

THE NATURAL HISTORY OF NYALA
TRAGELAPHUS ANGASI
(MAMMALIA, BOVIDAE)
IN MOZAMBIQUE

JOSÉ L. P. LOBÃO TELLO AND RICHARD G. VAN GELDER

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ABSTRACT

We made observations of nyala (*Tragelaphus angasi*) for more than 2000 man-hours primarily between September, 1971, and April, 1974, in Zinave National Park, Mozambique, and vicinity, mostly in a study area of approximately 32 sq. km., near Zinave Camp on the Save River. Data on habitat, climate, measurements, and age and growth of nyala are presented. In the study area 70 percent of the adults seen were females. The population of nyala in the study area increased from an estimated 175 to 250 in 1971 to more than 326 in 1973, for a density of about 10 nyala per sq. km. More than 60 percent of the nyala seen were adults. Nyala were seen alone or in groups up to 30 in number; 67 percent of the observations were of one to three animals. Males were seen alone twice as frequently as females. Nyala groups are not permanent, and individuals come and go. A subadult male was seen in association with at least 15 other individuals and an immature with 16 in eight and 13 days respectively. The strongest bond is probably between a mother and her young, but newborn nyala are left hidden in thickets for several weeks. The home range of male nyala is up to 10 sq. km., and does not change seasonally. The home range

of females is approximately the same size. No evidence of territoriality has been observed, and there is extensive overlap of home ranges of a number of males and females. Nyala are active in the daytime especially at temperatures between 20° C. and 30° C. and at night during the rainy season. They shelter from both sun and cold in thickets and at Zinave drink daily. In the dry season when food is less available nyala may wander 12 km. between sunup and sundown. Lions and leopards are the main predators of adult nyala, whereas baboons and raptorial birds are the principal predators of juveniles. Nyala are killed by man for trophies and meat. Nyala have a single offspring born after an eight and one-half month gestation period at any time of the year. Females may conceive within a week after parturition. Nyala are often seen in association with impala or baboons. Nyala eat leaves, fruits, flowers, twigs, and bark of more than a hundred species of plants. They are parasitized by ticks, flies, trypanosomes, and helminths. The social behavior of nyala is shown mainly by male displays and rituals for assertion of dominance without fighting. A hypothesis of the communicatory role of the white markings of nyala is presented.

SUMÁRIO

No Parque Nacional do Zinave—especialmente numa área de estudo, com cerca de 32 Km², próxima do Acampamento Zinave, na margem sul do Rio Save—estudaram-se inhallas (*Tragelaphus angasi*), durante mais de 2000 horas/homem, principalmente entre Setembro de 1971 e Abril de 1974.

Apresentam-se elementos sobre o habitat e clima assim como se fornecem notas biométricas e apontamentos sobre idade e crescimento da inhalla.

Na área de estudo, 70% dos animais vistos eram fêmeas. A população da espécie em causa, na mesma faixa, aumentou do número estimado de 175 a 250 em 1971, para mais de 326 em 1973, dando uma média de 10 inhallas por Km². Mais de 60% dos animais vistos eram adultos.

Foram encontrados isolados ou em grupos

variados, chegando estes a ter 27 animais. Em 67% das observações foram vistas de 1 a 3 inhallas. Os machos isolados foram avistados duas vezes mais frequentemente do que fêmeas sòzinhas. Os grupos não tinham constituição permanente e o mesmo animal ora vivia num grupo, ora noutro, ora ainda se encontrava isolado. Um macho sub-adulto foi visto, em 8 dias, associado, pelo menos, com 15 diferente indivíduos; um imaturo, em 13 dias, foi encontrado com, pelo menos, 16 diferentes inhallas. Provavelmente, a mais unida associação é a que existe entre a mãe e sua cria. Contudo, as recém-nascidos são deixados sòzinhos, nas brenhas, por longos periodos, durante várias semanas.

O espaço habitacional (home range) chega a atingir os 10 Km². Algumas das inhallas, senão todas, vivem no seu espaço habitacional durante

todo o ano. Não se observaram quaisquer sintomas de territorialismo e verificou-se uma grande sobreposição de espaços habitacionais, quer de machos, quer de fêmeas.

Durante o dia, as inhalas são principalmente activas quando as temperaturas rondam de 20 a 30° C. Refugiam-se, quer do frio, quer do calor, nas brenhas. No Zinave, bebem diàriamente e, durante a época seca, quando a comida é menos abundante, talvez percorram 12 Km., entre o nascer e o pôr do sol.

Os leões e leopardos são os principais predadores naturais das inhalas adultas; os macacos-cães, assim como determinadas aves de rapina, constituem os mais importantes inimigos dos juvenis. São abatidas também pelo homem, quer para troféus (fora do Parque) quer para a obtenção de carne.

Depois de uma gestação de 8 1/2 meses, é

parida uma só cria, a qual pode nascer em qualquer época do ano. As fêmeas talvez concebam durante a primeira semana após o parto.

O comportamento social da inhala é principalmente mostrado pelo macho, durante as exhibições (display) e rituais efectuados para a afirmação de domínio, sem ser necessário lutar pelo mesmo.

É apresentada uma hipótese sobre o papel desempenhado pelas marcas brancas do corpo, na comunicação interespecífica das inhalas.

Alimentam-se principalmente de folhas, frutos, ramitos, flores e cascas de plantas lenhosas, mas também comem certas herbáceas, principalmente durante a época das chuvas.

Associam-se frequentemente a impalas e macacos-cães.

São parasitadas por carraças, moscas, tripanossomas, e helmintas.

INTRODUCTION

The nyala (*Tragelaphus angasi* Gray, 1849) is one of the less studied large mammals of southern Africa. The paucity of information is in part due to the relatively small geographic range of the species (Sidney, 1965; Ansell, 1971; and fig. 1) and because in much of its habitat tsetse flies and malaria have discouraged visitors and agricultural (livestock) enterprise. Virtually all the literature prior to 1968 consists of taxonomic and morphologic descriptions and generalized and scanty accounts by trophy hunters.

We present data obtained in more than 1200 man-hours of observation on the Nyala Expeditions of the American Museum of Natural History: September 25-October 19, 1971; August 30-September 17, 1972; July 5-July 28, 1973; April 2-April 25, 1974, all in the Zinave region of the Save River in Mozambique. Supplementary data obtained by the senior author since 1963 at the Maputo Game Reserve near Bela Vista and at Gorongosa National Park near Vila Paiva de Andrada, and since June, 1969, on the hunting concessions of Moçambique Safarilandia (see Dalquest, 1965, map), by the junior author in the same area in September and October, 1968, and by field assistants at Zinave from 1971 to 1974 are included where they add materially or differ from our current observations.

Acknowledgments

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The Direcção dos Serviços de Veterinária de Moçambique kindly authorized these studies and provided Tello with appropriate and needed permits.

In the field we were continuously aided and encouraged in all ways by Baron Werner von Alvensleben, and assisted by Messrs. George Turner, José Saraiva de Carvalho, Ken Fubbs, Miguel

Guerra, Manuel Figueira, Ray Sparrow and his sons, Lionel Pereira, G. Cowan, Mr. and Mrs. Irving Kingsford in 1971, Mr. Russell N. Van Gelder in 1973, and Mr. and Mrs. Alan Blinken in 1974. Mr. Dennis Goodson was especially helpful in much of the radio-tracking.

We are indebted to Miss Patricia W. Freeman, Dr. Emil Dolansek, Mr. William Conway, and Miss Marie Lawrence for assistance in various phases of the project, and to Prof. J. Travassos Dias (Faculdade de Medicina Veterinária of the Universidade de Lourenço Marques) for identifications of the parasites and to Mr. Aurelio Balsaínhas of the Instituto de Investigação Agronómica de Moçambique for assistance in plant identifications.

Above all we are grateful to Messrs. England, Lucas, Wilson, Manuel and the late Sabão, our trackers, whose keen eyes, hard labor, and detailed knowledge enhanced every phase of the field studies. The photographs were taken by Mrs. Anne Kingsford, Mr. Russell N. Van Gelder, and the authors. The maps, drawings, and graphs were prepared by the Graphic Arts Department of the Museum under the direction of Mr. Joseph Sedacca.

We dedicate this work to the memory of Mabihane Chimungane Dzucule-Sabão—our chief tracker, friend, and field companion whose efforts and knowledge contributed so much to this study and who died at the age of 39 in 1973.

METHODS

We made most of our observations with binoculars ranging in power from 7 to 15 magnifications from a topless vehicle. Ordinarily animals were observed from 100 m. or more, as they generally moved away from us when we approached more closely. The flight distance in the open, however, did decrease during the course of the study from about 100 m. in 1971 to about 70 m. in 1972, and to about 60 m. in 1973 and 1974. The cover of thickets permitted us to approach more closely, however, and animals in thickets could be approached at 25 to 35 m. The nyala in the open tended to flee at about 300 m. or more from a man on foot.

In order to identify individuals we attempted to photograph nyala in 1971, but this was unre-

warding. That year we captured some animals by hand at night, but because it was hazardous we discontinued after some injuries to our capture team. Although there were a few nyala that we could recognize on sight by a particular horn conformation or unusual coloration, most of the animals remained difficult to distinguish from one another.

In 1971 we attempted to capture nyala using a drug, Parke, Davis and Company 744, administered from an extra-long-range (powder) Cap-Chur gun. Although we got satisfactory results from unrelated species, the drug did not work well on nyala, either causing death or failing to immobilize the animal. In 1972 with a revised composition for 744, we were also unsuccessful in immobilizing any animals. By experimentation we found that we could immobilize adult and subadult male nyala and adult females with 2.4 to 3.5 mg. etorphine hydrochloride (M-99) plus 5 to 7.5 mg. of acepromazine maleate (Acetylpromazine) or with 40 mg. of U.S. sublimaze R 4263-citrate (Fentanyl) plus 7 mg. of Acetylpromazine or 150 mg. Azaperone (Stresnil) for adult males and 30 to 40 mg. of Fentanyl plus 5 mg. of Acetylpromazine or 100 mg. of Azaperone for adult females. For the M-99 the antidote is 4 mg. cyprenorphine hydrochloride (M-283) intravenous, and for Fentanyl the antidote is 50 mg. nalorphine hydrobromide (Lethidrone).

Our standard and successful dosage was 3 mg. of M-99 with 7 mg. of Acetylpromazine or with 150 mg. of Azaperone for all classes. Our only mortalities when using these drugs were two females that died of capture myopathy ("white muscle disease"). Nyala may be especially susceptible to white muscle disease, and in captivity Selenium has been administered to improve viability of the young (Davall, 1965).

In 1971 we marked some animals with plastic ribbons around the neck, clipped to the ears with ear-tags, and on the tail. Those around the neck and the tail were quickly lost, but those on the ears lasted some weeks. At the same time we painted the horns of males, and this was found to last, in diminishing amounts, for up to a year. However, the sighting of marked animals again was seldom, and in 1972, we commenced putting collars containing radio transmitters on captured animals and continued this through 1974. These

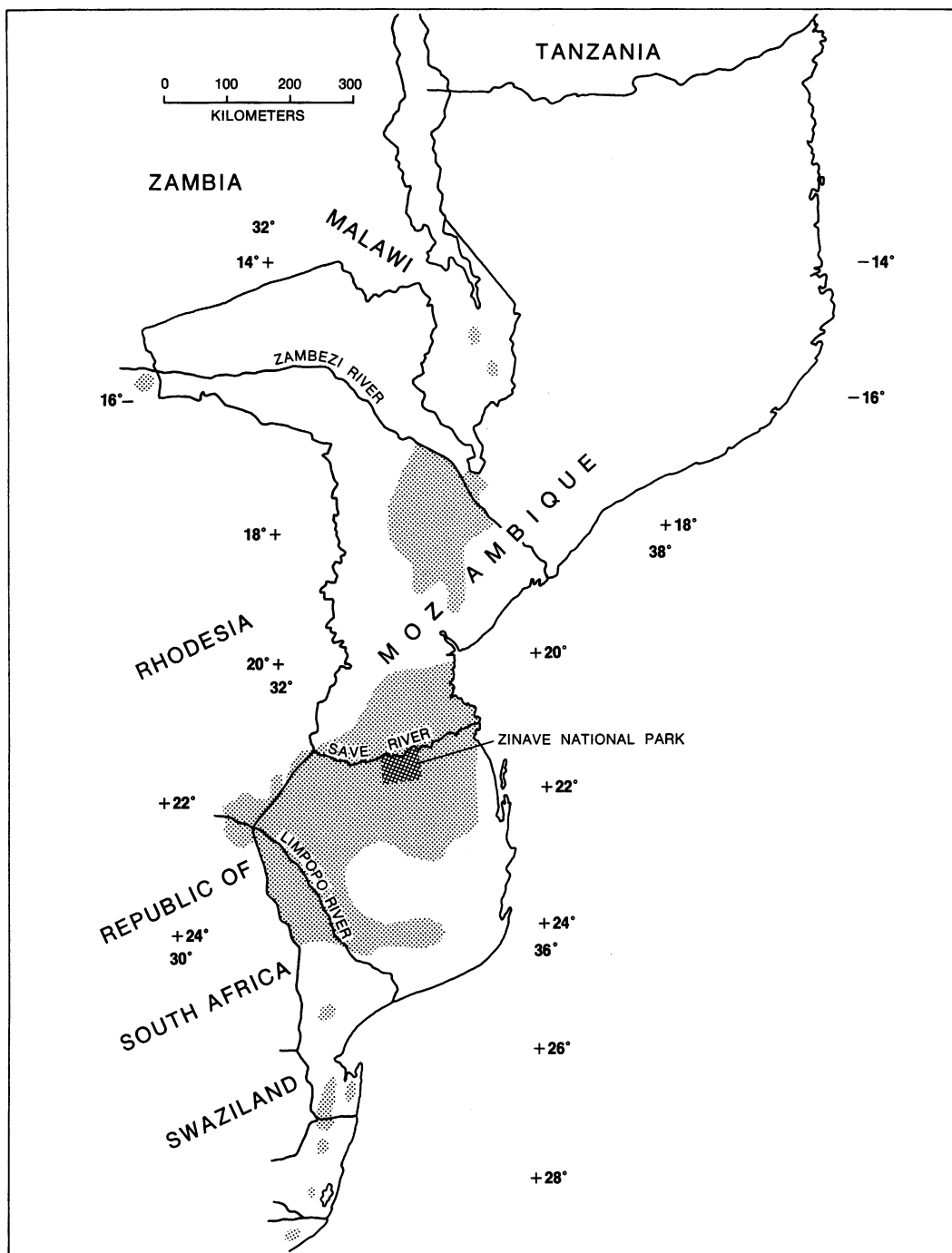


FIG. 1. Map of presently known distribution of *Tragelaphus angasi* (stippled) and Zinave National Park, Mozambique (crosshatched).

were manufactured for us by Dav-Tron (formerly Davidson Co. Electronics) of Minneapolis, Minnesota; the one- to two-pound radios did not seem to alter the behavior of the animals and enabled us to locate individuals again and to determine their movements.

We examined the stomach contents and took measurements of about 40 animals found dead, inadvertently killed by us, or killed by trophy hunters.

Plant names follow Gomes e Sousa (1966-1967).

LIFE HISTORY

Study Area. Most of our observations were made in a small portion of Parque Nacional do Zinave. Proclaimed in 1973, the Park occupies part of what was formerly Coutada No. 4 of Moçambique Safarilandia (see Dalquest, 1965, map). The north border of the park is formed by the south bank of the Save River from longitude 34° 02' 08" E, to longitude 33° 01' 51" E and the park extends southward to latitude 21° 53' 30" S at longitude 34° 02' 18" E and latitude 21° 41' 18" S (fig. 1). The area of the park is approximately 4200 sq. km. and the soil is mainly alluvial formations of laterite and calcareous Tertiary and Quarternary sands. In altitude the park ranges from 85 to 170 m., in places sufficiently accented to produce rolling country with slight ravines in places along the Save River. The only permanent water is in the river, although in most years (but not in 1971) there is water in Zinave Lagoon. Most of our observations were made in a study area extending about 6 km. to the west of Zinave Camp, the Park headquarters, and from the Save River to the south about 5 km. The study area comprises about 32 sq. km. (See map, fig. 16.)

There are no long-term weather data for the Zinave area, but records have been obtained from Massangena on the Save River, about 90 km. west of Zinave, and from Mabote, about the same distance south of Zinave. From Zinave the region becomes somewhat more arid from north to south as well as from east to west with fewer days of precipitation and less rainfall and with less marked seasonal temperature changes (see table 1).

The vegetation of the study area is savanna (mesic savanna of Tinley, 1969) typical of the subarid regions of Mozambique, which we characterize as two types of savanna-woodland: tree savanna and open tree-savanna, following Tinley.

The tree savannas occur on the flats and gentle undulations near the Rio Save. These generally gray, yellow, or red sandy soils have as their dominant tree *Acacia nigrescens* and other *Acacia*, *Ostryoderris stuhlmannii*, and *Bolusanthus speciosus*. Among the other trees in this habitat are *Adansonia digitata*, *Albizia versicolor*, *A. anthelminthica*, *A. glaberrima*, *Combretum apiculatum*, *C. mossambicensis*, *C. imberbe*, *Cassia abbreviata*, *Diospyros usambarensis*, *Dalbergia melanoxylon*, *Kigelia pinnata*, *Spirostachys africana*, *Sterculia rogersii*, *Uvaria caffra*, *Sclerocarya caffra*, *Grewia bicolor*, *Grewia* sp., *Lonchocarpus capassa*, *Xeroderris* sp., and *Terminalia sericea*. The herbaceous stratum in this zone is dominated by species of *Chrysopogon*, *Digitaria milangiensis*, *Digitaria* spp., *Enneapogon scoparius*, *Andropogon gayanus*, *Schmidtia bulbosa*, *Eragrostis superba*, *Panicum* spp., *Sporobolus marginatus*, *Aristida* sp., *Tragus* spp., and *Urochloa mossambicensis* and by herbaceous legumes and cucurbits, especially in overgrazed areas. In many localities this plant formation is influenced by termite thickets, secondary thickets, and thickets around seasonal pools, as well as thickets around the base of large trees.

Among trees and shrubs found in termite thickets are *Acacia* spp., *Balamites maughamii*, *Cordia* sp., *Euphorbia* sp., *Leconiodiscus fraxinifolius*, and *Ximenia caffra*. The climber, *Salvadora persica* is often the dominant plant and, in places, forms a pure community on a termite hill. The thickets around seasonal pools formed by rain water include *Acacia* spp., *Diospyros mespiliformis*, *Ficus* spp., *Cladostemum kirkii*, *Newtonia hildebrandti*. The climbers *Acacia kraussiana* and *Tragia kirkiana* are common.

The thickets at the base of trees are formed mostly around *Adansonia* (fig. 2). *Strychnos* is a common component of these thickets with many

TABLE 1
Climatic Data for Zinave Area

	Temperature (in °C)		Percentage of Relative Humidity		Rainfall (in Mm.)		Mean Number of Days Rainfall	
	Mean (Max. Min. Mean) Massangena ^a	Mabote ^b	Massangena ^a	Mabote ^b	Massangena ^c	Mabote ^d	Massangena ^c	Mabote ^d
January	27.4 (33.3-22.5)	26.2 (31.7-19.0)	69	72	191.7	114.6	11	5
February	27.2 (33.5-21.9)	26.0 (31.3-19.1)	71	75	114.4	129.0	9	6
March	26.9 (32.9-21.3)	25.8 (31.2-18.7)	66	73	34.2	67.8	8	3
April	24.7 (31.9-18.4)	24.8 (30.4-17.2)	66	72	30.4	21.1	4	2
May	21.3 (29.7-13.4)	23.0 (29.0-14.3)	65	68	9.4	14.9	2	1
June	19.0 (28.2-11.0)	21.3 (26.9-12.6)	66	71	25.2	9.7	3	1
July	18.7 (27.7-10.1)	21.1 (26.8-12.2)	63	70	1.6	2.0	1	1
August	21.5 (29.3-13.6)	22.2 (28.0-13.5)	60	72	6.4	7.7	2	1
September	24.0 (31.6-16.6)	23.7 (29.6-15.4)	55	68	4.9	13.0	2	1
October	26.0 (32.5-18.9)	25.0 (31.1-16.5)	54	66	15.7	15.2	2	2
November	26.8 (33.6-21.8)	25.9 (31.6-17.7)	60	68	101.9	59.9	8	4
December	27.1 (33.0-21.0)	25.8 (31.4-18.5)	66	72	129.1	120.4	11	5
Mean Annual Average	24.2 (31.4-17.6)	24.2 (29.9-16.2)	64	71	661.9	576.3	63	32

^a Average of 5 years through 1969.

^b Average of 26 years through 1969.

^c Average of 4 years through 1969.

^d Average of 27 years through 1969.

shrubs up to 2.5 m. high. Secondary thickets are common in those portions of the tree savanna that have been overgrazed. Common trees here are *Acacia* spp. and *Dichrostachys africana*. In all the thickets, the lower stratum is composed mainly of *Panicum maximum*, *Sansevieria* sp., species of Acanthaceae and Liliacea.

The open tree-savanna as well as savanna woodland are interspersed in the tree savanna, forming a mosaic. They are composed largely of

the same botanical species, and the two habitats differ mainly in the distance between the canopy of the trees. Like the tree savanna, the open tree-savanna also has termite thickets interspersed within it (figs. 3-6).

Just outside the study area, to the west, are large woodlands of *Colophospermum mopane*. Within the study area, mainly in the slightly lower areas, pockets of *Colophospermum mopane* woodlands occur. In depressions that were



FIG. 2. Baobab (*Adansonia digitata*) with thicket developing at base in a tree savanna of *Acacia nigrescens*.

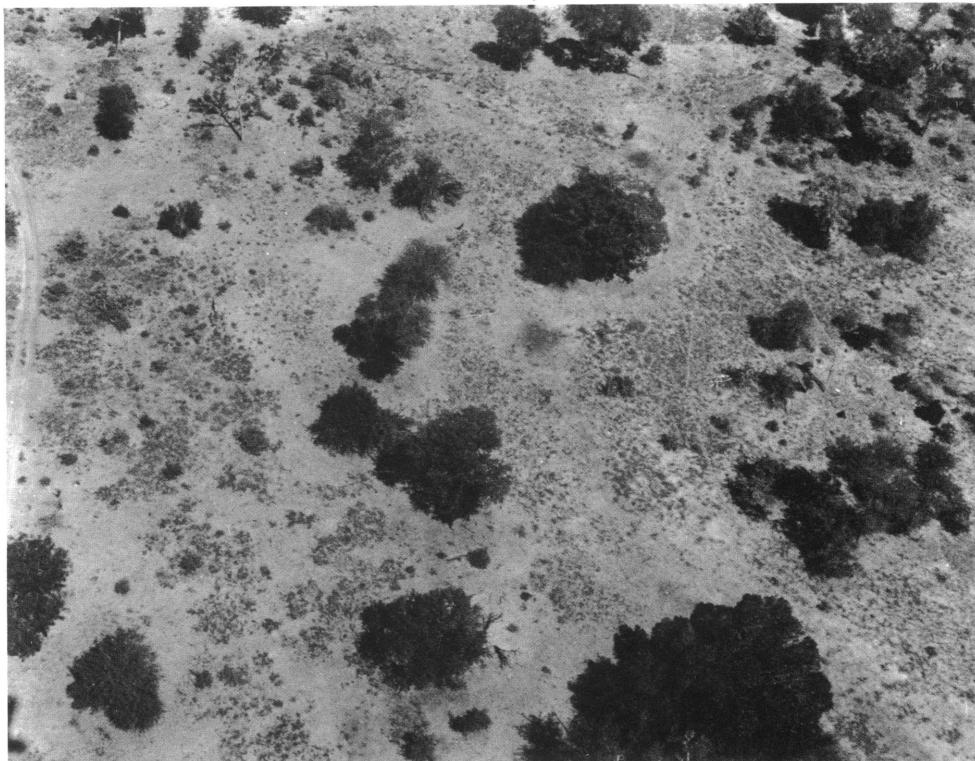


FIG. 3. Aerial view of open tree-savanna in a floodplain, with termite thickets.



FIG. 4. Tree savanna of *Acacia nigrescens* with thicket (at left) of *Salvadora persica* and *A. nigrescens*. Horizontal line on thicket is level of browse line in October, 1973. Legumes are invading floodplain in foreground. Animals are waterbuck. Photographed April 20, 1974.



FIG. 5. Savanna woodland with *Cassia*, *Combretum*, *Terminalia*, *Sclerocarya*, and a thicket mosaic.

heavily flooded during the rainy seasons in the past, but which have been drier the past few years, generally on black clay or sandy clays, *Colophospermum* has been invading.

Along the Save River, there are woodlands with *Acacia albida*, *Acacia xanthophloea*, *A. spp.*, *Albizia sp.*, *Combretum spp.*, *Ficus spp.*, *Hyphaene crinita*, and other trees, and the herbaceous stratum is scant. Termite thickets and small riverine thickets also occur in this habitat.

In grasslands that are usually in floodplains with dark clay or sandy clay soils, the herbaceous stratum is composed mainly of *Andropogon sp.*, *Hyparrhenia sp.*, *Chloris gayana*, *Ischaemum brachyatherum*, *Eriochloa borumensis*, *Panicum maximum*, *Setaria sp.*, *Sporobolus robustus*, and others. As a consequence of hydromorphologic

changes and heavy overgrazing, large portions of the grasslands have been invaded by several species of herbaceous legumes, cucurbits, and other herbs. These grasslands also are influenced by termite thickets, and in some places are invaded by *Acacia nilotica*, *Colophospermum mopane*, and *Dichrostachys africana*.

There are a few dry thickets within the study area comprised mainly of *Guibourtia conjugata*, with *Acacia sp.*, *Adansonia digitata*, *Strychnos innocua*, and *Spirostachys africana*. Outside the study area, where the nyala may occur, there are also thickets composed primarily of *Brachystegia glaucescens* and *Julbernardia globiflora*, riverine thickets mainly of *Cola sp.*, *Ficus sp.*, and *Mimosa obovata*, and other thickets of *Strychnos sp.*, *Dichrostachys*, and *Acacia sp.* There are also



FIG. 6. *Acacia nigrescens* savanna woodland.

dry forests composed mainly of *Guibourtia conjugata*, *Balamites maughamii*, *Dahlbergia nitidula*, *Drypetes gerrardi*, and *Gyrocarpus americanus*, woodlands of *Colophospermum mopane*, woodlands of *Acacia xanthophloea*, *Acacia* sp., *Ostrya oderris stuhlmannii*, and *Hyphaene orinita*, tree savanna with *Acacia* sp., *Albizia versicolor*, *Hyphaene orinita*, and *Lonchocarpus capassa*. On the sandy banks of the Save River there are large expanses of *Phragmites mauritianus*.

There is shifting cultivation in the region and on abandoned farms there are shrub thickets or shrub savannas, normally with invasions of some woody plants. At these places also are large patches of invading legumes, cucurbits, and other herbs (fig. 7).

Habitat. Although nyala were seen in a variety of habitats, the presence of thickets nearby is of considerable importance to their distribution.

In 1971 (September 28-October 14) we recorded the habitat occupied by 318 nyala (99 observations) and found that 40 percent of the animals (and observations) were in tree savanna with thickets, 23 percent (17% of the observations) were in open tree-savanna with thickets, and 11 percent (14% of the observations) were at the edge of thickets. By way of comparison, 8 percent of the animals (5% of observations) were in grassland, and fewer than 10 percent were in tree savanna, open tree-savanna, or woodlands without thickets.

In 1972 (August 31-September 16) we recorded 421 observations of 1642 animals according to the habitat where they were first observed and found the association with tree savanna even more evident. About 80 percent of both the number of observations and the nyala were in this habitat, and no more than 6 percent were

seen in any of the other habitats. In 1971 more than 70 percent of the animals were seen in association with thickets, and in 1972, 91 percent were seen in habitats that contained thickets. Chi-square tests indicate that this distribution was not random ($p \leq 0.01$). Similarly, Chi-square tests comparing the numbers of nyala seen in open tree-savanna with thickets and those in open tree-savanna without thickets are also highly significant ($p \leq 0.01$). The statistical tests confirm that the occurrence of nyala in habitats with thicket is not random and that the animals show a predilection toward tree savanna with thickets.

Although nyala were commonly seen in the open, they were never more than several hundred meters from a thicket and often were much closer. When frightened or chased, nyala run to a thicket, and if the cover is heavy, as during the

rainy season, they usually stop running and stand a meter or two inside it. When standing in a thicket, nyala can be approached much more closely than when they are in the open, and in our drugging activities we consistently shot them with darts at distances of 25 to 35 m. as they stood, screened by the branches and leaves of the thicket vegetation, watching us. In addition to providing a refuge from pursuers, thickets contain many of the browse species utilized by nyala, shade from the sun, refuge at night, and hiding places for the newborn. The dark color and light markings of adult males especially renders them almost invisible, even a meter within a thicket, because of the pattern of light and shadow there.

At the end of the rainy season, as in early April, 1974, nyala were much less observable than in the dry season, and often were found



FIG. 7. Secondary invaders on abandoned cultivated field (foreground) with secondary thicket including *Guibourtia conjugata* forming tree canopy in background.

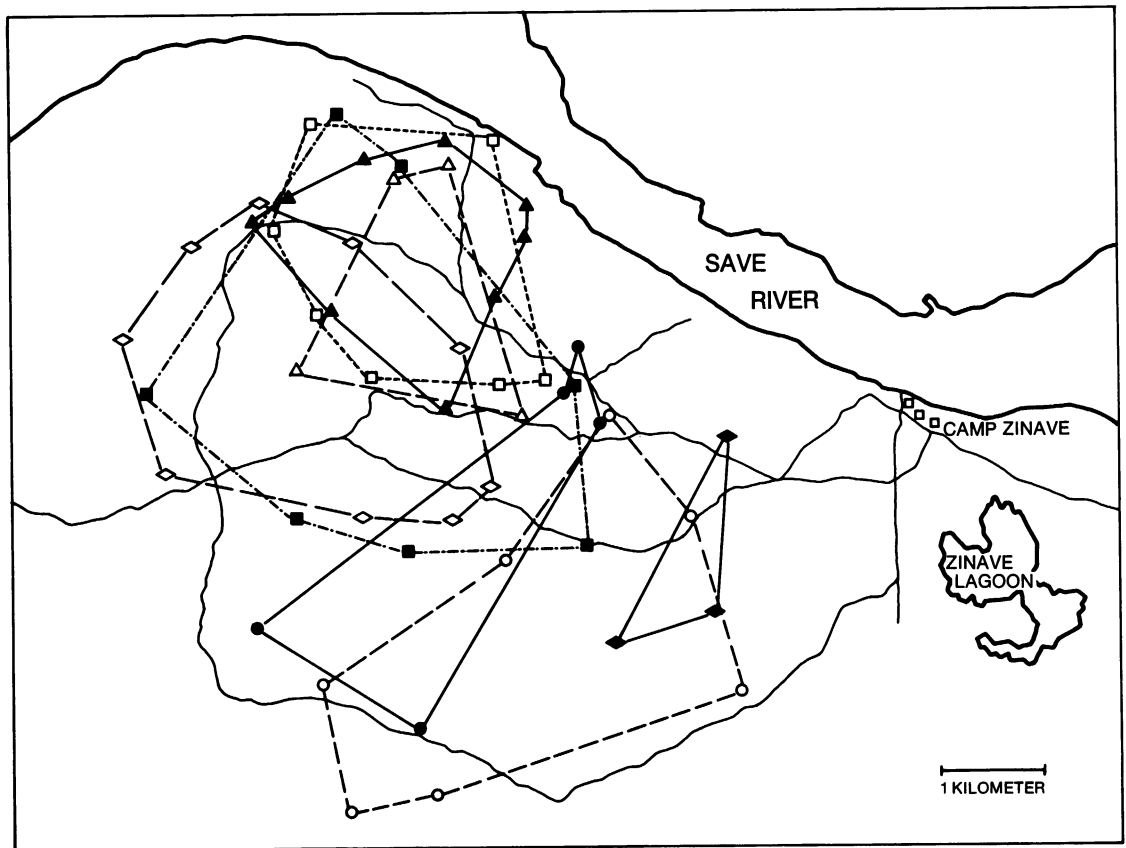


FIG. 8. Home ranges of eight adult nyala. Open triangles, Macaxulo; solid triangles, Keyser; open circles, Russell; solid circles, Old Man; open squares, Kubassa; solid squares, Ndliati; open diamonds, Djiweni; solid diamonds, Ham. See table 2.

lying down in the shade in a thicket when the temperatures were above 30°C . and were more active at night. In the dry season when it was cool, below 20°C ., and on overcast and windy days, the nyala seemed to remain in the thickets for longer periods, especially early in the morning.

When nyala were seen in the open, especially in the dry season, they were often feeding from the ground, picking up fallen leaves, or on their way to or from water or thickets. During the hotter, wetter season, they fed in the open especially on herbs, cucurbits, and legumes.

In Gorongosa National Park, nyala are found in habitats similar to those of the Zinave region, and also at the edge of dry forest (*Newtonia*, *Guibourtia*, *Acacia*, *Balamites*, *Adansonia*) but

do not go to grasslands where there are no thickets. In the Maputo Game Reserve and outside it, where nyala have been and still are heavily persecuted, they spend their time mostly within large thickets and at the edge of dry forest (Tello, 1972, 1973).

Nyala habitat has improved in many places in southern Mozambique as a consequence of ecological disturbance such as over-grazing by cattle or wildlife, shifting agriculture, or changes in soil-water relations resulting from slight changes in slope which encourages the growth of plant invaders and formation of mosaics of thickets that provide food and cover.

Home Range. Data on the home ranges of identifiable individuals were collected for 14 nyala from April to November in 1972 and 1973

(dry season), and from November, 1973, to May, 1974 (rainy season). In general, the home range of nyala does not seem especially large; it covers 4 to 5 sq. km. For nine adult males, the home range varied from one that was found over 9.5 sq. km. (34 observations), to another that was seen over only 1.3 sq. km. (four observations; fig. 8). The average for all the adult males indicated a home range of 3.9 sq. km.; for the five adult males that we had sighted more than 10 times, the average home range was 5.5 sq. km. The maximum distance between places where we saw known males varied from 2 km. to 4.5 km., averaging 2.9 km. For the five males sighted more than 10 times, the average distance was 3.2 km. (table 2).

Two subadult males had home ranges of 1.8

and 3.1 sq. km., with maximum distances of 2.7 and 3.5 km. One of these subadults was subsequently observed as an adult, and it is of interest to note that his adult home range was completely outside that plotted for him a year earlier when he was a subadult, and the maximum extent of the home range, although not the area, was somewhat greater as a subadult. The home range of an immature male, the albinistic Ndliati, was 2.5 sq. km. and lay entirely within the home range that we later determined for him as an adult (fig. 9). The home range of the other immature male was much smaller, but was determined by only eight observations over a one-week period (table 2).

Of the three females for which we have home range data, only that for Karina, observed 22

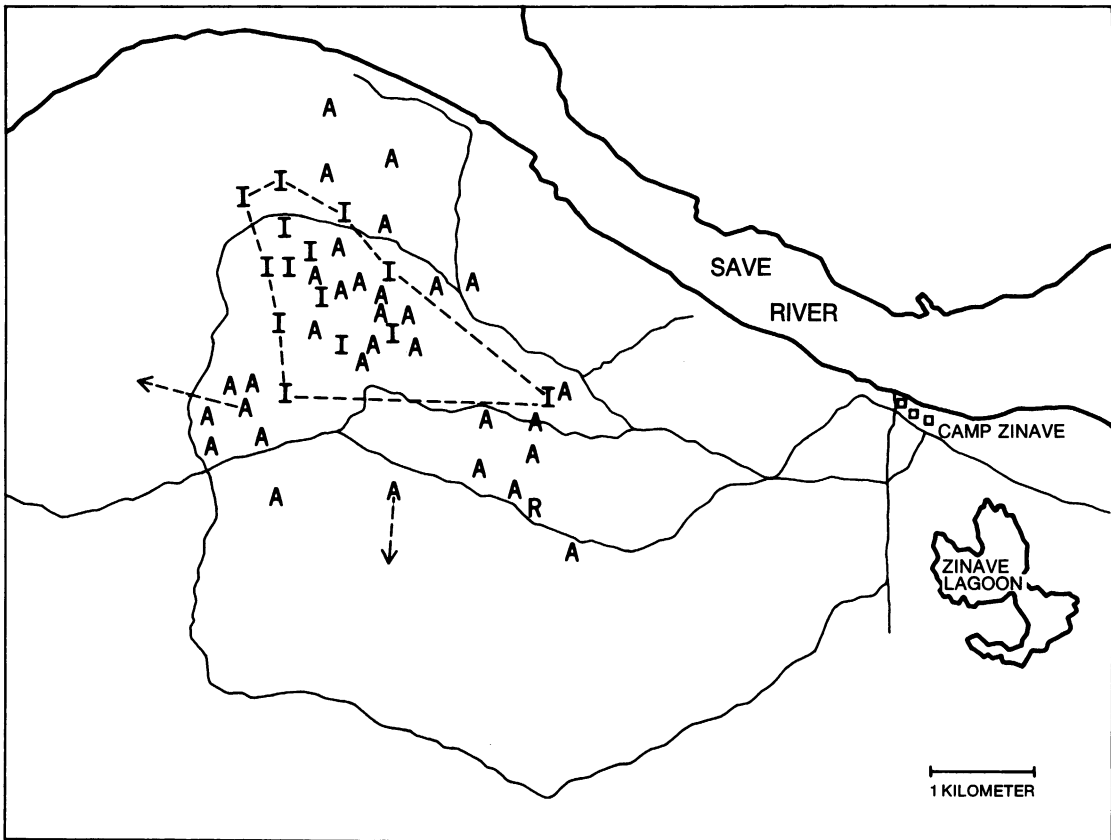


FIG. 9. Home range of albinistic male nyala, Ndliati. I indicates places where he was seen as an immature in 1972; A indicates places where he was seen as an adult in 1973; R indicates sole rainy season observation. Dotted lines ending in arrows show where animal was last seen running off.

TABLE 2
Home Range of Nyala

Sex	Age	Name	First Date	Last Date	No. of Observations	Maximum Distance between Observations (km.)	Area of Home Range (sq. km.)
M	Ad	Ham	9 VI 72	16 X 73	4	2.2	1.3
M	Ad	Macaxulo	21 IX 73	14 XII 73	6	2.4	2.6
M	Ad	Old Man	18 X 72	26 VII 73	5	3.8	4.3
M	Ad	Russell	12 VII 72	29 XI 73	13	4.3	7.3
M	Ad	Keyser	11 VII 73	3 XI 73	30	2.1	3.6
M	Ad	Djiweni	9 IV 73	29 X 73	13	2.4	3.4
M	Ad	Kubassa	10 VIII 73	8 IV 74	31	2.5	3.9
M	Ad	J	4 IV 73	17 IV 74	7	2.0	1.5
M	Ad	Ndliati	8 IV 73	17 XI 73	34	4.5	9.5
M	Imm	Ndliati	22 IV 72	5 XI 72	14	3.1	2.5
M	Imm	Gordon	7 IV 74	14 IV 74	8	1.8	0.9
M	Sad	Djiweni	9 IX 72	13 X 72	8	2.7	1.8
M	Sad	Mike	29 VII 73	1 VIII 73	14	3.5	3.1
F	Ad	Leslie	15 VII 73	1 VIII 73	4	1.0	0.4
F	Ad	Karina	14 VII 73	7 XI 73	22	3.5	3.6
F	Ad	3	7 IV 74	15 IV 74	4	1.3	0.5

Abbreviations: Ad, adult; Imm, immature; Sad, subadult.

times, is meaningful. She was seen over 3.6 sq. km. and the maximum length of her home range was 3.5 km., not greatly different from the average for all adult males, and supporting our general feeling that the home range of females is approximately the same size as that of males (table 2).

The home ranges of individual nyala overlap those of a great many other nyala. Six of the adult males that we observed in 1973 had home ranges that to some degree overlapped one another. There was one place where all six home ranges overlapped (fig. 8). Some of these identifiable males were seen traveling together, and also with other unidentified males, indicating that relatively large numbers of adult males share home ranges. The other two identifiable males observed in 1973 had home ranges that overlapped, but were exclusive of those of the other six. The home range of one subadult, Mike, overlapped in places the ranges of at least four other males but was, for the most part, exclusive of the home ranges of our identifiable males. The home ranges of the immature males overlapped

those of others in the same age and sex class as well as all other classes. The home ranges of females, likewise, overlap those of males.

The first two years our observations were made entirely in the dry season, and we had suspected that the concentration of nyala in the study area, where food seemed limited, was in response to the availability of drinking water in the Save River at that time. We had thought that, during the rainy season, the nyala would move away from the river and thus have a different home range. However, from our observations during the rainy season 1973-1974, we found our known individuals to be occupying the same home ranges that we had previously determined for them. Although some of our marked animals were not found, and we cannot demonstrate that they moved out of their dry season home range, all of those identifiable individuals, both male and female, that we did observe were in their dry season range. To some extent our failure to find some individuals was because the rainy-season vegetation effectively screened them from view. For example, although we did not locate the

albinistic male, Ndliati, during three weeks of daily observing in April, 1974, he was subsequently seen within the bounds of the home range that we had determined for him.

We have no information that would indicate that nyala are in any way territorial in the sense of their defending space against conspecifics either directly or by vocal, olfactory, or other form of marking.

Description. Lydekker and Blaine (1914) described the male nyala:

"Size medium, shoulder-height about 42 inches; nuchal and dorsal crest much longer than in preceding species [*Tragelaphus scriptus*], a profuse fringe of hair on throat and under-parts, and tail more bushy and longer; horns forming rather more than one complete turn; no white throat-band. General colour slaty grey, with a tinge of yellowish rufous; forehead rufous and orbital region fawn; upper lip and chin, two spots on cheek below each eye, an imperfect suborbital chevron, base of backs of ears, a chest-band, about fourteen more or less distinct transverse stripes on body, and a few spots low down on haunches, as well as a considerable proportion of the hairs in the dorsal crest, and the whole under surface of the tail, white; legs from just above the knees, and the backs of the front-shanks as well as the inner sides of the thighs and hocks, white; back of pasterns black; a pair of white spots on front of pasterns above hoofs."

Lydekker and Blaine (1914) characterized the females, which are hornless, as follows: "Female bright chestnut, with a dark face-blaze, a whitish chevron, and about eleven transverse stripes and a few haunch-spots white; dorsal stripe black, intersected with white where crossed by transverse stripes; no long mane or fringes."

To this we would amend or correct the height at shoulder, which in 17 adult males from the Zinave region averages 44 inches (112 cm.) and reaches a maximum of almost 48 inches (121 cm.). These correspond closely to measurements of adult males from Hluhluwe presented by Vincent et al. (1968). The coloration of mature males may be slaty gray, as Lydekker and Blaine stated, but also varies to dark brown, and in the field, depending upon how the light strikes them, the animals may appear almost black or even tan. The number of spots below the eye may be two

or three. The number of vertical stripes is generally less than 14 in the Zinave area, and in animals that we presume to be older, may be reduced to three or four. The most persistent stripe is in front of the hip, and there are always several white spots in the area of the knee. Anterior to the vertical white stripes the gray-brown hairs are slightly darker than the remaining body color, forming a shadow stripe of about the same width as the white stripe. These persist even after the white stripes are lost.

The chevron on the face of the female is variable, and we have sometimes thought that, with age, this mark diminishes in visibility. Roberts (1951, p. 311) implied that it is absent in females and young males, but we have found the chevron to be present in newborn of either sex, and in a number of fully adult females. The usual range in white vertical stripes on the female is from eight to 14, although we have counted as many as 18. In very young animals there is a large distinct white patch on the inner surface of each ear, and these are lost with age, and are not present in animals that we categorize as immature.

Both males and females have a small white dot on each side of the base of the tail.

There is considerable variation in color in the Zinave population. In 1971 several times we observed a female with very pale yellowish coloration. This female, incidentally, had a single horn on the right side about 170 mm. long. She was usually seen with two younger females of unequal size, both of which were also quite pale, one almost as pale as the horned female. We also observed an abnormally colored male, Ndliati, in 1972, 1973, and 1974. This animal was evidently erythristic, and was essentially palomino in color. Its right horn was normal, about 380 mm. long when first seen in August, 1972, but the left horn was deformed and was growing out parallel to the muzzle. At that time the palomino male was in our age category of immature male. In July, 1973, the deformed horn had turned ventral and then posterior and was growing into the skull just below the left eye. We drugged the animal and cut off part of the horn, which had entered the head about 20 mm. This nyala survived the surgery and was seen as late as April, 1974. Other authors have commented on color

TABLE 3
Measurements (in Millimeters) and Weights (in Kilograms) of Adult Nyala from the Rio Save Region

Measurement	Number	Adult ♂			Adult ♀		
		Mean	Standard Error	Deviation	Mean	Standard Error	Deviation
Total length	20	2103.0	25.4	113.5	2450	18.3	60.7
Tail length	22	427.5	5.5	25.7	470	6.9	21.8
Hind foot	21	474.3	6.4	29.2	557	4.0	13.4
Ear (notch)	21	193.5	1.9	8.8	205	2.2	7.2
Weight	13	107.5	3.2	11.6	126.5	1.8	5.2
Shoulder height	17	1121.5	14.3	58.8	1210	27.0	76.4
Chest girth	19	1094.7	14.3	62.5	1260	20.5	67.9
Horn length	22	645.9	10.3	48.4	755	—	—
Horn circumference	19	183.2	2.0	8.9	200	—	—
Horn, tip to tip	17	296.8	23.2	95.8	510	—	—

TABLE 4
Measurements (in Millimeters) and Weights (in Kilograms) of Subadult, Immature, and Juvenile Nyala from the Rio Save Region

Measurement	♂ Sad	♂ Imm	♂ Imm	♂ Imm	♂ Imm	♂ Imm	♀ Imm	♂ Juv	♀ Juv
Total length	2040	—	2015	—	1875	—	1803	1601	1311
Tail length	352	402	455	—	450	—	385	—	290
Hind foot	455	—	471	484	467	—	453	404	353
Ear	187	198	200	—	185	180	175	160	150
Weight	70.0	—	80.0	—	66.3	53.2	—	—	23.2
Shoulder height	1076	—	1015	—	1038	—	950	809	—
Chest diameter	894	—	1005	—	920	—	860	805	—
Horn length	516	520	315	352	215	272	165	106	—
Horn circumference	170	162	150	—	125	—	110	—	—
Horns, tip to tip	170	222	295	—	260	—	195	—	—

^aHorns palpable under skin.

Abbreviations: Imm, immature; Juv, juvenile; Sad, subadult.

aberrations in nyala (Dixon, 1964; Dorst, 1969). Dorst, incidentally, commented that females lack the white chevron between the eyes, which is not true of most in the Zinave region. On the north side of the Save River a female with horns about 600 mm. long and colored like an immature male with horns 250 mm. long was seen. The female's horns, although symmetrical and as properly shaped as those of an adult male, were noticeably thinner.

The measurements of some nyala from the Save River area appear in tables 3 and 4. Females average about 85 percent of the dimensions of males, and weigh about 40 percent less (figs. 10-12).

Dorst (1969) gave the weight of nyala from 220 to 280 lbs. (100 to 127 kg.). The mean weight of 13 adult males from the Zinave area is 107.5 kg., with a maximum of 126.5 kg.

Labuschagne and van der Merwe (1966) gave 310 lbs. (141 kg.) as a maximum, and J. Anderson informed us (*in litt.*) that an adult male at Ndumu Game Reserve in Zululand was weighed at 158.4 kg. (348 lbs.). The weight of nyala may vary seasonally and in response to population size (Keep, 1973a).

Ansell (1971), following Haltenorth (1963), stated that *T. angasi* has inguinal glands. We have found no evidence of inguinal glands in any of the numerous male nyala we have examined in the flesh or as skins, and suspect that Haltenorth may have mistaken the vestigial teats of males for these.

Nyala males do have a distinct tuft of black hairs between the false hooves of the hind feet. These tufts are often construed to be evidence of glandular tissue, but we have been unable to detect any secretion or distinctive odor from



FIG. 10. Two adult male nyala, with immature female in front of male at right. Subadult male is at left, and adult and subadult females are behind him.



FIG. 11. Adult female nyala.

these on fresh material and await histological examination to determine whether or not secretive tissue is present.

Age and growth. In the field, we recorded nyala in four size classes: juvenile, immature, subadult, and adult. These categories are roughly correlated with age and were based mainly on size, and in males on coloration and horn length. In general, our categories are more accurate for males than for females. Data on size classes and

growth rate have been presented by Vincent et al. (1968) and Rowe-Rowe and Mentis (1973). The former based their groupings on tooth eruption and tooth wear; the latter had animals of known age under observation. Figure 13 represents an attempt to correlate our categories with those of these other investigators on the basis of shoulder height and horn length.

Juveniles of either sex were from about 800 to 1200 mm. in total length and about 500 mm.

in shoulder height. At birth both sexes are colored alike, and resemble adult females, although the orange coloration may be even more intense in some. Newborn nyala have a

large patch of white hair on the inner surface of each ear, and we believe that this is no longer markedly evident by the time the juveniles reach three months of age. We included males with



FIG. 12. Adult male nyala, Ham, with collar holding radio transmitter.

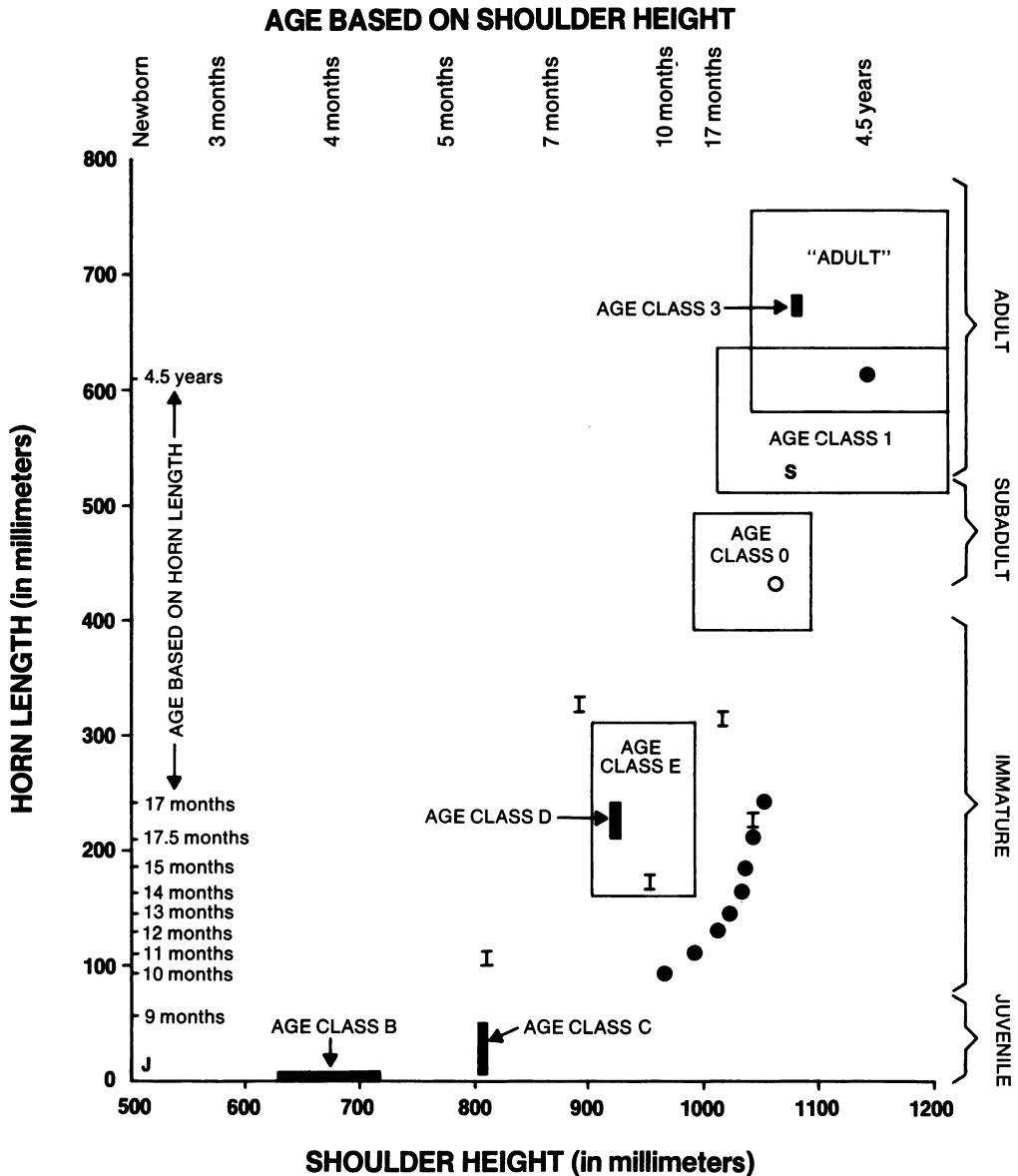


FIG. 13. Age-class correlations of male nyala from various authors (see text). *Left (vertical)*: horn length and ages according to length of horn of known-age individuals. *Bottom (horizontal)*: shoulder height and ages. *Top (horizontal)*: known-age individuals. *Right (vertical)*: age categories used in this paper, based mainly on horn length. Rectangles, parameters of age classes based on tooth eruption and shoulder height. Closed circles, horn lengths, and shoulder heights of known-age individuals. J, I, S, represent individual juveniles, immatures, and subadult males in this study.

horns up to 75 mm. in length in this category, which would probably encompass nyala up to about six months of age. Rowe-Rowe and Mentis

(1973) mentioned that males begin to lose their red color as early as four months of age, three months before horns are visible. In the field,

there is enough variation in the coloration of females so that we were unable to distinguish juvenile males by coloration alone before they had horns 100 mm. long. Juvenile females were identified on size alone, generally in comparison with adults nearby, and this category includes animals up to about 60 percent of the shoulder height of adult females, which size is reached at about three months of age.

Nyala that we called immature included males with horns from 75 to about 400 mm. in length (horns about twice as long as the ears) (figs. 10, 14). In these animals the horns have not yet begun to curve back toward the midline and are essentially straight. The animals observed by Rowe-Rowe and Mentis (1973) appeared distinctly browner than females at an age of five

months, before any horns were evident. In the field, however, we found that coloration is generally not useful for distinguishing males until their horns are more than 100 mm. long. Males are clearly recognizable by coloration alone at a long distance when the horns are 200 mm. in length. The progression of molt to adult coloration in males commences on the head and neck, and in an immature male with 200 mm. horns, the neck and muzzle were quite grayish. The fringe of hair on the rump, the posterior thighs, and the anterior part of the shoulder had attained adult coloration, but the body showed more of the coloration of a female. The dorsal crest of hairs was about 35 mm. long over the loins and shortest at the base of the neck. The vertical body stripes were changing from the



FIG. 14. Immature male nyala. Adult female torso is behind him.

juvenile white to that of the adult male, as described below, with the molt progressing from the shoulders posteriorly and from the midline of the back ventrally. The tail was black at the tip and it was dark along the midline and base, unlike that of females. An immature male with horns 300 mm. long showed the same darkening at the front and rear ends, but had a distinct gray-brown wash over the juvenile orange of the body. The progression of change to adult male white stripes was completed except for the flank stripe, which was complete except ventrally. The white body stripes of the juvenile males are completely replaced during molt. The body hairs of the stripes of females and juveniles of both sexes are white throughout, whereas the stripes of adult males are formed by horizontally growing, posteriad-directed hairs that have a white distal half and a darker, grayish base. This dark base forms a dark shadow stripe anterior to each white stripe. In older, adult males, which seem to have fewer white stripes, the shadow stripes of the dark hair base may be evident. This may represent wearing off of the white part of these hairs, but also there seem to be some darker tipped hairs anterior to the white stripes or in place of the former white stripes. On denuded study skins the white stripe locations are evident on the hairless skins as a paler color.

The dorsal crest of the immature male with 300 mm. horns was better developed than in the one with 200 mm. horns, and the juvenile female black of the midline was completely replaced by adult white and brown long hairs. The neck was adult brownish gray, and the hairs on it both dorsally and ventrally, were longer than those of the immature male with 200 mm. horns. The dorsal crest, however, is not fully grown to the adult length of 120 mm. until the male has horns more than 425 mm. in length. Similarly, the ventral fringe on the neck and belly seems to be the last to develop completely and can reach 150 mm. long in adults.

Immature females ranged from about 60 to 80 percent the shoulder height of adults, but were indistinguishable from them in color. We have no data concerning molt in females. Rowe-Rowe and Mentis (1973) mentioned that after three months of age the facial chevron of the female they observed became less distinct. We have

found the chevron on the face of females to be variable in its presence and distinctness, although we have sometimes thought that it is less evident in the older adult females.

Subadult males had full adult coloration and horns that ranged from about 430 mm. to about 500 mm. In these animals the horns have begun to curve back toward the midline, but have not yet begun another outward curve. Although colored like adults, many appeared somewhat paler, which might represent the lack of wear and soiling of the pelage. All were adult height at the shoulder, although generally they were lighter in weight. The categorization of females as subadults was generally made in relation to larger (adult) females visible, and these would be animals that were approximately 90 percent of adult height. As noted elsewhere, this size category, which would have animals six to seven months of age according to Rowe-Rowe and Mentis (1973), is one that we were least sure of determining accurately.

Adult males were those that had horns that had begun a second, outward curve and which had full adult pelage. The horns were generally more than 500 mm. long and the longest that we have measured were 755 mm. The world record length is 835 mm. (Best et al., 1962). In addition to the characters of length of horns and general body size and weight, we feel that there may be a progressive loss of white vertical stripes with age in adult males (fig. 15). Certainly the subadults and younger adults seemed to have more and perhaps brighter white vertical stripes than those we judged as old on the basis of their long horns. Adult females were determined on the basis of their size.

According to the chronology of Rowe-Rowe and Mentis (1973) females eight to nine months of age are of adult height and would be categorized as adults by us.

It is evident from figure 13 and from the data of Vincent et al. (1968) and Rowe-Rowe and Mentis (1973) that there may be considerable variation in the rate of growth and in the various size categories in relation to actual chronological age. In the group that we call immature, which would encompass males from six months to perhaps 20 or 24 months of age, the horns of animals grow from 75 mm. to more than 500 mm.



FIG. 15. Adult male nyala with vertical white stripes not evident. Dark shadow stripes are faintly evident.

or at a rate of about 23 to 30 mm. per month. This is confirmed by our field observation of an aberrantly colored male, Ndliati, with one normal and one abnormal horn. In September, 1972, Ndliati was classified as an immature and his normal horn was estimated at 380 mm. In July, 1973, Ndliati was drugged, and the horn was measured at 610 mm. The growth of about 230 mm. in 10 months tends to confirm the rapid growth of horns in nyala during the immature period. From the data of Rowe-Rowe and Mentis (1973), it would seem that the rate of horn growth slows considerably after the horns are

600 mm. From identifiable animals that we have watched over a two-year period, we would estimate that the rate of growth from 600 to 650 mm. takes about one year, and probably is even slower after that. There is, however, so much variation in horn shape and size that estimates of age based on length or shape of horn after the males are fully adult are likely to be erroneous.

Although our four size-categories are fairly well correlated with chronological age, they are not related closely to sexual maturity. Vincent et al. (1968) showed that males that we call immature have viable sperm in the testis and epididy-

mus. Males with horns as short as 161 mm. or with body weights as little as 54 kg. were sexually mature. Despite their potential for breeding, we do not believe that the male nyala that we classify as immature are reproducing. We think that they do not reach social maturity until our class of subadult at the earliest, and perhaps do not reproduce until they are fully adult.

Female nyala reach sexual maturity at about one year of age, and Vincent et al. (1968) noted that a female born on June 5, 1962, gave birth on February 13, 1964, when she was 20 months old. Rowe-Rowe and Mentis (1973) stated that a female gave birth when she was approximately two years old.

In captivity nyala have lived for 15 years 10 months and nine days (Crandall, 1965). In the course of our study, we have observed adult males from 1972 into 1974, but have no data on their actual chronological age.

Sex Ratios. Vincent et al. (1968) found 12 males and 16 females (and seven indeterminable) to be the sex ratio of fetuses. This ratio of 1:1.3 is not significant statistically for a sample of this size. Even if all seven of the unsexed fetuses were females, the ratio would not be statistically significant at the 0.05 level. Davall (1965) reported 42 males, 37 females, and four not sexed in 83 births at the Bronx Zoo from 1939 to 1964.

Davison (1971) found an overall sex ratio of 154 nyala killed in tsetse fly control operations to be 73 males to 81 females and not statistically significant from a presumed 1:1 sex ratio. (Our calculation of chi-square from Davison's data produces a different value from his, but still not significant.) Vincent et al. (1968) presented data on 90 individuals taken in a control program in Hluhluwe Park, of which 27 (30 percent) were males. This is a significant deviation from a 1:1 sex ratio, but we suspect that, because of the nature of the control operation, the killing was selective, rather than random, and perhaps that is why these authors do not discuss the sex ratio.

We have no meaningful data on fetal sex ratios, but sex was determined for nyala seen in 1971 and 1972 (2276 sightings). About 100 other observations of nyala, almost entirely of juveniles, were made but these individuals could not reliably be sexed. It is also likely that some

other juveniles recorded as females were actually males.

The 2276 observations were made, of course, on a population that probably did not number more than 350, and thus represents not only repeated counts of the same animal, but is mainly representative of the visibility of individuals. Assuming, however, that visibility was equal and that the repeated counts were in the same proportion as sexes actually in the population, our 2276 observations reveal 39 percent males, a highly significant ($p = < 0.01$) deviation from 1:1. In 1971 (797 observations) 255 males (32%) were seen and in 1972 (1479 observations) 626 (42%) of the animals seen were males. Both of these sets of observations indicate a highly significant difference in the ratios of sexes seen. Barnes (1972b) found the observed sex ratio of nyala in False Bay Park, Zululand, to vary from 1:2 in 1969 to 1:1.5 in 1970 and 1:1 in 1972. He could not account for this change other than to attribute the possibility of selective culling as having had an effect.

In general, adult males are more conspicuous than females in the open and during the day, but it may be that they are not so active as females in these places at these times and that we were actually counting a disproportionate number of females. There was a slight increase, from 28 to 31 percent, in the number of adult males seen between 1971 and 1972. This might be an artifact of sampling, or might also reflect the fact that hunting in the area had ceased and permitted a greater number of adult males to survive as well as increased their temerity because of less hunter harassment.

Our observed ratios of animals younger than adult indicated in 1971 that 43 percent were males ($p = < 0.03$), and in 1972 that 63 percent were males ($p = < 0.01$). Our more detailed breakdown for ages for 1972 indicates that 61 percent of the subadults were males, 67 percent of the immature nyala were males, and 5 percent of the juveniles were males. Although these data are statistically significant, we recognize not only that our samples for some of these groups are small, but that there may have been unconscious bias in our observations. In general, the higher number of nonadult males in both years is diffi-

cult to explain, assuming that the ratios may be true ones. The more rapid maturation of females is undoubtedly another factor in the preponderance of young males observed as well as the higher proportion of adult females seen.

Population Size and Density. All our observations of population size and structure were made in the study area of about 32 sq. km. In 1971 we recorded individual nyala 797 times over a three-week period. We have no way of knowing how frequently the same individual was counted. However, on one morning we drove the periphery of the study area and counted 101 animals, and we do not believe that the same individual would have been counted twice. Assuming, then, that there were a minimum of 101 nyala in the study area, there was one nyala per 0.32 sq. km. It would be quite logical to assume that there were more. Although visibility within the study area is varied, we assume that, on average, we were seeing about 0.5 km. into the study area; we would then have sampled a belt of area of 9 sq. km., giving a population density of one nyala per 0.09 sq. km. in the area sampled and, assuming uniform distribution within the study area, a total population of 350 animals. On the basis of subsequent counts, we believe that this extrapolated figure was too high for 1971, and that the actual number of nyala in the study area in 1971 was between 175 and 250 animals (one nyala per 0.18 to 0.13 sq. km.).

Another check on the validity of the 1971 population estimates may be gained from repeated observations of identifiable animals. These included several marked females, an albinistic individual, and several males with distinctive horn shapes. Of two marked females, one was never seen again, and the second was seen once again, in the same place where it had been marked, at approximately the same hour of the night, two days later. A very young male, perhaps less than two weeks old (weight 4.15 kg.) was not seen again after marking. The albinistic animal was seen a total of two times. One male with a recognizable horn configuration was seen four times. The maximum assumption, four observations, would suggest that the 797 sightings were made of a total population of 200 individuals. The animals that were seen only

twice would suggest a total population of 400.

In 1972 we saw nyala 1565 times in the study area. We did not make a circuit census as we had in 1971, but our impression is that there were considerably more nyala present than in 1971. We deliberately looked for one albinistic immature male several times and found him eight times. If the observations of this animal had been random as some of the sightings were, a total nyala population of 195 (one nyala per 0.16 sq. km.) for 1972 would be indicated. Two of the radio-tagged animals were found four and five times respectively, but these observations were not random. One radio-tagged nyala, however, was not relocated by radio because we were searching for him on the wrong frequency. Despite a twice-daily search in the area where he had been tagged, he was not seen from September 6 until September 13, when he was seen (not radio-tracked) again. This suggests a maximum population of 780 nyala (one nyala per 0.04 sq. km.) which we believe is too high an estimate. We suspect that the true number of nyala in the study area in 1972 was between 200 and 350 animals, or about one-third more numerous than in 1971.

On May 29, 1973 driving two cars in parallel lines 250 m. apart, but in different sections, we counted nyala in the study area and periphery; we saw a total of 381, of which 326 were actually within the study area (fig. 16).

Barnes (1972b) estimated the nyala population in the 22.25 sq. km. of False Bay Park, Zululand, not to have exceeded 1000 during the period of study. His counts (subject to the same errors as ours) suggest one nyala per 0.05 sq. km. in 1969, one per 0.06 in 1970, and one per 0.04 in 1971.

Population Structure. Our data concerning the structure of the nyala population is subject to the same bias as our data on sex ratios, i.e., that it is based on multiple sightings of the same individuals. Again, we present our data on the assumption that the proportions of ages and sexes that we observed were representative of the actual proportions present in the area, except as noted.

In 1971 68 percent of the nyala seen were adults and 32 percent nonadults, including the

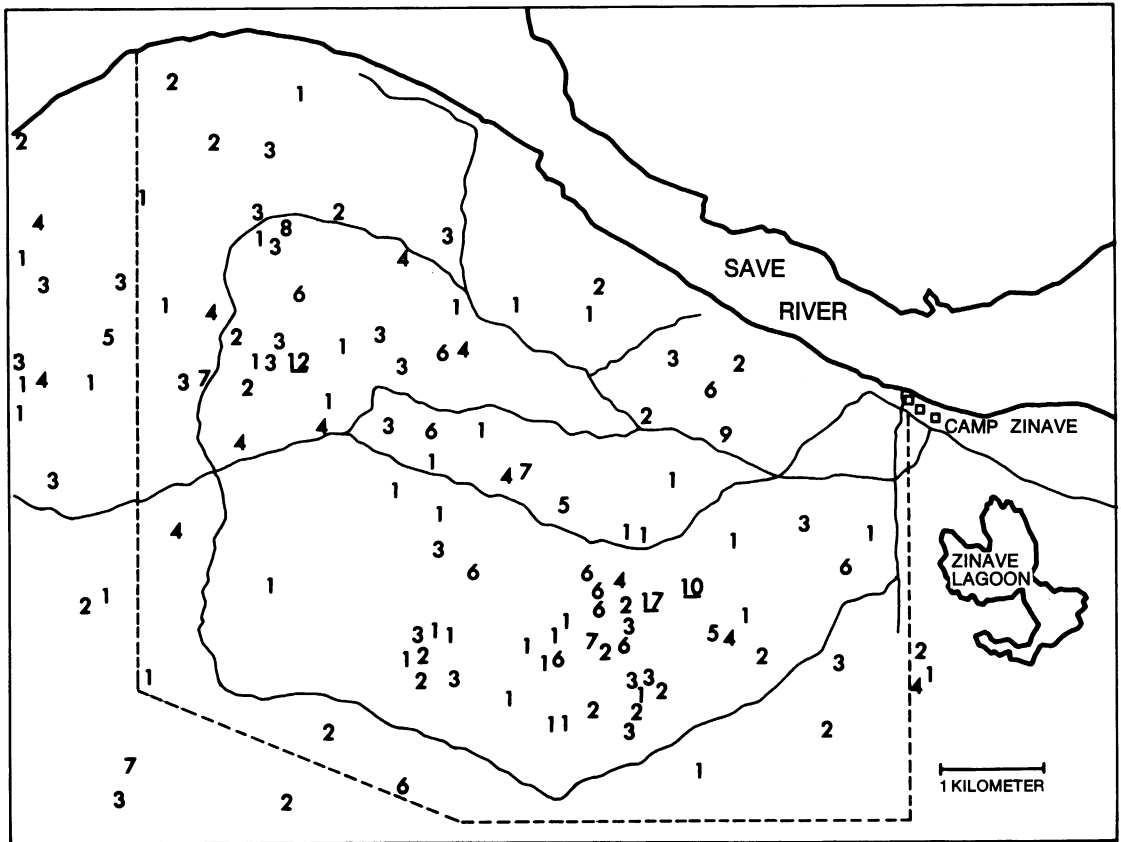


FIG. 16. Locations and numbers of individual *Tragelaphus angasi* seen during a census on May 29, 1973. Dotted line is approximate boundary of study area. Lines within study area are roads.

age classes subadult, immature, and juvenile. In 1972 61 percent of the animals seen were adults and 39 percent nonadult. The difference in percentages between these two sets of 756 (1971) and 1565 (1972) observations is highly significant ($p < 0.01$).

In 1972 when our identification of age classes was more reliable, the structure of the population, by classes, was 61 percent adults, 7 percent subadults, 24 percent immature, and 7 percent juvenile. According to Vincent et al. (1968) both the males and females of our subadult age class are reproductively mature, and if these are pooled with the adults, the population structure changes to 69 percent adult, 24 percent immature, and 7 percent juvenile.

Among the males in 1971, 58 percent were adults and in 1972, 47 percent were. The per-

centages of adults among the females for these two years were, respectively, 73 percent and 78 percent. For the 1972 data, by age class and sex, the percentages are: males, adult, 47 percent; subadult, 11 percent; immature, 41 percent; and juvenile, 1 percent; females, in the same order, 78 percent, 5 percent, 15 percent, and 2 percent. Only 23 percent of the juveniles were classified as to sex.

Demographically, the population structure in 1971 and 1972 is characteristic of a declining population—far more adults than young. We do not believe, at least from 1971 to 1972, that the population of nyala declined in our study area and, in fact, feel sure that it increased. In part the large number of adults observed in the population may be attributed to the relatively rapid maturation of nyala. Females, at least, born

between the time of the 1971 and 1972 observations could have achieved enough growth to be classified as adult.

In surveys made in 1969, 1970, and 1971 Barnes (1972b) found also a preponderance of adults in False Bay Park, Zululand. His age classes, however, differ somewhat from ours, and allowing for this variation, his reduced percentages of from 57 to 75 percent adults are not dissimilar from our own.

According to Vincent et al. (1968), one female produced her first offspring at an age of 20 months nine days, suggesting that sexual maturity was reached at about one year or even as young as 10 months 24 days. This might explain, in part, the high proportion of adult females we found. Males, we suspect, may take longer to reach the size that we call adult, even though some are physiologically capable of reproducing at sizes we call immature (see Vincent et al., 1968). This might account for the proportionally higher number of young males we saw each year.

The juveniles are poorly represented in our survey, and we do not believe that our observations are a valid representation of the number of juveniles in the population. For the first week or two, at least, of their existence baby nyalas are left in thickets by their mothers and thus are not readily observed, and even when they emerge, might not be seen by us because of their small size.

Differential mortality could account for some of the differences in population structure between 1971 and 1972, as well as for the adult heavy structure of both populations as a whole. We have no evidence to support or deny this idea, although we suspect that predation in the study area is probably higher on the juveniles than on the older animals. Baboons (*Papio ursinus*) and eagles are common in the study area (see Mortality) and signs of leopard (*Leo pardus*) were noted in 1972. However, we saw no dead nyala of any age nor other signs of mortality from natural causes in the study area in 1971 or 1972. There were no notable increases in the number nor kinds of potential predators between 1971 and 1972, nor was there increased poaching by human beings. However, an increasing impala (*Aepyceros melampus*) population was producing

a browse-line more than 1 m. above ground, and it is possible that there might have been higher juvenile mortality because small nyala could not reach food.

Keep (1973a) discussed the factors he believed led to a crash in a population of nyala in the Ndumu Game Reserve in Natal, South Africa, in October, 1970. Although he had no census of actual numbers of nyala present in the Reserve of 101.17 sq. km., some 50 carcasses were found in the last two weeks of October. Keep presented data that indicated lower mean weights of both males and females and mentioned the generally skinny appearance of the animals and the condition of the bone marrow. We also have noted the generally anemic appearance of nyala at Zinave at the end of the dry season, but have no high mortality at that time. Keep (*op. cit.*) attributed the die-off to the combination of a sharp drop in temperature together with heavy rainfall affecting the weakened animals. We have noted that nyala seem affected by cool weather, and the combination of temperature and humidity may well be major factors in limiting the distribution of the species. Although Keep (1973a) stated that there was no increase in parasites or in pathological conditions, he did indicate (Keep, 1973b) the presence of coronary aneurysms caused by a helminth in the population.

Group Size and Composition. Nyala were seen alone and in groups ranging in size from two to 27 animals. Most (73%) of the 688 observations were of nyala in groups, although the most frequent group size-class was of nyala seen alone (27%). Groups of two (21%) and three (18%) were also common, and these group classes, one to three, comprise 67 percent of the observations (fig. 17, table 5).

Of the 2446 nyala seen, most (375) were in a group size of three (125 observations), and the next highest number of animals (292) was in 146 groups of two animals. These are, respectively, about 15 and 12 percent of the animals seen. Solitary animals comprised 187 observations, or 8 percent of the total. More than half (1298) of all the nyala seen were in groups of five or fewer or alone (fig. 18, table 5).

Some shift in group-size frequency between 1971 and 1972 was noticed. Fifty-six percent of the 1971 observations of groups consisted of one

TABLE 5
Group Size of Nyala

No. of Animals in Group	1971			1972			Combined 1971 & 1972		
	No. of Observations	% of Observations	No. of Animals	% of Animals	No. of Observations	% of Observations	No. of Observations	% of Observations	No. of Animals
1	80	30.3	80	10.0	107	25.2	107	25.2	107
2	69	26.1	138	17.3	77	18.2	154	18.2	154
3	50	18.9	150	18.8	75	17.7	225	17.7	225
4	20	7.6	80	10.0	36	8.5	144	8.5	144
5	12	4.5	60	7.5	32	7.5	160	7.5	160
6	5	1.9	30	3.8	29	6.8	174	6.8	174
7	6	2.3	42	5.3	17	4.0	119	4.0	119
8	9	3.4	72	9.0	10	2.4	80	2.4	80
9	3	1.1	27	3.4	10	2.4	90	2.4	90
10	3	1.1	30	3.8	9	2.1	90	2.1	90
11	3	1.1	33	4.1	9	2.1	99	2.1	99
12	2	0.8	24	3.0	5	1.2	60	1.2	60
13	1	0.4	13	1.6	1	0.2	13	0.2	13
15	0	0	0	0	2	0.5	30	0.5	30
16	0	0	0	0	2	0.5	32	0.5	32
19	0	0	0	0	1	0.2	19	0.2	19
20	1	0.4	20	2.5	0	0	0	0	0
24	0	0	0	0	1	0.2	24	0.2	24
27	0	0	0	0	1	0.2	27	0.2	27
Totals	264	99.9	799	100.1	424	99.9	1647	100.1	1647
							688	99.7	2446

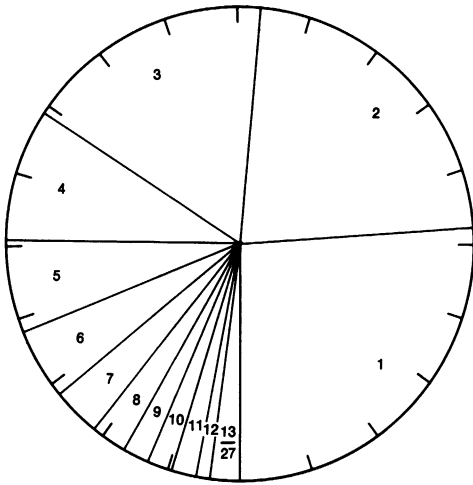


FIG. 17. Percentage of 688 groups of nyala in each group size class. Combined 1971 and 1972 data.

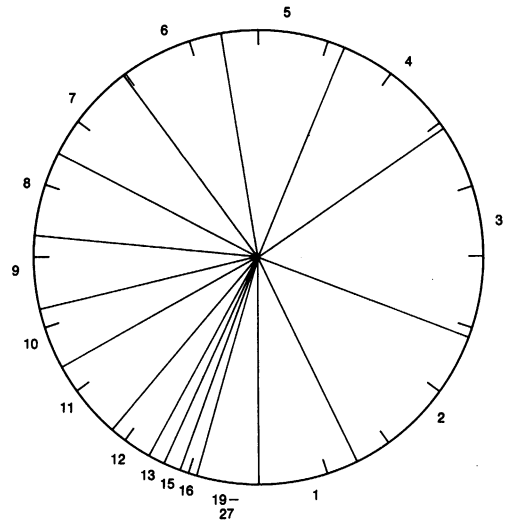


FIG. 18. Percentage of 2446 nyala comprising groups of various sizes. Combined 1971 and 1972 data.

or two animals; in 1972 only 43 percent consisted of one or two. The median in 1971 was 3.4 animals, and in 1972 five. These changes perhaps reflect the larger number of animals we suspect were in the study area in 1972, indicating that, to some extent, group size may be related to overall population size. However, Barnes (1972b) reported mean group-sizes of from 3.28 to 3.58 for four surveys from 1968 to 1971, with a total of animals ranging from 338 to 547. Likewise, there was little change from year to year of a median group-size of about two nyala despite possibly 60 percent more animals.

Of the 180 nyala seen alone in 1971 and 1972, 69 percent were males and 28 percent females; the remainder were unidentified as to sex. Adults comprised 74 percent, and of the adults 71 percent were males, 29 percent were females. Of the 43 nonadults seen alone, 72 percent were males, 28 percent were females. For 1972, when more detailed classes were recorded, the breakdown of 107 solitary individuals was 56 percent adult males, 8 percent subadult males, 15 percent immature males, 17 percent adult females, 1 percent subadult females, 3 percent immature females, and 2 percent nonsexed juveniles. In general, male nyala were seen alone more commonly than females, and adults were seen

alone more frequently than nonadults (table 5, fig. 19).

Twenty-one percent of the groups of nyala observed were of two animals (12% of the total animals observed). Of these groups of two, 17

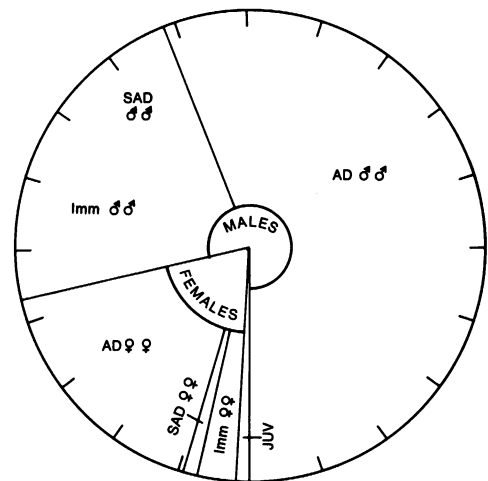


FIG. 19. Percentage of adults (AD), subadults (SAD), immature (Imm), and juveniles (JUV) of 107 solitary male and female nyala. 1972 data.

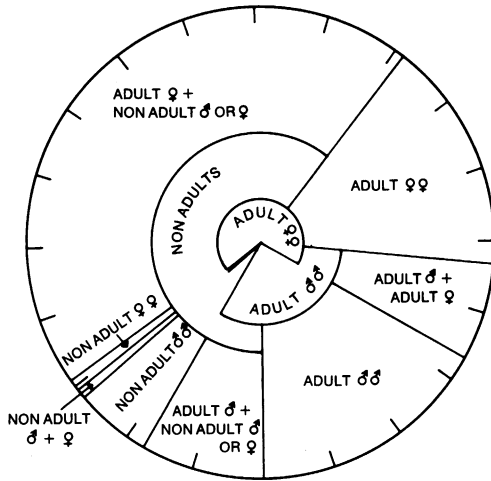


FIG. 20. Percentage of age and sex composition of 146 groups of two nyala. Combined 1971 and 1972 data.

percent were of two adult males together, and 16 percent of two females together. The most frequent composition (45%) observed was of an adult female with a nonadult. Of these 68 observations, 35 were of an adult female with a nonadult female, 26 with a nonadult male, and seven with a juvenile of undetermined sex.

The nine observations of nonadult females seen together in 1972 consisted of two groups of subadults, five of immatures, and two of juveniles. All of 12 adult females seen with nonadult males were with immature males. Sightings of an adult male and female together were not especially common, this combination being seen only 10 (7%) times. Of about equal occurrence was an adult male with a nonadult. Of 12 (9%) such observations, 11 were of an adult male with a nonadult male, and the other one was of an adult male with a subadult female. Once we saw an adult male with a juvenile (sex undetermined). Although we never observed nonadult males in pairs in 1971, we did see immature males together eight times (5%) in 1972. Once in 1971 we saw two nonadult females together, and once that year we saw a nonadult male and nonadult female together (fig. 20).

Of the 125 observations of nyala in groups of three, 42 (34%) were composed of adults only. Half of these groups consisted of adult males

only, and 11 of adult females only. Seven of the remaining 10 groups consisted of two adult males with an adult female, and only three were of one adult male with two adult females. Only twice did we see an adult male, an adult female, and a nonadult together. Except for 13 observations (11%) of one or two adult males with nonadults, and one of three subadult males together, the remaining 65 observations (53%) were of one or two adult females together with one or two nonadults. The most common of these was of one adult female with two nonadults (42 observations, 34%). Of the 25 observations in 1972 when the age class of the nonadults was determined, nine of the pairs of subadults were in different age classes (eight immature-juvenile, one subadult-immature). Except for one that contained two subadult females, all the others had two immature animals. Three of them had immatures of both sexes (fig. 21).

In groups of four, the most frequent of 51 observations was 14 (27%) of two adult females accompanied by two nonadults. The next most frequent composition (10) was of an adult male, two adult females, and a single nonadult (20%). Of all the groups that had one or more nonadults with one or more adult females (37; 73%), 15 (29%) also had one or two adult males present. Groups of four all the same sex or age were not

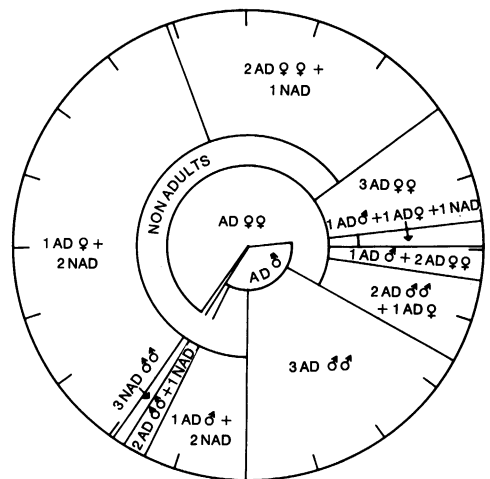


FIG. 21. Percentage of age and sex composition of 125 groups of three nyala. Combined 1971 and 1972 data.

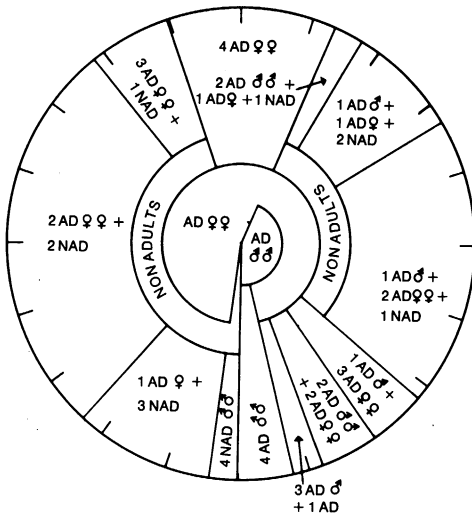


FIG. 22. Percentage of age and sex composition of 56 groups of four nyala. Combined 1971 and 1972 data.

commonly seen: two of four adult males, six of four adult females, two of two adult males and adult females, and one of three adult males, and one adult female. Once four immature males were seen in a single group. In the 15 groups that had adults of both sexes and nonadults, the ratio of adult males to adult females was 1:1.56 (fig. 22).

Thirty-four (77%) of the 44 groups of five nyala included one or more nonadults. The most frequently seen combination (18%) was three adult females and two nonadults, and four adult females and a single nonadult was a common grouping (11%). Adult males without adult females but with nonadults were also seen five times (11%), and combinations of adults of both sexes and nonadults were seen nine times (20%). Groups of five comprised only of one sex were seen eight times (18%), seven of these being all adult female groups. Mixed groups of adults were seen only in the combinations: two males and three females (one) and three males and two females (one). For the groups that contained adults of both sexes as well as nonadults, the ratio of adult males to adult females was 1:1.05 (fig. 23).

Groups of six nyala, comprising 5 percent of the observations, had none that contained only adult males, and only two (5.6%) composed

entirely of adult females. The combination of adult females and nonadults made up 50 percent of the observations, and combinations of adults of both sexes plus nonadults comprised 39 percent of the groups seen. Adult males with nonadults were seen twice (5.6%) and in each case all the nonadults were males. Six adult females together were seen twice, and once we saw six immature males as a single group. In the groups that contained adults of both sexes and nonadults the ratio of adult males to adult females was 1:1.55 (fig. 24).

In 80 groups of seven to 27 (which comprise only about 12% of all observations) all but one contained one or more nonadults, and only four did not have one adult female present. Slightly over 40 percent of these larger groups had no adult male in them, and the mean number of adult males per group, in those that had them, ranged from one (in a group of 19 and in two groups of 12) to six (in a group of 15), with an average 2.1 in 45 groups. The average number of males in the 29 groups sized from seven to 10 was 1.9, and for the remaining 15 groups sized 11 to 27 it was 2.4.

From these data on herd composition, no strong, clear picture emerges. The comments of hunters cited by Lydekker (1908) and Bryden (1899) are that: females might often be seen in

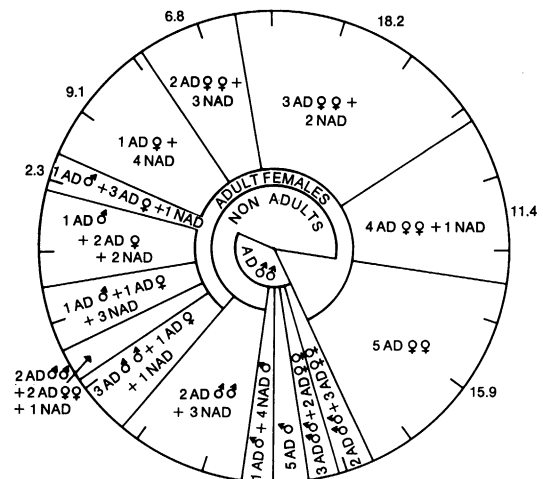


FIG. 23. Percentage of age and sex composition of 44 groups of five nyala. Combined 1971 and 1972 data.

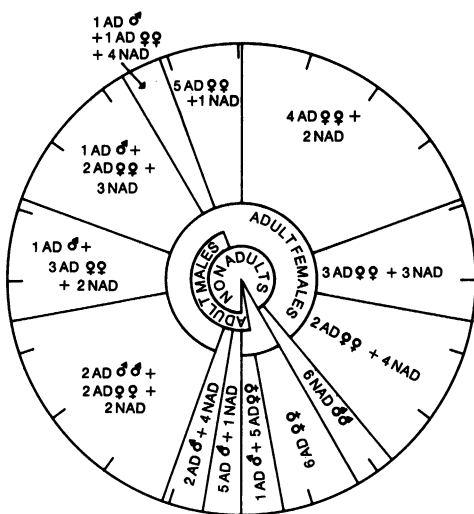


FIG. 24. Percentage of age and sex composition of 34 groups of six nyala. Combined 1971 and 1972 data.

large herds in 1854...never more than five together...not gregarious, but living either alone or in pairs, sometimes accompanied by last year's fawn...herds are small, although formerly were commonly much larger...does with their young and immature males are in herds by themselves, the adult rams living singly or associating together...one big ram accompanies a herd of does...a doe is only found alone when she has a newborn fawn...seldom find a doe alone although the old rams are so found...when the males separate from the females the former go in small troops, as many as eight being seen together...one herd of 16 of which four were big rams. Roberts (1951) stated that: "although to some extent solitary, they sometimes occur in herds of as many as thirty of both sexes and young, in small parties of females and young only, in pairs and even a couple of males together." Each of the above comments are encompassed in our observations. Other published quantitative data on herd composition include those of Davison (1971) whose summary of the composition of 123 groups (over a six-year period) indicates 36 percent solitary, 21 percent in twos, 25 percent in threes, and 10 percent in fours, and the remaining 8 percent consisting of

from five to eight in a group. These data correspond very closely to our findings (see fig. 17). Barnes (1972b) data for four years are also similar: 34 percent solitary, 24 percent in twos, 15 percent in threes, 12 percent in fours, and the remaining 15 percent of from five to 22 in a group.

In general, we find nyala are commonly seen alone or in small groups up to five, and less frequently in herds of six to 27 or more. Of the solitary animals males are seen alone about twice as frequently as females are. Of the nyala in groups adult males are seen in about one-third of them, whereas adult females are present in more than 70 percent of all groups and up to 100 percent of the larger groups. Nyala younger than adult occur alone in about a quarter of the observations, approximately equal to the frequency of solitary adult females. Lone juveniles are rarely seen and comprise less than 1 percent of the solitary nyala we observed.

The most frequent association of nyala in groups is of adult females with nonadults. Sixty-six percent of groups of two to eight animals had an adult female and nonadult in them. Only in the groups of two animals were fewer than half (45%) the observations of an adult female with a nonadult. In comparison, only 32 percent of groups sized two to eight had both an adult male and an adult female in them. There is an approximately equal percentage (31%) of association of an adult male with a nonadult, and only in two of the seven size classes was the adult male-female combination more prevalent than that of adult male and nonadult. Of the four groups' sizes, two, three, five, and six that had adult males in association with nonadults only of one sex, 92 percent were associations with males. By contrast, adult female associations with nonadults of only one sex in group size classes two to seven were about 40 percent with males and 60 percent with females. Group size does not seem to be influenced by the habitat frequented by nyala. In 1971 the 99 groups for which habitat was recorded averaged 3.2 animals with a range of 5.2 to none according to which habitat the groups were observed in. A Chi-square test for deviation in group size in the eight habitats observed was not significant ($P < 0.60$). Simi-

larly, for 1972 when 421 observations recording habitat were made, the group size averaged 3.9 (range 5.14 to none) in the eight habitats, but again there was no significant difference revealed by the Chi-square test ($P = < 0.60$). The average group size difference between 1971 and 1972 is not significant statistically.

The group composition of nyala may be better understood in light of our findings with animals tagged with radio transmitters and other identifiable individuals: the aggregations of nyala that we observed are not permanent groups, and the assemblages may be of extremely short duration. The transient nature of these groups is exemplified by observations of Ndliati, an albinistic male, over a short period of time. Ndliati was seen at 1700 hours on August 31, 1972, as part of a group of four, the other three being adult males. Five days later, on September 5, at 0900, Ndliati was again seen as part of a group of four, but this time the others were one adult male and two adult females. At 0837 on September 8, Ndliati was seen alone, but that afternoon at 1635 was part of a group of five composed of an adult male, an adult female, a subadult male, and another immature male. Twenty-four hours later, the albinistic male was one of a group of nine nyala: one adult male, three adult females, one subadult male, two other immature males, and an unsexed juvenile. The following morning at 0745 he was seen in a group of 10: four adult males and five other immature males. On that same day, September 10, at 1705, Ndliati was seen with another immature male. Our final record of this animal in this period was on September 12 when he was one of a group of 11 nyala: three adult females, three subadult males, two immature males, one immature female, and one unsexed juvenile. Over our period of observation of this individual as an immature animal, from April to November, 1972, he was seen in association with at least 14 other nyala, and most likely the number of actual associates was much higher. Our observations of other nyala confirm the transient nature of the groups observed. Table 6 presents data for 17 known animals with the minimum number, age, and sex of the others with which each was seen in association. Adult males were seen, on average, with at least 15

other individuals, subadult males with at least 10, immature males with at least 12, and adult females with at least 10 others. For the purposes of table 6, we considered any nonmarked animal seen in association with a marked one to be the same as one of the same age and sex seen with it before; the actual number of associates may well be double or triple these figures.

Identifiable adult males were seen alone in 34 percent of the times they were observed, whereas adult females were seen alone in 30 percent of the sightings. Subadult and immature males were seen alone 25 and 18 percent of the observations, respectively. The adult males had 34 percent of their associates as males, and the adult females had 31 percent of their associates as males, roughly the same proportion of sexes as were believed to exist in the population of nyala in the study area. Immature and subadult males, however, had a considerably higher percentage of male associates, 58 and 62 percent, respectively. Adult males seemed to associate more with other adult males than with younger males, as 74 percent of their male associates were adults. Subadult males had 54 percent adult male associates, 15 percent subadult male associates, and 31 percent immature male associates. Immature males had 36 percent adult, 21 percent subadult, and 43 percent immature male associates (table 6).

One adult male (five observations) was never seen in association with other nyala, and we believed him to be a very old individual. Another adult male (four observations) was never seen alone. One adult male (four observations) was never seen in association with any females, and one adult female (five observations) was never seen in association with any other females (table 6).

These data confirm our belief that nyala, although gregarious, do not have long-lasting associations and that the animals within a general area, the home range and its periphery, are known to one another and may associate for a while. The strongest bond is probably between that of a mother and her offspring, but how strong that is we do not know. We have observed females to leave newborn nyala quite readily, leaving them hidden in a thicket, and even to run from us so fast as to leave a small juvenile trailing

TABLE 6
Least Number of Other Nyala in Association with Known Individuals

Sex	Age	Name	Associates ♂		Ad	Associates ♀		Imm	Ad	Imm	Juv	No. of Associates	No. of Observations	No. of Times Alone
			Ad	Sad		Ad	Sad							
M	Ad	Russell	3	1	0	5	1	0			1	10	14	6
M	Ad	Ham	2	0	1		15				4	22	4	0
M	Ad	Keyser	3	0	0	3	1	1			1	9	21	7
M	Ad	Kubassa	6	1	2		27					35	27	5
M	Ad	Old Man	0	0	0		0	0			0	0	5	5
M	Ad	Macaxulo	5	0	0		12					17	5	2
M	Ad	Djiweni	6	1	1		15					23	13	5
M	Ad	Ndliati	8	2	2		12					20	29	8
M	Ad	J	2	0	2		0	0			0	4	7	5
M	Sad	Djiweni	4	1	3		0	0			0	14	8	2
M	Sad	Mike	3	1	1		0	1			0	7	8	2
M	Imm	Ndliati	4	3	5		0	0			3	19	14	1
M	Imm	Gordon	1	0	1		0	1			1	5	8	3
F	Ad	No Name	1	0	1		10					12	9	1
F	Ad	Leslie	0	0	0		0	3			1	6	4	1
F	Ad	3	2	0	2		0	0			0	4	5	3
F	Ad	Karina	8	0	1		17				1	27	12	4

Abbreviations as in table 2.

her far behind. We have also seen a female followed by a small juvenile that was not the same one of the same size that had been following her a few days before. (See also Mortality and Social Behavior.)

In general females tend to aggregate more than males, and are invariably well represented in the larger groups. The presence of a large number of adult males in mixed herds is not common. In seven groups of 15 or more that were seen in 1972, the number of adult males ranged from none to six, and averaged 2.6. The ratio of adult males to all others in these groups was 1:7.3. When seen with one or more other nyala, the average group size for our identifiable adult males was: Russell, 4.0; Ham, 8.7; Keyser, 3.3; Kubassa, 7.0; Old Man, 0; Macaxulo, 8.0; J, 1.5; Djiweni, 5.6; and Ndliati, 4.5. The two subadults (table 6) averaged 4.2 and 2.2, and the two immature males, 5.8 and 3.0. The adult females averaged: No Name, 3.6; Leslie, 3.0; Three, 2; Karina, 3.8.

Although immature males are seen alone, immature females are not commonly seen out of the company of other nyala. In 1972 somewhat over 20 percent of the solitary nyala seen were immature or subadult males, and of the nyala seen in groups of two animals, about 5 percent of the observations were of nonadult males together, whereas two nonadult females together comprised less than 1 percent of the groups of two seen. From our data, we suspect that as immature males grow older, they gradually associate more and more with males of their own or older age-classes, leaving the company of their mothers and their predominantly female groups, while the young females tend to remain in the company of the largely female groups.

Food. In the Save River region, nyala are primarily browsers of a diversity of plant species. By examination of stomach contents or by direct observation of animals feeding, we have identified 108 kinds of plants utilized by them (table 7). Leaves are the main food, and 85 percent of the species were utilized for leaves. Fruits of 39 percent of the species were also eaten, 13 percent of the species had twigs eaten, and 10 percent were utilized for flowers. The only species for which bark was recorded as food is the baobab

(*Adansonia digitata*) which also provides nyala with flowers and fruit. Werner von Alvensleben reported (personal commun.) seeing nyala feeding on bits of bark dropped by elephants stripping baobabs; nyala also profit by eating leaves from branches from other trees torn down by elephants.

Among the more important foods from the standpoint of providing leaves, twigs, flowers, and fruits are several species of *Acacia*, especially *A. xanthophloea*, and *Salvadora persica*, *Spirostachys africana*, species of *Strychnos*, *Thylachium africanum*, *Ziziphus mucronata*, and a variety of legumes. Some species, such as *Salvadora persica*, are so heavily used by nyala and other browsers that a browse line was evident 1.3 m. from the ground in 1971. In 1972 that line was about 1.6 m., and in 1973 the browse line appeared to be nearly 2 m.

In the stomachs of 30 nyala taken in all months except March, May, and December we have identified some 57 kinds of plants. Seventeen (30%) of the species were found in stomachs only from June to October, representing the dry season (months with less than 30 mm. of rainfall), and 16 (28%) were found only in stomachs of animals killed from November through April, the rainy season. Twenty-four of the species (42%) were found in stomachs both of the dry season and of the rainy season, and these included species of *Acacia*, *Diospyros macrocalyx*, species of *Drypetes*, *Salvadora persica*, *Strychnos innocua*, *Spirostachys africana*, *Thylachium africanum*, and grasses (table 8). In the dry season, nyala feed much from leaves that have fallen to the ground, and we have also seen males thrash branches above their heads with their horns to dislodge leaves. Females accompanying such males also benefit from the fallen leaves.

In the rainy season when there is a greater diversity of green vegetation, nyala probably feed on more kinds of plants than indicated by our data. Unfortunately, only eight of the 30 stomachs (26%) are from the wet months, and we noted from the stomachs of the three animals killed in April that there were a number of other plants present that we have not yet identified. The three April specimens were killed in 1974, a year in which the rains were heavy in March and

TABLE 7
Plants Eaten by Nyala

	Leaves	Twigs	Flower	Fruit	Bark
<i>Acacia clavigera</i>	x	—	x	x	—
<i>Acacia nigrescens</i>	x	x	—	x	—
<i>Acacia nilotica</i>	x	x	x	x	—
<i>Acacia xanthophloea</i>	x	x	x	x	—
<i>Acacia</i> spp.	x	x	—	x	—
<i>Adansonia digitata</i>	—	—	x	x	x
<i>Adenium multiflorum</i>	x	—	—	—	—
<i>Afzelia quanzensis</i>	x	—	x	—	—
<i>Albizia anthelminthica</i>	x	—	—	x	—
<i>Aristolochia petersiana</i>	x	—	—	—	—
<i>Artabotrys brachypetalus</i>	x	—	—	x	—
<i>Artabotrys montiroea</i>	x	—	—	—	—
<i>Balanites maughamii</i>	x	—	—	x	—
<i>Berchemia discolor</i>	x	—	—	—	—
<i>Bolusanthus speciosus</i>	—	—	x	—	—
<i>Brachystegia glaucescens</i>	x	—	—	—	—
<i>Brachystegia</i> sp.	x	—	—	—	—
<i>Canthium</i> sp.	—	—	—	x	—
<i>Carpolobia conradsiana</i>	—	—	—	x	—
<i>Cassia</i> sp.	—	—	—	x	—
<i>Cissus rotundifolia</i>	x	—	—	—	—
<i>Cissus</i> sp.	x	—	—	—	—
<i>Cleistanthus holsti</i>	x	—	—	—	—
<i>Cleitochlamys kirkii</i>	x	—	—	—	—
<i>Coffea</i> sp.	—	—	—	x	—
<i>Colophospermum mopane</i>	x	x	—	x	—
<i>Combretum butyrosom</i>	x	—	—	—	—
<i>Combretum imberbe</i>	x	—	—	—	—
<i>Combretum molle</i>	x	—	—	—	—
<i>Combretum</i> spp.	x	—	—	—	—
<i>Combretum</i> sp. (focane) ^a	x	—	—	—	—
<i>Combretum</i> sp. (gulawossico) ^a	x	—	—	—	—
<i>Cordyla africana</i>	—	—	—	x	—
<i>Courbonia glauca</i>	x	—	—	—	—
Cucurbitaceae indet.	x	—	—	x	—
<i>Cynancum</i> sp.	x	—	—	—	—
<i>Deinbollia xanthocarpa</i>	x	—	—	—	—
<i>Dichrostachys africana</i>	x	—	—	—	—
<i>Digitaria milangiensis</i>	x	—	—	—	—
<i>Digitaria</i> spp.	x	—	—	—	—
<i>Diospyros macrocalyx</i>	x	—	—	—	—
<i>Diospyros mespiliformis</i>	x	—	—	—	—
<i>Diospyros usambarensis</i>	x	—	—	—	—
<i>Drypetes gerrardi</i>	x	—	—	—	—
<i>Drypetes mossambicensis</i>	x	—	—	—	—
<i>Ficus sycomorus</i>	—	—	—	x	—
<i>Ficus ingens</i>	—	—	—	x	—
<i>Ficus</i> spp.	—	—	—	x	—
<i>Garcinia livingstonei</i>	x	—	—	x	—
<i>Gardenia spatulifolia</i>	x	—	—	x	—

TABLE 7—(Continued)

	Leaves	Twigs	Flower	Fruit	Bark
Gramineae indet.	x	—	—	—	—
<i>Grewia bicolor</i>	x	—	—	—	—
<i>Grewia caffra</i>	x	—	—	—	—
<i>Grewia occidentalis</i>	—	—	—	x	—
<i>Guibourtia conjugata</i>	x	x	—	x	—
<i>Hugonia orientalis</i>	x	—	—	—	—
<i>Hyphaene crinita</i>	—	—	—	x	—
<i>Indigofera</i> sp.	x	—	—	—	—
<i>Kigelia pinnata</i>	x	—	x	—	—
<i>Landolphia</i> sp.	x	—	—	x	—
<i>Lecaniodiscus fraxinifolius</i>	x	—	—	—	—
Leguminosae (shrub invaders) different species	x	x	x	x	—
<i>Leptactinia</i> sp.	x	—	—	—	—
<i>Lonchocarpus capassa</i>	x	—	—	x	—
<i>Maerua angolensis</i>	x	—	—	x	—
<i>Maerua</i> sp. (shipinga) ^a	x	—	—	—	—
<i>Manilkara mochisia</i>	x	—	—	—	—
<i>Maprounea africana</i>	—	—	—	x	—
<i>Markhamia obtusifolia</i>	x	—	—	—	—
<i>Millettia stuhlmannii</i>	x	—	—	x	—
<i>Mimusops obovata</i>	x	—	—	x	—
<i>Mimusops zeyheri</i>	x	—	—	x	—
<i>Mimusops</i> sp.	x	—	—	—	—
<i>Olex dissitiflora</i>	x	—	—	—	—
<i>Ostryoderris stuhlmannii</i>	x	—	x	—	—
<i>Panicum maximum</i>	x	—	—	—	—
<i>Panicum</i> spp.	x	—	—	—	—
<i>Phyllanthus kirkii</i>	x	—	—	—	—
<i>Piliostigma thonningii</i>	x	x	—	x	—
<i>Pyrenacantha kaurabassana</i>	x	—	—	x	—
<i>Pyrenacantha</i> sp.	x	—	—	—	—
<i>Rhus</i> sp.	x	—	—	x	—
<i>Salvadora persica</i>	x	x	x	x	—
<i>Sansevieria</i> sp.	x	—	—	—	—
<i>Sclerocarya caffra</i>	x	—	—	x	—
<i>Setaria chevalieri</i>	x	—	—	—	—
<i>Solanum panduraeforme</i>	x	—	—	x	—
<i>Spirostachys africana</i>	x	—	x	x	—
<i>Sterculia rogersii</i>	x	—	—	—	—
<i>Strophanthus grandiflorus</i>	x	—	—	—	—
<i>Strychnos innocua</i>	x	x	—	x	—
<i>Strychnos mitis</i>	x	x	—	x	—
<i>Strychnos spinosa</i>	x	—	—	x	—
<i>Strychnos stuhlmannii</i>	x	x	—	x	—
<i>Strychnos</i> sp. (kangala) ^a	x	—	—	—	—
<i>Stylochiton natalense</i>	x	—	—	—	—
<i>Talinum</i> sp.	x	—	—	—	—
<i>Tamarindus indica</i>	x	—	—	—	—
<i>Terminalia prunioides</i>	x	—	—	—	—
<i>Terminalia sericea</i>	x	—	—	—	—

TABLE 7—(Continued)

	Leaves	Twigs	Flower	Fruit	Bark
<i>Thylachium africanum</i>	x	x	x	—	—
<i>Tricalysia</i> sp.	—	—	—	x	—
<i>Urochloa mossambicensis</i>	x	—	—	—	—
<i>Uvaria caffra</i>	x	—	—	x	—
<i>Vepris</i> sp.	x	—	—	—	—
<i>Vitex</i> sp.	—	—	—	x	—
<i>Xylia torreana</i>	x	—	—	—	—
<i>Ziziphus mucronata</i>	x	x	—	x	—

^aShangaan name.

continued into the first week of April. An adult female and an adult male taken on the ninth and thirteenth of April, respectively, had been feeding on twigs and leaves, grass, legumes, and cucurbits. The dry weight of the stomach contents of the female revealed 3 percent leaves and twigs, 26 percent grass, 29 percent legumes, and 42 percent cucurbit leaves, stems, and fruits. The male had (dry weight) 64 percent leaves and twigs, 18 percent grass, and 18 percent cucurbits.

We have found grass in the stomachs of nyala from most months of the year, ranging from none or a trace to as much as 65 percent of the volume of the wet stomach contents. Estimates were made of the percentage of browse and grass, by volume, in the stomachs of 20 nyala killed throughout the year except in March, May, and December. On average, 12 percent of the volume of the stomach contents consisted of grasses and herbs (median 10%), with a range from 65 percent to none. Jeremy Anderson, who was studying nyala at the Ndumu Game Reserve in Zululand, informed us (*in litt.*) that when the grass sprouts after the rains start, nyala feed on it almost exclusively. We have observed nyala eating short, sweet grass, *Setaria chevalieri*, at the edge of lagoons. Brad House, Curator of Mammals at the New York Zoological Park, informed us that the herd of 20 or more nyala exhibited in the "African Plains" setting do not eat the grass and it is necessary to mow it.

The wet weight of the contents of the stomachs of four adult males averaged 11.1 kg. (range 15.6-7.2), about 10.6 percent of the average total weight of the animal. Five females had stomach contents that averaged 4.3 kg. (4.8-3.9), or about

7 percent of the total weight. Two immature males were intermediate in both weight and percentage of total weight between adult males and adult females.

Barnes (1972a) reported 47 species of plants eaten by nyala in False Bay Park, Zululand, in April, 1969, 1970, and 1971. Only two of the species he listed, *Grewia caffra* and *Terminalea sericea*, are common to both our list (table 7) and his. Vincent et al. (1968) found nyala stomach contents in Hluhluwe Game Reserve, Zululand, to be about 70 percent browse and 30 percent grasses. Of their list of 27 species of plants utilized by nyala there, eight are known to be eaten by nyala in the Save River region. Best et al. (1962) commented that nyala "seem to be exclusively browsers, only eating grass when this is young and tender. The main diet consists of leaves and tender twigs, pods and various fruits, such as the so-called 'Kaffir oranges' which they will eat when these have fallen and are lying practically rotten on the ground. There is probably some unknown factor which limits their distribution to the isolated areas they inhabit, but a good deal of investigation, notably by the late Lt.-Colonel Stevenson-Hamilton, has not succeeded in ascertaining exactly what this is. It has been observed that Nyalas only inhabit dense bush where the undergrowth is very thick and the vegetation includes the growth of a peculiar species of cactus and other associated plants. It has been suggested that some bulb or root is essential to the existence of the Nyala, but this, so far as the Editors are aware, has not yet been confirmed." In our investigations we have not found any specific association with cactus, which

	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Acacia</i> spp.	—	—	—	1	—	1	1	1	3	2	2	—
<i>Adenium multiflorum</i>	—	—	—	1	—	—	—	—	—	—	—	—
<i>Azela quanzensis</i>	—	—	—	1	—	—	—	1	1	2	—	—
<i>Albizia anthelminthica</i>	—	—	—	—	—	—	—	—	1	3	1	—
<i>Aristolochia petersiana</i>	—	—	—	—	—	—	—	1	—	—	—	—
<i>Artabotrys brachypetalus</i>	—	—	—	1	—	—	—	—	—	—	—	—
<i>Artabotrys monteroae</i>	—	—	—	—	—	—	—	1	—	—	—	—
<i>Balanites maughamii</i>	—	—	—	—	—	—	1	—	—	—	—	—
<i>Berchemia discolor</i>	—	—	—	—	—	—	—	1	—	—	—	—
<i>Brachystegia</i> sp.	—	—	—	—	—	1	—	—	—	—	—	—
<i>Cissus rotundifolia</i>	—	—	—	—	—	—	—	1	1	—	—	—
<i>Cissus</i> sp.	—	—	—	—	—	—	—	1	—	1	—	—
<i>Cleistanthus holsti</i>	—	—	—	1	—	—	—	—	—	—	—	—
<i>Colophospermum mopane</i>	1	—	—	—	—	—	—	4	4	1	1	—
<i>Combretum molle</i>	1	—	—	—	—	—	—	—	—	—	1	—
<i>Combretum</i> sp. (focane) ^a	—	—	—	1	—	—	—	—	—	1	—	—
<i>Combretum</i> sp. (gulawossico) ^a	1	—	—	—	—	—	—	—	—	—	—	—
<i>Courbonia glauca</i>	—	1	—	—	—	—	—	2	2	1	1	—
<i>Deinbollia xanthocarpa</i>	2	—	—	—	—	—	—	—	—	—	—	—
<i>Diospyros macrocalyx</i>	1	—	—	2	—	1	1	2	—	1	1	—
<i>Diospyros mespiliformis</i>	—	—	—	—	—	—	1	—	—	—	—	—
<i>Drypetes gerrardi</i>	1	—	—	1	—	—	1	2	2	2	—	—
<i>Drypetes mossambicensis</i>	—	1	—	2	—	—	—	5	2	2	1	—
<i>Garcinia livingstonei</i>	—	—	—	—	—	—	—	—	—	—	1	—
<i>Gardenia spatulifolia</i>	—	—	—	—	—	—	1	—	—	—	—	—
Gramineae indet.	2	1	—	3	—	1	2	2	5	4	1	—
<i>Grewia bicolor</i>	—	—	—	1	—	1	—	—	—	—	1	—
<i>Guibourtia conjugata</i>	—	—	—	1	—	—	2	1	1	2	—	—
<i>Hugonia orientalis</i>	—	—	—	1	—	—	—	—	—	—	—	—
<i>Lecaniodiscus fraxinifolius</i>	—	—	—	—	—	—	—	—	4	3	—	—
<i>Lonchocarpus capassa</i>	—	—	—	—	—	—	—	—	—	1	1	—
<i>Maerua angolensis</i>	1	—	—	—	—	—	—	—	1	2	—	—
<i>Maerua</i> sp. (shipinga) ^a	—	—	—	—	—	—	—	—	1	2	—	—
<i>Manilkara mochisia</i>	—	—	—	—	—	—	—	—	3	1	1	—
<i>Markhamia obtusifolia</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>Millettia stuhlmannii</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>Mimusops obovata</i>	—	1	—	—	—	—	—	—	1	—	1	—
<i>Mimusops zeyheri</i>	—	—	—	3	—	—	—	—	—	1	1	—
<i>Olax dissitiflora</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>Ostryoderris stuhlmannii</i>	—	—	—	—	—	—	—	—	—	—	1	—
<i>Phyllanthus kirkii</i>	—	—	—	2	—	—	—	—	—	—	1	—
<i>Pyrenacantha kaurabassana</i>	—	—	—	1	—	—	—	4	1	—	1	—
<i>Pyrenacantha</i> sp.	1	—	—	—	—	—	—	—	—	—	—	—
<i>Salvadora persica</i>	2	1	—	2	—	—	1	—	7	2	1	—
<i>Sclerocarya caffra</i>	1	—	—	—	—	—	—	—	—	—	1	—
<i>Solanum panduraeforme</i>	—	—	—	2	—	—	—	—	—	—	—	—
<i>Spirostachys africana</i>	1	—	—	1	—	1	2	3	4	2	1	—
<i>Sterculia rogersii</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>Strophanthus grandiflorus</i>	1	—	—	—	—	—	—	—	—	—	—	—

TABLE 8—(Continued)

	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Strychnos innocua</i>	1	—	—	3	—	—	3	2	2	3	—	—
<i>Strychnos mitis</i>	1	—	—	1	—	—	3	—	2	—	1	—
<i>Strychnos</i> sp. (<i>kangala</i>) ^a	—	—	—	2	—	—	—	—	—	1	—	—
<i>Talinum</i> sp.	—	—	—	—	—	—	—	—	—	—	1	—
<i>Tamarindus indica</i>	—	—	—	—	—	—	—	1	—	—	—	—
<i>Terminalia prunioides</i>	—	—	—	—	—	—	—	—	1	—	—	—
<i>Thylachium africanum</i>	1	—	—	2	—	1	—	4	3	6	2	—
<i>Xylia torreana</i>	—	—	—	1	—	—	—	—	—	1	—	—
No. stomachs examined	2	1	0	3	0	1	3	5	7	6	2	0
No. species	16	5	—	24	—	7	12	19	26	24	23	—
% species	28	9	—	42	—	12	21	33	46	42	40	—
% species from this month in all stomachs from this month	19	100	—	8	—	100	17	5	4	4	9	—

^aShangaan name.

is not native to Africa, nor have we any evidence of nyala feeding on euphorbs (called "cactus" locally) or on roots or bulbs.

Although in the Save River region nyala feed extensively on the cucurbits and legumes that grow in overgrazed areas and in lands abandoned by shifting agriculturists, they rarely invade cultivated areas. In this regard they differ markedly from bushbuck (*Tragelaphus scriptus*), and the only cultivated plant that we have heard that nyala eat is watermelon leaves and stems.

Drinking. In the Zinave region, during the dry season, nyala probably drink once a day, generally after dark. We have observed nyala moving toward the river between 1700 and 1730 hours, walking slowly and browsing along the way. The high level of human population close to the river may be why nyala drink at night, for elsewhere, where human beings do not live, we have observed nyala drinking between 1200 and 1400 hours, the hottest time of the day. During the hot, rainy summer nyala may have less need of drinking water, as the leaves on which they browse are more succulent. At this time, also, there are pools of water throughout the study area where the animals can drink without going to the river. Normally, by September, most of these pools have dried, and the nyala drink from the river. We know of some places, not in the study area, where nyala seem to persist for some

months during the dry season in the absence of free drinking water. Davison (1971) also reported nyala in Rhodesia persisting for a number of months in the absence of surface water and concluded that water is not essential for their existence, and Roberts (1936) also noted the presence of nyala 10 to 15 miles from drinking water.

Defecation and Urination. Unlike some of the other antelopes in the area, especially impala, nyala are not often seen defecating or urinating, nor do they seem to have particular sites for the deposition of excrement or urine as is common to impala at some times of the year. The few occasions that we saw females urinating indicate that they squat slightly and do not raise the tail more than to arch it. Males arch the tail, but do not squat when urinating.

We have not seen females defecating and have only two observations of males doing so. The individuals that we followed all day (see Movements) were not seen to urinate or defecate when in our view. A male seen defecating on November 7, 1973, stood with the hind legs slightly spread and elevated his tail over the back to a point where it formed an angle of 20 degrees with the plane of the back, and spread it to show the white hairs of the underside. Another male that was seen defecating did not raise and spread the tail, but only arched it.

Nyala droppings are roughly barrel-shaped,

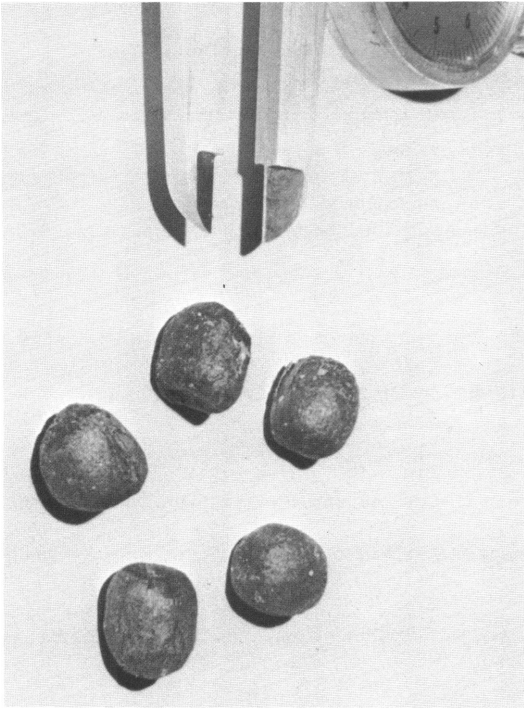


FIG. 25. Nyala feces. Caliper tips are 10 mm. apart.

slightly indented at one end and rounded at the other. They are about 11.5 mm. in diameter and 13.2 mm. in length. In the dry season, at least, they do not stick together (see fig. 25).

Reproduction. Although Brand (1963) gave the gestation period of nyala as six months, the preponderance of evidence indicates a longer time, about eight and one-half months (Mentis, 1972). Females are capable of conceiving at one year of age; Vincent et al. (1968, footnote) presented data for a female that gave birth at 20½ months, and subsequently at intervals of 9½ and 11½ months. Evidently, female nyala may come into heat within a week or so after parturition (Mentis, 1972), and calving intervals may be as short as 257 days.

Births of nyala throughout the year are generally reported (Brand, 1963; Vincent et al., 1968; and others; see Mentis, 1972), but some authors have reported possible peaks from September to December in the Pretoria Zoo (Brand, 1963), from August to November in Kruger Park (Fairall, 1968) or September to October in Kruger

Park (Stevenson-Hamilton, 1912) or in August at Ndumu Game Reserve (Mentis, 1972). Davison (1971) found fetuses from June to November in Rhodesia and lactating females in February and from July to December. If females breed at one year of age, and if females may conceive within a week of their parturition, and if there are calving peaks, the following year should see a peak about three months earlier. It is perhaps noteworthy that all the suspected peaks of calving are near the end of the dry season or just before the summer rains. Small calves would be much more visible at that time of year, which might give an impression of a lot of calves at those times. The data from the Pretoria Zoo, of course, would not be so constrained. Crandall (1965) reported 83 births in all months except August, September, and October at the Bronx Zoo. However, these data are biased because the nyala are housed indoors and the male(s) are separated from the females during the winter (December to March).

Our data concerning reproduction are relatively scant. Our only observations of copulation were on October 18, 1971, and July 23, 1972. In the first a male was seen to mount a female, making several penetrating thrusts, and then dismount and move off behind the female. The second involved an adult male that joined an adult and subadult female. After chasing off two adult males, described in the section on Social Behavior, the male put his neck over that of the adult female for 30 seconds, just after the female had urinated. She urinated again and this time the male exhibited "Flehmen"—took urine in his mouth, sniffed, raised his head and withdrew his upper lip—and then mounted the female and copulated for a few seconds.

We believe that nyala breed throughout the year in the Zinave area. We have noted newborn animals or term fetuses in mid-February, late April, mid-September, and the end of October, as well as small nyala that we estimated to be less than one month old in February, March, April, June, July, August, September, October, and November (table 9). In part these data reflect the intensity of our field work during these months, and the absence of data from other months, especially December and May, reflect less time in the field. At times we have thought that there might be a birthing peak near the end of the dry season,

TABLE 9
Records of Pregnant or Lactating Female Nyala in the Zinave National Park Area and Observations
of Baby Nyala Estimated to be Less than One Month Old

Month	Day	Observation
January	21	Female killed; had male fetus with crown-rump length 355 mm., weight 2.1 kg.
February	15	Female killed; had male fetus near full term with total length 790 mm., (crown-rump 570 mm.), weight 5.5 kg.
	15	Baby about one week old
	15	Baby about one week old
	16	Female killed; had male fetus near full term with total length 810 mm., (crown-rump 570 mm.), weight 5.0 kg.
	28	Female killed; had male fetus with crown-rump length 160 mm., weight 170 gm.
March	14	Baby about one month old
April	4	Baby about one month old
	4	Baby about one month old
	4	Female killed, some milk in udder, none in teats; had female fetus with crown-rump length 145 mm., weight 250 gm.
	15	Female killed, some milk in udder, none in teats; had female fetus with crown-rump length 240 mm., weight 168 gm.
	16	Baby about two weeks old
	22	Newborn male, with umbilical cord, wet, total length 893 mm., hind foot 283 mm., ear 115 mm., height at shoulder 530 mm.
June	13	Baby about two weeks old
	13	Baby about one week old, total length 815 mm.
July	7	Baby about one week old
	9	Female killed; was lactating
	10	Baby about one week old
	12	Female killed, was lactating
	16	Baby about one month old
	21	Baby less than one month old
	28	Baby less than one month old
August	9	Female less than one month old (killed by baboon)
	17	Female found dead; had male fetus with total length 641 mm., weight 2.1 kg.
September	3	Baby less than one month old (killed by baboon)
	8	Baby less than one month old
	10	Female killed; had fetus with crown-rump length 25 mm.
	10	Female killed; was lactating
	10	Female killed; had female fetus with crown-rump length 435 mm., weight 5.2 kg.
	14	Baby less than two weeks old
	15	Baby less than two weeks old
	16	Newborn, still wet
	21	Baby less than one month old
	25	Baby about three weeks old
October	7	Baby about one week old
	15	Baby about two weeks old (killed by baboon)
	18	Copulation observed
	28	Female killed, not lactating; had female fetus near term with total length 830 mm., weight 5.2 kg.
November	1	Baby less than one month old
	3	Baby less than one month old (killed by baboon)
	8	Baby less than one month old

but this may be the result of the increased visibility at those periods of the year as well as our increased number of observations then. Mentis (1972) indicated that only single births are recorded for nyala, and our limited data confirm this.

Nyala probably give birth in the cover thickets, and during the day on September 16, 1973, a newborn female, still wet, was found on the top of a termite mound in a thicket. The mother ran off when the car approached. The ground was damp where the afterbirth might have been and we presume that it had been eaten by the mother. The baby was marked and put back where it had been, but it did not stay quiet and tried to follow us without any indication of fear. She nuzzled the nose of one of us who was lying on the ground. The baby was sturdy and could walk virtually without staggering. She was able to walk down from the top of the termite mound without falling. About 2200 hours on April 22, 1974, we found a newborn male nyala, still wet and with about 100 mm. of umbilical cord. The mother ran off as we approached. There was a damp spot on the ground, but no afterbirth. The baby was marked, but did not try to follow us. This birth evidently took place in the open, not in a thicket.

On a few other occasions we encountered very small nyala in thickets, and we believe that for the first few weeks of their lives the babies are left by the mothers in the thickets. On two or three occasions we saw very small animals following an adult female, and in some of these instances, when we followed, the adults and babies ran into a thicket, but later only the adults emerged. When hiding in a thicket, the baby lies flat on the ground with the head and neck extended and the chin touching the ground; the ears are pressed flat against the neck. We have never seen baby nyala nursing, and we believe that this takes place in the cover of a thicket.

At birth, nyala measure from 810 to 830 mm. in total length (about 40% of adult male total length) and weigh from 4.15 to 5.5 kg. (4.5% of adult male average weight). They are about 493 mm. (475 to 530 mm.) in shoulder height (44% of adult male height; fig. 26). The fetal sac and fluids, including a 5.2 kg. term female fetus, weighed 8.1 kg.

We have seen baby nyala estimated to be less than one month old in February, March, April, June, July, August, September, October, and November. We have found females with term fetuses in February and October. We found one female with a male fetus with a crown-rump length of 160 mm. and a weight of 170 gm. at the end of February, and a dead female found in July had a 641 mm. fetus that weighed 2.1 kg. Lactating females have been found in April, July, and September. Females with small fetuses and with milk in their udders have been found, further supporting the data that they may breed shortly after parturition. See table 9.

Activity. Where heavily persecuted, nyala tend to be very secretive and shy, and crepuscular or nocturnal. In the Zinave area and other protected regions, they are active throughout the day and spend most of the night in thickets. During the rainy season, when much green food is readily available, they seem to spend more time in the shade of thickets especially during the hotter parts of the day (30° C. or higher) and perhaps do more feeding at night. In the dry season they are not only more easily seen, but must wander more widely in order to find food and water and thus tend to be more active during the day. In the dry season, when the mornings are cool, nyala tend to remain in the thickets later. The thickets seem to trap some warmth, and we have noticed that on overcast and windy days nyala also seem to remain longer in the thickets. During the heat, especially at midday, the nyala also shelter from the sun in thickets or the shade of trees.

In July, 1973, we followed an adult male and an adult female each carrying radio transmitters from about 0830 until about 1700. Although we tried to remain far enough from the animals to avoid influencing their movements, we also tried to observe what they were doing. Although we suspect that our presence may have caused these individuals to move more than they might ordinarily have, we feel that the activity and movements that we record in the following lists are representative of the animals' activities during the dry season. Both walked some 10 to 12 km. in a roughly oval path that was entirely within the home range of each of the animals as previously and subsequently established (fig. 27).

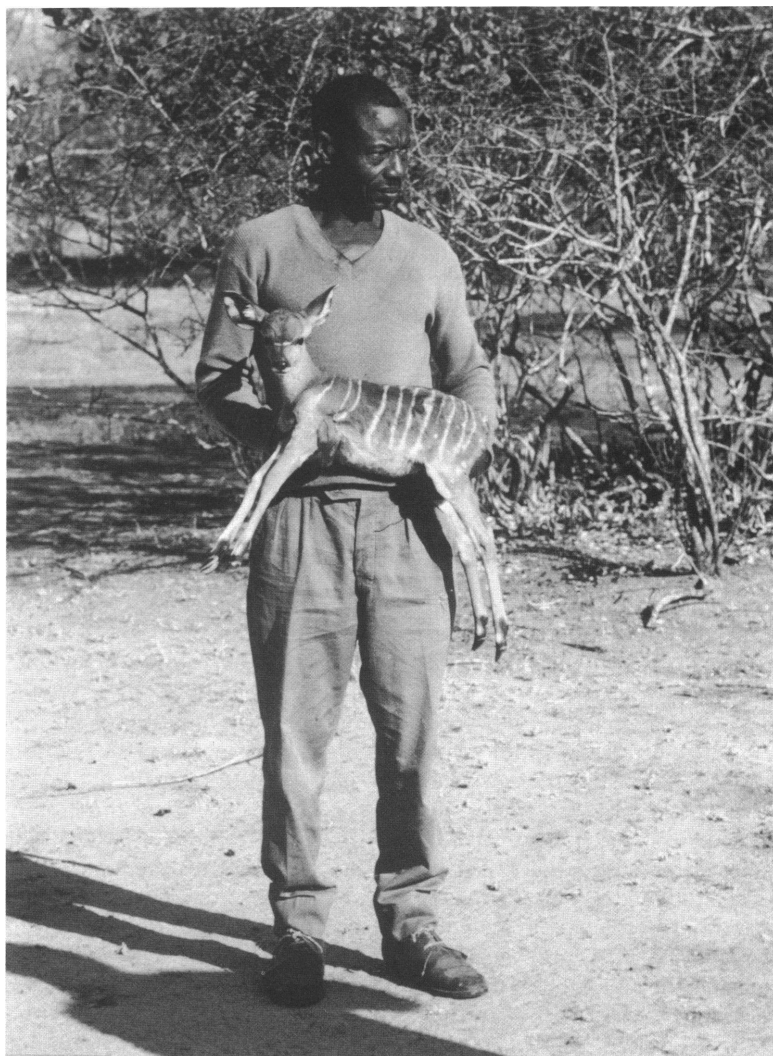


FIG. 26. England with very young male nyala, weight 4.15 kg., October, 1971.

Daily Activity of Keyser, Adult Male
July 17, 1973

- 0825 Sight Keyser alone.
- 0827 Walking south toward thicket, moving along edge, tail twitching.
- 0830 Standing in shade in thicket, 21 seconds later moved off slowly with much tail flicking. Shade temperature 26° C. Another male in thicket with female.
- 0834 Keyser in thicket watching us at 60 m.; did not join other male or female.
- 0837 Keyser walking in sun between thickets to about 3 km./hour and stopped in thicket.
- 0848 Sun temperature 26.5° C., shade temperature 26° C.

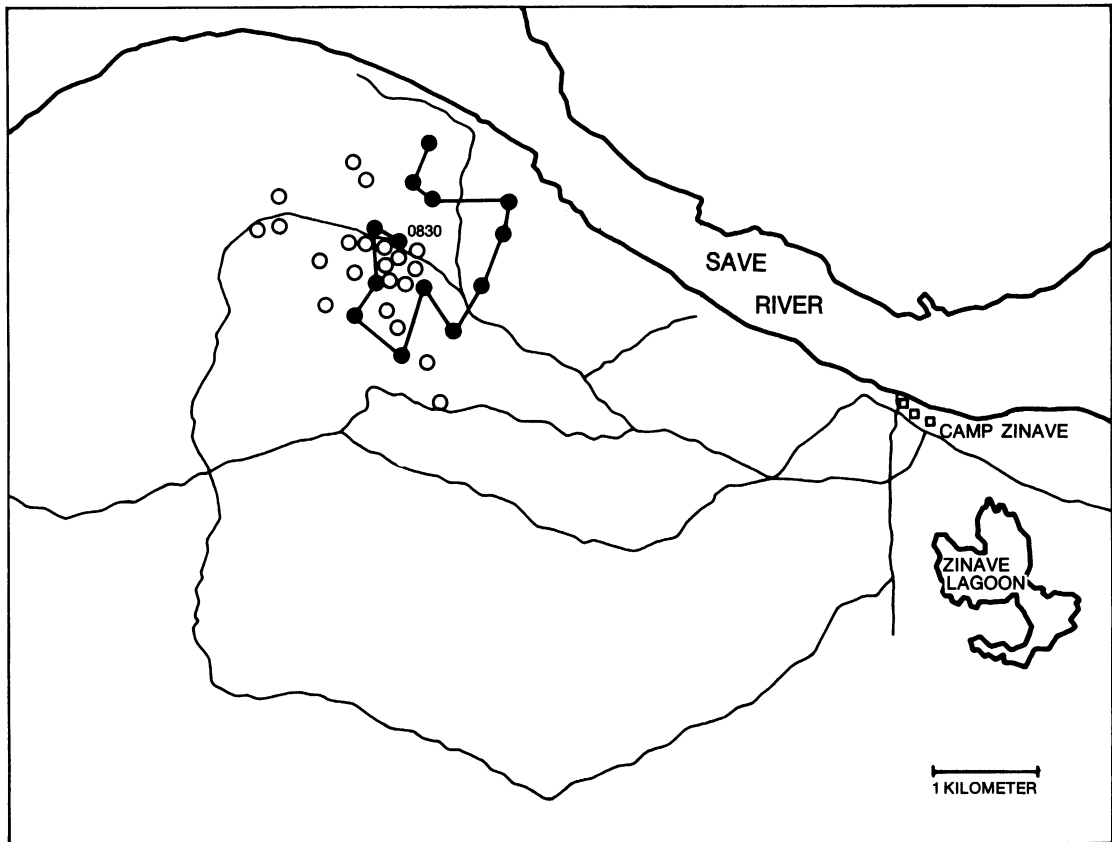


FIG. 27. Movements of Keyser, an adult male nyala (solid circles with connecting lines) over a single day, starting at 0830 hours. Open circles are other records, where Keyser has been observed.

0851 Walked to thicket and although not visible to was walking in thicket as determined by 0952 radio.

0956 Seen drinking from pool of stagnant water in thicket. Walked away when we stopped. Sun temperature 29° C.

1002 In thicket, not visible.
to
1055

1100 In shade watching us, then ran off, walking to in open 2.5 to 3 km./hour.

1105

1105 Sporadically eating leaves from ground for to several minutes; then walking between 1130 thickets, picking leaves from ground as he moved. Went into thicket. Sun temperature 36° C.

1134 Moved into thicket where another male was 50 m. away. The other made head-down display toward Keyser, then turned slowly broadside to Keyser and put crest down and turned head.

1138 Keyser encountered another male, no displays, and they separated going in 45-degree directions.

1140 Keyser approaches another male, who erects crest, stands at 30 m. with head up. Keyser stops and displays, head high, crest up, tail down, and other male moves off with crest down. Keyser noses own right flank, then feeds from ground.

1145 Keyser passes another male who goes into head-up display at 30 m. Keyser also displays head up. Keyser moves off feeding,

- and the other also feeds. Other male had tail arched.
- 1150 Keyser displays head up, tail arched, state-ly walk to another male in head-up display. The other turns away. Keyser feeds from ground after displaying.
- 1150 Keyser walking, picking leaves from to ground, browsing in thickets. He is joined
1217 first by one male, then by second male, all feeding from ground under same tree.
- 1221 Keyser still feeding from ground in same spot. Other two males have moved off. Shade temperature 28° C., slight breeze.
- 1225 Keyser feeding from ground, walking to through thickets. Two other males nearby.
1305 Sun temperature 30° C., slight breeze. Keyser seen standing in shade, ruminating.
- 1305 Had moved 300 m. while we stopped for to lunch. Standing alone in thicket. Shade
1345 temperature 30.5° C., slight breeze.
- 1352 Moving through thickets, feeding from to ground. Once levered a branch between his
1420 horns. Walking at about 1.5 km./hour.
- 1425 Keyser passed by adult female Leslie; Keyser follows.
- 1430 Keyser alone again, no sight of Leslie.
- 1437 Eating leaves from the ground in thicket, to then ruminating.
1444
- 1445 Standing still in thicket, probably ruminat-
to ing.
1509
- 1509 Walking slowly from thicket to thicket, to feeding from ground.
1614
- 1617 Standing in shade of baobab, ruminating.
- 1621 Walks off, sometimes feeding from the to ground, heading toward river. Sun temper-
1700 ature 30° C., no wind.
- 1702 Keyser joins group consisting of four adult females, one subadult female, two imma-
ture females, an immature male with 75 mm. horns, and one with 25 mm. horns.
- 1707 Other group has gone away, Keyser alone to again and walking slowly toward river,
1745 sometimes feeding from ground. Air temperature 28° C. Sun is down at 1717.
- Karina, Adult Female
July 18, 1972
- 0826 Located Karina with adult male, another female, small juvenile, immature male with 75 mm. horns, and another immature, unsexed.
- 0831 Karina ran off with group.
to
0836
- 0842 Karina walking, probably alone, moved to into large thicket and stood there. Shade
0958 temperature 25° C.
- 0958 Left thicket and walking in open with an to adult male and another adult female.
1010 Three walking together, feeding from ground. Male is probably the one seen with Karina at first sighting.
- 1014 Karina standing under tree, perhaps rumi-
to nating, others have moved off. Sun tem-
1030 perature 29.5° C., slight breeze.
- 1030 Karina ran from thicket for 30 m., stopped in shade, and then started walking. Male
1150 appeared to be following. Karina followed by male at about 10 m. walking and going into thicket. Sometimes eating leaves from ground.
- 1157 Karina and male still walking slowly, feed-
ing from ground. Joined adult female, sub-
adult female, and immature male with 225 mm. horns.
- 1159 Karina and male parted from group. Stand-
to ing in shade, ruminating.
1209
- 1209 Karina and male join the same three ani-
to mals and follow them.
1218
- 1218 Karina and male separate from others and enter thicket where there is standing water. Four minutes later they leave thicket running with three other nyala and some impala. Something, not thought to be us, scared them.
- 1224 Karina and male leave other nyala and to impala and move off together, feeding
1233 from ground and enter thicket.
- 1237 Karina and male with three or four other nyala.
- 1247 Karina and male alone together in tree savanna.

- 1250 Suddenly Karina and about five nyala running, Karina with tail up, followed by one bull, then two more that displayed for one and a half minutes, one bull with tail showing white, but both bulls with head up walking parallel, then going in the direction of Karina.
- 1255 Karina with three adult females and immature male; two bulls walking off in other direction.
- 1257 One adult male now heading back toward Karina and female.
- 1301 Karina with male approached by another male. The two males go into head-up displays with tails flared and showing white. First male walked toward and parallel to second male and as it neared his rump gave a run and leap past his rear, then continued to display walking off. Second male now drops his display and picks food from ground. Karina pays no attention during two minutes this took. The horns of both males are about equal length.
- 1312 Karina now following a male (not the one that had been with her all morning), and original male is 50 m. in front of him, walking and picking leaves from ground.
- 1340 Two males with Karina, second male closer, original male 65 m. away, ruminating in shade.
- 1341 Original male starts to walk toward Karina and second male. Walked toward him and both displayed head up but with tail arched, not straight up. Walking parallel 15 m. apart. Then original male walked to other male and made head-up, tail-up display, passing broadside to lowered head of number two who backed away, turned; then both males walked parallel. Karina feeding from ground. Original male passes close enough to lowered head of number two to receive horns in his side, if latter had thrust head forward and had not backed away.
- 1346 Original male together with Karina again, both feeding from ground; number two male is 120 m. away.
- 1350 Karina walking and feeding from ground.
- 1357 Karina and original male walking slowly, 3 to km./hour, no sign of male number two.
- 1419 Browsing from tree, feeding from ground,

male following. They go into thicket. Sun temperature 34° C.

- 1425 Karina and male join adult male and two immature females and follow.
- 1427 Karina and male in thicket; others are gone. Feeding from ground. Baboon passes
- 1438 male 10 m. away, but male does not lift head.
- 1511 Karina and male have walked about 250 m. in half hour, are in thicket, possibly ruminating. Shade temperature 30.5° C., slight breeze.
- 1535 Both animals in thickets, not moving to much, perhaps ruminating. They are relatively near river, and have traveled about 11 km. during day.

Social behavior. Nyala have been described variously as solitary to herd animals, and until now no quantitative data on their assemblages or descriptive material on their social behavior has been presented. From our observations we believe that the nyala in our study area represent a loose and flexible aggregation and that the species exhibits a limited repertoire of observable behaviors.

We have no evidence that nyala are in any way territorial. We have found no evidence of territorial marking or defense, no restricted birthing season, and we have observed unantagonistic associations of two or more adult males with or without females at all months of the year. From radio-tracking and repeated observations of identifiable individuals we have determined that there is considerable overlap in the home ranges of many males as well as females and that one individual may be seen in association with a large number of other individuals or groups, or be seen alone, within a period of a few hours. We now believe that all the resident nyala within a specific area know and recognize one another and associate freely among their spectrum of known associates.

Among the adult males, we believe, a dominance hierarchy exists, and we have seen a number of times a dramatic sequence of displays and movements that we interpret as challenges and status rituals. The main components of these displays are the erection of the dorsal white crest, the elevation of the tail, the position of the head,

and the manner of walking. All the displays that we have seen have been between fully adult males, and although we have seen interactions between an adult male and an immature male, the activity was clearly a different one.

The displays between adult males have been seen in two main contexts—between males only and between males of which one was accompanying a female. Most of the time when two adult males come together there are no displays, and the animals generally walk or feed side by side, separated by 1½ m. or more, or trail one another the same distances. Once, however, a male ran out of a thicket from which we had probably startled him toward two males we had been following. All three males erected their dorsal crests and elevated their tails. The two that we had been following lowered their heads so that their horn tips faced slightly forward and stood still, facing the same direction, parallel to each other, their bodies at right angles to the path of the third male. The last, with mane erect, had his tail arched but did not display the white underside, and had his head held high and neck arched, horns vertical. He commenced a high-stepping, slow, deliberate mincing walk in a direction to pass in front of the heads of the other two. These maintained their position and stance while the third male passed in what we call the “stately walk” about 4 m. in front of them and continued walking away from them. When he was about 30 m. past them, all three animals relaxed their crests and positions and the original two males continued walking side by side into a thicket.

We have interpreted this sequence of events to represent status displays between two individuals known to each other toward another who is a stranger. We believe that the head-down, horns-forward position is that taken by the more dominant animals, and that the stately walk, while a challenge, is that of the subordinate or less secure males. The triggering of these displays may well be flashing expanse of white, as when the underside of the tail is displayed and fanned out. One male nyala whose ears we had marked with white plastic streamers seemed to undergo an unusual number of challenges during the hours we followed him, but many of them seemed rather half-hearted. We suspect that these challenges were triggered by the flashing of white from the

streamers, or because they made a known individual appear initially as a stranger.

Displays between adult males were seen only once during our joint observations in September and October, 1971, several times in September, 1972, and almost daily in July, 1973, and not at all in April, 1974. To some extent these variations may be the result of our specific objectives in observation in these years or the decreased visibility in 1974, but we feel that the data for 1971-1973 reflect a real difference in male-male displays. It was noted that after July, 1973, the frequency of displays diminished markedly.

We assume that, in the absence of females, the displays between males are a status determination, as there seemed to be no food, space, or other item as an object of immediate possession or competition. In none of these displays did the exhibiting males remain together afterward, but always continued their separate ways.

We have concluded that the head-up, stately walk is the display of the subordinate or less secure individual, and that of the head-down, horns-forward position is that of the dominant animal. None of the displays are given face to face, and most commonly the subordinate animal walks by the head of the dominant one at a distance of several meters or more—well out of the range of injury that could result if the dominant male should choose to thrust his horns forward.

Maberly (1963) mentioned this male display, but indicated that the head-down position is combined with the “stiff, mincing gait,” a combination we have not observed. He further noted that a tame nyala male that had become an “affectionate member of the household does this always as a sign of pleasure and ‘greeting.’” Unfortunately, he did not give details of the head positions, and the animal could be either indicating a dominance threat or a subordinate display. At the Bronx Zoo in New York an adult nyala bull approached by one of us within his paddock went into a standing head-down dominance-threat display as described above. In another field observation, six males were walking single file, but were also passing one another. As the passer came up on the level of the one in front of him, the one in front raised his dorsal crest slightly and lowered his head slightly. As soon as the passer was a head-length in front, the

display ceased. The animals were passing about 1 to 1½ m. apart.

Our conclusion that the standing, head-down position is dominant and that the head-up, stately walk is subordinate is reinforced by our observations of displays by males that were with females. Our first such observation in October, 1971, involved an adult male and female that we were watching as they were standing in the open about 40 m. from a thicket behind them. Suddenly the male put down his head, erected his mane, and flipped his tail up onto his back somewhat over on the right side, exposing the bright white underside. About 10 seconds later an adult male emerged, from the right, from behind the small thicket with his head up, crest erect, and tail arched, but not exposing the white. This male made his stately walk at right angles to the plane of the body of the head-down standing male, passing some 30 m. behind him. As the stately walker passed the midline of the standing male, the latter flipped his tail over to the left side of his back, thus keeping the white underside exposed to the male now moving away from him. About 50 m. apart, both animals lowered their crests and returned to usual attitudes, the first male following the female that had wandered a little distance off. In this case the stationary animal maintained his association with the female, while the stately walker continued on his way.

Another observation of display between males when one was accompanying a female was somewhat more complex. At 1312 hours on July 18, 1973, an adult male was displaced from his association with a female that he had been accompanying since we had started following her at 0826 hours. Twenty minutes before, however, there had been several males moving toward the two and displaying. Ten minutes before, a male had approached the male that had been with the female and both had gone into a head-up display with their tails erect and flared out. The two were walking parallel to each other and when the newcomer approached the original male, he made a run and leap past his rear and continued to walk off still displaying. The original male dropped his crest and fed from the ground. We did not see the details of the activity that resulted in male number one being displaced by

male number two, as we were partially screened from the animals by a thicket and were some 200 m. away. By the time we were in a position to observe clearly, the second male was 3 m. from the female and the first male was some 50 m. away. The two males and the female were now feeding from the ground on fallen leaves. The males were about equal in size and in length of horns.

After about 30 minutes the displaced male erected his mane, arched his tail, and commenced a stately walk over the 65 m. that now separated him from the female and second male. The two males walked, heads-up, parallel to one another, 15 m. apart. The second male assumed the head-down stance, with his body broadside to the path of number one, but with his tail arched, not straight up or over on his back. His head was perhaps lower and his horns were pointing forward more than we have observed in any other male. Number one continued his stately walk with his tail erect and came to pass the head of number two so closely that had the latter desired to thrust his horns forward, he could easily have penetrated the other's side. Instead, number two abruptly backed away, withdrawing his head out of thrusting range, and then turned away and began a stately walk away from number one who was now approaching the standing female. In a few seconds both males had dropped their crests and were feeding from the ground, and number two wandered off and was soon out of sight. Number one continued his association with the female for the rest of that day.

In this instance, we believe, the challenge by number one to regain his association with the female was strong enough to require the second male, temporarily holding the dominant position, to enforce his dominance with a thrust of the horns at the side of the challenger. By failing to do this and backing away, the first male again assumed the dominant status and the second male wandered off.

A third observation involved a charge by a male. On July 23, 1972, an adult male was seen following an adult female and a subadult. Two males approached the trio from the rear and one side, and the accompanying male turned broadside to the other two males, erected his crest, low-

ered his head, and charged a few meters at them. The two males ran off and the male rejoined the females again. The adult female urinated, and the male put his neck over her neck and remained that way for some 30 seconds. The female urinated again, and the male turned and tasted the urine, sniffed, raised his upper lip, and then copulated briefly with the female. The latter then started walking again with the male following with his nose very close to her tail. Another male with horns longer than those of the first male started following the group. When he approached the first male, however, the latter again displayed his crest and when the second male did not stop, the first lowered his head and charged, and the intruder ran off. The first male again returned to following the two females.

All of our observations of displays between males have been of animals when displaying parallel to one another—side by side—or with one animal at right angles to the other, either at the front or rear. In no case have we seen a face-to-face confrontation during a display. In fact, face-to-face encounters by male nyala, with or without display, are so exceptional that we suspect that there is deliberate avoidance of such a meeting. Once in 1974 a startled male running around a thicket came face-to-face with one feeding from the ground and that one immediately threw its head high and back, exposing the broad white band on the chest, and the first animal quickly turned away from the other. Another observation was identical, except that both animals were running when they came face-to-face, and both threw their heads back before each turned away.

Fighting between adult male nyala seems to be extremely rare. We have never observed it, nor have our knowledgeable Shangaan trackers. However, on August 15, 1973, G. Cowan reported (field notes) two males in a thicket fighting: "horns locked with heads down—on all four feet—a pushing competition. Unlocked horns twice, not lifting heads more than parallel to ground before head on clash with some force. Only slight twisting of head and neck, manes of the neck mostly up, although at base of back relatively flat. Alternately gaining ground until one got tangled in thicket nearly falling over. Victor did not take a cheap shot at exposed flank

but looked up at vehicle as did loser and both fled." Car was 10 m. away and neither paid attention to it when it drove up. The fighting observation lasted two minutes. Roberts (1951) mentioned two males "playfully clashing their horns together" at night. Some male nyala skins show scars that might have resulted from horn wounds, but the majority do not.

On a few occasions we have observed adult male nyala thrashing low bushes with their horns in mock fighting. As mentioned under Food, nyala males also thrash branches to drop leaves that would otherwise be out of reach. When the ground is soft during the rains, nyala males are sometimes seen with mud caked on the ends of their horns, and have been seen plowing with them. Field assistant G. Cowan reported (field notes) in July, 1973, seeing two males at a water-hole dig their horns into the mud quite forcefully before drinking, and in April, 1974, we killed an immature with 200 mm. horns that were caked with mud to the base. The function of this is not known. At the Bronx Zoo, in the spring when the nyala are released from indoor winter confinement for the first time, the adult male has been seen plowing the ground with his horns. Deane (1962a) described a male nyala at Hluhluwe in South Africa digging its horns into moist soil one at a time and moving its head back and forth. He believed that the animal was sharpening its horns.

Behavioral interactions between adult males and males of other ages or between them and females were rarely observed by us. In September, 1973, a subadult male was seen approaching an adult male that gave a brief display of dorsal crest, to which the subadult responded with a slight raising of the crest on the neck and moved 2 m. away from the adult. While feeding from the ground, this subadult again approached the adult without any reaction by either of them. In October, 1971, an adult male, with an adult female, and an immature male and female turned and made a head thrust at the immature male (horns 180 mm.). The adult male was following the female by about 15 m. and he was followed by the immature female 20 m. behind; the immature male was 8 m. behind her. When the adults stopped, the younger nyala approached within 1 m. of the adult male. Without erecting

the crest or tail, the adult male turned, lowered his head, and thrust at the immature male, who dodged away. This was repeated 10 seconds later. The immature male then walked parallel to the adult, but when he dropped behind was again subjected to a lowered head and thrusts and again 10 seconds later the same thing occurred. The immature male dodged around and moved to walk 8 m. in front of the adult and between him and the adult female. Ten minutes later the immature male had dropped back and was 15 m. behind the adult, and eventually the two immatures were 4 m. apart and trailing 40 m. behind the adult male who was now 60 m. behind the adult female. Of note here is the fact that the adult male threatened the immature male only and only when it was close behind him. When the immature was parallel to or in front of the adult he was ignored. Both the females seemed to pay no attention to these activities and continued walking. In August, 1973, the senior author leading a hunting party on the north side of the Save River came upon two adult males and one adult female. One male was shot, and at the sound, the other male ran strongly at the female and attempted to horn her before running off.

Except for the observations of copulation mentioned in the section on reproduction, and observations of "Flehmen," adult males do not seem to exhibit much social behavior toward females. When in mixed groups of nyala, males walk usually in single file and tend to be nearer the rear of the groups than the front, although it is not uncommon to find them anywhere in the line. They seem not to be spaced apart from the others to any noticeable degree. Similarly when associated with other adult males only, no specific organization has been noted except that two males together may commonly walk more or less side by side 5 or more m. apart, rather than behind one another.

Behavioral interactions between adult females have not been apparent to us. While there do seem to be some spatial parameters for single-file walking, these are not strong, and although two or three body lengths apart seems most common, they may trail one another by only a head length. The groups of females and young or of mixed ages and sexes are so transient that we have not been able to determine whether there is

any consistent leadership, and we doubt that dominance exists among adult females. The leading animal in a group is, however, most commonly an adult female, and when a group consists of only one adult female and some young, the latter are usually following rather than leading.

On August 27, 1973, from 1130 to 1245 hours, nine nyala were observed lying in the shade of a tree ruminating. They formed four groups: two adult females, an adult female and a juvenile, an immature male and immature female, and two immature females. Each member of these pairs was close enough to the other to be able to engage in licking the face, ears, neck, and shoulders of the other, as well as licking themselves on the shoulders and legs. The only other occasion that we have observed mutual grooming involved a juvenile licking the neck of an adult female. We assume that mothers lick newborn nyala. Nyala hairs have been found in the stomachs of two of the females we dissected. The ninth member of the above assemblage, an adult male, lay apart from the others and did not engage in grooming either others or himself, but we have at other times seen males licking themselves on the tail, base of the tail, or hind leg. Such licking may serve to remove ticks, which are abundant in the ears of nyala, and we have found an engorged tick in the stomach of a male nyala. We do not know whether adult males engage in mutual licking. Males also scratch their shoulders with their horns by tilting their head back and scratching behind their ears with a hind foot.

As with adults males, female nyala rarely encounter one another face-to-face and perhaps engage in specific but unnoticeable activity to avoid this. The only face-to-face encounter of which we have knowledge was between an adult female and a very young baby, in which some form of greeting behavior, face-to-face, with muzzles touching took place. As mentioned elsewhere, newborn nyala, although capable of standing and walking almost immediately after birth, do not regularly follow their mothers for at least several weeks. We have not observed nursing, but on one occasion strange behavior by a known female was displayed as we approached, in a car, a thicket near which she was standing. Instead of walking or running off, she seemed agitated and peered at

the car and then looked at the thicket several times. Then she ran in a circle, stopping from time to time to look either at the car or the thicket. This lead us to suspect that she might have just given birth and had a baby secreted in the thicket. As we emerged from the car, the female ran off and stopped to watch us at a distance of 50 m.—much less than normal for a nyala to remain from a man on foot. A search of the thicket did not reveal a baby, but our suspicions were nevertheless strengthened some weeks later when this female was seen followed by a small juvenile.

Unlike many other artiodactyls, nyala mothers do not seem to attempt to defend or even watch their babies. Several times we chased females with juveniles estimated at less than one month of age. If the animals reached a thicket, the female always emerged, continuing to run, leaving the baby hiding in the thicket. A few times, however, the mother ran off at full speed, and the baby was left behind. The baby eventually ran off in a different direction to some form of cover while the adult went out of sight another way. How or if the mothers relocate their babies in these instances we do not know. Once (April, 1974) we found two juveniles hiding together in a thicket, one estimated at one month old and the other at two or two and one-half months. Robbins (1972), however, described a female nyala clearly defending a newborn calf from attacks by bateleur eagles (*Terathopius ecaudatus*).

When juveniles are old enough to follow their mother, they do not stay any closer to her than do other nyala when following one another, i.e., several body lengths away. In fact, when we observed a group that contained several adult females and several juveniles or even several adult females and only one small juvenile, we could never be sure which adult was the mother.

The urge to follow seems to be somewhat stronger in females and young nyala than in adult males, but an animal of either sex or age that is alone will generally, even if briefly, turn to follow a nearby group of walking nyala. A single nyala, usually a female, walking within a herd of impala is not an uncommon sight.

Other than two observations of "Flehmen," we have also twice seen adult males smelling at

the base of the tail of females. The latter either paid no attention or had the tail pressed close against the anus and vulva and curled under the body. Otherwise, we have not noted any signs of olfactory communication. Nyala are not especially endowed with external glands, and we have pointed out elsewhere in this paper that we believe Haltenorth's statement regarding inguinal glands in the males to be in error. The evidence for pedal glands is also inconclusive. Nyala presumably have a good sense of smell, although under the conditions of our investigation, their awareness of us came from sound and sight first. Other than the horn thrashing described earlier, which we do not believe involves marking, nyala seem to have no particular defecation or urination spots or other forms of marking, unless digging in soft soil with the horns is such a device. Similarly, nyala do not seem to display any sizable amount of tactile communication, and other than the observation of mutual licking described before, nyala do not usually touch one another.

If nyala engage in much vocal communication, it is either inaudible to us or quite uncommon. Compared with the two other tragelaphines that are common in the area, bushbuck and kudu (*Tragelaphus strepsiceros*), nyala are relatively silent. Nyala are capable of a bushbuck-like bark, but this is seldom heard, and in our experience has been made as a result of an animal being startled, as, for example, when one was surprised by a stealthy approach on foot. Roberts (1951, p. 311) described a "loud double-bark" that he attributed to nyala. Another sound that we have heard is a reverberant "ooooonk," somewhat drawn out. We have heard this from injured female animals that we were restraining, and on one occasion this sound was heard at night, and the next morning a female nyala was found close by, killed by a leopard. Cowan (field notes) described perhaps a similar sound by a female that was separated from her very young calf by the car, and which could not seem to decide whether to flee or to go to the calf.

The lack of strong evidence for extensive vocal/auditory, tactile, or olfactory communication, tends to confirm our belief that much of the behavior of nyala is oriented through sight. The virtual absence of behavioral interactions between adult males and females can be attributed

to the enormous difference in size, the horns, color, and shape between them. The sexual dimorphism in nyala is the greatest of all the tragelaphines and among the greatest of any ungulates. If males are dominant over females, the assertion of this or the demonstration of masculinity would be largely unnecessary as there is no mistaking a male for anything but a male. The pattern of spots and stripes on both males and females, the consistency of some markings and the variability of others had led us to hypothesize what these markings communicate to nyala.

A large expanse of white, as an exposed underside of the tail, an erect dorsal crest of a male, or the exposure of the band of white on the chest is essentially a warning. To a lesser extent the chevrons on the face of the male also serve this function. When males display their dorsal crests to one another the animals are always in a position to view each other broadside, either by walking parallel or at right angles to one another, but never head-on or head to tail. This broad line of white, running the length of the body, functions, we believe, in male-to-male dominance communication. The flashing of the white underside of the tail, both by females and males, is essentially a warning of an interspecific threat, and in our experience, the hairs of the underside, at least in males, are not flared out as they are when the white undersurface of the tail is utilized in intraspecific behavior related to status between males. The white band on the throat usually is not conspicuous, but as we have noted, when two males accidentally ran toward one another head on, one threw his head back, exposing the large white expanse low on the throat, and the other male stopped and turned away.

The vertical stripes of the body are most conspicuous in females and younger males, and their number and intensity are variable. If they serve a communicatory function, rather than a protective one as cryptism, then the message may be species or individual identification or may be a neutral, no-warning or no-threat message. In some males, at least, the fact that these stripes may be scant or scarcely visible, leads us to attribute a relatively minor role to them as mechanisms of communication.

Nyala of either sex also have white spots on the side of the face, at the knee, and at the base

of the tail. Although white spots may be present elsewhere, nyala are consistent in having these, and we believe that they, too, play an important role in the behavior of this species. The visualization of white spots communicates a condition that permits approach. The consistent presence of dots on the knee area, lateral to the mammary glands of the female could serve as an orientation and learning device for the suckling newborn. The association of dots with allowing permissible approach could also lead to following behavior, utilizing the two dots at the base of the tail. The presence of the white patches in the ears of juveniles, likewise, may serve to encourage the mother to approach her baby head-on in a thicket, an approach not otherwise employed by nyala (fig. 28).

The white spots on the cheeks and chin and the white spots on the legs may enhance recognition of individuals, permit animals to cross at right angles to one another, and facilitate the mutual grooming described earlier. The tips of the horns of nyala are whitish, but we do not know how this may relate to visual communication, except that from the rear and from the side they provide additional white spots that might encourage approach. From the front, however, approach is not encouraged, and here the facial chevron, brighter than the horn tips, may dissuade it. The chevron is consistent and bright in all males, but in females it is not always present, perhaps fading most in older animals (figs. 29, 30).

The position of the head and tail, when combined with erection of the crest, communicates social information by the males. We believe that a male nyala with his head lowered (and the horns facing vertically or slightly forward), standing still, with the crest erect and the tail either arched, erect, or flopped over onto the back to display the white underside is showing the most dominant stance. A challenge is generally displayed by a male that is walking, has the crest erect, but has the tail arched and the head held high with the neck arched. The head-down position was used to threaten an immature male, as described earlier, and the head-down, standing-still position was used by a male that continued his association with a female when challenged by a display from an animal with crest erect, neck



FIG. 28. Very young nyala. Note conspicuous white patches in ears. These are lost by three months of age.



FIG. 29. Adult male nyala, showing conspicuous white markings on nose, lip, cheek, and horn tips.

and tail arched, performing a stately walk. Numerous other observations of displays of the crest with the tail arched, but walking normally, have not resulted in any further interaction and indeed often ended with association of the two males for a while. The only exception to the hypothesis that the head-down position is dominant occurred in the case of the male attempting to regain his association with a female (described earlier). In that instance, the head-down animal was approached so closely by the stately walker that he had only the alternatives of thrusting with his horns or withdrawing; he did the latter, and gave up his association with the female to the other male.

The preceding analysis of the role of the markings in nyala is, of course, highly speculative

and is based on a large number of disjunct observations rather than on continuous observation of known individuals. Because there do not seem to be strong permanent groupings among nyala, we presume that visual communication must be somewhat standardized and uniform to enable aggregations to form and reform.

The tragelaphine antelope tribe includes, in its broadest sense, the bongo (*Tragelaphus eurycerus*), the bushbuck, the mountain nyala (*T. buxtoni*), the lesser kudu (*T. imberbis*), the greater kudu, the sitatunga (*T. spekei*), the nyala, and the elands (*Taurotragus oryx* and *T. derbianus*). These species have variously been arranged in monotypic genera (e.g., *Boocercus* for bongo, *Strepsiceros* for greater kudu, *Ammelaphus* for lesser kudu, *Limnotragus* for sitatunga, *Nyala* for



FIG. 30. Adult male nyala, head on, showing how nose chevron and white markings on lips form conspicuous bars.

nyala, and other arrangements reviewed by Ansell, 1971). The behavior of this group has been little studied, but in general what has been published does not suggest territoriality for this group. At least, nyala do not seem to show it, nor has it been observed in various studies of both kudu, mountain nyala, bushbuck, or eland. Various types of aggregations or associations seem to be the rule.

The display behavior reported by Waser (In press) for bushbuck is remarkably similar in many of its components to that which we have seen in nyala. Bushbuck and nyala are noteworthy for the absence of much fighting between individuals, especially males. Waser recorded only two instances of mild aggression between males in more than 200 hours of observation of bushbuck, and we have yet to observe adult males fighting in more than 1000 hours of joint observation, although others (p. 372) have seen it. It has been popular in the literature of behavior to imply that aggression is as characteristic of a mammal as a head or lungs. We prefer not to regard an attack against another species in defense of young or home as equatable with a fight with or a threat to a conspecific (as does Ewer, 1968, pp. 155-157). We regard threats or fighting as particular behavior patterns which may be utilized to satisfy different motives. Much of what is described as aggression in the behavioral literature seems to us to be motivated by a desire for status. If status, or dominance, can be achieved without threat or fighting, then aggressive behavior against conspecifics need not be a part of the regular behavioral repertoire. We suspect that the size, strength, and weapons of adult male nyala are so obvious to the smaller, hornless females that no aggressive behavior is necessary to express male dominance over females. Similarly, we suspect that the status of males in relation to other males is learned by immature males associating with adult males and by rare threats with the horns. Subsequently, dominance may be maintained by the male displays we have described and without necessitating actual fighting other than in exceptional instances.

Walther (1964) presented much information on the behavior of tragelaphine antelopes. Unfortunately, much of his data is based on observations of captive animals in zoos; all his nyala data

are based on the unpublished study of the Bronx Zoo's herd made by Burckhardt, and many of his generalizations for the tragelaphines as a group are not confirmed by our field observations. Among our disagreements are his generalizations that mutual grooming is frequent and extensive, that males frequently thrash trees or bushes with their horns, that young females tend to attack young males, that there is much "playing," and that except during flight from danger, movements of the tail have no great significance in social life. Overall, Walther often finds that the bushbuck is an exception to his generalizations for the two species of kudu, and the sitatunga, and he tends to ally the nyala behaviorally with the last three species. We find that the nyala, to a considerable extent, bridges the behavioral gap between the bushbuck and the more social species and believe that phylogenetic conclusions must await more detailed field studies of all of the species, especially the sitatunga.

Animal Associates and Competitors. Although nyala were most commonly associated with other nyala, it was not a rare sight to see one or more nyala in with a herd of impala, waterbuck, or kudu, or a herd of nyala interspersed with a troop of baboons. With the latter it was generally a search for common food that brought the two species together, and we once watched nyala eating parts of *Strychnos spinosa* dropped by baboons. For the associations of nyala with impala, waterbuck, or kudu, a common search for food may have been one attraction that brought the species together, but we believe that the tendency to herd and follow in these antelopes, and to follow in nyala, also plays a role.

Nyala generally responded to impala alarms and vice versa. Often our observations of nyala were interrupted because impala, startled by some cause other than us, started running near the nyala and caused them also to take flight. Generally when we startled nyala into flight, nearby impala would start to run.

When we saw nyala interspersed with baboons, we got the impression that each species was ignoring the other, as we saw no signs that would indicate that one was paying especial attention to the activities of the other. We have noted that baboons may be important predators of juvenile nyala, but our observations lead us to

believe that baboons are not opportunistic killers of young nyala, and are not normally reacted to as predators by the nyala. For example, in November, 1973, a juvenile female nyala was drinking at a pool in a thicket with a large troop of baboons alongside her. Neither species showed any interest in the other. Our beliefs are supported by observations in Gorongosa National Park where baboons are known to prey on young bushbuck, but the two species have been seen interspersed without noticeable concern. We suspect that baboons kill small antelopes only when they decide to hunt them, rather than taking advantage of every opportunity to do so. North of Gorongosa Park, the senior author saw a troop of baboons in a semicircle, closing in on a lone juvenile nyala. The male baboons were barking and advancing, and the nyala seemed disoriented and turned away as they barked, eventually walking directly to and being caught by the observer. Hunting of hares (*Lepus* sp.) by baboons appeared to involve most or all the adults of a troop and was well organized, but it is probably an outgrowth of insect hunting and is more opportunistic. The hunting of small antelopes seemed ordinarily to involve only adult males in the hunt, but Paul Dutton (personal commun.) reported a large troop of baboons chasing a juvenile nyala.

Red-billed oxpeckers (*Buphagus erythrorhynchus*) are not uncommonly seen associated with nyala, and we have seen them picking at ticks on the inside ears, on the neck, flanks, anus, and belly of both male and female nyala. The oxpeckers also peck at open wounds.

Competition for food varies with the time of year. It is during the dry season that competition may be most intense. During and just after the rains, those species that graze as well as browse may compete less with nyala, which seem to prefer browse. Impala, in particular, of which there were more than 3000 in the study area, became prime competitors for browse as the grass disappeared during the progression of the dry season. Our observations are that an increasing browse line, from 1.3 m. in 1971 to 1.6 in 1972 and to almost 2 m. in 1973, would put intense pressure on the nyala, especially the smaller ones. The impala not only have alternative foods, if available, but also make more use of grass during

the rainy season when the nyala are still primarily browsing.

Smaller antelopes such as gray duikers (*Sylvicapra grimmia*), steinbok (*Raphicerus campestris*), and suni (*Nesotragus moschatus*) have become increasingly scarce in the study area, possibly as a result of the heavy grazing by impala and the browsing both by impala and nyala. As competitors, presently few in number, they are probably of little importance to nyala. Probably a reduction in cover is as important as the competition for food in having an effect on the populations of these smaller antelopes. Noticeable changes have been wrought to the thickets and shrubs by browsing impala and nyala. With such a high browse line as existed in 1973 there was virtually no cover in the thickets used as refuge by suni and no shrubs to hide duikers and steinbok. We believe that this, as much as anything else, has caused their numbers to decline.

Bushbuck may compete somewhat with nyala, but most of this would be in the riverine habitat and during the dry season. When there are grass and herbs, as during the rainy season, bushbuck would compete much less with nyala. Eland (*Taurotragus oryx*) are so scarce in the study area that their competition with nyala can only be minimal. In the rainy season only, waterbuck compete with nyala for cucurbits, legumes, and grasses such as *Digitaria*.

Among the other browsers, kudu are the main competitors with nyala. Their numbers have increased in the study area during the four years of study, but still are not large. The adult kudus generally can browse at higher levels than nyala and thus may not be in direct competition with them, but during their first year, young kudus are direct competitors with nyala. During the peak of the dry season when nyala feed mainly on leaves and fruits that have fallen to the ground, kudus are in direct competition with them.

Elephants (*Loxodonta africana*) also compete with nyala for many of the same species of browse, and juvenile elephants and adults may browse at the same levels as adult nyala. Adult elephants may provide some food for nyala by pushing over trees that had leaves or fruits out of reach of the antelopes and also in dropping fruits and bark from higher levels. On the whole, we

suspect that despite the direct competition a limited number of elephants in the study area would be generally beneficial to the nyala by keeping some of the trees short. The same might also be true for kudu activity. As with most of the other species, elephants compete most with nyala during the dry season, when they come through the study area on their way to water. In 1973 there were at least 150 elephants traveling through the study area to the river each night in March and April and from August to December, with much effect on the vegetation made by the elephants, some of it in prime nyala habitat.

Among the other species that inhabit the study area and are known to feed on some of the leaves, fruits, or other parts of plants that are used by nyala are bush squirrels (*Paraxerus cepapi*) and red squirrels (*P. palliatus*), baboons, vervet (*Cercopithecus aethiops*) and samango monkeys (*Cercopithecus mitis*), side-striped (*Canis adustus*) and black-backed jackals (*Canis mesomelas*), civets (*Viverra civetta*), and some of the birds, including green pigeons (*Treron australis*), brown-headed parrots (*Poicephalus cryptoxanthus*), brown-necked parrots (*Poicephalus robustus*), purple-crested loeries (*Gallirex porphyreolophus*), trumpeter hornbills (*Bycanistes bucinator*), crowned hornbills (*Tockus alboterminatus*), golden orioles (*Oriolus oriolus*), black-headed orioles (*Oriolus larvatus*), and cape glossy starlings (*Lamprocolius nitens*). Ostrich (*Struthio camelus*) in the area are known to feed on *Salvadora persica*, a major item in the diet of nyala.

Man is also a competitor of nyala both for food and for space. The riverine habitat of the study area is heavily populated by man and consequently much of it is unavailable to nyala for habitat and is used only at night when the antelopes go to the river to drink during the dry season. Although the presence of agricultural crops removes original nyala habitat in the tree savanna, grassland, and riverine sites from use by these antelopes, the transient nature of the shifting farms eventually provides food for them. The legumes, cucurbits, shrubs, and thickets that succeed on the abandoned farms eventually provide food and cover for nyala, especially at the end of the rainy season.

Human beings also use a number of plants uti-

lized by nyala, especially the fruits of *Carpolobia conradsiana*, *Cassia petersiana*, *Coffea* sp., *Ficus* sp., *Grewia* sp., *Hyphaene crinita*, *Manilkara mochisia*, *Maprounea africana*, *Mimusops obovata*, *Mimusops zeyheri*, *Sclerocarya caffra*, *Strychnos innocua*, *Tricalysia* sp., *Uvaria caffra*, and *Vitex* sp.

Parasites and Diseases. We have recorded the ticks *Boophilus decoloratus*, *Hyalomma truncatum*, *Amblyomma pomposum*, *Rhipicephalus muhlensi* from nyala in the Save region as well as the wingless fly, *Echestyphus paradoxus*. In general, nyala in the Save region are not heavily parasitized by these ectoparasites, the ticks generally being found around the anus and in the ears. It is our impression that the ectofauna is heavier as the dry season progresses. Dixon (1964) reported *Amblyomma hebraeum* as well as the *Boophilus* and *Rhipicephalus pravus* and *R. maculatus*, and *Amblyomma hebraeum* from nyala at the Ndumu Game Reserve. We have found the above two species of *Rhipicephalus* on other bovids in the Save region, but not yet on nyala, although it is possible that some are infected.

Vincent et al. (1968) reported *Rhipicephalus evertsii*, *R. appendiculatus*, *R. maculatus*, *Amblyomma hebraeum*, and *Boophilus decoloratus* as ticks collected from nyala in the Hluhluwe Game Reserve and also the hippoboscids fly, *Echestyphus*. Keep (1971), reporting on ectoparasites from nyala in Zululand, listed *Amblyomma hebraeum*, *Ixodes pilosus*, *Haemaphysalis silacea*, *Rhipicephalus evertsii*, *R. pravus*, *R. appendiculatus*, *R. simus*, *R. maculatus*, *R. sanguineus*, *R. muhlensi*, *Boophilus decoloratus*, and the fly, *Echestyphus paradoxus*. We have found *Rhipicephalus appendiculatus* on kudu and *R. sanguineus* on other bovids at Zinave, but not on nyala, and we have recorded *R. simus* on wild suids. Ticks found on other tragelaphines in the Save region, but not on nyala, include *Rhipicephalus neavei*, *R. masseyi*, and *Hyalomma ethiopica*.

Except for a single unidentified nematode found in one animal, nyala in the Save region seem to be relatively free of helminth parasites. One adult female did have a heavy infestation of sarcocysts of unknown cause, and an old adult female that was killed had an undetermined

Widespread skin disease. Keep (1971) listed a number of internal parasites from nyala in Zululand and recorded (1973b) coronary vein aneurysms caused by the helminth *Cordophilus sagittus*.

In general, we found the nyala around Zinave to be only lightly infected with parasites or diseases.

Mortality. We have recorded lions (*Leo leo*), serval (*Felis serval*), leopards (*Leo pardus*), spotted hyenas (*Crocuta crocuta*), baboons (*Papio ursinus*), eagles, and pythons as predators of nyala. Of 24 animals killed by predators, six were by lions. Two of these six were adult males, three were immature males, and one was not sexed. Five of these lion kills were made in an eight-day period in September, 1970, in the vicinity of Alves de Lima camp north of the Save River. The nyala were concentrated around a small lagoon, the only nearby water, and a group of lions was in residence. Leopards are perhaps a more important predator of nyala, and we have records of 10 kills made by them. Of these, six were adult males, two were immature males, one was an adult female, and one was not sexed. Baboons are predators of young nyala, and we recorded four kills, each a juvenile female less than two months of age. In October, 1972, we found a serval eating a juvenile nyala, and we have also recorded the killing of a juvenile female less than two months old, by a tawny eagle (*Aquila rapax*). In July, 1973, we found a dead spotted hyena which had the hooves of a small nyala in its stomach, and in June, 1974, a python was seen swallowing a subadult female nyala.

It is worthy of note that of the 14 animals of known sex that were killed by lions and leopards, 13 were males, suggesting some selection by these predators. The lions' kills are regarded as somewhat exceptional by us, and we believe that of lions and leopards, the latter are probably more important predators of adult nyala. Many of these data have come from outside our particular study area, and to our knowledge, there have been no lions in the study area during the course of our study.

From our data, the major predator of juvenile nyala is the baboon. Although we suspect that in most cases the predation is on juveniles that are alone, having been left in a thicket by the mother, we have observed a baboon catch a juve-

nile nyala when it was accompanied by its mother $\frac{1}{2}$ m. away. This was not in a thicket but in the open tree savanna. Baboon kills of nyala in thickets would not readily be noticed by us. Jeremy Anderson (*in litt.*) informed us that at the Ndumu Game Reserve in Zululand, cheetahs (*Acinonyx jubatus*) kill adult female and young nyalas, but not adult males. He also reported black-backed jackals attacking weakened adults.

Although we recorded a tawny eagle preying on juvenile nyala only once, we suspect that this is more common and perhaps a major mortality factor for juvenile nyala. Robbins (1972) reported a bateleur (*Terathopius ecaudatus*) attacking a newborn nyala. Eagles, particularly crowned eagles (*Stephanoaetus coronatus*), and bateleur eagles are abundant in the study area and do prey on a variety of small antelopes including oribi (*Ourebia oribi*), gray duiker (*Sylvicapra grimmia*), and bushbuck (*Tragelaphus scriptus*), as well as juvenile nyala. The jackal buzzard (*Buteo rufofuscus*) is another potential predator of small nyala.

Spotted hyenas and wild dogs (*Lycaon pictus*) are quite uncommon in the study area and in the Zinave region in general. We have no way of knowing whether the hooves found in the stomach of the dead hyena were obtained from carrion or from predation. Davison (1971) reported a nyala killed by wild dogs.

Pythons prey on nyala in our area, and in June, 1974, a python about 4 m. long was seen swallowing a subadult female nyala. Deane (1962b) reported a juvenile nyala killed by a python (*Python sebae*) in Natal, and Dixon (1966) also reported pythons preying on nyala at Ndumu.

Some nyala may be trapped in mud and drown or be killed by crocodiles, especially at the end of the dry season. In October, 1968, an adult female was pulled from the mud at the edge of Zinave Lagoon where she evidently had been trapped overnight. Other animals in the muck had been nibbled by crocodiles. Murray (1962) reported a 12-foot crocodile (*Crocodilus niloticus*) killing an adult female nyala in Natal, and Dixon (1966) also reported crocodiles killing nyala.

Barnes (1972b) mentioned that 107 nyala (59% adult, 12% immature, 30% juvenile) died

presumably of natural causes in False Bay Park, Zululand, from 1968 to 1971, but did not mention the mortality factors. Of 67 that were sexed, 39 (58%) were males.

Man is the main cause of nyala mortality in the vicinity of the Save River. From January, 1970, to October, 1971, 146 nyala were killed by poachers, and these can represent only a small fraction of the mortality caused by man. Of the 81 recorded in 1970, 13 were males, 14 females, and the remainder not sexed. In 1971, 29 males, 15 females, and 21 not-sexed nyala were killed by poachers, mainly in wire snares. The 81 nyala recorded in 1970 represent 10 percent of all the animals found killed in snares (812); 45 of these nyala were on the south side of the Save River in what is now the national park. In the park a total of 297 animals were found of which nyala were the second most frequent (15%) and impala the most frequently caught (37%). On the north side of the river, where 515 illegally killed animals were found, nyala represented 7 percent. The others, in decreasing order of abundance, were wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), buffalo (*Syncerus caffer*), and waterbuck (*Kobus ellipsiprymnus*).

Trophy hunters, restricted to the north side of the Save River since 1970, killed 67 male nyala in 1970. The total recorded mortality by man in 1970 accounts for 148 nyala, of which 54 percent were killed by poachers and 46 percent were males shot under license.

We have no quantitative data on nyala dying from causes other than predation by man and other carnivores. We received word, however, in October, 1971, that dead nyala were seen near Alves de Lima camp, north of the Save River, where the lagoon that had contained water for at least 12 consecutive years had dried. Close to the Save River nyala utilize free drinking water throughout the dry season. Elsewhere in Zinave National Park nyala may persist for several months without free drinking water.

Keep (1973a) reported high mortality of nyala in Ndumu Game Reserve in October, 1970. He attributed the death of the animals to their weakened condition resulting from overpopulation and consequent lack of food, combined with unusually wet and cold weather (see Population Structure).

Potential for Ranching. In the Save River region, nyala inhabit lands that are marginal for standard agricultural practices. The presence of tsetse flies has limited the opportunities for raising livestock, and endemic malaria and bilharzia, relatively low annual and seasonal rainfall, and limited soil resources have discouraged extensive human occupation and limited crop raising to shifting agriculture. Nyala and other ungulates are abundant in the area, and we have investigated the potential of utilizing nyala for meat production. Table 10 lists the weights of four adult males, five adult females, and two immature males and their organs. The mean total weight of three adult males, 110.9 kg., is slightly, but not significantly, higher than the mean of 13 adult males appearing in table 3, and that of the five adult females, 62.2 kg., is not significantly different from that given for eight adult females (table 3). The weight of the dressed-out carcass of four males averaged 66.75 kg., or about 60 percent of the total weight. The carcass-weight of the adult females averaged 37.4 kg. and was also 60 percent of the total weight.

Keep (1971) found the dressed-out weight of adult males from Ndumu Game Reserve in Natal to average 57 percent of the total average weight of 109 kg. and that of adult females to average 56 percent of the total average weight of 63 kg. Some differences in techniques may account for the differences in our percentages. Keep also found that the average edible lean meat was about 42 percent of the total weight. Thus, a 63 kg. male carcass would produce about 46 kg. of edible lean meat, and about 26 kg. of edible lean meat would be available from a 37 kg. female carcass. In addition, there would be another 2.7 kg. of edible heart, liver, and kidneys from males and 1.6 kg. from females.

Inasmuch as domestic livestock in Africa dress out to 44 to 50 percent of total weight (Keep, 1971), the productivity of nyala is evident. As these antelopes inhabit lands not highly suitable for domestic livestock, mature rapidly, subsist largely on browse and other species not utilized by domestic animals, and do not normally invade croplands, they present a high potential for game ranching. Keep (1971) discussed other aspects of the possible utility of nyala as ranch animals.

TABLE 10
Organ Weights (in Kilograms) of Nyala

	26 X 73	29 XI 73	21 I 74	13 IV 74	28 II 73	26 X 73	21 I 74	9 IV 74	15 IV 74	22 IV 74	22 IV 74
	♂ Ad	♂ Ad	♂ Ad	♂ Ad	♀ Ad	♀ Ad	♀ Ad	♀ Ad	♀ Ad	♂ Imm	♂ Imm
Total Wt.	113.74	—	99.8	119.1	62.0	68.06	60.0	54.85	66.0	66.3	80.0
Carcass Wt.	67.3	58.10	63.0	78.6	40.1	38.85	36.0	34.10	38.0	39.90	49.1
Heart	0.58 ^a	0.60 ^a	—	0.95	0.50 ^e	0.47 ^a	— ^a	0.60 ^a	0.39 ^e	0.50 ^e	0.49 ^e
Lungs	1.02	1.00	—	—	0.70	1.00	—	1.30	0.52	0.67	0.89
Liver	1.85	2.02	—	2.20	1.20	1.00	—	1.35	1.10	1.40	1.50
Spleen	0.23	0.30	—	0.30	0.20	0.20	—	0.32	0.18	0.41	0.23
Kidneys	0.34 ^a	0.425 ^a	— ^c	0.33	0.2 ^e	0.26 ^b	— ^b	0.30 ^b	—	0.25	0.20 ^e
Stomach Full	18.4	16.67 ^a	10.9	10.50	6.8 ^e	6.60	6.0	6.05	6.90 ^e	7.00	10.6
Stomach Empty	2.8	3.00	2.83	3.30	2.2	—	1.65	2.00	2.08 ^e	1.80	2.1
Intestine	5.4 ^d	4.70 ^{a,d}	3.80 ^d	6.65 ^d	2.8 ^d	2.55 ^{b,d}	— ^a	2.50 ^b	3.25 ^{c,d}	2.70 ^{d,e}	3.3 ^{d,e}
Backbone Fat	0 ^a	0 ^b	0.221	0.26	0.60	0 ^a	— ^b	0.40	0.167	0.106	—
Mesentary	—	—	— ^c	2.42 ^c	—	—	— ^b	0.15 ^c	—	—	0.135 ^e
External	—	—	—	—	—	—	—	—	—	—	—
Kidney Fat	0 ^a	0	0.164	0.20	0.400	0 ^b	0 ^b	0 ^b	0.138	0.111	0.060
Internal	—	—	—	—	—	—	—	—	—	—	—
Kidney Fat	0 ^a	0	— ^c	0.007	— ^c	0	0 ^b	0	0.004	0.004	0.004
Head, Skin, Feet	—	15.90	—	—	—	6.60	—	—	—	—	—
Fetus and Sac	—	—	—	—	1.0	8.10	4.0	1.35	1.15	—	—
Fetus Only	—	—	—	—	—	5.20	2.1	0.250	0.168	—	—
Testis	0.069	0.075	0.050	0.060	—	—	—	—	—	0.021	0.035

^aNo fat.

^bTrace of fat.

^cWith fat.

^dFull.

^eExcluding fat.

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