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The social organisation and aspects of behaviour of the nyala *Tragelaphus angasi* Gray, 1849

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Abstract

Investigated the social organisation and behaviour of the nyala *Tragelaphus angasi* to provide information which would assist in the management of the species in the game reserves of Zululand, South Africa. Distinct social groupings were recognised and their formation and composition discussed. Visual and vocal communication are noted and discussed. The most important aspects of social behaviour and behaviour related to the environment are described, and conclusions as to the form of social organisation found in nyala are made.

1 Introduction

The group size frequency of nyala has been described by DORST and DANDELLOT (1970) and TELLO and VAN GELDER (1975). Groups range in size from one to about 30, but two or three are the most common. TELLO and VAN GELDER (1975) give a detailed breakdown of the various groups they recorded and described their transient nature. They concluded that although nyala are gregarious, long-lasting relationships are not formed.

WALTHER (1964, 1974) described behaviour patterns of Tragelaphines primarily from observations on captive animals. The patterns he recorded for the nyala are from the unpublished observations of BACKHAUS but some of these were seen in the wild population studied

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by TELLO and VAN GELDER (1975). TELLO and VAN GELDER (1975) believe nyala males have a dominance hierarchy and interpret the agonistic displays between males as challenge and status rituals. LEUTHOLD (1974), however, has tentatively placed the Tragelaphine social organisation in an intermediate category.

Daily activity of nyala has been commented on by SMITHERS (1966) and DORST and DAN-DELOT (1970) and covered in more detail by TELLO and VAN GELDER (1975). The latter authors also found that nyala had overlapping home ranges within their study area, a mean of 5.5 km² for males and 3.6 km² for females.

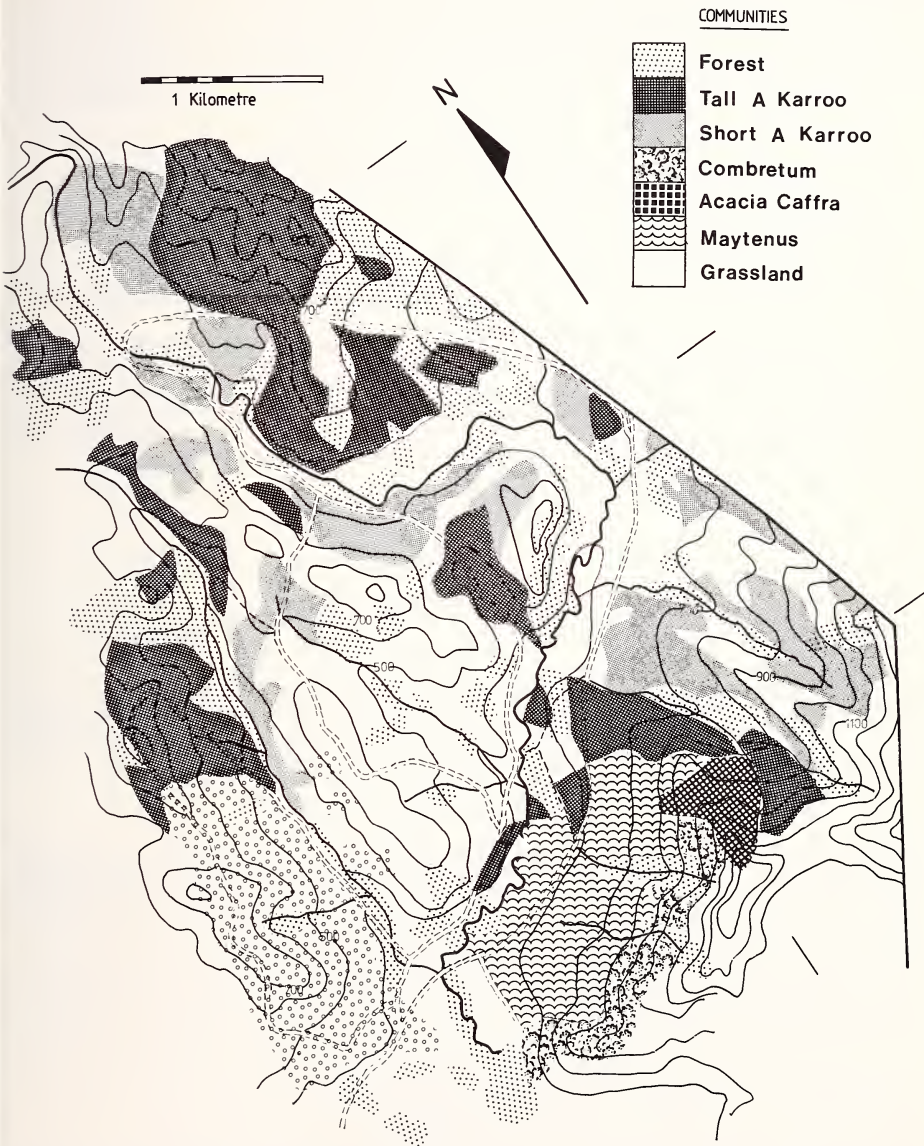


Fig. 1. The major vegetation communities in the Hluhluwe Game Reserve study area

2 Study areas

Most of the data were collected between June 1972 and August 1973 in an area of approximately 1750 ha on the middle catchment of the Manzimbovu river (32°6'E, 28°2'S) in Hluhluwe Game Reserve, Zululand. These were supplemented by observations made in other Zululand reserves, namely Ndumu (32°15'E, 26°53'S) and Mkuzi (22°15'E, 27°38'S). In Ndumu, animals were culled for management reasons and findings on age criteria and reproductive physiology were used in several aspects of the behavioural study.

The topography in the Hluhluwe study area (Fig. 1) was hilly, with differences in altitude of up to 160 m. Of the seven major vegetation communities recognised, all but the forest and *Combretum* community were regarded as being secondary. The present form of the remainder is the result of the influences of fire, game populations and management by man.

a. Forest. The canopy of this moist, semi-deciduous community is closed and the forest margins are clearly defined. Small, isolated patches of forest occur in some of the other communities.

b. Tall *Acacia karroo* community. This community is a result of the previous invasion of grassland or tree savanna by *Acacia karroo*; the average height of these exceeds 2 m. The ground cover is dense, composed of grasses and shrubs with an average height of about 1.5 m.

c. Short *Acacia karroo* community. This community, where invasion of the grassland is taking place, is also secondary. The average height of the community is about 1.5 m.

d. *Combretum* community. This is situated on the north-facing slopes in the south of the study area. *Combretum molle* is the dominant tree.

e. *Acacia caffra* community. As with the previous community, it occurs on the periphery of the study area and no observations were made therein.

f. *Maytenus* community. This community is where degraded grassland and tree savanna has been invaded by the shrub *Maytenus madagascariensis*. The average height of this fairly dense scrub is about 1.5 m.

g. Grassland. Scattered in this community are clumps of forest and patches of *Acacia caffra* and *A. karroo* scrub. There are also isolated trees, mainly *Sclerocarya caffra*, *Zizyphus mucronata* and *Schotia brachypetala*.

The grass cover, averaging 1 m in height, consists primarily of *Themeda triandra*, *Hyparrhenia filipendula*, *Sporobolus* sp. and *Eragrostis superba*. In the low-lying areas near the Manzimbovu river, where soils are heavier, *Panicum maximum* and *Cyperus textillis* are dominant.

3 Methods

3.1 Anatomical structures relevant to behaviour

3.1.1 Glands

Patches of skin from between the horns, the sides of the face and the region of the false hooves on the hindfoot, were collected from an adult male. These were preserved in 10% formal saline, subsequently dehydrated in alcohol, cleared in xylene and embedded in wax. Sections of the tissue were wax-embedded, cut at 6 µm and stained with Meyer's haematoxylin and examined microscopically.

3.1.2 Body conformation

The torso of the nyala male gives the impression of being laterally compressed. If this was so, it would have the effect of increasing the surface area presented in a lateral display. To investigate this, the lateral silhouettes of nyala and impala *Aepyceros melampus* were compared. The latter is one of the few species where no lateral display is present in its behaviour patterns (SCHENKEL 1966; WALTHER 1974). The silhouettes were measured planimetrically from photographs and the percentage comprised of the torso alone was calculated. In addition, the measurements and formulae of MOEN (1973) were used to calculate the surface areas of 12 nyala males and 21 impala males. The percentage surface areas, comprised of the torso in each species, were then compared.

3.2 Social behaviour

3.2.1 Observations

Data were recorded primarily from direct observations of animals. Activity of undisturbed animals was recorded at 4 min intervals as has been done by SPINAGE (1968) and JARMAN and JARMAN (1973).

The study area in Hluhluwe was visited on 171 occasions for periods of between two and 29 hours, during which 354 hours were spent actually observing nyala. It was impossible to follow animals by vehicle because of the terrain, or on foot because of their wariness. Therefore, once animals were lost from view, observations were terminated.

In Ndumu, where conditions were unfavourable for observing nyala, observations were made only during the course of other work.

Some useful observations were also made on tame freeranging nyala on farms (S. LOMBARD, pers. comm.; T. SKINNER, pers. comm.).

3.2.2 Sex and age classification

The sex and age classes used which were based on parameters of body size and, in the males, horn development are described in Table 1. The chronological ages of the classifications are not comparable between sexes because it was possible to allocate more field age classes to males than to females. The classification of 'subadult' females was of necessity subjective; these were animals estimated at between 10 and 14 months old. 'Adult' females were those older than 14 months but the younger animals were again classified subjectively.

Table 1

Sex and age criteria used in the study of nyala behaviour

class		sex
<i>Female</i>		
I		Body height below belly-line of adult female
II		Larger than I but less than III. Upper limit is subjective
III	Subadult	Subjective class, animals obviously not quite adult
IV	Adult	Animals obviously mature
<i>Males</i>		
I		Body height below belly-line of adult female
II		Horns visible but shorter than ear, upper limit of this class is approximately 14 months
III		Horn length between one and two ear lengths, animals between 14 and about 24 months old
IV	Subadult	Horns greater than two ear lengths but have not completed second twist, body size smaller than adult. Two to three years old
V	Adult	Adult size and colours, horns completed second twist
VI	Adult	Adult size and colour, horns in third twist

3.2.3 Recognition of individuals

With nyala, it was possible to recognise individual males by their differences in horn conformation and the arrangement of the spots on the sides of the face. I found that the body stripes and spots were too complex for me to be able to use for rapid identification and I was therefore unable to recognise females on the basis of natural markings.

3.2.4 Marking and radio telemetry

Despite the disadvantages in marking animals, as outlined by WALTHER (1972) it was decided that the marking of some animals, particularly females, was essential. As much of their time was spent in cover, it was also considered necessary to use radio telemetry.

Nyala in the study area were captured either by the method described by DENSHAM (1974) or by immobilization with etorphine hydrochloride (M 99, Reckitt and Sons). Animals were marked with coloured plastic eartags or fitted with individually recognisable collars, or collars bearing a radio transmitter. These transmitters employed the same circuit as that described by ANDERSON and HITCHINS (1971). Four nyala males and six females were fitted with radio transmitters and a further seven animals were marked, either with eartags or collars (Table 2).

Table 2

The recognizable marked and instrumented nyala in the Hluhluwe Game Reserve study area

Sex	Age class	Individual code	Period under observation (days)	n sightings or relocations
M	VI	G	121	33
M	VI	E	184	21
M	VI	C	108	20
M	VI	D	208	10
M	VI	A	348	16
M	V	O	202	10
M	V	H	140	10
M	VI	Q	92	9
M	VI	DD	171	6
M	V	I	113	5
M	V	Sn	97	2
M	II ¹	WR	116	8
M	II ¹	WB	116	10
F	IV	N	190	90
F	IV	K	169	63
F	IV	T	164	52
F	IV	L	163	35
F	IV	J	183	37
F	IV	M	171	17
F	IV	RL	5	3
F	IV	GL	141	7
F	IV	g	153	2
F	III ¹	GY	117	8
F	III ¹	WL	78	8
F	III ¹	WR	366	13
F	IV	WB	123	9
F	II ¹	YL	161	8
F	II ¹	YR	1	1
F	II ¹	GL	354	3
F	II ¹	Y	1	1

¹ age class when tagged.

4 Results and discussion

4.1 Composition and grouping of the population

4.1.1 Sex and age ratio

The composition of the population, estimated at about 150 animals, was based on the classification of 951 animals. These results, adjusted to a base of 100 adult females, are shown in Table 3. It was apparent that a large proportion of the adult females was incorrectly classified as sub-adults. As the age span of sub-adult females is only four months, the ratio of subadult to adult females is excessive and consequently considered invalid. The lower limits of the males and female adult classes differed and therefore these could not be statistically compared. It was however valid to compare the sex-ratio of all animals Class III and above; this ratio (341 : 422) was found to differ significantly from parity ($\chi^2 = 8.59$, $p < 0.01$). There was no obvious seasonal change in composition of the population.

Table 3

Sex and age composition of the nyala population in the Hluhluwe Game Reserve study area, calculated to a base of 100 adult females

Sex	Age class	Ratio: 100 females
M + F	I + II	58.4
F	III	31.1
F	IV	100.0
M	III	2.5
M	IV	1.6
M	V	28.3
M	VI	73.5

Table 4

The social groupings of nyala recognized in the study

Social grouping	Description
1. Lone calves	Class I and II animals – no other nyala seen within 200 m of them
2. Lone subadult ♀♀	No other ♀ or young seen within 200 m of them
3. Lone adult ♀♀	No other ♀♀ or young seen within 200 m of them
4. Lone juvenile ♂♂	Class III, IV and V ♂♂ – no other animals seen within 50 m
5. Lone adult ♂♂	Class VI and VII ♂♂ – no other animals seen within 50 m of them
6. Male group	Two or more ♂♂ which remain together for more than 5 minutes
7. Family unit	Adult ♀ accompanied by her young from one or more generations (Fig. 7).
8. Female groups	Two or more adult ♀♀ or family units
9. Mixed groups	Single ♀♀ or family groups accompanied by one or more ♂♂ of Class V or older which remain for 5 minutes or more.

4.1.2 Social groupings

A total of 492 sightings of nyala groups were made and these ranged in size from lone animals to a group of 21. The mean group size was 2.38 and the typical group size (JARMAN 1974) was 4.56.

From these data, it was possible to distinguish nine types of social groups. These are defined in Table 4.

a. Lone young. Neonate nyala are not precocial but undergo a “lying-up” or ableiger phase (TELLO and VAN GELDER 1975). Although no lone Class I animals were recorded in the study area, two were seen in Ndumu and one was found “lying-up” after field work had been completed.

In tame animals, it was noted that it was only when a young animal was between 10 and 14 days old that it was first seen with its mother. I believe that when lone young were seen afoot, it was a result of the family unit, (e), having been disrupted by the courtship behaviour which occurs during the post-partum oestrous cycle of the dam.

b. Lone adult females. Only 8.4% of the adult females were seen alone, this being significantly lower ($p < 0.001$) than those occurring in groups. Circumstantial evidence suggests that most of the lone females seen are animals which are tending a calf during its “lying-up” phase. Of the seven lone females collected in Ndumu during the study, five were lac-

tating heavily and their uteri showed signs of recent parturition, two animals still had placental remains in their rumena. In the study area, the instrumented female J was seen alone on two successive days and then 16 days later, accompanied by a Class I calf. Observations made on tame free-ranging animals support this hypothesis.

Table 5

The frequency distribution of lone ♂♂ and male group size classes

Group size	1	2	3	4	5	6	7	8	9	10
n observed	200	75	23	19	4	5	0	2	2	0
% Frequency	63.0	2.2	6.6	5.4	1.1	1.4	0	0.6	0.6	0

Table 6

The frequency distribution with which lone animals of each sex and age class were observed

Sex	Age class	n Single	Total observed	% Single
M and F	I	0	11	0
M and F	II	5	121	4.13
F	III	4	73	5.48
F	IV	24	287	8.36
M	III	5	64	7.81
M	IV	1	8	12.50
M	V	33	148	22.30
M	VI	161	349	46.13

c. Lone males and male groups. Lone males were the most commonly encountered group size (Table 5) also found by TELLO and VAN GELDER (1975). The age class distribution of lone nyala (Table 6) showed that with increasing age, nyala males, like those of lesser kudu (LEUTHOLD 1974), became more solitary ($\chi^2 = 51.9$, $p < 0.001$).

From the distribution of male group size classes (Table 5), the mean group size was 1.75 and the typical group size was 2.73. Despite the greater frequency with which lone males were seen than groups of males, significantly more males were sighted in groups than alone ($p < 0.001$). There was, however, no significant difference in the number of sightings of recognisable males alone (30) or in groups (18).

The male groups were not the comparatively stable bachelor groups which have been described in other bovidae (SCHENKEL 1966; ESTES 1969; DAVID 1973) but were short-term associations. From observations of known males, the transient nature of the groups described by TELLO and VAN GELDER (1975) was confirmed. The readiness with which male groups were seen to form and disband suggests that the duration of male group stability lasts an hour or two at the most. An example of the associations recorded for a known adult male (C) are shown in Table 7. Males were seen joining groups three times and leaving groups twice.

The younger males, Classes III and IV, associated significantly more ($p < 0.01$) with males of similar age rather than with older animals. Of 37 male groups containing Class III and IV males, 27 had two or more of this age group present. The positive associations of a young male with others of the same age may be because in a group of similar age animals, he has some opportunity for asserting dominance over others. Although no data on the permanence of young male associations were collected, it is probable that these are more permanent than the associations of adult males.

Table 7

Resightings of an adult ♂ (C) and associated animals

Date	Group
16.1.73	Captured with two adult females (T and J)
19.3.73	With female group (n = 6)
23.3.73	With Class IV male
25.3.73	Alone
26.3.73	Alone (06h20)
26.3.73	Alone (18h03)
8.5.73	With another Class VI male
29.5.73	Alone
18.7.73	With two adult males
19.7.73	Alone
22.7.73	Alone
22.7.73	Alone

Males become more solitary with age and, as post-mature growth continues, they become progressively more dominant. When dominance is asserted in a display, the only disadvantage to the loser is that if an oestrous female is present, he is prevented from mating with her. Therefore, although large adult males have no advantage in being solitary, slightly smaller males are at a disadvantage when in their company and it is in their own interests to avoid the company of the larger males. The increased solitariness of a large male is probably a consequence of avoidance by other males rather than his intolerance of them.



Fig. 2. A nyala family unit, the adult female is accompanied by a Class II calf with an elder calf (behind) which is now classified as a sub-adult

d. The family unit and female group. A family unit consisted of an adult female accompanied by one or more offspring (Fig. 2) whereas a female group was where two or more adult females were present with or without offspring. The frequency with which different sized aggregations of females and young were recorded (Table 8) includes data from mixed groups from which the numbers of sub-adult and adult males have been subtracted. The mean family unit/female group size was 4.07 and the typical size 5.61. Sixty two of the groups of two and three animals were fully classified and of these, 60 (96.7%) consisted of an adult female with one or two offspring. Only two observations were of two adult females.

Table 8

The size class distribution of family units and female groups

Group size	2	3	4	5	6	7	8	9	10	11	12-20	21
n observed	37	29	30	12	7	4	4	7	0	1	0	1
% frequency	28.0	21.9	22.7	9.1	5.3	3.0	3.0	5.3	0	0.8	0	0.8

Confirmation that the small groups were "family units" is shown by the repeated observations of an instrumented female, N, and her eartagged Class II calf YL. A coefficient of association (COLE 1949) was calculated on the number of times the animals were seen together or separately. Between 28/2/73 and 9/5/73, the coefficient of association for N and YL was 1.00 (n sightings - 5), indicating a perfect association, but from the subsequent sighting of N (31/5/73) until the final sighting of YL on 8/8/73 (n - 6), the coefficient was 0.75, indicating a reduction in the amount of times YL spent with its mother. At this stage, YL was between nine and 12 months old.

The meeting of family units to form a female group was seen twice and the breaking up of a female group into family units five times.

The family unit was the most stable of all nyala social groupings encountered but the association with other family units to form female groups appears to be almost as transient as the association of lone males to form male groups. This is illustrated in Table 9 which shows the successive group sizes in which known females and family units were recorded.

Table 9

The successive group sizes in which known ♀♀, and family units were recorded

Female M	5	3	4	3	3	2	2	1	—
Female N	5	5	3	4	1	4	1	3	4
Female T	3	1	5	4	6	—	—	—	—
Female WB	3	3	4	4	8	4	3	3	3

There is some evidence that particular family units may associate together more often than they do with others. The females J and K were caught together and from the degree of toothwear, J was found to be younger than K. Of the 18 resightings of these females and their young, both females (and young) were seen together seven times (Table 10). The coefficient of association was 0.77 and as this exceeds 0.50, it indicates a positive association of the two units. It is believed therefore, that J was an elder offspring of K's and when seen alone, the former was tending her first calf during its "lying-up" period.

In many cases, the aggregations of family units into female groups and, if joined by males into mixed groups, were engendered by some local attraction afforded by the habitat. The

focus could be either trees in fruit, a single water point or a flush of new grass growth after a burn. During August 1971 in Ndumu, a group of 31 was seen on the Pongolo floodplain where, in September 1970 G. SCHÜTTE (pers. comm.) saw a loose aggregation of over 100 animals. No seasonal change in group size was apparent although the larger temporary feeding aggregations must be seasonal as the attractions which cause them are of a seasonal nature.

Table 10

The association of two known ♀ nyala over a period of eleven months

Date	Observation
28. 2.73	♀♀ K and J
2. 3.73	J feeding alone
7. 3.73	K with small Class I calf and Class V ♂
18. 3.73	J and K in company of six other ♀♀ and young, J and Class I calf
1. 4.73	K with another adult ♀ (assumed calf lost)
12. 4.73	K with J and calf and another adult ♀
13. 4.73	K with J and calf and six other ♀♀ with young
9. 5.73	K with J and calf, and another ♀ with Class II calf
17. 5.73	K with J and calf, and another ♀ with Class II calf
25. 6.73	J alone (assume calf lost)
21.11.73	K with Class I calf and a subadult ♀
15.12.73	K with Class II calf and J and two adult ♀♀ with Class II calves

Table 11

The occurrence of nyala ♂♂ of different age classes with family units or female groups

Age class	With ♂♂ or alone	With ♀♀	p Value
I	0	100 ¹	<0.001
II	3	33 ²	<0.001
III	28	19	N. S.
IV	37	6	<0.001
V	181	5	<0.001
VI	510	29	<0.001

¹ This value is an assumption as no Class I animals were seen other than with an adult ♀. –
² This figure includes only those Class II ♂♂ which were positively sexed. In reality, it is higher (see 7.1).

e. Mixed groups. These groups comprised one or more males of Age Class V. The occurrence of nyala males of all age classes with female groups is shown in Table 11. The younger Class I and Class II males were members of a family unit, hence their highly significant ($p < 0.001$) occurrence with females:

In Class III males, there was no significant difference in the number of times they were seen with or without females. These animals are between 14 months and two years old. The younger animals are pubertal but by the upper limit of this class, males have attained the charcoal-grey colour coat of an adult male and their testicular development is the same as that of adult males.

The greater frequency with which adult males are found away from females is highly significant ($p < 0.001$). Adult males were seen with adult females more often than is shown in Table 12 but these associations with females were for less than five minutes. In these brief as-

sociations, an adult male, finding himself in the vicinity of a family unit or female group, would walk up to them, "test" the adult females for oestrus and then wander on.

The mixed group centred around an oestrous female is the most durable and will last for about two days, i. e. the duration of the oestrous cycle. In each of the six sightings of pairs (Table 12), the male was showing courtship behaviour and the female therefore was presumed to be in oestrus.

Table 12
The group size frequency of mixed nyala groups

Group size	2	3	4	5	6	7	8	9	10	11	12	13	14	15
n observed	6	4	4	6	3	1	2	1	1	—	—	—	—	1
% frequency	20.7	13.8	13.8	20.7	10.3	3.4	6.9	3.4	3.4	0	0	0	0	3.4

The largest aggregations of nyala were all recorded in open habitats. This tendency for ungulates which live mainly in cover in small social groups, to form larger aggregations when in the open, has been described in other ungulates (PEEK et al. 1974; HIRTH 1977; LEUTHOLD 1970; WALTHER 1972a).

The aggregation of a species into larger groups as a means of providing greater security from predators, has been suggested by CROOK and GARTLAN (1966), JUNGUS (1971) and by ESTES (1974). HIRTH (1977) has also suggested that the larger groups may be formed to improve feeding efficiency on extensive, even swards. The large aggregations of nyala are not cohesive and the sub-groups within these, pay little attention to one another. This lack of cohesion, as compared to that in herds of plains game, infers that security from predators is a secondary feature of the aggregation and that its formation is centred around feeding.

4.1.3 Conclusions on social grouping

The social grouping of nyala is similar to that found in the lesser kudu *T. imberbis* (LEUTHOLD 1974) and sitatunga *T. spekei* (OWEN 1970). The group sizes of nyala in Hluhluwe were slightly larger than those found in lesser kudu (Table 13). They were smaller but not significantly so (Students' *t* test) than those recorded by TELLO and VAN GELDER (1975) for nyala in Zinave.

The basic social group is the family unit, consisting of an adult female and her progeny. As the typical female group size is 5.61, it is obvious that family units commonly band together to form female groups. From the evidence provided by females J and K, it is likely that the smaller family groups have a structure very similar to that found in elephant *Loxodonta af-*

Table 13
The mean and typical group sizes of sitatunga, lesser kudu and nyala

Species	Mean size	Typical size	Source
Nyala	3.55	6.35	TELLO, & VAN GELDER 1975
Nyala	2.48	5.20	This study
Lesser kudu	2.50	2.95	JARMAN 1974
Sitatunga	1.36	1.69	OWEN 1970
Bushbuck	1.29	1.55	JARMAN 1974

ricana (DOUGLAS-HAMILTON and DOUGLAS-HAMILTON 1975). The adult females are related, one probably the elder daughter of the other.

Group size within African bovids has recently been examined from two angles. ESTES (1974) assumed that the early forest dwelling bovids were solitary and that with the transition from "closed" to "open" habitats, they underwent a "socialisation" process. Gregariousness evolved primarily as a predator avoidance strategy as more open habitats were occupied. JARMAN (1974) related grouping and behaviour to the animal's body size, feeding style and predator avoidance strategy.

Nyala are intermediate feeders (ANDERSON 1978) and fit into JARMAN's (1974) feeding class C but their social organisation and behaviour fit more appropriately into his class B in which are the selective feeders. This discrepancy is comparatively minor and may to some extent be explained by the fact that although nyala are intermediate feeders, whether they browse or graze, they do so selectively. Furthermore, as JARMAN (1974) has acknowledged, discrepancies may be expected when an attempt is made to subdivide a continuum.

4.2 Socialbehaviour

4.2.1 Communication

4.2.1.1 Olfactory communication

No glands were present in the samples of skin taken from the sides of the face or between the horns, but the pedal glands described in the thickened skin around the false hooves by POCKOCK (1910) were very obvious. The purpose of these glands were not investigated and I can only speculate that they serve as an advertisement for the presence of the animal within the area.

Contrary to the findings of HALTENORTH (1963), TELLO and VAN GELDER's (1975) observation that nyala have no inguinal glands was confirmed.

Nyala males test females for oestrus by smelling briefly at the base of the tail. "Flehmen" (SCHNEIDER 1930) is only shown if the female is in oestrus. It appeared that oestrus could be detected without actually testing the female's urine, presumably from odours arising from the moist vulva which are derived from urine.

4.2.1.2 Visual communication

a. Pelage and body conformation. Perhaps the most striking aspect of the sexual dimorphism of the nyala is the difference in male and female pelage. The basic coat colour of the adult male is a charcoal-grey whereas that of the female is a red-brown. In the adult male the long fringe of hair on each side of the belly and hind legs, together with the erectile ridge of hair running along the spine, have the effect of increasing the surface presented in a lateral display by up to 40%. In addition, the torso of the nyala male has the appearance of being laterally compressed, in cross-section being more elliptical than oval. The torso of the nyala male comprises 67% of its lateral silhouette whereas that of the impala, which does not have a lateral display, is 58.1%. The surface area of the torso of 12 nyala males made up $49.5 \pm 0.45\%$ ($\bar{x} \pm \text{SEM}$), and that of impala $43.1 \pm 0.36\%$ ($\bar{x} \pm \text{SEM}$). The difference, tested by Students' *t* test, was highly significant ($p < 0.001$) and this, together with the difference in composition of the silhouettes, is I believe, related to the importance of the lateral display in nyala behaviour and its absence in the behaviour of impala.

Sexual dimorphism is a common feature amongst Tragelaphines and probably reaches its greatest expression in the nyala. The dominance ritual and lateral display are the criteria on which sire selection is achieved. As a result, there has been selection towards large male size and the strategically situated hair crest and fringes. These latter serve only to exaggerate body size and the only benefit accrued from this is the enhancement of mating opportunity. Simi-

lar features which increase the lateral display have evolved in other species, for example the dewlap and dorsal ridge of the gaur *Bos gaurus* (SCHALLER 1967).

The benefits of size dimorphism in enabling a greater number of females of some species to exist on a limited food resource, have been discussed (JEWELL 1966). In some dimorphic raptors (REYNOLDS 1972), there is niche separation and this has also been suggested in dimorphic ungulates (GEIST 1974). The dimorphism of nyala does not confer either of these benefits nor do nyala males play a role in the defence of female and young. Therefore, the only function of this dimorphism must be social communication with the aim of obtaining mating rights.

Mating rights themselves have one disadvantage. OWEN-SMITH (1977) maintains "any form of mating competition must result in some reduction of life expectancy on account of the time and energy expended and risks of injury incurred in interactions with other males". While this applies to species with a rutting peak, conceptions in nyala are more scattered in time (ANDERSON 1978) and relatively little energy is expended in any dominance ritual.

Life expectancy in the large males is however reduced. The largest males have the greatest energy requirements and when food quality and availability become limited towards the end of the dry season, these males have the lowest condition levels. When further stress is experienced, mortality is biased towards adult males (ANDERSON 1978). Logically, the males which die will be those in the poorest condition, i.e. the biggest. Here we have a situation which parallels GEIST's (1971) findings in mountain sheep.

The neotenic appearance of young males is retained for some time after puberty. Although they look like females, adult males are aware of the sex of these young males as no adult male was seen "testing" a young male. These young males elicit no agonistic behaviour from adult males and are therefore not driven from the family unit until they become larger and darker than the females.

There is a survival value in the young post-pubertal male remaining with the female unit as long as possible as once he leaves, he will no longer be part of any cohesive social group. This is less important in seasonally breeding ungulates where young evicted males experience a common fate and form bachelor herds.

b. Horns. In ungulates, horns are in most cases the mechanism whereby dominance and ranking are achieved and may be used in either ritualized displays or in fighting (EWER 1968; GEIST 1971; WALTHER 1974).

Only the male nyala has horns; these commence growth at about six months and become more noticeable when they exceed the ear length at about 16 months. The horns are used in various agonistic displays but their size alone does not appear to have a role in determining rank or dominance.

4.2.1.3 Vocal communication

a. Alarm bark. The alarm call, a staccato dog-like bark, is the most commonly encountered call. It conveys a warning to other nyala and is given when man or a large carnivore is sighted. The reaction of other nyala to the bark is immediate flight.

b. Bleat. A distress "bleat" is uttered by both sexes. It is commonly heard when animals are entangled in game capture nets and was once heard when an adult male was being killed by lions. A similar but lower pitched bleat was heard once when a female had become separated from her calf. The calf bleated and the female returned and rejoined it.

c. Clicking. S. LOMBARD (pers. comm.) heard a tame female make a soft throaty clicking sound which was only audible at a distance of less than 5 m. It was heard more often when the female was in oestrus or when she was tending a very young calf. A similar call has been described in bushbuck *T. scriptus* (JACOBSEN 1974), uttered by a tame female when searching for her calf. This call was not heard during the study, presumably because it is so soft.

The random meeting of animals in an area is sufficient to obviate the need for any vocalisation to contact conspecifics and nyala are essentially silent.

4.3 Behavioural patterns

4.3.1 Agonistic behaviour

Some aspects of agonistic behaviour might have been seen but not recognised, an example being the avoidance of one male by another before any behaviour could take place. Those which were recognised have been described in order of increasing aggressive intent.

a. Horning the ground. In the study area population, the animals observed horning the ground were all adult males in Classes V and VI. However, males as young as 18 months were seen horning at a waterhole in Mkuzi Game Reserve.

Horning did not appear to be directed towards other animals. It was frequently executed when the male was alone, and if other animals were present, they showed no noticeable reaction to the horning male.

Horning generally took place in the moist soft ground (Fig.3) next to the river or waterholes (Mkuzi). The horns would be thrust forward into the ground and then wrestled and twisted upwards to free them. As in other African bovids, where horning has been described, the forehead makes contact with and is rubbed against the ground (JOUBERT 1970,



Fig.3. An adult male horning the soft moist ground at the edge of a waterhole

1972; UNDERWOOD 1975; JACOBSEN 1974). These authors consider the possibility of scent transference but in nyala, where no glands are present in the skin of the forehead, and as the action is not directed to faeces or urine, it is unlikely that any scent transference occurs.

It has been speculated that the horning in bushbuck and sitatunga may be some form of territorial advertising (WALTHER 1964) but as nyala are not territorial, this cannot be the motive. Furthermore, as the action is not released by a conspecific, it is not redirected aggression and is perhaps symbolic of a behaviour pattern which no longer has a role in the social behaviour of nyala.

b. Weaving and thrashing of vegetation. The distinction between weaving and thrashing by nyala males was clearly noticeable. Weaving was the rather unhurried rubbing of vegetation, usually the stem of a small bush, between the horns and along the sides of the face by moving the head up and down. Thrashing was more violent and the bush was attacked, the horns pointing forwards and the head moving almost in a figure "8" pattern. These actions may be executed individually or one may run into the other.

In weaving, the rather deliberate movement suggests that the animal is marking the stem with a secretion as is done by impala (JARMAN 1975) and eland *Taurotragus oryx* (UNDERWOOD 1975). However, no scent or secretion was detected on the bushes which had been rubbed. Unlike the fraying done by roe deer *C. capreolus* (PRIOR 1968), there was no obvious damage to the bush which might serve as a sign to other nyala.

Weaving was seen four times and only Class VI males were involved. On the three occasions in which weaving occurred in the company of others, the other animals showed no discernible reaction to the activity. The context in which weaving was done was never obvious.

Thrashing was seen seven times and all instances were in the company of other animals which showed no reaction. In four observations, thrashing was clearly linked to aggression. Twice thrashing was done by a male immediately after losing a dominance encounter and once, a Class VI male, consorting with a female, thrashed a bush when a Class V male approached to within about 40 m. The latter responded immediately by turning and walking away from the pair.

Thrashing by an animal either after a dominance encounter or before a potential encounter, is regarded as being redirected aggression, as defined by WALTHER (1974). However, where thrashing occurred without apparently being released by a conspecific, its context remained obscure.

c. Pawing the ground. Pawing the ground with a forefoot was seen only three times during the entire study. It was done exclusively by Class VI males.

Twice the circumstances were considered "stress" situations. The animals were encountered at close quarters and pawing, linked once with ground horning, and the second time with thrashing, appeared to be directed at my vehicle. In the third observation, a male in the company of three others, weaved and then pawed the ground, the activity being ignored by the other males.

WALTHER (1964) maintained that Tragelaphines lacked the ground-pawing complex present in the behaviour of *Bos* species. It is still present in the nyala but it was never observed in any intraspecific encounter. Where pawing occurs in other ungulates (HAFEZ et al. 1969; SCHALLER 1967; WALTHER 1974), it forms part of an aggressive behaviour pattern.

d. Dominance display. The components of the dominance display have been outlined by WALTHER (1964) and TELLO and VAN GELDER (1975). These I have divided into three phases, based on their degree of intensity.

In the first phase, a male will not disrupt a "routine" activity (walking, feeding, etc.) but will half raise the dorsal ridge of hair. It is believed that this merely signifies that the male is aware of another's presence. The display becomes more intense in the second phase when the dorsal ridge is fully erected, the head held high and the animal moving with a very characteristic gait (Fig. 4). In this "Imponiergang" (WALTHER 1964) or "stately walk" (TELLO and VAN GELDER 1975), the legs are raised higher than normal, displaying the orange lower legs



Fig. 4. The nyala dominance display. The dominant male on the left has entered the third phase of the display while the submissive male on the right is in the second phase of the display and is turning away to terminate the encounter

and the movement is slow and deliberate. As this phase becomes more intense, the “Imponiergang” becomes slower, the tail is half raised and the neck is lowered until it is in line with the body, the horns held forward (Fig. 4). In its final phase, the animal stops walking and only moves to orientate the side of its body to its opponent. The tail is erected over the rump and the white hairs on its underside are fanned out. The head is lowered and the horns are held pointing forward.

e. Sparring. I saw sparring three times in the study area and twice in Mkuzi. In all cases, the animals involved were evenly matched and only once were they fully mature Class VI males.

Sparring was initiated by the animals lowering their heads and placing their foreheads “carefully” together. The animals then pushed against each other (Fig. 5) until one broke off the encounter with a quick sidestep, the other not pursuing the “loser”.

Alternatively, after pushing against each other, both animals would stop and then hold their heads up and sideways on to each other, WALTHER’s (1964) “Kopfseitwärtswenden”. The sparring would then either be resumed or one would break off the encounter by displacement grooming or feeding. On one occasion, mutual facial grooming took place between two bouts of sparring.

It appeared that, „Kopfseitwärtswenden“ was an appeasement rather than a threat gesture as it is in some species (WALTHER 1974). Rather than a “present” (GEIST 1971), where the horns are shown to the opponent, it appears as the “displaced alarm display” seen in wildebeest *Connochaetes taurinus* (ESTES 1969), bontebok *Damaliscus dorcas* (DAVID 1973) and eland (UNDERWOOD 1975).



Fig. 5. Sparring consists of pushing against each other while the horns are locked together

f. Horn clash. As opposed to sparring, the horn clash, seen twice, was a clear expression of a high level of aggression. In both instances, it occurred when a Class VI male was consorting with a female which, in view of his courtship behaviour, was presumably in oestrus. On each occasion another slightly smaller male approached the others and, without hesitation, the consorting male rushed at the intruder. The single clash of horns was so swiftly delivered and parried that it could not be described. The smaller animal hastily retreated while the larger, not following-up any advantage, returned to the female.

g. Fighting. Fighting, as opposed to sparring, was seen once. TELLO and VAN GELDER (1975) remarked on this and I am aware of only two fights which had been witnessed in the Zululand reserves.

In the fights witnessed by SCHÜTTE (1967) and myself, the striking feature was the animals' ferocity and the fact that at no time was any lateral display used; they faced each other at all times. At the site of another fight, one combatant was found killed by a horn thrust through the parietals. This, and the presence of large scars on the necks of many adult males, bear testimony to the danger to the individual of fighting.

h. Aggressive behaviour of females. Only two observations of female aggression were made; in both instances, they were directed towards another female. What precipitated the action was not known but the aggressor in each case lowered her head and ran at the other animal, butting her on the abdomen. The recipient in each case moved away and continued feeding.

4.3.2 Patterns of submissive behaviour

Submissive behaviour patterns are included in this section as they generally result from agonistic behaviour and form part of every dominance encounter.

a. Male submissive behaviour. There were clearly recognisable submissive signals in a dominance encounter but there may have been others too subtle for me to discern. The submissive animal would cease pilo-erection and start a displacement activity such as "Kopf-

seitwärtswenden", the "head-and-tail sweep", grooming or feeding. Head flagging, which WALTHER (1964) interprets as a peace offering, „Friedensangebot“, was seen once but not in the study area. While flagging, the submissive animal stepped backwards, away from the still displaying dominant animal.

Only once was a male seen showing submission by holding the head downward-forward and laying the horns back on the neck, this being one of the most common submissive postures used by ungulates (WALTHER 1974).

b. Female submissive behaviour. If submissive behaviour was shown towards other females, I did not recognise it. The submissive posture adopted towards the male during courtship was holding the head and neck downwards and forward.

4.3.3 The dominance ritual

The cause of the ritual, where agonistic and submissive behaviour patterns are combined, is obvious when it occurs in the presence of an oestrous female. However, most observations of the ritual were observed in the absence of females and some took place between males, which shortly beforehand, had been feeding peacefully together. In the study area, I saw 25 dominance rituals and the outcome was clear in only (36%) of these. Whenever a ritual occurred in the presence of an oestrous female, a conclusive outcome was reached but in the displays between males in casual encounters, inconclusive outcomes often resulted.

The ritual starts when one animal, not necessarily the larger, enters phase one of the dominance display. This may take place up to 50 m from the male to which the display is addressed. Why this first phase of the dominance display is ignored in most encounters is not known; it may be that the animals are known to one another and are confident of their status. The challenge is accepted when the animal to which it was addressed goes into a second phase of the display. There are occasions when the threat may be directed at and returned by more than one male. What initiates such an encounter was not determined.

At this stage, the outcome may be settled by one animal showing submission or both animals may show displacement activity with the outcome remaining unclear. Alternatively, the ritual will progress with one animal adopting the third phase of the display while the other slowly circles him. This is identical to the movements of the lateral display in the gaur (SCHALLER 1967).

The animal which exhibited the third phase of the display always achieved dominance in the encounter (Table 14). Where both animals entered this phase (seen once), the outcome was uncertain as both broke off into displacement grooming.

Table 14

The situations and outcomes of observations of interactions where the second and third phases (see text) of the nyala dominance display were recorded

Activity of addresser	Activity of addressee(s)	Outcome of encounter	n Observations
Second phase	No reaction	Not observable	8
Third phase	No reaction	Not observable	2
Second phase	Submission, no display	Submission by addressee	2
Second phase	Second phase	No clear outcome	5
Third phase	Second phase	Submission by addressee	7
Third phase	Third phase	No clear outcome	1
Second phase	Different species	—	1

Animals obviously bigger than their opponents, always proved to be dominant in the outcome of a ritual. Where animals of the same body size contested dominance, the deciding factor was too subtle for me to discern. There was no indication that horn size had a role in deciding dominance (in Fig. 4, the male with the smaller horns is dominant).

The evolution of horns and fighting techniques has been reviewed by GEIST (1966) who concluded that their development has been primarily to serve in intraspecific social conflicts. Although nyala horns play a role in the dominance ritual, horn size, unlike cattle (BOUISSOU 1972) and red deer *Cervus elaphus* (LINCOLN et al. 1970) is less important than body size.

The predominant feature of the nyala's repertoire of agonistic behaviour is the dominance ritual. Dominance displays such as this have evolved to reduce fighting and the possibility of sustaining an injury which might itself lead to death or render the animal more susceptible to death by predation (GEIST 1974). The outcome of the dominance ritual is decided by body size and the anatomical features which serve to emphasize this.

The sparring which occurs mainly in the younger males (Class II to V) may serve to give them the experience to realize that opponents larger than themselves are likely to win any physical encounter. Therefore, as animals become larger and the risk of serious injury greater, the incidence of sparring decreases and dominance is achieved by the display alone. This change in agonistic behaviour with age, where potentially dangerous behaviour is replaced by displays, has been described in other ungulates (ESTES 1974; SPINAGE 1969; KITCHEN 1974).

4.3.4 Reproductive behaviour.

a. Testing females for oestrus. Testing for oestrus takes place whenever males come into contact with females during the course of their daily activity. Foci of activity such as waterholes and fruiting trees enhance the chances of visual contact between males and family units. I saw male/female meeting and "testing" 127 times, and among these, only two females were found to be in oestrus. Three male/female meetings were seen where "testing" did not occur.

On joining a female or female group, males test for oestrus by smelling briefly at the base of the tail of adult and sub-adult females (Fig. 6a). In this initial test, the male does not smell the vulva and in contrast to some other ungulates where this form of stimulation causes the female to urinate (EWER 1968), this action elicits no response from the female. The urinary pheromones which signify that a female is in oestrus are apparently powerful enough to be detected without the urine itself having to be sampled.

The testing of females is done by all males of Class IV or older and when a group of males encounters a female group, all the males test the adult and sub-adult females. Although some young (Class III) males have the general appearance of females, none was ever seen tested by older males.

Nyala show the typical lipcurl of "Flehmen" (SCHNEIDER 1930; ESTES 1972) but this is only in response to the testing of an oestrous female (Fig. 6b). Normally, when testing females which are not in oestrus, the male merely raises his head and slightly opens his mouth in the less exaggerated "Flehmen" shown by some gazelles (ESTES 1967, 1972).

Nyala males were twice seen encountering oestrous females and a further 12 oestrous females were seen with one or more males already in attendance. In these instances, whenever the females were tested, the full "Flehmen" lipcurl was exhibited.

b. Oestrous behaviour. In the field, oestrus could not be detected in the absence of any male activity to reveal the female's condition. S. LOMBARD (pers. comm.) observed that his tame female became restless and agitated during oestrus and vocalised frequently with the "clicking" call.

Of six oestrous cycles which LOMBARD (pers. comm.) observed, overt oestrus lasted approximately two days and the females permitted copulation for a period of about six hours towards the end of this period. Observations on an instrumented female M tended to confirm this as she was seen at 10h10 on 30/6/73 with a consorting male. At this stage, she re-

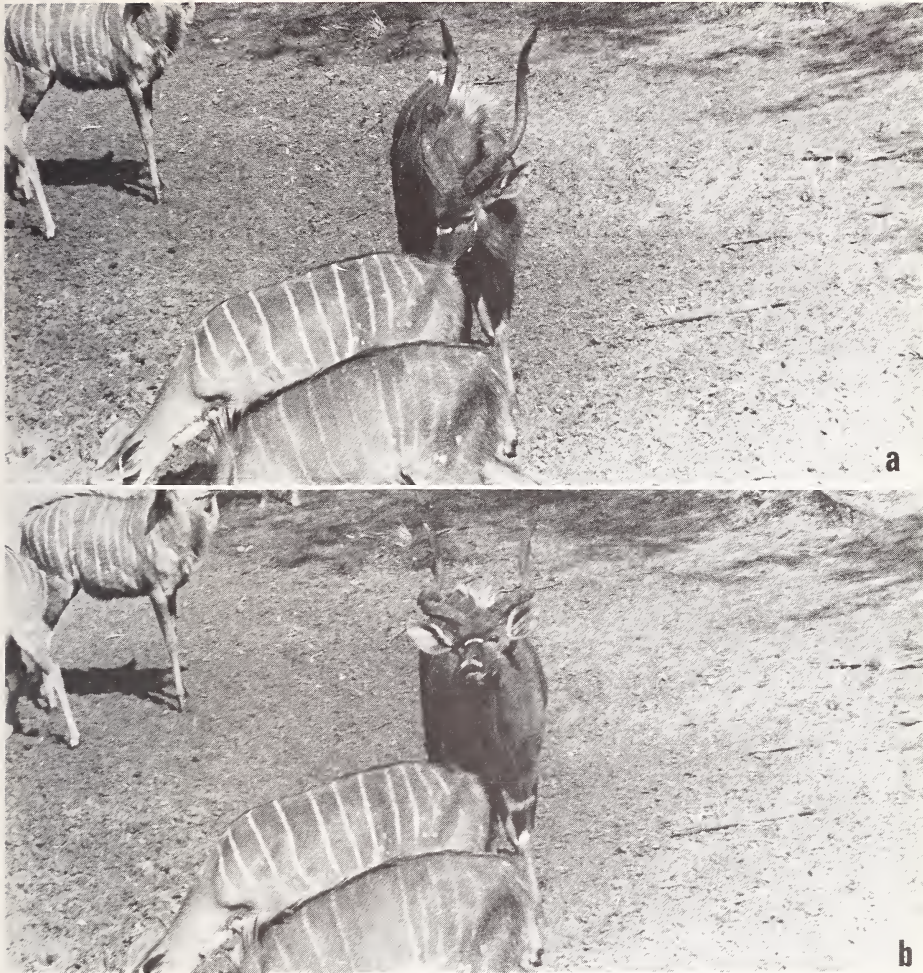


Fig. 6. a: Male testing a female for oestrus by smelling at the base of the tail; b: "Flehmen" is exhibited only if the female is found to be in oestrus

jected all his attempts to mate with her and first permitted mating at 09h45 the following day.

c. Courtship and mating. On testing a female and finding her to be in oestrus, the male's first reaction is to move up to her and align his forequarters against her hindquarters in the mounting-intention posture. In all my observations of this initial approach, the female rejected the male's advance by moving away.

The male then follows closely behind her, holding his head and neck stretched forward (Fig. 7a), "Überstrecken", which WALTHER (1974) regards as typical of courtship in Tragelaphines. He repeatedly smells her vulva and frequently pushes his head between her hind legs; BUCHNER and SCHLOETH (1965) termed this "inguinal nuzzling". BUECHNER and SCHLOETH (1965) cite BURCKHARDT (in litt. but never published) as having recorded inguinal nuzzling in nyala and WALTHER (1958) noted it in lesser kudu. In both species, it was only recorded prior to copulation and as it appears to be an infantile action, it may have an appease-

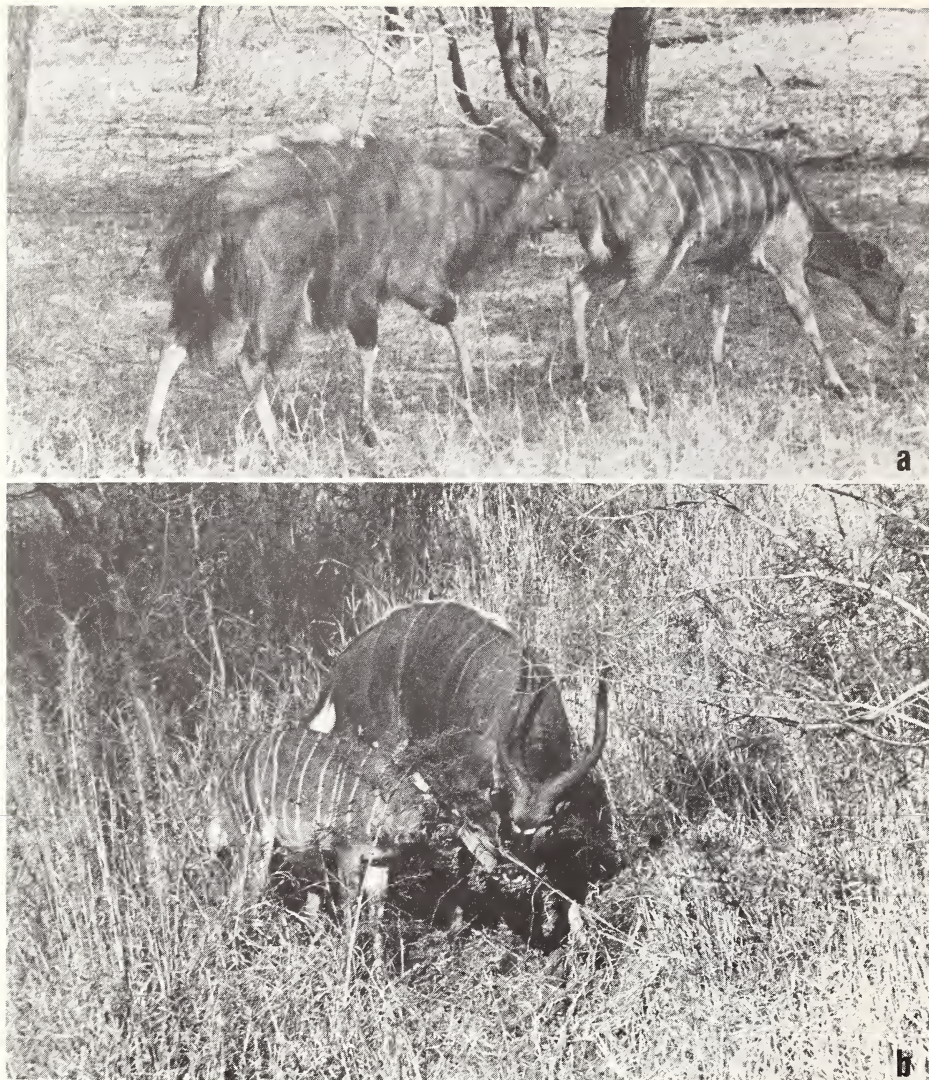


Fig. 7. a: If the female is not receptive she moves off, the male following with his head and neck stretched forward. In this case the female is holding her head in the submissive posture and it was assumed that she was almost receptive to the male's advances; b: As the female becomes more receptive, the male blocks her movement away from him. (This female is fitted with a collar and radio transmitter)

ment function. This nuzzling may be conducted so assiduously that the hindquarters of the female are lifted off the ground.

The female shows little reaction to these initial advances though she may sometimes hold her head and neck in the submissive posture when being tested (Fig. 7a) or while walking. Should she remain stationary for more than a few seconds, the male will assume the mounting-intention posture, and if she is unreceptive, her only recourse is to move off. Those oestrous females which were seen with consorting males were not accompanied by any younger animals and it is likely that the action of the courting male or males has a disruptive effect on



Fig. 8. a: After blocking the female, the male then presses her neck down into a submissive posture; b: While keeping his head across her neck and withers, the male moves to assume the mounting-intention posture

the normal daily activity of the female unit, resulting in a temporary break in the mother-young bond. This was supported by the observations on female M. During the period she was observed while in oestrus, there was no sign of any calf, yet when she was collected, 32 days later, she was lactating and was accompanied by a calf of approximately nine months old. In Ndumu, two oestrous females were collected during courtship. One was experiencing a post-partum oestrus and the other was lactating but had apparently calved some weeks previously.

This initial phase of pre-copulatory behaviour continues until the female no longer moves off after the testing and inguinal nuzzling. The duration of this lasts at least 24 hours during which the consorting male may have been replaced by progressively more dominant males.

Although the female no longer walks away from the male, she moves a little each time the male takes up the mounting-intention posture. The male then moves to block these small movements of the female. He stands slightly obliquely and shoulder to shoulder with the female (Fig. 7b). He then manoeuvres her into a submissive posture (WALTHER 1974) by pressing her neck down with his own (Fig. 8a), an action which may have to be repeated a number of times until the female remains in this submissive attitude. The male, keeping his neck across her withers, moves to the mounting-intention position (Fig. 8b) and then, with his head still pressed down on her back, mounts. The copulatory position is typical of that in all Tragelaphines (WALTHER 1964). The male's body is held low and touching the back of the female and his head is pressed down along her withers.

The courtship and mating involving female M was the only complete sequence I observed and this was terminated prematurely by the animals being disturbed. Once mating had been accepted by the female, it occurred four times in a period of 48 minutes. Copulation lasted between four and 10 seconds, the male making rapid pelvic thrusts (8–16) while the female remained motionless.

That the adoption of the submissive posture by the female is the eventual cue for mating, can be seen when non-receptive females in oestrus have to lower their heads to drink. When this occurs, any consorting male will immediately mount the female who will quickly move off to avoid copulation.

There appears to be no post-copulatory behaviour pattern other than a repetition of the blocking and pressing down of the female's neck which occurs prior to copulation.

Important in the reproductive behaviour of nyala is the duration of the oestrous cycle (about two days) and the fact that mating is permitted only at the end of this period. During the period prior to mating, the female will be attractive to any male she may encounter in her home range. This male will immediately start courting her and as the courtship behaviour is very distinctive, the pair may attract other males which have seen them but are too far away to be aware that the female is in oestrus.

The competition for the right to mate with the female may last for nearly two days and this allows a certain amount of sire selection to occur.

4.3.5 Parturition and post-partum behaviour of female and calf

a. Parturition. Parturition itself was not seen but I was able to observe a calf born in the game pens in Hluhluwe and its mother, from approximately three minutes post-partum (PP) until four hours PP.

WEBB (1974) described the birth of an nyala in captivity. A notable feature of this birth was that two other females assisted the dam in cleaning the calf. In the post-partum behaviour that I observed, although other females were present in the pen, they did not assist in cleaning the calf. The female first ate the membranes then licked the calf for nearly 20 minutes. She then ate all the straw bedding which had been soiled by the birth. The calf first attempted to stand at 20 minutes PP and was successful at 74 minutes PP. Its first attempt to suckle at 120 minutes PP was unsuccessful and it was only at 199 minutes PP that it succeeded in drinking. The female lay down briefly at 30 minutes and 60 minutes PP, and on each occasion, she half rose on her forequarters and appeared to be straining. This was repeated at 127 minutes PP when the placenta was expelled. She immediately rose, licked her vulva and began eating the placenta. A sub-adult female which then joined her, ate approximately half the placenta.

b. Reactions of calf to external stimuli. At 30 minutes PP the calf was able to shake its head in an apparent attempt to dislodge flies. A sudden noise at 55 minutes PP caused the calf to immediately adopt the "lying-out" posture with the head and neck held flat along the ground. It maintained this position for 11 minutes despite the fact that the other animals present paid no attention to the noise.

c. Reactions of female and calf to conspecifics. During and immediately after the birth, the other nyala in the pen did not react towards the female and calf. When the female first lay down (30 minutes PP), a Class II calf came up and groomed her ears, then briefly smelt the calf.

On its second attempt to suckle, the calf tried to drink from a strange female. This female ignored the calf but the mother manoeuvred her away by butting her under the belly with her head and neck.

The sub-adult female which had earlier eaten half the placenta, attempted to suckle from the female. This was rejected by the female, pushing her away with her forehead.

d. "Lying-up". The "lying-up" periods observed by S. LOMBARD (pers. comm.) were between 10 and 14 days. In the study area, I saw the marked female J alone over a period of two days, then 16 days later, accompanied by a calf less than one month old. I presume that the minimum "lying-up" period in this case was 18 days.

The sites in which nyala have been found "lying-up" in Zululand are all in some form of cover (N.P.B. records) and although TELLO and VAN GELDER (1975) record finding two young "lying-up" together, only single young have been found "lying-up" in Zululand.

4.3.6 *General behaviour*

a. Leadership within the family unit and group. Within the family unit, leadership is clearly with the adult female but when two or more units join to form a female group, no ordered leadership was detected.

b. Leadership within male groups. When male groups formed, there was no apparent leadership when a male asserted dominance via the dominance ritual; no visible advantage was discerned in the absence of an oestrous female.

c. Relationships to other herbivores. Nyala pay little attention to the presence of other herbivores. They will avoid larger herbivores if the latter move towards them but show no alarm in doing so.

Kudu and impala both react to the alarm calls of nyala and look for the source of the alarm. Nyala were seen to react similarly to the alarm calls of impala and baboon.

Although essentially herbivorous, baboon *Papio ursinus* have been recorded killing and eating small nyala calves (N.P.B. records; PIENAAR 1969; TELLO and VAN GELDER 1975). In spite of this, nyala do not avoid the company of baboon and are frequently seen beneath trees in which they are feeding, eating the dislodged fruit and leaves.

d. Reaction to carnivores. Nyala alarm calls were heard in response to the presence of lion *Panthera leo* and hyaena *C. crocuta* and presumably the reaction to other large carnivora would be similar.

e. Reactions to man. Where they have been hunted, nyala are wary of man, their reaction being the same as it is towards carnivores. In addition, it is likely that they confine more of their activity in open habitats to the night time. This accounts for the early view that nyala are secretive (STEVENSON-HAMILTON 1947). As TELLO and VAN GELDER (1975) point out, where afforded protection, nyala extend their activity pattern into daylight hours and lose their shyness of vehicles.

In all the Zululand reserves with the exception of False Bay Park, nyala are wary of people on foot. Around the campsite at False Bay however, nyala have become habituated to man and some, having been fed, now actively approach people in the hopes of reward.

f. Play. TELLO and VAN GELDER (1975) disagree with WALTHER (1964) over the fact that there is "much playing" in the behaviour of nyala. My observations confirm this as, during the entire study, only once was an instance of playing observed; a Class II calf rushed around its mother for approximately 20 seconds.

4.3.7 Conclusions on social organisation

TELLO and VAN GELDER (1975) believe nyala to have a dominance hierarchy but the main characteristic of such a hierarchy, namely the simultaneous presence of several adult males together with females in the same group (LEUTHOLD 1974) is absent. As yet, no quantitative data on known male: male interactions have been obtained and consequently, the existence of a hierarchical system has yet to be demonstrated.

The ecological tenets outlined by GEIST (1974) suggest that nyala should have a hierarchical system as do the prolonged postmature growth and sexual dimorphism of the males (ESTES 1974; GEIST 1974). Furthermore, in a species where reproduction may occur at any time of the year, as is the case with nyala, a hierarchical system is more advantageous than the territorial one (GOSS-CUSTARD et al. 1972). Nyala may be expected to show a hierarchical system yet this is not apparent, and in view of this doubt, LEUTHOLD (1974) groups the Tragelaphine social organisation in an intermediate category, between a hierarchical and a territorial system.

OWEN-SMITH (1977) has recently outlined the four basic male mating strategies, and being non-territorial, there are two alternatives into which the nyala may be grouped. These are a stable ranking dominance as is found in buffalo *Syncerus caffer* (SINCLAIR 1974) and eland (UNDERWOOD 1975), and the temporary dominance asserted in the presence of an oestrous female, as occurs in mountain sheep (GEIST 1971a) and caribou *Rangifer tarandus* (LENT 1965). There is no stability in male groups and no evidence that there is a stable ranking within any particular area. It is also difficult to visualize how a stable ranking system could exist with the nyala's spatial organisation of overlapping home ranges. A male may have a different ranking in different parts of his home range, depending on the number and sizes of males whose home ranges overlap various segments of his own home range. When it is recognised that this must also apply to all the males whose home ranges overlap with his, the system appears to be too complex to be viable.

I believe that the nyala's social system or mating order is based on a temporary dominance. On all occasions when an oestrous female was observed during courtship, dominance was fiercely contested whereas in a stable ranking dominance, this would be less likely to occur. Females, when in oestrus, may also attract a male whose home range is outside her own, for example when meeting takes place at a waterhole. When she returns to her home range, he will follow her, and if possible, continue to consort with her until she permits mating. With their given spatial organisation, a temporary dominance system is more appropriate than a dominance hierarchy for the nyala mating system as the latter would result in chaos rather than order. I suggest that it is probably the system found in other Tragelaphines with the exception of the eland.

As the Tragelaphines do not display territoriality, one should consider why their alternate form of social organisation is more efficient as a means of enhancing reproductive success. Much of the argument used by BARRETTE (1977) to illustrate why the muntjac *Muntiacus muntjak* is not territorial is applicable to the Tragelaphines. Because they live in closed habitats at comparatively low densities, territories would have to be fairly large to contain sufficient adult females to make the holding of a territory worthwhile. The territories would also necessarily have to be large in order to affect conspecific males at all.

In a closed habitat, the maintenance of a large territory would, without scent marking, place a high demand on both the energy and time of the territorial male. In open habitats, animals have the advantage of visual communication which means less energy expenditure in advertising and defending a territory than would be necessary in a closed habitat. In closed habitats, the reward in terms of mating opportunity, in exchange for energy and time expenditure, is potentially greater with the Tragelaphine social system than it would be with a territorial one.

4.4 Behaviour related to the environment

4.4.1 Activity

The observation of activity patterns was biased in that it was only activity in the open which could be recorded. Furthermore, when the majority of animals were sighted, they were aware of my presence and generally ceased their previously undisturbed activity. For these reasons, activity was examined in two ways.

a. Seasonal activity patterns. All sightings of animals in the open, regardless of their activity, were first grouped seasonally and then into time classes of one hour. To account for variations between time classes and time actually spent in the study area, the data were treated as follows:

$$\frac{n \text{ animals seen in time class } x}{\text{total time in study area during time class } x}$$

These animals: time ratios were then illustrated by taking the highest class ratio as being 100 and treating others as a percentage thereof (Fig. 9). These data (Fig. 9) give a picture of overall "activity in the open" in hour classes between seasons.

A further breakdown into specific activities was made from 1736 records of the activity of undisturbed animals. Three activity types were quantified: (1) feeding; (2) resting, either standing or lying down; and (3) other, which encompassed undisturbed travel, grooming, drinking and intraspecific behaviour patterns. Within each time class, the data for each activity type were summed and their percentage calculated. As their overall patterns were very similar, the spring and summer activity patterns were grouped together as were those of autumn and winter (Fig. 10).

b. Daily activity. During the day, feeding took place primarily in the early morning and late afternoon. There was a marked difference in feeding activity between the hot spring and summer months, and the cooler autumn and winter months. During the former period, no animals were seen between 10h00 and 14h00; those seen between 09h00 and 10h00 in spring (Fig. 10) had all been disturbed.

During spring and summer, animals were seen resting in the open only during the cooler hours of the day. I assumed that during the middle of the day, when animals were in cover and hidden from view, that they were inactive like the conspecific bushbuck (JACOBSEN 1974). In the cooler months between 10h00 and 15h00, nyala were seen resting in the open or in lightly shaded sites.

There was no apparent pattern in the occurrence of intraspecific behaviour patterns, but there was a peak in drinking activity towards midday during autumn and winter. During this period in the study area, most observations of animals drinking were made between 09h00 and 13h00. OWEN-SMITH (1965) presented data on the drinking times of game in Mkuzi during mid-summer (January). These data probably approximate the drinking times of nyala in Hluhluwe at the same time. In the study area during the spring and summer, few observations of drinking were made and at this time, surface water was abundant and widespread. If there was a drinking peak at midday, this could not be detected as animals were in cover.

TELLO and VAN GELDER (1975) attribute the greater frequency with which nyala are seen during the day in the dry season to their need to wander more widely to find food and water. Neither of these factors is thought to have influenced the amount of time nyala spent in the open in Hluhluwe Game Reserve.

An assessment of 24 hours' activity was made from instrumented animals during May and June. The number of "active" signals received in each time class was converted to a percentage (Fig. 11). There was a decrease in activity between midnight and sunrise, and a marked drop in activity between 13h00 and 14h00. The decrease in activity after midnight has been confirmed by P. HANCOCK (pers. comm.) while using night viewing equipment to observe hippo *Hippopotamus amphibius* in Ndumu.

c. Activity in response to weather. As outlined above, during hot weather, nyala enter cover and it was during the middle of the day that most "resting" was recorded. When resting during this period, animals were only seen standing; presumably this is because, as in the red kangaroo *Megaleia rufa* (RUSSELL 1971), it permits a greater surface area for evaporative cooling than lying down.

The response of nyala to rain and cold was to remain in cover and during these conditions,

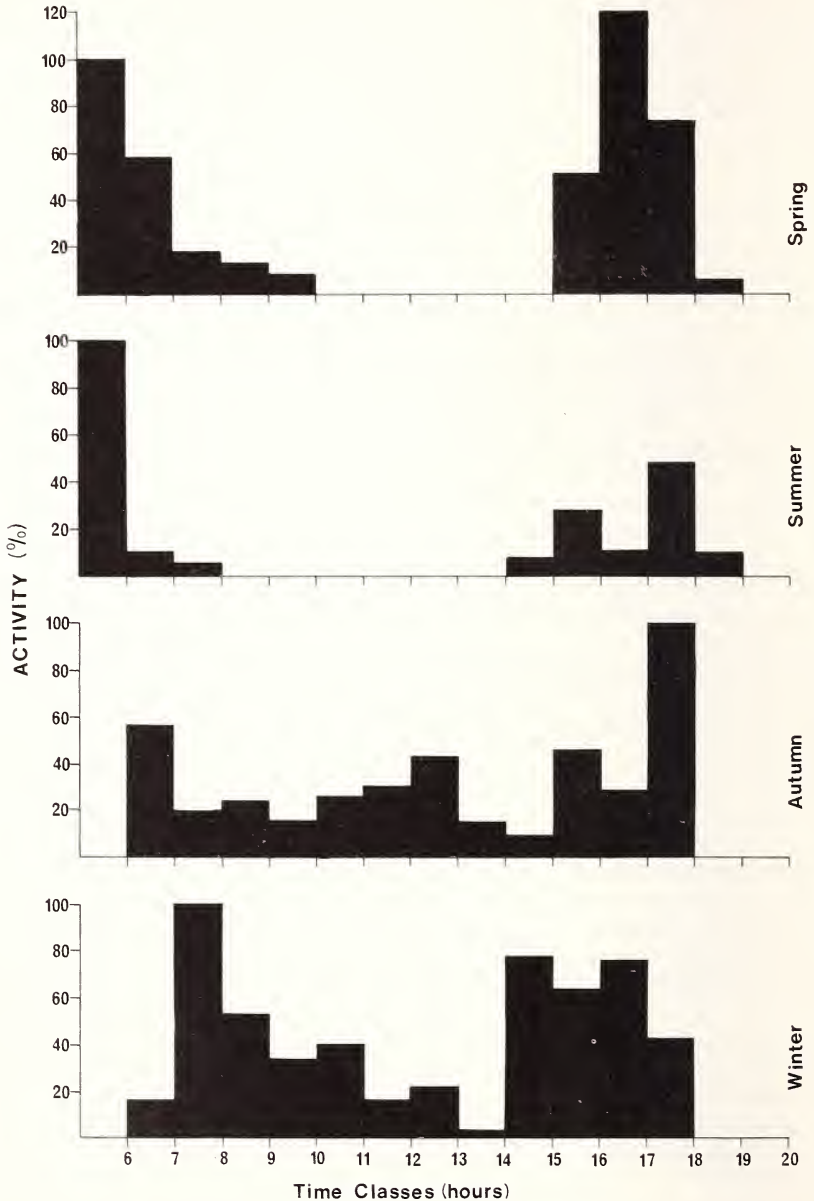


Fig. 9. Seasonal differences in diurnal "activity" of nyala in Hluhluwe Game Reserve. (For the explanation of the calculation of "activity %", refer to text)

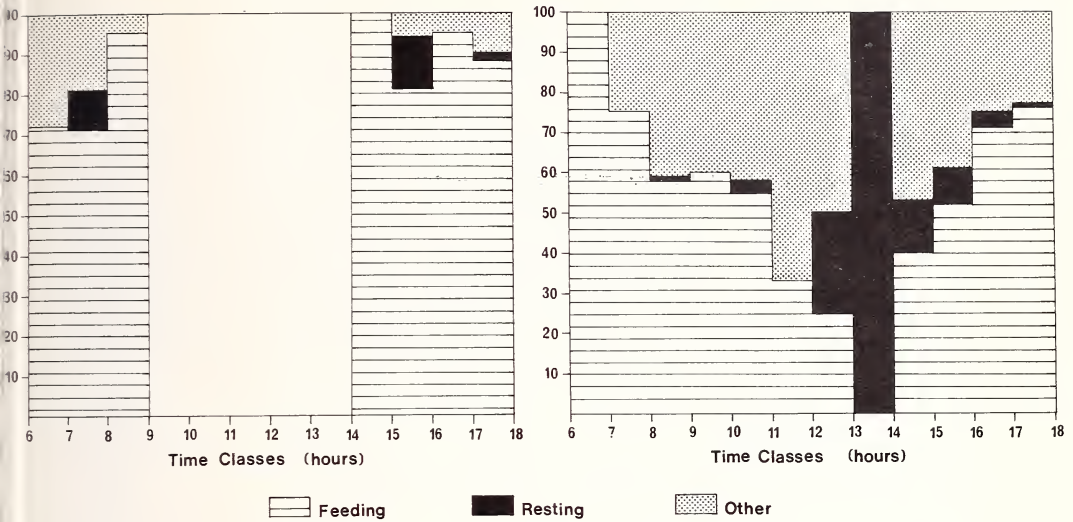


Fig. 10. The patterns of observed activity of nyala during spring/summer (above) and autumn/winter (below)

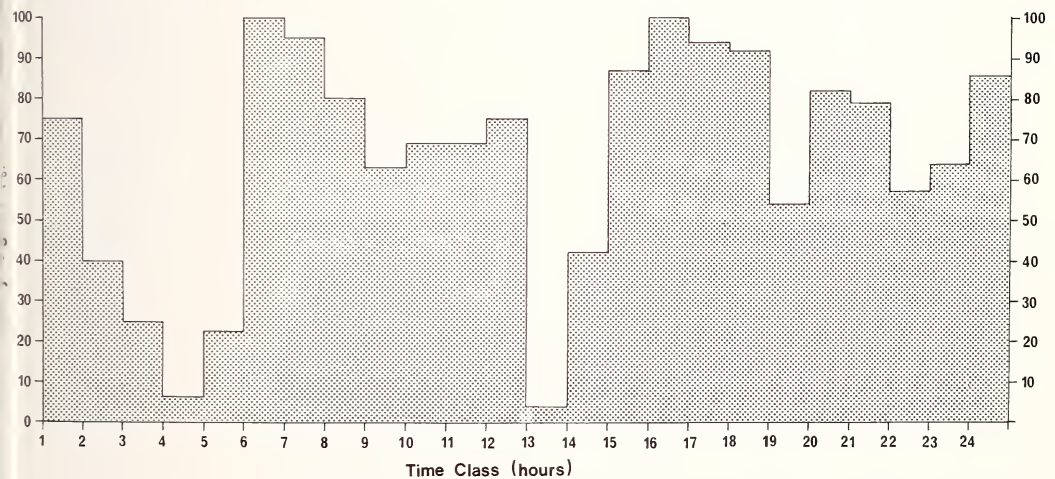


Fig. 11. An assessment of 24-hour activity during May and June (winter), determined from 496 telemetry readings

nyala were rarely seen, regardless of the time of day. It is perhaps pertinent that two of the three sightings of nyala lying down during the day were made during cool weather while there was a light drizzle. This may have been a reaction to the weather conditions as their exposed surface area was decreased and heat loss thereby reduced.

It would appear that thermoregulation is the main factor responsible for the seasonal changes in their activity in the open. During hot weather they seek shade and in inclement weather shelter, thus highlighting the importance of closed cover as a component of nyala habitat.

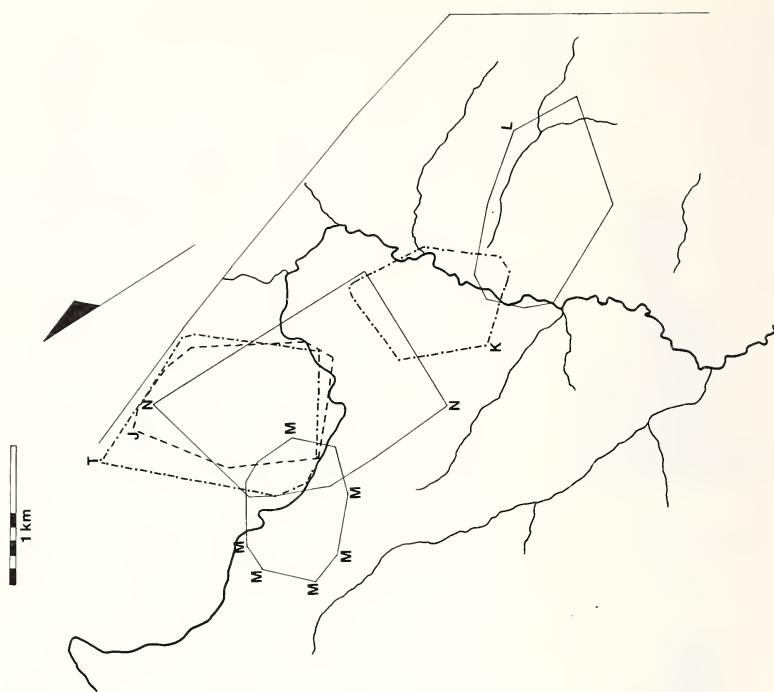


Fig. 13. The minimum home ranges of six nyala females in Hluhluwe Game Reserve. There were at least another 15 adult females whose home ranges overlapped with these animals, their home ranges were not known

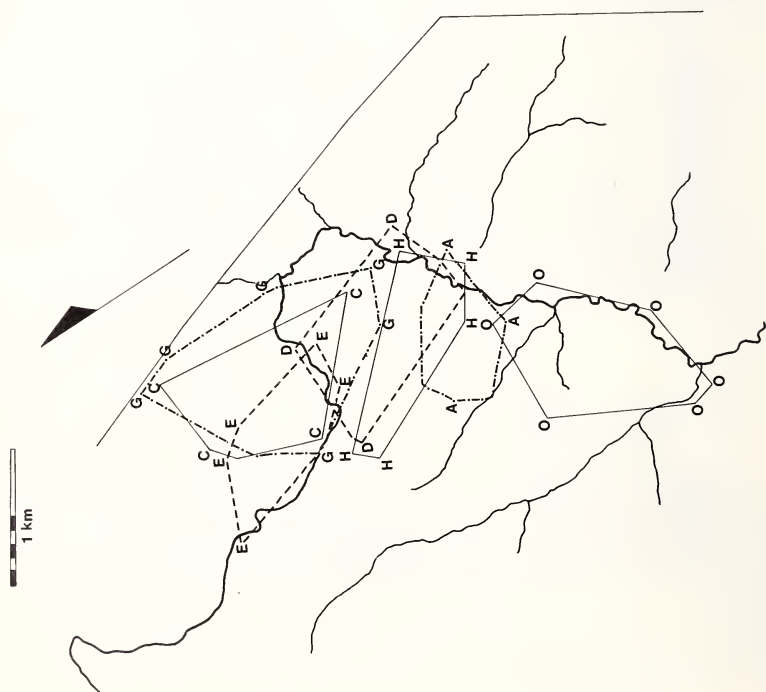


Fig. 12. The minimum home ranges of seven nyala males in Hluhluwe Game Reserve. A minimum of 17 other adult males occupied that portion of the study area in which the home ranges are illustrated, their home ranges were unknown

4.4.2 Spatial behaviour

No data were collected which might suggest that nyala of either sex were territorial. This confirmed TELLO and VAN GELDER's (1975) findings that the non-exclusive and overlapping areas occupied by nyala were home ranges as defined by WALTHER (1972).

a. Home range size. Using the data on the resightings of recognisable or marked animals and the relocation of instrumented animals (Table 2), the areas of activity of animals were plotted using the "Minimum Area" method (STICKEL 1954). Only the data from animals which had been relocated 10 or more times were used (six males and six females).

The size of each minimum area polygon (Fig. 12 and Fig. 13) and the amount of each vegetation type within each polygon, were calculated (Table 15). The mean home range size for adult males was $0.65 \pm 0.099 \text{ km}^2$ ($\bar{x} \pm \text{SEM}$) and for adult females, $0.83 \pm 0.16 \text{ km}^2$ ($\bar{x} \pm \text{SEM}$). There was no significant difference in home range size between sexes.

Table 15

The minimum home range sizes of 13 nyala home ranges and the vegetation community percentage composition within each

Animal	Sex	Minimum area (km ²)	Forest	Tall <i>Acacia karroo</i>	Short <i>Acacia karroo</i>	<i>Combretum</i> community	<i>Acacia caffra</i>	<i>Maytenus</i> sp.	Grassland
G	M	1.05	26.3	23.9	11.1	—	—	—	38.6
E	M	0.43	25.9	40.2	—	—	—	—	33.3
C	M	0.68	22.3	40.4	11.7	—	—	—	25.6
D	M	0.86	11.2	10.5	27.2	—	—	—	51.1
A	M	0.38	11.4	9.1	—	—	—	—	79.5
O	M	0.77	14.3	4.5	—	—	—	0.6	80.5
H	M	0.39	19.2	35.2	15.8	—	—	—	29.8
N	F	1.39	11.5	33.3	1.9	—	—	—	36.2
K	F	0.48	32.3	42.2	—	—	—	—	54.6
T	F	1.16	24.2	36.8	—	—	—	—	39.0
J	F	0.74	37.1	45.0	—	—	—	—	17.9
L	F	0.78	13.4	39.9	—	1.9	16.4	19.6	8.7
M	F	0.42	16.4	32.5	14.1	—	—	—	37.1

There was extensive overlapping of home ranges, both within and between sexes. Monopolized zones (JEWELL 1966) and core areas (KAUFMANN 1962 in JEWELL 1966) were not detected and judging by the indifference with which conspecifics are treated, it is unlikely that they occur. Insufficient data were obtained to enable observations on home range size of sub-adult males.

b. Habitat components of home ranges. Of the vegetation types within each home range, the one which appeared to be the most essential was forest which in all cases, constituted more than 10% of the home range. The tall *Acacia karroo* and grassland communities occurred to varying extents within each home range but their presence did not appear to be important whereas forest provided essential escape cover and shade throughout the year.

A source of available water was present in each home range. This may be essential to animals which are used to year-round water availability but, as DAVISON (1971) and TELLO and VAN GELDER (1975) have described populations which survive some months of the year without drinking, it does not apply generally.

c. Diurnal and nocturnal use of the home range. The data from some instrumented animals showed that there were parts of the home range which animals only occupied at night (Fig. 14). The most accurately known male and female home ranges showed that the areas occupied at night comprised up to 27.6% (N) of the entire home range. The areas occupied at

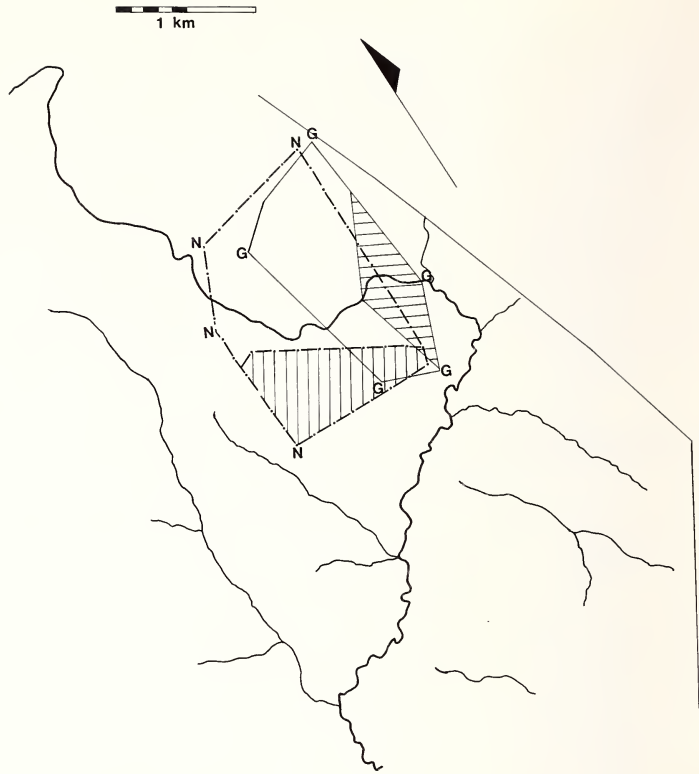


Fig. 14. The areas of nocturnally used home range (shaded) of a nyala male (G) and female (N)

night were primarily open, and grassland and short *Acacia karroo* scrub comprised a significantly greater percentage of the nocturnally occupied part of the home range than that occupied by day (male G, day home range 49.7%, night home range 92%, $p < 0.001$; female N, day home range 38.1%, night home range 95.3%, $p < 0.001$).

In Ndumu, the most open vegetation communities were the floodplains and their occupancy by nyala was almost exclusively at night.

Although the data for the individual animals (N and G) showed that there were areas exclusively occupied at night, other animals were occasionally seen in parts of these areas during the day. With prolonged observations, I suspect that the animals would eventually have been recorded in these open areas during the day. The data do, however, indicate that open areas within the home range were used more often at night than during the day. This differs to TELLO and VAN GELDER's (1975) findings that in Zinave, Mocambique, the nyala spend most of the night in thickets.

d. Dispersion. A female nyala, on the birth of her first calf, will remain in the vicinity of her parental family unit and these two units will frequently associate for short periods of time. Because of this prolonged association, dispersion by females is probably a very slow process.

There is no adequate information on the dispersion of males from the family unit; in their case, there is some coercion to leave the family unit. When a male has reached the Class III age class and the adult female comes into oestrus, larger males will not tolerate his presence in the vicinity of the female and he will be displaced. He may return to the family unit once the

female is no longer in oestrus but as the average female in Zululand experiences three oestrous cycles between pregnancies (ANDERSON 1978), he will be repeatedly driven from the group. At this stage, Class III males are found more often in association with males than females, but whether this is within the parental home range or not is not known.

e. Seasonal changes in home range. By the end of March 1973 the river in the study area stopped flowing and a month later, surface water was available at only three points along its course.

As successive pools dried, recognisable animals extended their known home range to encompass the nearest available pool. At this stage of the dry season, nyala from the adjoining catchment to the west of the study area came to drink on the river and immediately thereafter, returned to their former home range. This distance from the middle of the adjoining catchment to the drinking point in the study area was only 2.1 km.

f. Permanence of home ranges. On completion of the study, the last sightings of surviving marked and recognisable animals were all within their home ranges. Sightings of marked animals, made by other observers some time after completion of the study, showed no changes in their known home range. One adult female (RW) was seen in June 1975, 27 months after being marked, less than 500 m from the site of her original capture.

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Zusammenfassung

*Über soziale Organisation und Verhalten des Nyala, *Tragelaphus angasi* Gray, 1849*

Die hier vorgelegten Ergebnisse beruhen auf Beobachtungen, die im Zeitraum April 1971 – August 1973 in Wildreservaten des Zululandes durchgeführt wurden. Die Daten wurden in Hluhluwe erarbeitet und in Ndumu und Mkuzi ergänzt.

Die soziale Organisation der Nyala basiert auf der Mutterfamilie, bestehend aus dem Muttertier und ihren Nachkommen. Die charakteristische Gruppengröße von 5,61 wird gebildet aus zwei oder mehr Mutterfamilien. Diese Gruppenbildung beruht nicht auf Zufall, sondern wird begünstigt durch verwandtschaftliche Bindungen.

Die Söhne verlassen die Mutterfamilie im Alter von 14–24 Monaten und suchen die Gemeinschaft von anderen Männchen auf, bevorzugt von solchen gleichen Alters. Die Größe dieser Männchengruppe wird mit 2,73 charakterisiert. Diese Gruppen sind nicht fest gefügt und selten länger als während eines Tages konstant. Mit fortschreitendem Alter und zunehmender Körpergröße werden die Männchen dominanter und immer mehr Einzelgänger.

Die Nyalamännchen sind nicht territorial, der Erfolg bei der Werbung beruht auf temporärer Dominanz in Gegenwart eines brunftigen Weibchens. Die Dominanz wird begründet durch Imponierverhalten mit seitlicher Schaustellung unterstützt durch Körpergröße und Aufrichten des Haarkammes.

Männchen und Weibchen bewohnen Areale, die sich überschneiden und im Untersuchungsgebiet etwa 1 km² groß sind. Diese Wohngebiete können, wenn kein Oberflächenwasser vorhanden ist, vergrößert werden. Die Töchter verbleiben später im oder nahe dem Wohngebiet der Mutter. Der Umfang der Wanderungen der Söhne nach Verlassen der Mutterfamilie ist noch nicht eindeutig erkennbar.

Die Nahrungsaufnahme der Nyala findet statt in den Stunden des frühen und späten Tageslichtes. Wasserstellen werden zumeist in den späten Morgenstunden aufgesucht, wenn möglich täglich. Während der heißen Tagesstunden oder bei ungünstiger Witterung verbleibt die Nyala im Dickicht, welches sich im Wohnbereich befinden muß. Wenn das Verhalten der Nyala nicht durch Menschen beeinflusst wird, wird der größte Teil des Tages im vergleichsweise offenen Gelände verbracht.

In Jagdgebieten hingegen wird dichter Busch bevorzugt. Man kann die Nyala jedoch vorsichtig an Menschen gewöhnen.

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