to combat and the males usually just move into the reverse parallel position afterwards. Outside the CR, head turning has been seen by females when being sniffed by a male. The female turns her muzzle around towards the male in the same way as may occur during the CR. Nose touching has occasionally been seen when two bachelors are grazing close together. They may walk up to each other, stretch their muzzles cautiously towards each other and briefly touch noses before continuing grazing.

Secondly, it sometimes happens that a male does not submit to being sniffed, but leaps away when the other male comes to sniff him (F=0.30). He may just give a little jump or really cavort away from the other male. Usually he swings round to face him when leaping away and this led to horn contact (Fig.42) in about 16% of cases. This was not counted as combat since it was not performed on the knees. The males would just touch horns very briefly and then back away from each other immediately, or move forward into reverse parallel. It would appear, then, that a male does not always trust the close approach of the other and since cavorting away is an aggressive response one must assume some aggression implicit in the act of approaching and sniffing.

6. <u>Lateral Presentation</u> (F=0.44; %=35)
<u>Lateral Presentation to Hindquarters</u> (F=0.51; %=36)

Lateral presentation is a position of challenge. This is most clearly seen when a territorial male runs up to a bachelor or another territorial male who is crossing his territory, as in the first of the transcribed rituals. The defender plants himself squarely in the path of the invader, presenting his side to the other's face, and stops him dead in his tracks. He carries his head as high as possible during lateral presentation. The invader normally walks round behind a presenting defender.

FIGURE 40. Unilateral anus sniffing with head turning by the male being sniffed.

FIGURE 41. Nose touching. Two males about to touch noses during the Challenge Ritual.

FIGURE 42. Horn contact without combat. The two males touch horns following anus sniffing.

FIGURE 43. The males walk during the Challenge Ritual.

During the CR, in the course of moving about, one male would assume the lateral presentation pose and I counted it if ever I saw one of the males standing broadside in front of the other (Fig.44). However, in this situation it is not a very clearly defined action in bontebok and seemed to me to be of doubtful display significance. It was observed almost as frequently by the invader as by the defender (F=0.20 cf. F=0.24). The defender does not usually meet the invader with lateral presentation at the start of a CR as Estes records for wildebeest.

Another position of doubtful significance, but nevertheless quite often assumed, is that of lateral presentation to the hindquarters. One male would move forward out of reverse parallel and stand behind the other, broadside on, so that his side was presented to the other's rear (Fig.45). This position could be maintained for some appreciable time and is presumably less provocative than normal lateral presentation.

<u>7. Circling</u>. <u>Mutual</u> (F=0.10; %=9); <u>In Front</u> (F=.08; %=6) <u>Behind</u> (F=0.22; %=19).

Three types of circling are seen during the CR, all of which are performed when in the reverse parallel position. In mutual circling the 2 males move round each other virtually on the spot and return to reverse parallel at the end. During circling in front, one male turns out of reverse parallel, walks right round the head of the other male and returns to reverse parallel on the other side of him. The most common of the three types of circling is circling behind, when one male walks out of reverse parallel and walks round behind the other male, coming up on the other side of him, so that both males end up side by side and facing the same way. This latter manoeuvre nearly always resulted in the male not responsible for the circling turning at once back into reverse parallel. As mentioned above, the parallel position is considerably more provocative than reverse parallel, so it would seem that the male responsible for the circling is giving a mild threat. It might be supposed that turning and deliberately walking round in front of the other male contains some threatening element. In general, I got the impression that these circling movements had no special signi-

FIGURE 44. Lateral presentation. The male on the left presents his side to the other male who looks away.

FIGURE 45. Lateral presentation to hindquarters.

ficance but were performed perhaps just to release tension, since the males usually spent much of the ritual standing in reverse parallel. None of them were common.

8. Head Dip (F=3.67; %=84). Grazing (F=1.40; %=70).

Head dipping (Fig.32) is the action of abruptly lowering the muzzle to the ground, in the grazing attitude, and then raising it again after only a second or two. It is the second most frequently performed action in the CR and is usually to be seen while the males are standing reverse parallel and particularly after anus sniffing. When walking out of the reverse parallel position also males usually dip their muzzles low in the grazing attitude. The important thing seems to be the lowering of the head, and this is interpreted as appeasement since head low in the grazing attitude is as far removed as possible from the threatening head up posture.

Grazing is also an important activity in the CR(F=1.40). In some cases, where the male takes only a few desultory mouthfuls before looking up or changing to some other activity, it is clearly only a displacement activity. I only recorded cases of grazing where the males were really grazing, (Fig.38). For a full discussion of the role of grazing during the CR see Estes p.332 et seq. I will only summarise his main arguments here in point form:

1. Grazing under conditions where conflicting attack/escape drives may be assumed is termed "agonistic grazing".

2. Agonistic grazing is, or began as, a displacement activity, consistently selected because it represents the motor pattern closest to the head-low submissive posture.

3. Grazing is one of the few maintenance activities that can be continued indefinitely and has the advantage of being both dynamic and distinctive.

4. Grazing in the CR is indistinguishable from normal grazing and yet it is so integrated that it may be right to regard it as a ritualised activity rather than purely as a displaced one.

5. Grazing is a purely neutral activity, neither threatening nor submissive. It is a natural-looking pose that cannot be

mistaken for threat, but reveals no lack of confidence either.

9. Glandular Weaving (F=0.55; %=28)

Glandular weaving has already been described in Section VI.B.4, but it is interesting that it should play a fairly important role in the CR, being recorded in 28 of 100 rituals (Fig.36). It would appear to be entirely out of context here and it is therefore assumed to be pure displacement, though it was not distinguishable in performance from that occurring in a normal context. It is further assumed to be a neutral activity since it does not appear to have any display function. The significance of its occurrence during the CR can be judged from the fact that, as related in Section VI.B.4, during the rut it was seen in normal circumstances approximately once in 12 hours per territorial male, whereas during the Challenge Ritual it could be expected at least once for every 12 minutes of CR activity. (Since F=0.55 and the mean duration of a CR was 6.5 minutes.)

It seems to me that the reason for its selection during the CR is twofold. Not only is it neutral and distinctive, having no releasing value for attack, yet not being submissive in character, but it also has the advantage, like grazing, of being an activity which can be continued for an appreciable length of time. As Estes points out, other displacement actions such as scratching and grooming can only be repeated.

10. Urination (F=0.61; %=47) and Defaecation (F=1.19; %=61)

Excretory behaviour is common during the CR and as related in Section VI.B.5, is believed to have a threatening function. While one male is defaecating or urinating the other usually just stands and head flags close by (Fig.33). Sometimes while one is defaecating the other immediately moves to sniff his anus (Fig.34). Excretion is quite often performed while standing in the reverse parallel position.

Two things are interesting about excretory behaviour during the CR. Firstly, the males often adopt a deepcrouch posture while defaecating, which is not seen outside the ritual, (Fig.46). I recorded deepcrouch posture in 45 out of 119 defaecations during the CR (38%). Secondly, though often adopting the posture for excretion the males by no means always do actually urinate or defaecate. Unfortunately, due to the action being too quick or to my being too far away or unsighted, I was unable to ascertain in every case whether true excretion had in fact occurred. Equally, there were a number of cases where I was quite sure that it had not. Both these facts seem to show that it is the adoption of the posture that is the important thing, and not the urination or defaecation itself. The adoption of a deepcrouch serves to exaggerate the defaecation posture and make it more impressive. It seems clear that the excretory posture does indeed serve a display function and that this is of an intimidatory nature.

11. Cavorting (F=0.82; %=38)

Cavorting in bontebok is the action of leaping into the air with all 4 feet off the ground and kicking out with the hind-legs or, at lower intensity, of leaping just sufficiently to bring the forelegs clear of the ground (Fig.37). To the uninitiated eye it looks just like play or sheer 'high spirits'. Its true aggressive nature was explained in Section VI.A. Cavorting could occur at any stage during a ritual, but particularly following anus sniffing and soil horning. It was thought at first that cavorting would only be seen in high intensity encounters, perhaps leading to a fight, but it soon became clear that this was not so and that most cavorting was at low intensity and did not necessarily provoke any response from the other participant. Estes recorded cavorting only 27 times in 100 rituals for wildebeest which is only about $\frac{1}{3}$ the frequency I recorded for bontebok. I have never seen the racing and cavorting along a common boundary in bontebok that Estes saw in wildebeest. All in all, cavorting seems to be "quieter" in bontebok which perhaps accounts for it being more frequent. Outside the CR I have very rarely recorded cavorting in females, but I have seen it in the games of lambs and amongst yearlings, who may race around kicking up their heels this way and that.

12. Soil Horning (F=0.65; %=34). Combat (F=.03; %=3)

Soil horning (Fig.35) has been described in Section VI.B.5. It is performed during the CR by either male alone or by both simultaneously and at varying levels of intensity. They usually choose a dung site to horn on and head shaking and/or cavorting usually follows horning. During the CR, defaecation follows horning in only around 50% of cases. The most spectacular horning is to be seen when the 2 males horn the soil simultaneously facing each other on their knees (Fig.47). This happened in only 5 rituals and is listed as "Facing" in Table 12. Here it is a high intensity threat display as the aggression felt towards the rival is redirected against the ground. Once I saw a male lie down for a few seconds after horning the soil during a CR before getting up and defaecating - the only time this was observed to happen.

True combat on the knees is rare in bontebok and was only observed 3 times in 100 rituals (Fig.48). On 2 other occasions the males were seen facing each other on their knees in combat position (Fig.49) and making intention movements to engage horns but not actually doing so. All these cases were either preceded or succeeded by soil horning. The fights were all of only a few seconds duration and did not result in injury to either party. Their foreheads are pressed flat to the ground during combat and their horns pass either side of the opponent's neck so that damage is scarcely possible.

Once a male was seen to get up after horning the soil and rush at his opponent, who was just standing a few yards away, without any warning and to get home with a horn thrust in the shoulder, which caused the other to limp for a few days afterwards. This was the only time injury was known to be caused. No victor or vanquished emerged from these fights and the males usually got up afterwards and stood close together or returned to reverse parallel before moving apart and returning to their own territories. I have not seen one serious fight in 15 months fieldwork and indeed, apart from the gentle jousting of yearlings (Fig.55), I have seen no fighting at all outside the context of the CR. This is in marked contrast to the serious fighting Estes records for wildebeest in the Ngorongoro Crater. I have relatively frequently seen springbok fighting in the Bontebok Park and Estes (1967) reports that fighting is common amongst Thomson's gazelles.

FIGURE 46. Deep crouch defaecation performed only in the Challenge Ritual.

FIGURE 47. Soil horning in the combat position, facing each other on their knees.

FIGURE 48. Combat during the Challenge Ritual. Neither male suffered injury.

FIGURE 49. Facing on knees in the combat position, preparatory to engaging horns.

13. Head Nodding (F=0.27; %=12)

Head nodding in bontebok is fairly conspicuous and of frequent occurrence though, as a matter of fact, it is not very prevalent during the CR. It is a widespread display among ungulates and yet, as Estes remarks, "its meaning has seldom been determined". I have seen it in bontebok in a wide variety of situations and in animals of both sexes and all age classes including very young lambs. Estes quotes Walther (1966) who interprets nodding in the black wildebeest as a threat display derived from the intention movement to jab with the horns. Von Richter (pers. comm.) says that the motor pattern has changed to express the mood of restlessness or "let's go!". Certainly, it seems clear to me that it is a display of social significance as the animals transmit their mood from one to another, and not, for instance, anything to do with fly larvae in the nasal sinuses, as some authors have suggested.

In bontebok, head nodding is contagious within the group so that if one starts nodding the others follow suit. It is also seen in lone animals. If a mother walks off head nodding, her lamb, following at heel, does likewise. It also seems to be connected with the hot weather, as it is seen most often on particularly hot days, and I did not record it during the winter months. Groups can be seen standing around on hot days in the 'hot weather position', with muzzles very low and chins tucked well in (Fig.21), as described in Section VI.B.1. This position is particularly associated with head nodding as the animals usually make frequent restless movements of a few yards this way and that accompanied by pronounced head nodding. A territorial male will walk towards a group of intruding bachelors on his territory with head nodding and they give way steadily before him also at a walk and also head nodding. If a territorial male has just chased an interloper off he may stop at his border, look at the fleeing buck with head held high and then nod the head once or twice in a definite fashion. Animals, when disturbed and forced to move off, often nod the head as they walk away. These last three examples seem to show the element of threat or defiance implicit in head nodding (in the last case it is rather a question of defying the observer), but in my experience head nodding could be seen in almost any situation - for instance when just walking from one spot to another during grazing, (Fig.50). A territorial male may nod while walking up to a female before displaying to her and females have been seen to nod while being sniffed.

In general, it characteristically accompanies movement, and so in my opinion it is reasonable to suggest that it expresses the mood of restlessness. The motor pattern itself seems to be contagious so that one restless animal can infect a whole group. Estes suggestion that head nodding is directed primarily at inferiors and not at equals would explain why this rather conspicuous behaviour pattern is not common in the CR, which is essentially a confrontation of ranking equals.

14. Alarm Snort (F=0.32; %=6)

The alarm display in bontebok consists simply in inspecting the source of the disturbance with head held as high as possible and then giving the alarm snort - usually several uttered in succession (Fig.51). The alarm posture is indistinguishable from normal 'proud' posture and I have therefore recorded alarm behaviour only when the alarm snort was heard. This in fact happened in only 6 rituals and usually it was the observer the animals regarded as the source of alarm - though in no case was there any good reason for this. Once it was some men working in the veld and once the alarm bark of a grey rhebuck set the bontebok off snorting, which often happened outside the context of the CR. Though, in every case, the presence of the observer gave the animals a point of visual fixation yet, having given the alarm display, they did not move off. It is easy to accept Estes' thesis that this is a pure displacement action. In a situation of tension, the animals suddenly, and simultaneously, discover a matter requiring their urgent and joint attention, thus sidestepping their mutual confrontation. In the sense that it sidestepped the issue, alarm snorting seemed to be rather effective; for in the few cases where it was observed the males moved apart shortly after the performance of the alarm display.

FIGURE 50. A territorial male walks, head low, head nodding.

FIGURE 51. Alarm display. Both males inspect an imaginary source of disturbance.

15. Comfort Behaviour. Head-to-Flank (F=0.78; %=37)
Grooming (with muzzle) (F=1.20; %=56)
Scratching (with hindfoot) (F=0.90; %=44)

Minor comfort or maintenance movements such as foot stamping (F=.05), ruminating (F=.02), and shaking the coat (F=.03) which last is normally seen when the animals are standing in the rain, do occur in the CR, but the most important by far are the head-to-flank movements, grooming the coat with upward strokes of the muzzle and scratching of the forward half of the body with the hindfoot, (Fig.54).

In the head-to-flank movement the muzzle is swung round in an arc to the shoulder or flank as though shooing flies (Fig.52). This is presumably a similar movement to the Head-and-Tail-Sweep of wildebeest (Estes) in which, in addition to the head movement, the tail is swept across the face. In the bontebok CR this head-to-flank movement is not nearly so vigorous or so frequent as it evidently is during wildebeest rituals (Estes F=2.08). Head-to-flank movements are also sometimes seen outside the context of the CR where they presumably have the function of shooing flies. The same movement has been seen following kneeling and horning sessions (Fig.53) and also when two males face each other on their knees in the combat position. This has also been reported for hartebeest by Dowsett and Backhaus. Thus suggests that perhaps the movement originated in marking the flanks with the secretion of the preorbital gland. However, from what I have seen in bontebok it would seem safer to regard it simply as a fly-shooing movement. Its significance in the CR is uncertain but it is probably, as Estes suggests, just a displaced comfort movement. Unfortunately, I have no data on the normal frequency of occurrence of the movement to uphold this idea.

The appearance of all kinds of comfort behaviour in the CR is assumed by Estes to be pure displacement - that is to say 'irrelevant' behaviour performed as an outlet of tension in a situation where conflicting drives are being motivated. He goes on to say (p.331) that the impetus for displacement grooming could stem from turning the head away from the opponent (Walther 1964), and that indeed interacting wildebeest usually groomed on

FIGURE 52. Head-to-flank movement performed by the male on the right, while the other male looks away.

FIGURE 53. Head-to-flank performed after soil horning, while still on the knees.

FIGURE 54. Scratching (displaced) with the hindfoot.

FIGURE 55. Two yearling males play-fighting at low intensity.

the side away from the opponent. This gave rise to the idea that if comfort movements by bontebok during the CR were really displaced it should be possible to prove it. Accordingly, while engaged on 12 hour daily activity studies I recorded the duration and frequency of normal grooming and scratching in a number of one hour periods each day. Grooming was recorded by counting the number of upward strokes of the muzzle involved. While scratching, the movement of the hindfoot is too fast to be able to count the strokes and so I counted to myself and recorded the duration in seconds. The duration of comfort behaviour during the CR was recorded in a similar manner and then compared with normal comfort behaviour.

The results obtained are as follows: in the first place I recorded whether the animal performed the behaviour on the side nearest the opponent or away from him and then tested the observed and expected frequencies by means of Chi-square. This yielded a negative result. In my sample during the CR I recorded comfort behaviour performed 88 times on the side away from the opponent and 70 times on the side nearest him. This was not statistically significant ($Chi^2 = 2.05$; $p < 0.2 > 0.1$). Thus it would appear that the animals are indifferent as to which side they groom. This perhaps casts doubt on the idea that comfort behaviour during the CR arose from the act of turning the head away from the opponent.

However, with regard to the frequency and duration of grooming and scratching I got some highly significant results. This is based on the thesis that displacement behaviour is incomplete and therefore of briefer performance, (more perfunctory), than the same behaviour performed in its normal context and also that since the behaviour is performed 'out of context' it would be performed relatively more frequently, (as an outlet of tension), during the CR than normally.

The results are presented in Table 13 where application of the "t" test showed that in duration the grooming and scratching occurring in the CR is very significantly shorter ($p < .001$ in both cases) than that occurring normally. The normal frequency, I recorded as the number of events occurring per one hour

Table 13. Duration and Frequency of Normal and Displaced Comfort Behaviour

Activity	No. of Events	Units	Range	Mean	SD	t	DF	p
Normal Scratching	101	Duration Seconds	½-11	3.99	2.45	7.05	172	<.001
CR Scratching	73	Duration Seconds	½-9	2.44	1.57			
Normal Grooming	92	Duration Strokes	1-34	7.46	6.9	4.38	187	<.001
CR Grooming	97	Duration Strokes	1-17	5.01	3.1			
Normal Scratching	42 hours	Frequency Events/hr.	0-29	6.45	5.5	1.86	51	<.1>.05
CR Scratching	11 hours	Frequency Events/hr.	3-14	8.18	3.71			
Normal Grooming	42 hours	Frequency Events/hr.	0-25	6.43	5.33	4.62	51	<.001
CR Grooming	11 hours	Frequency Events/hr.	5-18	10.91	4.5			

CR = Challenge Ritual

observation period for 42 hours of observations. The 10.92 hours of CR observations were divided into eleven approximately one hour periods. Here the frequencies of both scratching and grooming were higher during the CR than occurred outside it, with grooming showing a particularly marked increase (Table 13). Thus, for grooming, $t=4.62$ and p is $<.001$ showing that the frequency of grooming was very significantly higher during the CR than in normal context. The result with scratching was not so clearcut, for though its frequency was higher during the CR than outside it, it falls just short of statistical significance ($p<0.1>.05$).

Overall, though, it is clear that comfort behaviour within the CR is both significantly briefer and more frequent than occurs normally and we are therefore justified in calling it displaced. It is interesting that while in normal context scratching is fractionally more frequent than grooming (6.45/h against 6.43/h), during the CR it is the rate of grooming which rises significantly to become far more frequent than scratching (Table 13). During wildebeest CR's, on the other hand, Estes found the reverse, scratching ($F=0.96$) being more frequent than grooming ($F=0.58$). The reason for this seems obscure.

If we return to the idea that grooming arises from the act of turning the head away from the opponent, this would fit in with the prominent head flagging of bontebok and would account for the significant increase in grooming activity during the CR. When standing close to each other, and during the approach, the two males would look round in all directions except at each other. Thus, once the head is turned, perhaps the natural thing for the animal to do is to groom itself in a gesture of 'embarrassment'. There were many occasions when this explanation was clearly indicated. This was so particularly, for instance, during unilateral anus sniffing. While one male was sniffing, the one being sniffed would turn its muzzle right round to the other, and then groom its flank in what seemed to be a gesture of pure embarrassment.

Estes suggests that the adoption of the head low posture, which frequently occurs during the CR, disinhibits scratching of the head, which action requires the head to be lowered before its normal performance. It seems to me that the adoption of the head low posture, accompanied by standing on 3 legs in order to scratch, puts the animal at somewhat of a disadvantage and would render it less able to deal with any sudden move on the part of its adversary. Perhaps this helps to explain the smaller relative rise in the frequency of scratching in bontebok. It does not explain why wildebeest should scratch more often than groom. Possibly bontebok spend more time with their heads up during the CR than do wildebeest and this is reflected in the greater amount of displaced grooming. Estes does remark that the head-up posture is "not constantly or always maximally displayed" in the wildebeest CR. In the bontebok CR, as long as the males are just standing, the head is usually held as high as possible.

E. Post-Ritual Behaviour

Specific behaviour was quite often observed at the termination of the CR, most commonly redirected aggression, sexual behaviour, and defaecation or soil horning as presented in Table 14.

As can be seen from the Table, specific post-ritual behaviour is more often seen on the part of the invader than the defender. This is because he usually has some distance to walk before reaching his own territory again, so that he has opportunity on the way to stop and perform various actions. Sexual behaviour is most commonly observed as both males return to their females with display run and sniff their vulvas. As already mentioned, males usually display to their females upon returning to their territory after any absence. Redirected aggression also occurs, usually on the part of the invader. He breaks off on his way back to his own territory to chase any yearling or other male who happens to be in the vicinity. He may run some distance in order to chase the other male and the chase itself is usually quite vigorous, showing a high level of excitation. Quite often too, the male will stop to defaecate or to kneel, horn the soil and defaecate, sometimes several times, on his way back to his own territory. At the conclusion of 3 rituals, one

TABLE 14

Summary of Post-CR Behaviour

	Chasing	Display to Females	Defaecate	Horn Soil & Defaecate	Urinate	Scratch
% of sample of 100 rituals	9	41	16	9	3	4
By I	8	29	11	7	1	4
By D	2	27	6	3	2	0

I=Invader; D=Defender.

male was seen to urinate.

It was noteworthy that all these actions are aggressive in nature or imply threat, and sometimes several actions are performed by one or both males - as for instance, when a male stops to horn the soil and defaecate and then runs to his females with display run. Overall, in 61% of my sample of 100 rituals specific behaviour was observed at the conclusion of the encounter. This seems to show the high level of tension involved during the CR, which is not apparent to the casual observer, and this requires outlet once the males are apart again. For the most part, the males appear quite relaxed and at ease during the ritual and it is hard for the observer to guess the high level of the inner conflict occurring. The importance of "saving face" is apparent in the unhurried and dignified movements of the males.

F. Discussion

Darling (1952) makes the interesting observation that " ... territorial behaviour as a whole is a social phenomenon, and it has survival value". Observing the occurrence in wildebeest CR's of social grooming behaviour which did not seem to fit in with the general picture of agonistic relations between the two males, Estes quotes Darling (op. cit.) (incorrectly) in support of his idea of the possibly social nature of these mainly agonistic encounters between territorial neighbours.

Darling, however, conceived his idea in relation to breeding birds: "I would like to put forward the hypothesis that one of the important functions of territory in breeding birds is the provision of periphery - periphery being defined as that kind of edge where there is another bird of the same species occupying a territory. One pair of warblers in a wood have, in effect, no territory at all; they are merely existing in space. But by pushing up against each other, rather than spreading themselves out, the birds are giving themselves peripheries, ... ". Darling led the evidence of Rinkel (1940) that Lapwings breed in territories, a number of which are always found together. Far from avoiding clashes, the birds sought opportunities for them. The males seemed to need them and the emotional stimulation they gave.

Thus, Estes wished to extend this suggestion, that territorial conflict was actually sought for the sake of stimulation, to wildebeest CR's. At first sight it is rather an attractive idea. Fisher (1954) later elaborated on the insight of Darling, also with regard to breeding birds, and Estes quotes him (also incorrectly) in further support: " .. the effect of the holding of territory by common passerines is to create "neighbourhoods" of individuals which are masters of their own definite and limited property, but which are bound firmly, and socially, to their next door neighbours by what in human terms would be described as a dear enemy or rival friend situation, but which in bird terms should more safely be described as mutual stimulation".

Since these words were written ornithologists seem to have treated the idea of mutual stimulation with some reserve. While I believe that it is a valid concept, to formally prove it is another matter. Evidence came to light which caused Fisher himself (op. cit.) to reject Darling's hypothesis of a 'threshold' level of stimulation necessary for successful breeding by colonial species, when it was found that the lack of success of some small colonies was due not to the failure to reach this critical 'threshold' stimulation, but to the birds being young pioneers making their first attempt to breed.

In any case, it seems to me that one can clearly see some, at least, of the biological advantages to birds of colonial breeding. One may discern a greater degree of protection from predators, the attraction of larger numbers of females to the colony leading to more young being produced in polygamous species, the facilitation of feeding due to successful feeders leading other birds to the feeding grounds etc. The mutual stimulation aspect may occur in the more rapid and synchronised attainment of the correct hormone levels leading to synchronous breeding and hence better survival of young. To apply these kinds of argument to territorial mammals such as bontebok or wildebeest seems to me fraught with difficulty.

SUMMARY

1. The behaviour of the bontebok was studied in the Bontebok National Park, Swellendam, for 15 months. The Park contains about 250 bontebok in an area of 10.8 sq. miles.

2. The bontebok is a gregarious antelope and its social structure comprises bachelor herds, nursery herds and territorial males.

3. The bontebok is a strongly seasonal breeder, the main calving season being September through October and the rutting season January to mid-March.

4. Nursery herds consist of females and young which have a limited home range. Core areas of some home ranges varied from about 10 to 70 acres. Females are not very gregarious, the largest number of females seen in one group being only nine. The average nursery herd was three females and 1.5 lambs. Nursery herds are semi-exclusive associations of particular females which may remain in the same home range for more than 12 months at a time. These associations of females impart considerable stability to the population. The nursery herds are distributed throughout the territorial network.

5. The bachelor herd consists of males of all ages above one year plus yearling females. Lambs of both sexes leave their mothers at about one year of age to join the bachelors. The bachelors show the strongest tendency to aggregate; up to 75 being seen together. This is a loose association of animals which follow the same general daily routine but may split up into smaller groups which move independently at any time. The bachelors moved at will and grazed anywhere in the Park. There was no marked tendency for animals of the same age to form subgroups in the bachelor herd. There is no clear social hierarchy within the bachelors and it is rare to see a bachelor herding, chasing or threatening another. Ex-territorial males join the bachelors, if they abandon their territory, where they are as amicable as the rest.

6. Territorial behaviour was studied by capturing and marking 14 territorial males. The mean density of territorial males in

the Park is approximately 2.5 per sq. mile (1.1 per km^2) with a maximum density of 4 per sq. mile (1.5/km^2). Mean spacing varied from about 320 yards to over ½ a mile. The average radius of movement about a central point in the territory was about 190 yards. Territorial males are distributed throughout the Park.

7. Territorial males herd and court any females on their territory, addressing special courtship displays to them and endeavouring to keep as many females as possible on their territory. Some males were often alone but others were always with females. In some cases the same individual females remained on the territory of the same male for the duration of the study period.

8. Despite the attentions of the territorial male the females are free to come and go as they please. The male is attached to his property and not to the females.

9. A quantitative study of daily activity showed that a territorial male, on a year round basis, spends 54.7% of his time grazing, 22.7% ruminating, 10.0% resting and 12.7% in 'other' activity. The female spends 64.9% of her time grazing, 20.8% ruminating, 9.5% resting and 4.7% in other activities. The other activity of the male is mostly (55-60%) referable to sexual behaviour, defence of territory and Challenge Rituals with other males.

10. Bontebok are territorial throughout the year. At least three males were known to retain the same territory for the duration of the study period. There is reason to believe that some males may hold the same piece of ground for the duration of their adult lives.

11. Though precise data is lacking, males do not establish territories before three years of age. It is probable that the general age is nearer to five years before a male becomes territorial.

12. The adult males at Swellendam are divided approximately 50 : 50 into territorial and bachelor males. There is no evidence of strong competition for territories from the adult bachelors. There appears to be plenty of space in the Park for

the establishment of new territories and some old territories that were vacated remained vacant for some months.

13. The territorial system is stable with very little interchange of males on territories. Only three males were known to have abandoned their territories during the study period.

14. Bontebok males defend their territory throughout the year by chasing away any intruding males. Chasing is ritualised and no physical contact or injury to either party resulted. Intruding males always gave way before the territorial male and no fighting in defence of territory was seen.

15. The various ways of advertising territory are discussed. Marking of territory, unless an actual mark is set which can be sensed by conspecifics, is rejected. The functions of the mere presence of the male on his territory, the presence of conspicuous dung sites scattered about the territory, the possible use of secretions of the preorbital gland and behaviour patterns such as kneeling and horning the soil followed by defaecation are discussed.

16. The territorial status quo is maintained by regular ceremonial encounters between territorial neighbours. These are called the Challenge Ritual and are analysed in detail.

17. The Challenge Ritual contains a rich behaviour repertoire. There are at least 30 different action patterns. The average duration of the Challenge Ritual was 6.5 minutes with a range from one minute to 23 minutes. During the rut about 30% of the male's total 'other' activity is spent in the Challenge Ritual. This occupied a mean of about 35 minutes a day during the rut and fell to 20½ minutes a day in the winter. In general, the territorial males engage each neighbour in a Challenge Ritual, on average, once a day but it is not uncommon for a male to have several encounters in a day, or none, with any particular neighbour.

18. The Challenge Ritual is assumed to be a challenge of fitness to hold property. Only territorial males, which are responsible for all mating in the population, have the self-assurance to go through the complete ritual. Bachelors, if engaged by a territorial male, run away. The system thus ensures that only the most dominant males will be able to hold on to a territory.

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