

THE ECOLOGY AND CONSERVATION OF BLUE DUIKER

AND RED DUIKER IN NATAL

by

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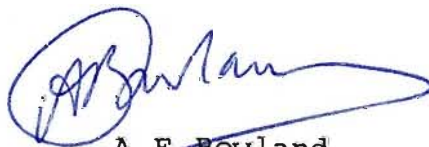
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PREFACE

The research described in this thesis was carried out from the Department of Zoology and Entomology, University of Natal, Pietermaritzburg under the supervision of Professor M.R. Perrin and Dr D.A. Melton over the period April 1985 to December 1988.

This research, unless indicated to the contrary in the text, is my own original work. It has not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.



A E Bowland

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Natal Parks Board allowed me to work at Charter's Creek and Kenneth Stainbank Nature Reserves. Natal Parks Board staff are thanked for their help, particularly Dick Nash, Christo Grobler and Dr. Mike Keep.

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Blue duikers for captive studies were provided by Wallace Rosevear from his farm at Highflats.

Umdoni Park Board of Trustees allowed me to study blue duikers at Umdoni Park and provided accommodation.

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I would like to thank my parents for their love and support, moral and financial.

I am grateful to my wife, Jane, whose help in this project, from its inception to the final deadline, has been invaluable.

ABSTRACT

The ecology of blue duikers Philantomba monticola and red duikers Cephalophus natalensis was studied in three lowland coastal evergreen forests in Natal. Variation in population densities, estimated with numerous census techniques and between and within study areas permitted comparisons of habitat parameters. Both species are strictly diurnal, and are active between 18 and 40% of the nycthemeral cycle. Usually a pair of blue duikers occupy a permanent territory of about 0,7ha while red duiker home ranges, between 2 and 15ha, overlap extensively with each other and those of blue duikers.

Habitat quality of both species is determined by canopy cover (stem densities, spatial patterning, and, diversity of the tree and shrub layers), tree to shrub ratios, and, bedsites. The main dietary item, freshly fallen leaves, is not that of a high-concentrate feeder as hypothesised. Food appears to be abundant while condensed tannins have no influence on duiker densities.

Management recommendations include land acquisition, forest ecology research, monitoring interaction with other species, genetic aspects, translocations and captive propagation.

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CHAPTER 1

INTRODUCTION

The Forest Biome

"A forest is a plant community having a continuous tree stratum, with or without a shrub and/or herbaceous stratum" (Geldenhuys et al. 1988).

Indigenous, evergreen forests form the smallest and most widely dispersed biome in South Africa and occur as a series of disjunct patches along the eastern and southern margins of the southern African subcontinent (Figure 1.1, Cooper 1985, Geldenhuys and Knight 1989). They cover less than 1,0% (2 000 km⁻²) of the land area (Geldenhuys and Knight 1989), with approximately 1 000km⁻² scattered throughout Natal (Figure 1.1; Cooper 1985).

The patchy distribution of indigenous forests ranges from sea level to 1700m a.s.l. between the latitudes 27° and 34°S (Geldenhuys et al. 1987). The canopy is evergreen to semi-deciduous, depending on soil nutrients and moisture conditions (Geldenhuys and Knight 1989). Generally, forests occur in areas with an annual rainfall of 500 to 1950mm, with summer and winter rainfall regimes, on a variety of geological formations (Rutherford and Westfall 1986, Geldenhuys et al. 1987).

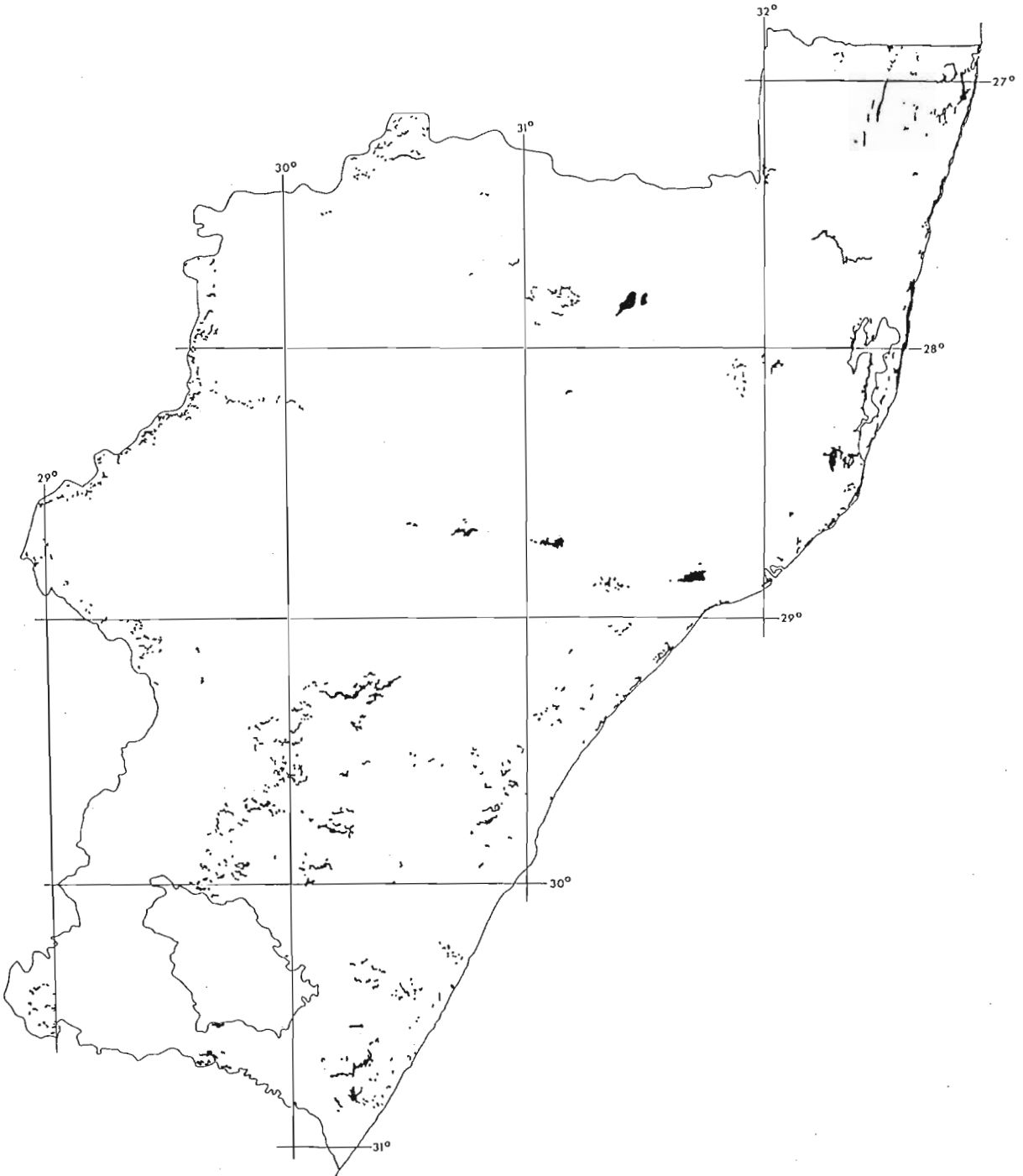


Figure 1.1 Indigenous evergreen forests of Natal (after Cooper 1985).

Distributional patterns of the scattered forest remnants reflect the physiographic, geological and climatic factors influencing the development of forest. Geology is diverse, giving rise to soils which differ significantly in nutrient status and water relations thus greatly influencing forest composition (Geldenhuys 1983). Forests of subtropical coastal areas occur on a variety of substrate types as indicated by descriptions such as sand forest, dune forest and swamp forest (Phillips 1973, Moll and White 1978). The afro-montane forests, on different geological substrates, occur on summits and along upper slopes of mountains (Geldenhuys 1983).

Forests in Natal range from lowland sub-tropical forests of the Indian Ocean coastal belt (Moll and White 1978) to the Afro-montane forests of the uplands (White 1978). Cooper (1985) identified six broad forest types in Natal (Table 1.1).

Table 1.1 Forest types of Natal and Kwazulu (after Cooper 1985) showing those inhabited by forest duikers (+=duikers present).

<u>Forest type</u>	<u>Area covered</u> (ha)	<u>Blue</u> <u>Duikers</u>	<u>Red</u> <u>Duikers</u>
Montane <u>Podocarpus</u>	9273		
Mistbelt mixed <u>Podocarpus</u>	30868	+	
Coast scarp forest	15076	+	
Coast lowlands	8777	+	+
Sand forest	5986		+
Riverine forest	1887		+
Swamp forest	4843		
Dune forest	14491	+	+

History of Forests

Forests of Africa, South America, Australia, India, Antarctica and Madagascar were all linked on the southern continent, Gondwanaland, before Africa separated from these landmasses about 100 m.y.B.P. (Axelrod and Raven 1978). Evidence suggests that mixed evergreen forest covered the larger part of Africa until the eastern escarpment formed and separated the moist coastal belt from the arid interior (Geldenhuis 1983).

In southern Africa forests covered large areas during the early Tertiary, but subsequently fragmented due to environmental changes including increasing aridity (Axelrod and Raven 1978). Changes in climate during glacial-interglacial cycles of the Quaternary probably caused forests to expand and contract (Moreau 1966, Van Zinderen Bakker 1978).

About twenty glacial-interglacial cycles, each lasting about 100 000 years, have occurred over the past two million years (Tyson 1986). Glacial maxima would have seriously affected the extent of evergreen forest (Van Zinderen Bakker 1978) and disjunct distributions of forest fauna must date back at least to the time of the last glacial maximum (Lawes 1987).

During the Holocene, after the the cool Pleistocene, conditions suitable for forest expansion occurred about 7000 years B.P. while the period 7000 to 2000 years B.P. was characterised by very high temperatures with reduced precipitation resulting in forest regression (Geldenhuis 1983).

Man and forests

Worldwide, man has had a long association with forests. In southern Africa there is escalating pressure on the forest biome for food, fuel, medicine, building materials and raw materials for furniture and handicrafts. Forests have also provided shelter, maintained water quality, reduced soil erosion and acted as natural firebreaks, yet man plays the major role in deforestation. Forests are cleared for agriculture, forestry and subsistence utilisation (Cunningham et al. 1988).

Sustainable forest use and prevention of further deforestation therefore requires sensitivity to ecological and social issues. It also requires political support for money and manpower to manage forest areas, to provide alternatives to our exploited forest resources (e.g. woodlots, cultivation of medicinal plants) and to allow for economic growth and expansion away from agricultural practices causing forest destruction.

Importance of forests

Forests, usually situated in high rainfall areas, prevent soil erosion in catchments and along waterways, while on steep gradients they play an important role in binding soil (Cunningham et al. 1988). Dune forests assist in preventing driftsand formation.

Multi-layered dense forest canopies reduce velocity and effective intensity of raindrops (Whitlow 1983). Forest soils have high organic matter content and thus absorb considerable quantities of

water. The above two effects decrease runoff and increase soil water storage. The net overall effect is that forested areas improve water quality and reduce and regulate total stream flow. This has important implications for catchment management and life time of dams.

Aesthetic and cultural values of forests are psychologically important (Geldenhuys et al. 1987); they have a traditional cultural significance as burial sites (e.g. Dingaan in Hlatikulu Forest, Cunningham et al. 1988), and there is economic potential for recreation and tourism (Geldenhuys et al. 1987).

Forests are amongst the most faunistically and floristically rich biomes known and are thus important in terms of conservation of genetic diversity. Although forests cover a small area of South Africa, we have no idea what the minimal critical size is required to support these forest communities and maintain species diversity. The effect of distance between forest patches (isolation) on species diversity is unknown (Cunningham et al. 1988, Geldenhuys and Knight 1989).

Forest fauna

Distribution patterns of extant sylvicolous species in southern Africa are assumed to be the consequence of vegetation adjustments following climatic cycles of the late Quaternary (Moreau 1966, Stuckenberg 1969, Lawes 1987). Some forest mammals, though integral components of forest biota, are often shared with neighbouring biomes (Table 1.2), while others, the "forest endemics", are inextricably linked to the forest biome and their fate is determined by its survival.

Forest duikers

In Natal, the sub-family Cephalophinae (family Bovidae) is represented by three genera, each represented by a single species. The common duiker Sylvicapra grimmia, a savanna species, is widespread through the region while the two forest species, the blue duiker Philantomba monticola and the red duiker Cephalophus natalensis are localised and confined to forested areas. Blue duikers, the smallest antelopes in southern Africa, stand about 30 cm at the shoulder and weigh 4-5kg. Red duikers, about 45cm at the shoulder, weigh 12-14kg. Blue duikers and red duikers (referred to collectively as forest duikers), prominent components of a vulnerable biome, are protected by law and are classified as rare in the South African Red Data Book (Smithers 1986).

Motivation for the study

Both species have declined over much of their range in recent years. The main contributory factor to this decline is the erosion of habitat. In view of the vulnerability, mainly via habitat loss, of these two antelopes, sound management practices are essential. The preparation and implementation of effective conservation plans are inhibited by the lack of basic ecological information on either of the two species. Consequently the Provincial nature conservation authority, Natal Parks Board, initiated and approved a priority project on the ecology and conservation of blue duikers and red duikers, with the following broad objectives:

- to investigate the habitat requirements of each species (in allopatry and sympatry) with particular reference to food and spatial requirements,

- to evaluate the extent and consequences of inter- and intra-specific competition, and,
- to make recommendations on a conservation policy for forest duikers.

I examined population densities, temporal and spatial patterning, habitat, diet, and food resources of populations of red duikers at Charter's Creek and Kenneth Stainbank Nature Reserve, and blue duikers at Umdoni Park and Kenneth Stainbank Nature Reserve.

CHAPTER 2

DISTRIBUTION AND STUDY AREAS

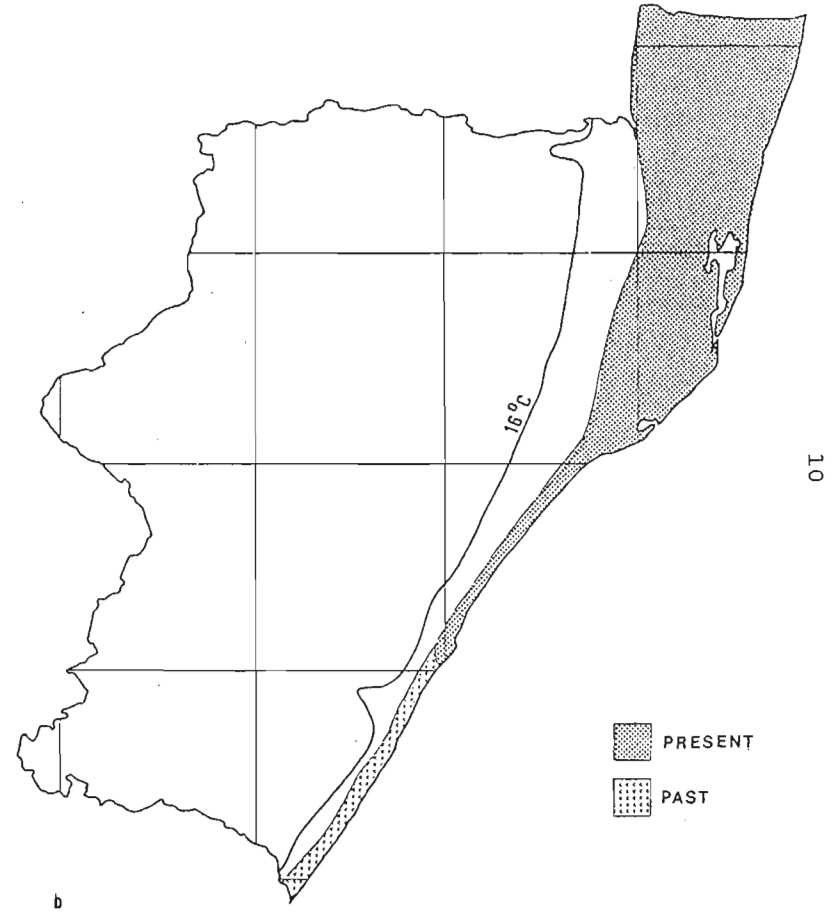
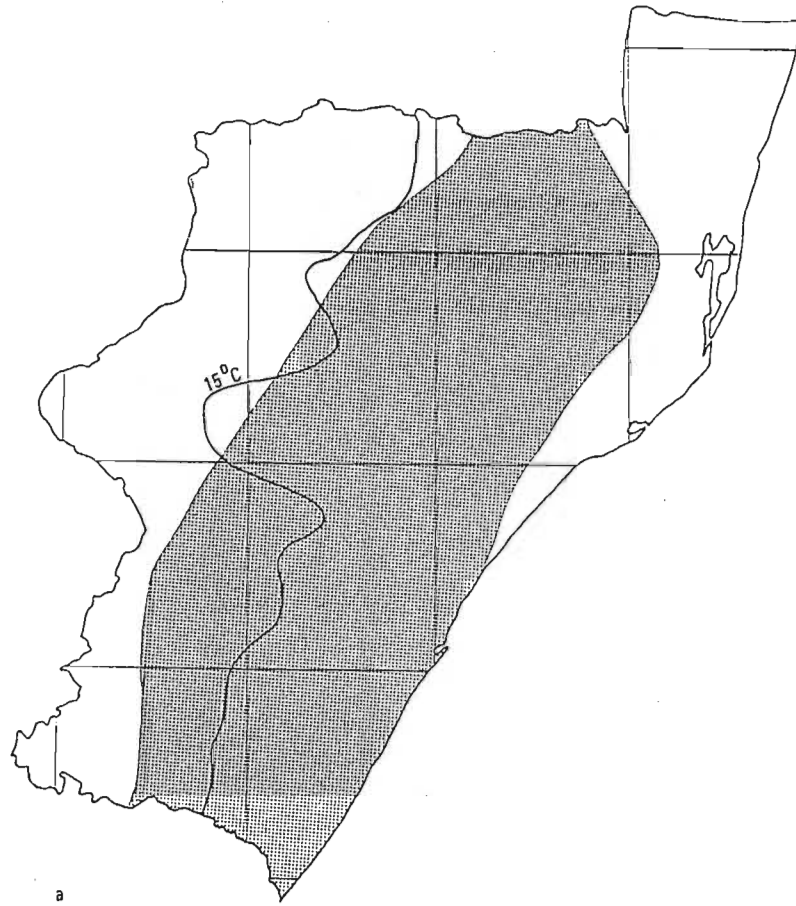
Distribution

Blue duikers are widely distributed through Africa south of the Sahara, with their range extending from parts of West Africa to the coastal areas of the Cape Province. They occur in eastern Nigeria; southeastern Sudan; western and southern Uganda; southwestern and southeastern Kenya; western, northwestern, southwestern and extreme southeastern Tanzania; throughout Zaire, the Congo Republic, and Gabon; western Angola; northeastern Zambia; the highlands of Malawi; northern Mozambique; and eastern Swaziland (Smithers 1983, Happold 1987).

In South Africa they occur in the Magaliesberg Mountains in the Transvaal (Cooper 1985), and along the coastal region and marginally inland in Natal and the Cape Province, as far south as George (Skead 1980, Smithers 1983).

In Natal their distribution extends from the coast inland to areas not exceeding 1500m, generally following the 15°C effective temperature isoline (Vincent 1962, Stuckenberg 1969, Howard and Marchant 1984). The coastal distribution digresses inland north of Durban at Umdloti (Figure 2.1).

Red duikers are confined to the eastern seaboard of Africa. They occur in northeastern Zaire; southern Sudan; western Uganda;



10



 PRESENT
 PAST

Figure 2.1 Forest duiker distribution in relation to effective temperature isolines (Stuckenberg 1969) in Natal, (a) blue duikers and (b) red duikers.

southern Kenya; northern, eastern, and southern Tanzania; eastern Mozambique; northern Malawi; and, Swaziland (Smithers 1983).

In South Africa they occur in the eastern Transvaal and Natal, where their northward distribution along the coast from Durban extends inland keeping east of the 16°C effective temperature isoline (Stuckenberg 1969, Cooper 1985, Howard and Marchant 1984). Recent re-introductions south of Durban (Bourquin and van Rensburg 1984, Henderson pers. comm., Roseveare pers. comm.) have been made into their former range, which, until recent times, extended as far south as Pondoland (Fitzsimons 1920, Du Plessis 1969; Figure 2.1).

The status of duiker populations within their range is difficult to determine. Habitat outside protected areas, vulnerable to overexploitation (Chapter 1), is probably no longer suitable and many forests have simply disappeared through deforestation (Evans *et al.* 1986). Even in some protected areas, e.g. Hluhluwe Game Reserve (Chapter 5), habitat has been adversely modified.

Study Areas

Five study areas in Umdoni Park (Umdoni), Kenneth Stainbank Nature Reserve (KSNR-A, KSNR-B, and KSNR-C; Figures 2.2 and 3.4), and Charter's Creek (Charters), were selected for intensive study on the following criteria :

1. the existence among them of sympatric (syntopic) and allopatric populations of the study animals,

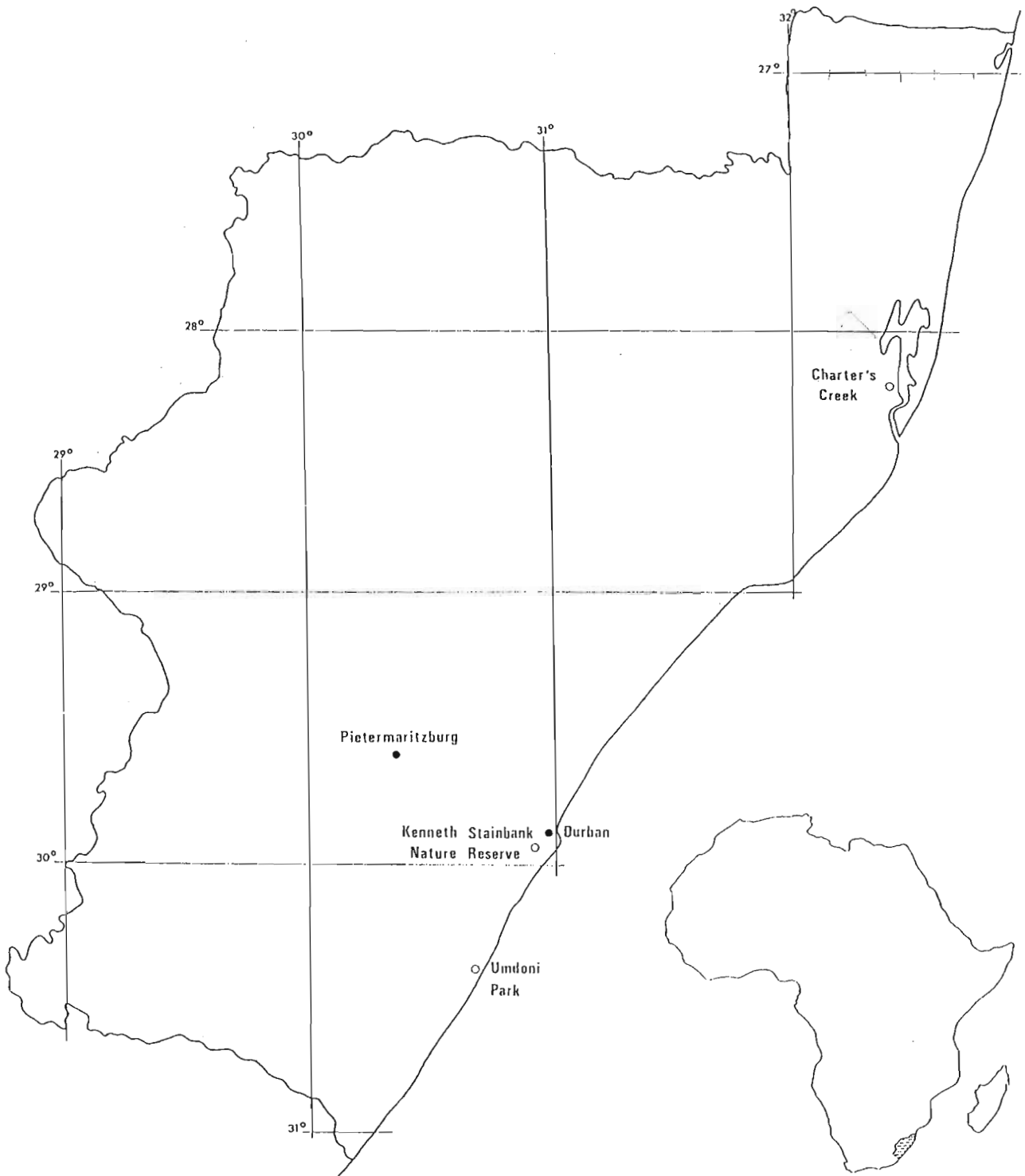


Figure 2.2. The location of study areas in Natal.

2. the study animals were present in relatively high densities, and,
3. environmental parameters were similar.

Compliance with these criteria facilitated the evaluation of assimilated data on a comparative basis; differences and similarities were then used to identify and confirm or reject previous interpretations of duiker ecology.

The study areas (Figure 2.2, Table 2.1) lie within the Natal Coastal belt, Philips bioclimatic subregion No.1 (Phillips 1973). The indigenous, evergreen forests in this region are classified by Acocks (1988) as Veld type I: coastal forest and thornveld; subcategory coastal belt forest. In all study areas, prevailing winds are from the northeast and southwest; there is no frost and mist is minimal.

Elevation is below 150m and topography is generally undulating to flat but with steep inclines adjacent to rivers. Sandy, regosolic soils, derived from coast dunes, are underlain by Karoo sediments and Recent to Tertiary sands with a greater proportion of Table Mountain Sandstone and basement rocks along the South Coast (Phillips 1973).

The southwestern projection of KSNR (i.e., KSNR-A, Figure 3.4) was initially chosen as an intensive study area. During the project it became clear that duiker densities differed substantially on a very localised scale (Chapter 3). It was decided to use this phenomenon to investigate comparative aspects of habitat utilization, food availability and food habits. Consequently,

KSNR-B, with low duiker densities, and KSNR-C, with high duiker densities, were incorporated as intensive study areas.

Other forest ungulates occurring in the study areas are listed in Table 2.2. The feeding niche of forest duikers (Chapter 6) avoids direct competition with forest cohabitants, except in areas of overlap between red duikers and suni (Lawson 1986), but their impact on vegetation structure may adversely affect habitat quality for the duikers.

Table 2.1 Environmental characteristics of the study areas.

	<u>Umdoni</u>	<u>KSNR</u>	<u>Charters</u>
Rainfall:			
Mean annual (mm)	1314	1210	1044
October to March (%)	70	70	66
Temperatures:			
Mean annual (°C)	20,3	20,1	20,8
Mean daily range (°C)	7,8	10,7	9,8
Maximum/Minimum (°C)	36/7	40/4	43/2
Co-ordinates	30°42'E 30°23'S	30°56'E 29°54'S	32°25'E 28°13'S
Size (ha)	205	214	150
Administrators	Umdoni Park Trust	Natal Parks Board	Natal Parks Board
Date founded	1918	1963	1939

Note: Climatic data for KNSR were taken from Louis Botha Airport (4km distant) and for Umdoni from Southbroom (80km distant).

Table 2.2 Ungulates coexisting with forest duikers in three forest communities (+=present).

	<u>Umdoni</u>	<u>KSNR</u>	<u>Charters</u>
Nyala <u>Tragelaphus angasii</u>			+
Bushbuck <u>T.scriptus</u>	+	+	+
Common duiker <u>Sylvicapra grimmia</u>	+	+	+
Impala <u>Aepyceros melampus</u>		+	
Bushpig <u>Potamocheorus porcus</u>			+
Warthog <u>Phacochoerus aethiopicus</u>			+
Zebra <u>Equus burchelli</u>		+	

CHAPTER 3

POPULATION DENSITIES

Conservation and management aimed at forest fauna are impeded by the lack of knowledge about many forest animals. Not only is it essential that the presence of a species is known but that its abundance is known and monitored. Thus, dependable and accurate (or relatively accurate) techniques for estimating population densities are an essential management tool.

Difficulties imposed by dense vegetation in conducting population density estimates of forest dwelling mammals are well documented (Schmidt 1983, Seydack 1984, Collinson 1985, Allen-Rowlandson 1986, Lawson 1986, Koster and Hart 1988). The non-social habits and secretive behaviour of many forest ungulates inhibit direct observation (Koster and Hart 1988) such that only a few of the numerous game census techniques available (Collinson 1985) can be realistically applied in forest habitats (Seydack 1984).

When selecting a technique to estimate population density, factors taken into account should include:

1. specific objectives of the investigation, e.g. monitoring changes in population levels in response to management strategies, calculating harvest levels, determining minimum viable populations,

2. goals of the census, e.g. index or absolute estimate, minimum amount of accuracy, precision, and repeatability, and
3. practical and ecological criteria, e.g. vegetation characteristics of the area, behaviour of the animal.

Six methods, i.e. drive counts, line transects, variable and fixed width transects, dung-heap counts, and territory mapping, were compared with respect to the above factors to evaluate their suitability in estimating population densities of forest duikers, and to assess their efficacy and precision. Ultimately, the reason for this part of the study was to estimate duiker densities in each study area or habitat condition so that, when related to environmental parameters such as habitat and food quality (Chapters 5 and 6), limiting factors could be identified.

Methods

Where possible, counts were conducted during the dry season (August and September) when understorey vegetation was relatively sparse, and visibility was best to locate animals and their dung-heaps. (Study areas in which estimation methods were applied are indicated in parenthesis, after the method is identified).

Drive counts (KSNR)

The basic principles of this method are described by Overton and Davis (1969) while its adapted application to KSNR is described by LeRoux and Morty (1985). Drive counts, repeated over three consecutive days, are conducted annually by NPB personnel. The best count does not usually occur on day one as the observers familiarise themselves with the procedure, habitat and duikers. Hence, the difference between counts on day 2 and day 3, expressed as a percentage of maximum count, were used to indicate "accuracy".

Since not all habitat surveyed was suitable for forest duikers, ecological density was computed, i.e. number of animals per unit of habitat area (Odum 1971). The area of suitable habitat, i.e. forest and forest patches, was calculated from aerial photographs taken in May 1987.

Population densities were estimated with the formula:

$$\text{Ecological density} = \frac{\text{number of duiker}}{\text{area of suitable habitat (ha)}}$$

Variable width transects (Umdoni, KSNR, Charter's Creek)

Strip transect sampling is based on the concept of sampling a long, narrow two dimensional strip of a given length and width, and hence area (Seber 1973). The width of the transect may be fixed or variable. Variable width was generally favoured, so as to include as many animals as possible in the sample, thereby improving precision and reducing bias (Caughley 1977).

At Umdoni, a seldom-used vehicle access track provided an adequate sampling line whereas at KSNR the "Red Duiker" hiking trail conveniently formed a sampling line through prime duiker habitat where animals were accustomed to pedestrian traffic. At Charter's Creek both minor service roads and swept footpaths served as sampling lines.

Sections of the sampling lines meandered so the shortest distance from the point where the animal was sighted, or from where it fled, to the sampling line was measured. Mean animal-to-sampling line distance gave the effective strip width. Transect lines were sampled repeatedly on consecutive days, weather permitting, with a trained observer. Data from counts made in heavy rain were discarded, since not only did subdued light beneath the canopy reduce visibility but animals were inactive in wet weather.

Forest duikers are diurnal and their activity peaks in early morning and late afternoon (Chapter 4). Consequently, sampling

was undertaken during early morning, beginning a half hour after dawn, and late afternoons, two hours before dusk. Human activity, if any, usually occurred between 09h00 and 16h00 thereby avoiding conflict with sampling procedures.

Transect lengths were measured on the ground. Minimum sampling effort, i.e. number of replicates, was determined by plotting cumulative population density estimates. Frequency distributions of animal-to-sampling line distances were plotted to monitor duiker response to observers. Seasonal differences in animal-to-sampling line distances were compared (Student's t-test) to evaluate the effect of vegetation density on observer visibility and subsequent population estimates.

Population densities were estimated with the formula (Collinson 1985):

$$\text{Density} = \frac{y}{2L.w}$$

where: y = total number of animals seen along transect line
 L = length of sampling line
 w = effective strip width (= mean animal-to-sampling line distance).

Standard strip transects (Charter's Creek)

With this technique an area of predetermined width (w) and length (L) is sampled, all animals on or crossing the strip during the sampling are counted (Collinson 1985). Two separate fixed strips were sampled. The first was along a forestry service road with wide, mown verges (length 1207m, mean width

13.4m) and no canopy overhead. The second strip (length 1036m, mean width 11.5m) was along the cleared area beneath power lines also with no canopy overhead.

Population densities were estimated using the formula (Collinson 1985):

$$D = \frac{y}{a}$$

where D = density of red duikers per unit area
 y = number of red duikers in or crossing the strip
 a = area of the strip x number of repetitions

Line transects (Charter's Creek)

Line transect methods involve estimating a density function directly from a one-dimensional sampling line (Eberhardt 1978). These methods, outlined by Burham *et al.* (1980), have an advantage in that they are based on models that are statistically valid (Collinson 1985).

At Charter's Creek the sampling line, divided into a number shorter straight sections to accommodate change of direction, was along narrow forest roads and specially cut footpaths, swept free of "noisy" leaf litter, beneath mainly closed canopy. Distance from observer, measured with a range finder (Ranging Opti-meter 620, effective range 15 - 180m), and compass bearings to the duiker and of the sampling line, were recorded at each sighting. Perpendicular distances from the sampling line to animals closer than 15m were measured with a tape-measure. Data were processed with Apple Transect Ver. 2.3

and 2.5 programmes (Goodman 1984) which are abridged versions of the original programme Transect written by Laake et al. (1979).

Dung-heap counts (KSNR, Charter's Creek)

This method simply converts the number of dung-heaps into an estimate of the animal population in the census area. Forest duikers deposit pellets in discrete groups or dung-heaps, usually comprising 30+ pellets, in middens dotted throughout the animal's territory. Dung-heaps were identified and counted in 85 sampling plots by two observers moving abreast along 125m² (5x25m), randomly located plots in forest.

Diameter of dry pellets, measured with calipers in the field, was the key feature used to distinguish similar faecal pellets of the two duiker species. Sixty-six pellets collected from the rectums of 12 wild caught blue duikers and 40 pellets from four wild caught red duikers were air-dried, measured and compared. Both mean length (blue = 7.9mm, red = 9.2mm) and mean diameter (blue = 5.1mm, red = 6.2mm) of pellets differed significantly between species (diameter $t=18.36$, $p<0.01$; length $t=4.77$, $p<0.01$). Since the standard deviation of the pellet diameter showed no overlap between species (blue = 5.1 ± 0.2 mm, red = 6.2 ± 0.4 mm), however, diameter was chosen as the more reliable field identification feature.

Rate of pellet decay was obtained by monitoring fresh dung-heaps in the forest. After 40 days the pellets began to crack

and disintegrate at KSNR in the dry season whereas at Charter's Creek, during spring, invertebrate activity had rendered dung-heaps unidentifiable within two hours.

Daily (24h) dung-heap deposition rates of 2.03 for blue duikers and 2.29 for red duikers was determined for captive animals, on a diet of antelope cubes, apples, and carrots, over 21 days (A. Pinchen pers. comm.). Captive blue duikers on a natural fruit diet in Zaire averaged 4.9 depositions per day (Koster and Hart 1988).

The influence of diet on defaecation rates has been noted by numerous workers (Neff 1968, Collinson 1985, Koster and Hart 1988). The diet of forest duikers in the wild is difficult to duplicate in captivity and I assumed that captive animal defaecation rates approximated those of wild animals.

Population densities were estimated from the formula (Seydack pers. comm.):

$$\text{Density} = \frac{n \times K}{N \times t \times d}$$

where: N = number of sample plots
 n = number of dung-heaps
 t = number of days pellets remain intact
 d = daily dung-heap deposition rate
 K = constant to express density per ha
 (80 in the case of 125m² plots)

Territory mapping (KSNR)

In territory mapping, animal density was derived by multiplying the number of territories by the mean number of occupants per

territory and relating the product to the amount of suitable habitat.

The number of territories may be estimated in several ways:

1. by recognising territory holders, and hence their spacing,
2. by estimating mean territory size by radio tracking, and degree of overlap, and,
3. by learning to identify individual territory occupants by repeated sightings in particular localities.

The second method was used in this study. Each territory was presumed to have two occupants; territories with a pair plus an immature offspring may offset single occupant territories.

Densities were estimated with the formula:

$$\text{Density} = \frac{t \times n}{A}$$

where: A = area of suitable habitat
 n = number of animals per territory
 t = number of territories (A/m)
 m = mean territory size

Localised variation in duiker densities

Drive counts suggest that forest duiker densities at KSNR have been constant since 1985 (Table 3.1). These counts are expedited by partitioning the reserve into manageable counting blocks. During the count the animal tally in each block is recorded; the grand total of counting blocks yields the duiker population estimate for KSNR.

Localised variation in duiker density was evident by comparing ecological densities in counting blocks. Ecological densities were derived through dividing the mean number of duikers counted in each block over a four-year period (1985-1988) by the area of suitable habitat it contained. A digital planimeter was used to determine habitat areas from a 1:5000 aerial photograph taken in 1987.

Adjacent counting blocks with similar duiker densities were consolidated into larger units to suppress 'edge effect' and facilitate further investigation. Two extreme forest communities, in terms of duiker densities, were selected for intensive examination.

Pecuniary cost of each method

Manhours required in the field to conduct each survey were recorded. Labour input was discriminated between semi-skilled (e.g. game scouts, field assistants) and skilled (e.g. researchers, biologists, wildlife managers) personnel.

Results

Drive counts

In KSNR (214ha) only 80ha are suitable habitat for the blue duiker and 128ha suitable for red duikers. Density estimates for each species have been fairly constant since 1985 (Table 3.1). The drive count method is a total count rather than a sampling technique, since by its assumptions it counts the whole population and therefore precludes statistical tests of sampling. The index of accuracy was 6,9% ($\pm 1,1$) for blue duikers and 8,4% ($\pm 1,7$) for red duikers (Table 3.1). It is expected that the true population differs by no more than these margins from the estimate.

Variable width transects

The forest duiker population was sampled three times (August 1987 and 1988, April 1987) at KSNR and once at Umdoni (March 1990). Accumulative estimation graphs indicated that fewer than 10 replicates (13 in the case of Umdoni) render population estimates unreliable, while its robust nature was exhibited by repeatability and precision of the estimates from temporally separate samples (Figure 3.1).

Table 3.1 Number of duikers counted on day 2 and day 3 of drive counts in KSNR (after NPB unpublished report) with percent difference between counts and estimation of density (animals ha⁻¹).

Year	Day of count	Blue duikers			Red duikers		
		animals counted	% difference	density estimates	animals counted	% difference	density estimates
1981	2	109	6,4	1,36	29	6,4	0,24
	3	102			31		
1982	2	128	3,8	1,66	46	2,1	0,37
	3	133			47		
1983	2	105	2,9	1,31	60	6,7	0,47
	3	102			56		
1984	2	94	5,3	1,17	45	11,1	0,35
	3	89			40		
1985	2	100	10,7	1,40	46	10,9	0,36
	3	112			41		
1986	2	94	12,1	1,34	48	2,0	0,38
	3	107			49		
1987	2	113	5,3	1,40	42	17,6	0,40
	3	107			51		
1988	2	93	8,8	1,28	44	10,2	0,40
	3	102			49		
mean			6,9			8,4	
SE			±1,1			±1,7	

Frequency distributions of animal-to-sampling line distances suggested that duikers sometimes move in response to approaching observers before they are sighted (Figures 3.2 and 3.3). No trend was observed in red duikers but an apparent 'safe' distance for blue duikers is 15m in sparser vegetation (August, Figure 3.2) and 7,5-12,5m when vegetation is more luxuriant (March and April, Figure 3.2). This behaviour violates a basic assumption of the method and can result in under estimation of population density.

Transect data are summarised in Table 3.2. Seasonal changes in vegetation density affected visibility, mean animal-to-sampling line distances were greater in the dry season (August) than at the

end of the wet season (April), but only significantly so in the case of blue duikers (Table 3.2). Population estimates are listed in Table 3.3.

Data collected for line transects at Charter's Creek were applied to this method to show how the results obtained differed between methods (Table 3.3).

Standard strip transects

Red duiker density estimates beneath the power lines averaged 2,07 animals ha^{-1} and were much lower, 0,91 animals ha^{-1} , along the forestry service road (Table 3.3).

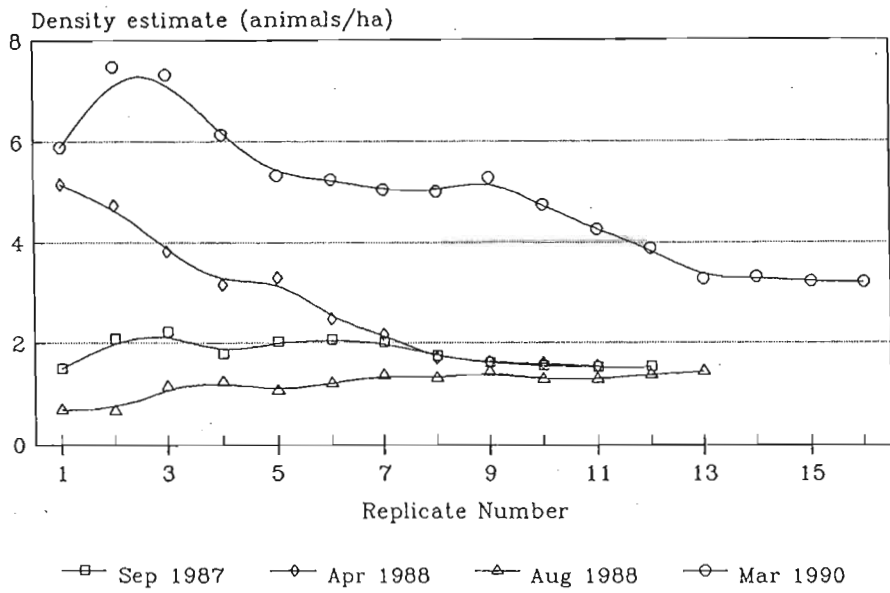
Table 3.2 A summary of variable strip transect data from sampling conducted at KSNR.

	Blue duikers			Red duikers		
	Aug 87	Apr 88	Aug 88	Aug 87	Apr 88	Aug 88
Transect length (km)	27,7	25,4	33,6	32,7	29,9	43,1
Number of replicates	12	11	14	12	11	14
Number of animals recorded	58	45	73	26	19	31
Mean animal-to-sampling line distance (m)	6,9	5,7	7,6	12,1	9,9	11,1
Comparison of distance means:						
Students t tests:	Aug 87 p =	0,13	0,23		0,19	0,27
	Aug 88 p =	0,23	0,04*	0,27	0,38	

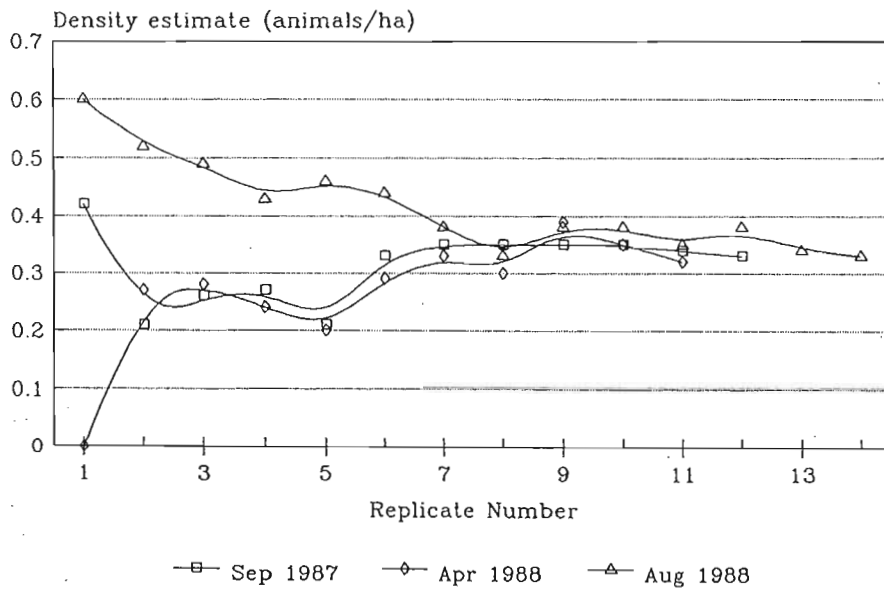
* difference significant ($p < 0.05$)

Table 3.3 Estimates of forest duiker population densities (animals/ha) in three study areas using different methods.

Study area	Date	Drive counts		Line transects		Variable strip transects		Standard strip transects		Dung heap counts		Territory mapping
			n		n		n		n		n	
Blue duikers:												
Umdoni	Mar 90					3,20	71					3,1
KNSR	Aug-Sep 88	1,4	113			1,53	58			2,38	205	2,7
	Apr 88					1,55	45					
	Aug 88	1,3	102			1,44	73					
Red duikers:												
KNSR	Aug 87	0,4	51			0,33	26			0,8	78	
	Apr 88					0,32	19					
	Aug 88	0,4	49			0,33	31					
Charters				1,59	247	2,58	250	2,07	37			
								0,91	25			

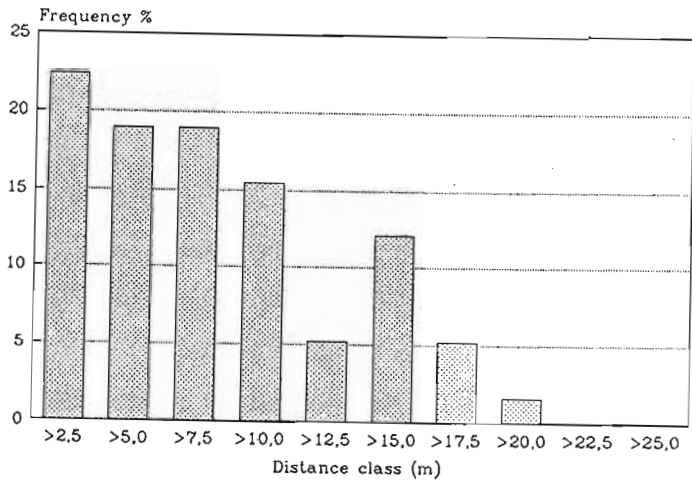


a

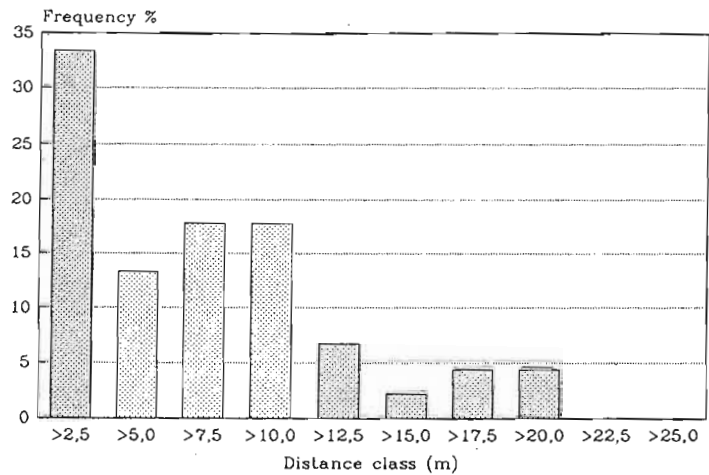


b

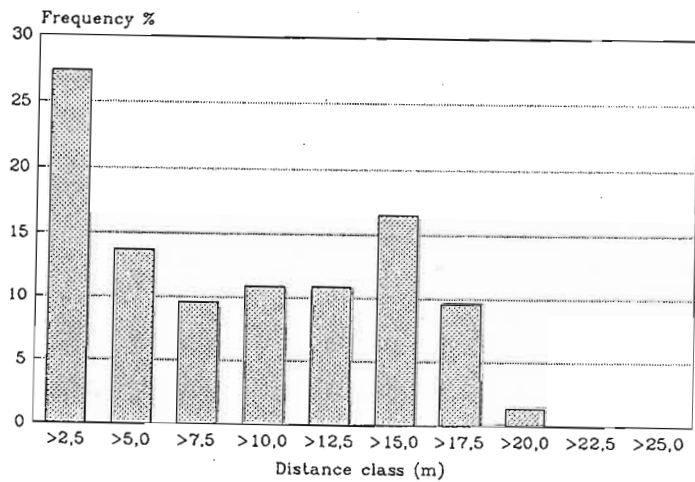
Figure 3.1 Cumulative estimates of (a) blue and (b) red duiker population densities to indicate minimum sampling effort.



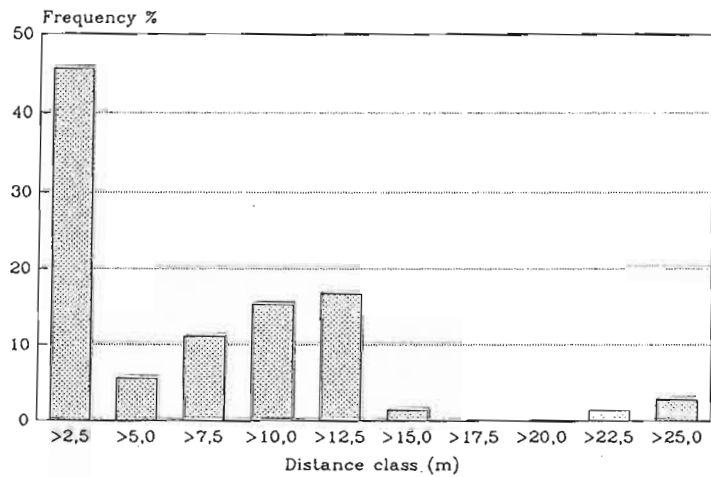
August 1987



April 1988

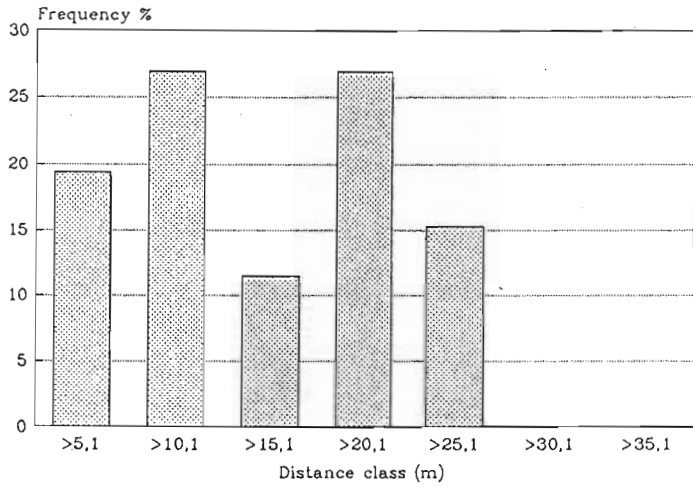


August 1988

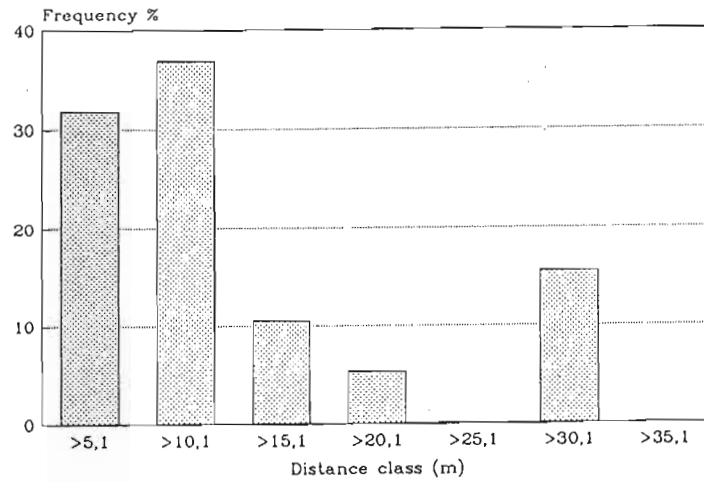


March 1990

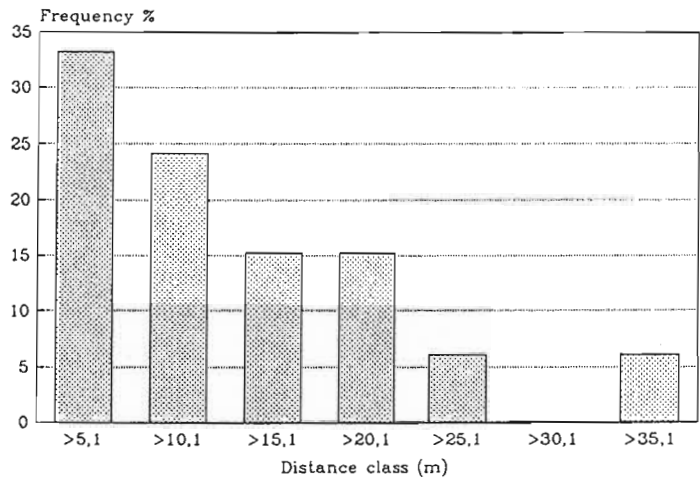
Figure 3.2 Frequency distribution of animal to sampling line distance for blue duikers.



August 1987



April 1988



August 1988

Figure 3.3 Frequency distribution of animal to sampling line distance for red duikers.

Dung-heap counts

Two hundred and five blue duiker and 78 red duiker dung-heaps were located in 85 sampling plots at KSNR. Sampling intensity was 1.33% for blue duikers and 0,83% for red duikers. Estimates of duiker population densities at KSNR from these data appear in Table 3.3. The late spring dung-heap count at Charter's Creek, rendered non-viable by invertebrate activity, was abandoned.

Line transects

Replicate sampling (n=15) was conducted along a 1749m transect during November 1987, 247 red duikers were sighted. The density estimate from line transect data was 1,59 red duikers ha⁻¹ (95% CL=1,32-1,83; Table 3.3).

Territory mapping

Radio tracking data (Chapter 4) showed that blue duiker pairs, sometimes with subadult offspring, occupy permanent territories which fluctuate very little throughout the year. Mean territory size at KSNR was 0,74ha and at Umdoni 0,65ha. However, red duiker home ranges overlap extensively, up to 100% in some cases; a feature which disqualified the application of this technique in population estimation.

The estimated number of blue duiker territories at KSNR was 108 and in 150ha of forest at Umdoni was 231. Density estimates at

Umdoni (3,1 animals ha⁻¹) approximated results from variable width transects, whereas at KSNR, 2,7 animals ha⁻¹ agreed with dung-heap counts: but was almost two-fold strip transect and drive count estimates (Table 3.3).

Variable duiker densities

Duiker densities varied locally throughout KSNR. Two areas were selected for intensive study, KSNR-B with the lowest densities (0,9 blue duikers ha⁻¹ and 0,3 red duikers ha⁻¹) and KSNR-C with the highest densities (1,6 blue duikers ha⁻¹ and 0,6 red duikers ha⁻¹; Figure 3.4). These two forest communities provided an opportunity to investigate the role of habitat and food quality as determinant factors of duiker densities (Chapters 5 and 6).

Costs

Minimum costs, in terms of manhours, for each technique are summarised in Table 3.4. Dung-heap counts and transect methods are by far the most economical while drive counts and territory mapping involve a substantial financial investment.

Table 3.4 Cost, in terms of manhours, of conducting various population density estimation techniques for forest duikers.

	<u>Semi-skilled</u>	<u>Skilled</u>
Drive counts	450	60
Transects (line, fixed and variable width)	50	50
Dung heap counts	20	20
Territory mapping	-	600+

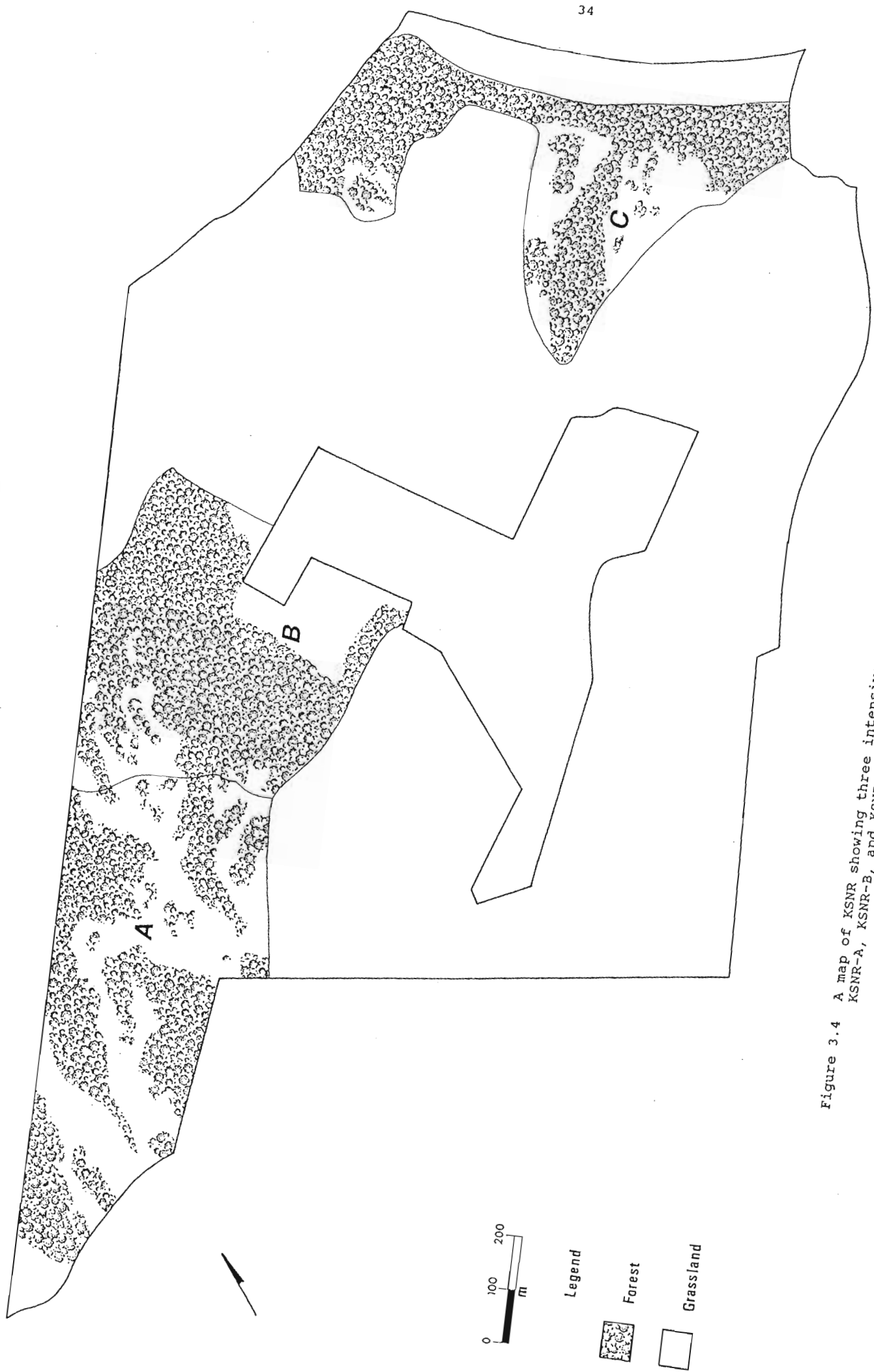


Figure 3.4 A map of KSNR showing three intensive study areas, KSNR-A, KSNR-B, and KSNR-C.

Discussion

All estimation methods have their limitations, and so a pragmatic approach should be adopted when evaluating and choosing a method. Some methods, though rejected because they have no measure of error, may be useful and informative in wildlife management. Because of the limited precision and accuracy of most techniques, it is desirable to use two or more independent methods to estimate population densities.

Drive counts

The merits of using this technique to count forest dwelling antelope are outlined by Le Roux and Emslie (in prep.). However, drive counts are not always successfully employed, and in some cases they have proved to be unreliable and biased (Tyson 1959, Downing, Moore and Knight 1965 vide Koster and Hart 1988). The intensity of drives and diligence of beaters vary in ways difficult to quantify, and the number of animals that do not flush cannot be counted (Koster and Hart 1988).

The accuracy of the results rely on the following assumptions (Collinson 1985):

1. no individual animal is counted by an observer more than once,
2. no individual animal is enumerated by more than one observer, and
3. all animals occurring in the census area at the time of the census are counted.

Blue duikers are territorial (Chapter 4) and not easily driven from their territories. When driven by observers, they hastily double back at the territory boundary, sometimes undetected, or they hide in thick understorey vegetation until the line of beaters has moved on. This response, also noted in the suni Neotragus moschatus by Lawson (1986), violates the third assumption and results in undercounting bias (Seydack 1984).

The experience and skill of counting line observers at KSNR accounted for a high degree of concurrence in that the mean percentage difference between counts approximated 10%. The number of undetected animals was probably low; since observers, aware of the blue duiker's skulking behaviour, concentrated on flushing the animals by beating thick vegetation with sticks.

The efficiency of observers was monitored by the sighting of two radio-collared red duikers in the 1988 counts. The marked animals were recorded by observers five times out of a possible six (Bowland 1990). The accuracy of this technique, as executed in KSNR, permits verification of estimates from other methods.

The primary disadvantage of this method (Seydack 1984, Collinson 1985, Lawson 1986) is the high labour input or pecuniary cost (Table 3.4). However, though not suited as a routine technique over large areas it is acceptable for small nature reserves and vulnerable species (Seydack pers. comm.).

Variable width transects

In many cases the only option available for sampling duikers in forests is to use an existing road or path as a sampling line. In some circumstances, conditions may in effect conform closely to a conventional design, which are seldom strictly random, systematic or representative (Collinson 1985).

Strip transect results are biased unless certain assumptions hold (Collinson 1985):

1. no animals move into or out of the approaching observer's range of visibility before being detected,
2. no animals are counted more than once by the observer traversing the sampling line, and,
3. sighting distances of the animal are measured from the exact point of detection and all measurements are recorded accurately.

Koster and Hart (1988) found that direct counts from transects proved impractical, as animals were difficult to detect because they moved away from the observer. The problem was not extreme in KSNR, where, though accustomed to pedestrian traffic, forest duikers sometimes moved in response to observers. Though this behaviour may affect the accuracy of the method, population estimates, when compared to those of drive counts, are similar for blue duikers and only slightly lower for red duikers.

No measure of error can satisfactorily be attached to this method (Knott and Venter 1987). However, consistent estimates, despite changes in season and visibility, indicate that the method is

robust regarding precision and repeatability, provided sufficient replications are made. Observer bias may occur where an untrained field assistant has not developed a search image for the animals. Blue duikers in particular are cryptic, especially in subdued light at dawn and dusk, beneath the forest canopy.

Variable width transects provide a reliable, simple and economic method to estimate forest duiker densities, especially in forests outside reserves. Invariably a jeep track or footpath traverses forest and forest patches which can be used as a sampling line.

Standard strip transects

The forest on either side of the road at Charter's Creek contained high duiker densities. However, though the road was suitable for me to conduct sampling, it was clearly avoided by the animals and serves to exemplify that the sampling line must accommodate the behaviour of the animal.

Red duiker densities along the road were lower than elsewhere: animals probably avoid this area because of noise and disturbance from timber haulage vehicles, palatability of food reduced by dust, and lack of cover (Chapter 4).

Line transects

The main disadvantage of line transect sampling arises if the estimator chosen to model the density function curve is incorrect,

since the population estimate is likely to be biased (Burnham *et al.* 1980, Collinson 1985). Further, when compared with variable-strip transect methods, other disadvantages are (Collinson 1985):

1. the analysis and interpretation of the results require more skill and the use of a computer,
2. more skill is mandatory in applying the field procedure, e.g. estimates are sensitive to rounding errors,
3. estimates are prone to bias arising from animal response to approaching observers, and,
4. the sampling line must be straight and clearly demarcated.

This method is generally unsuitable to estimate red duiker population densities. Apart from the stringent requirements of data capture and processing, the behaviour of the animal and the nature of its habitat are incompatible with field procedure prerequisites. In particular, the tendency of red duikers to move in response to observers and the requirement of a straight line are prohibited by dense forest vegetation.

Dung-heap counts

Dung-heap counts have proved useful in temperate zones to estimate population densities (Neff 1968). Some local authors (von Gadow 1978, Lawson 1986) suggest the use of this technique should be more fully explored in this region. However, Koster and Hart (1988) found that counting dung-heaps on fixed plots in tropical rain forest in Zaire was difficult, since animal densities were low, pellet decay was rapid, and pellets were rare and hard to find.

The conversion of animal sign estimates to population density estimates depends on assumptions that are difficult to meet (Collinson 1985):

1. the rate and degree of dung-heap disintegration vary markedly with invertebrate activity and prevailing weather conditions,
2. dung-heaps are sometimes deposited on top of existing dung-heaps, and,
3. daily defaecation rates vary with diet, age and season (Neff 1968, Collinson 1985, Koster and Hart 1988).

Von Gadow (1978) reports blue duiker dung-heaps in the Tsitsikamma forest remaining intact for 20-29 days while Lawson (1986) recorded suni dung-heap longevity of 60 days. Koster and Hart (1988) estimated that the maximum longevity of blue duiker pellets in tropical rain forest was 18 days. In this study dung-heaps were in good condition up to 40 days after deposition. Different climatic regimes within the census area contribute to variability in decay rate (Seydack pers. comm.).

Koster and Hart (1988) found a close agreement between densities derived from dung-heap counts and drive count estimates, whereas at KSNR dung-heap counts are almost double those of drive counts and strip transects. Problems related to meeting the assumptions of this technique are not easily overcome and it should not be used if other options are available.

Territory mapping

Many workers, mainly conducting bird counts, regard this method as an absolute and reliable density estimate (Franzreb 1981).

Territory mapping requires that every territory and its occupants in the census are accounted for. This requirement can only be met with use of radio tracking techniques which are expensive and time consuming.

The modification and application of territory mapping to estimating densities of forest dwelling antelope has a number of limitations:

1. the delineation of territories without the use of radio tracking is difficult,
2. it is impractical, if not impossible, to measure every territory in the census area,
3. territories in sub-optimal habitat, necessarily larger, and territories temporarily vacant, if such a phenomenon takes place, are not easily identifiable and thus not catered for in the estimation, and,
4. unpaired animals, floaters (animals without territories), and juveniles still living with parents are difficult to identify, no provision is made for them in the calculation.

Franzreb (1981) found that bird censusing territory mapping produced higher density estimates than variable strip transects; the results of each method were influenced by habitat structure and bird behaviour.

At Umdoni there is close agreement between densities derived from territory mapping and variable strip transects. The habitat at Umdoni is of high quality (Chapter 5), all territories probably abut and are occupied. At KSNR, inferior patches, in terms of habitat quality, are unoccupied (Chapter 5) and this results in an overestimation of blue duiker densities.

Wildlife management procedures and ecological research projects usually call for pragmatism. In view of this, the variable width transect method appears most suitable, and is recommended for population estimation of forest duikers.

CHAPTER 4

TEMPORAL AND SPATIAL PATTERNS

Introduction

The concept of home range is an important one in the interpretation of the behaviour of mammals; it relates to the restricted area within which individuals live and the manner in which they use this living space (Jewell 1966).

Although the term home range is used by many ecologists, there is disagreement over its meaning and the appropriate way to measure and represent it is a persistent problem (Jewell 1966, Anderson 1982, Samuel et al. 1985); for the purpose of this study it is defined as (Jewell 1966): "That area over which an animal normally travels in pursuit of its routine activities."

The object of this study was to correlate forest duiker home range characteristics (size, fluctuations, overlap, and core areas) and activity patterns with environmental factors.

Forest duikers are, by the nature of their behaviour and habitat, difficult animals to study with regard to spatial distribution. Very little information on movement patterns can be gathered from direct observations; consequently activity patterns and home range characteristics of forest duikers were surveyed by radio tracking.

Methods

Capture, handling, and immobilisation of forest duikers are described in Appendix A. Orientation in the forest was achieved by reference to tagged posts representing grid square intersections on study area map overlays which were located and marked on the ground. There is no known method for a priori choosing grid size (Anderson 1982), however, it should be small relative to home range area but no smaller than the limitations in the accuracy of the tracking system (MacDonald et al. 1980). For blue duikers a 20mx20m grid square provided an optimum focus while 50mx50m was appropriate for red duikers.

Radio collars

Each locally made transmitter (van Urk, University of Potchefstroom), potted in fibre glass gel, had its own frequency in the 144-148Mhz range and was securely attached to a durable collar. Radio collars, made from 3-ply machine belting, were sheathed in "sterkolite" to prevent abrasion of the animal's neck. Radio collars had a mass c. 150g for blue duikers, c. 170g for red duikers and transmitters, powered with Tadiran TL 2200 3,6v Lithium batteries, had a potential lifespan of 400 days.

Receivers and antennae

Transmitter signals were monitored with portable Yaesu FT290R transceivers. Two bar Yagi directional aeriels gave sufficient orientation to confidently pinpoint an animal to a grid square.

Radio tracking

The undulating topography of the study areas and capacity of the forest vegetation to absorb and diffuse transmitter signals rendered tracking from permanent stations in the forest impracticable. Any anomalous data were abandoned. Unobtrusive paths, usually coinciding with grid cell boundaries, were made in the forest to facilitate "predictive" tracking (MacDonald 1977).

Pathways, swept of "noisy-underfoot" litter one day prior to data capture, and the concealing nature of the vegetation permitted a disturbance-free approach to within 10-15m of blue duikers and 30-50m of red duikers. This method ensured precision and facilitated constant accuracy in pinpointing radio tracking locations ("fixes") to a grid cell. A characteristic change in transmitter signal pitch, when getting close, not only warned that an animal's flight zone was being encroached upon but enhanced accuracy of the fix. When an animal's position was in doubt cross-bearings were taken from alternate positions.

Tracking usually commenced at 04h00 and ceased at 20h00 with spot checks between 11h00 and 01h00. Forest duikers are diurnal, since periodic 24h tracking sessions confirmed that they are seldom active at night. Information recorded included animal identification number from transmitter frequency, time, and position.

Tracking sessions, with a minimum duration of five days, were planned for each season in all study areas. It was important to ascertain that tracking session duration was adequate to collect

biologically meaningful data. Minimum tracking duration, therefore, was derived from time taken to obtain sufficient fixes such that additional fixes did not significantly increase range area.

Radio tracking data were collected during two periods. In the developmental period location data were collected on an ad hoc basis day and night. These data were only useful in the computation of home range area. In the second period, time-interval predictive tracking required that where possible fixes be taken every half-hour for blue duikers and every hour for red duikers. Time-interval data enabled the calculation of activity patterns and home range size, including range overlap and fluctuation, and delineation of core areas.

Activity patterns

Activity state, stationary or active, was determined from radio tracking locations, in that where consecutive fixes were the same stationary behaviour was scored, while active behaviour was scored where they differed. The ten dark hours, 19h00 to 05h00, were scored as stationary following preliminary 24h continual recording.

Animals were presumed to move in straight lines between closely-timed fixes. The number of grid cells traversed, related to time of day, was used as an index of activity.

Home range size estimates

Home range estimates vary greatly with type of data analysis and selecting the appropriate method to quantify home range is difficult because there are no standards of accuracy. Literature relating to home range estimation is extensive; Mohr and Stumpf (1966), Sanderson (1966), Jenrich and Turner (1969), Van Winkle (1975), Anderson (1982), and Spencer and Barrett (1984) are among numerous authors who have scrutinised and reviewed home range models and their application.

Consequently, radio tracking data were analysed with the Mcpaal program which uses a number of different models to estimate home range area. Five models were chosen to process duiker location data: grid cell count; minimum convex polygon (Mohr 1947); minimum concave polygon (Stickel 1954); 95% ellipse (Jenrich and Turner 1969; Koepl, Slade, and Hoffman 1975); and, the harmonic mean measure (Dixon and Chapman 1980).

The harmonic mean measure has certain advantages over other methods of calculating home range areas; the harmonic mean, unlike arithmetic mean models, is always located within the area under consideration, it is relatively insensitive to movements within the home range, and the mean centre is a close approximation of the true activity centre (Dixon and Chapman 1980). Despite some inaccuracies in home range depiction by outer isopleths, Spencer and Barrett (1984) found the harmonic mean measure to be an advance over previous methods of calculating home range area.

Based on intimate knowledge of duiker home range, such as boundaries and centres of activity (e.g. bedsites and foraging areas), gained from the radio tracking method used, I found the harmonic mean measure to be the most realistic and accurate in reflecting home range size and utilisation. Consequently, this model was used consistently to predict the location of the perimeter and centres of activity of duiker home ranges.

Home range core areas

Most animals do not use the entire home range area with equal intensity (Dixon and Chapman 1980, Samuel et al. 1985). Certain areas, termed core areas, are used more frequently than any other areas and usually contain bedsites, refuges, and a regular food source (Ewer 1968). Spencer and Barrett (1984) found that harmonic mean isopleths containing 25% and 75% of the loci accurately defined core areas. Since duikers are stationary for lengthy periods, the 25% isopleth was used to identify core areas, particularly bedsites.

Seasonal fluctuations of the home range

In many African ungulates seasonal movements, even of small scale, are ecologically important in that they enable animals to utilise shifting food resources (Leuthold 1977). Shifts in individual duiker home ranges were monitored by superimposing seasonal home range plots to determine the extent of the shift.

Home range overlap

Where radio-collared animals were caught in close proximity to each other their home ranges (with core areas and common reference points), were superimposed to show overlap or segregation.

Temporal separation

Extensive overlap of red duiker home ranges, including core areas, indicated minimal spatial separation of individuals. A system whereby mutual avoidance allowed the temporal partitioning of the same area by several individuals was investigated. Inter-individual distances, estimated from the epicentres of grid squares, were measured only when either of the two individuals under scrutiny was in the area of overlap.

Frequency histograms of estimated inter-individual distances at simultaneous fixes were drawn to indicate the most frequent distance (rank class) between collared individuals.

Results

Constraints on radio tracking data can occur if the radio collar hinders or has any adverse effects on the animal. A collared pair, B4 and B7 (Table 4.1), not only maintained their territory during the study (18m+) but also reproduced. Further, the neck of study animal B18 showed no sign of abrasion or callousing when the collar was removed after 12m. These events suggest that radio collars had negligible, if any, influence on duiker activity.

Tracking effort

Measures of tracking effort are shown in Table 4.1; 20 animals (six females and four males of each duiker species) were fitted with radio collars. Premature failure of transmitters restricted the collection of reportable data to only 12 individuals. Minimum tracking duration was substantially less than five days; in most cases the entire home range was revealed after three days (Table 4.2). On average each tracking session yielding 152 fixes for blue duikers and 90 for reds.

Activity patterns

Forest duikers spend a large proportion of the day engaged in sedentary behaviour. Blue duikers were stationary for 33,1 to 50,0% of daylight hours (05h00-19h00) and red duikers 24,3 to 69,3%, while both duiker species were relatively more active in habitats of higher quality (Table 4.3).

Table 4.1 Summary of collared animals, radio-tracking effort and transmitter reliability (K=Kenneth Stainbank Nature Reserve, C=Charters Creek, U=Umdoni Park, Numbers identify individuals, M=male, F=female, ▲=month radio-collar fitted, ※=tracking session, *=premature transmitter failure, #=collar removed).

Year			1985		1986								1987					1988				
	Month		10	11	01	02	04	06	08	09	10	11	12	01	03	04	05	06	11	04	05	06
Blue duiker:																						
K	B1	F			▲			※			※	*										
K	B2	M			▲			※			※	*										
U	B4	M				▲	*															
U	B5	F				▲	※	*														
U	B7	F				▲	※	※			※	※		※	※				※			
U	B18	M					▲	※			※	#										
K	B22	M							▲		※											
K	B23	F							▲		※											*
K	B24	F							▲		※											*
K	B27	F								▲	*											
Red duiker:																						
K	R1	M	▲	*																		
K	R8	F														▲					*	
C	R9	F															▲				※	
K	R10	M															▲				*	
K	R11	F															▲				*	
C	R20	M																		▲	*	
C	R21	F																		▲		※
C	R22	F																		▲		※
C	R23	M																		▲		※
C	R24	M																		▲		※

Table 4.2 Minimum tracking duration for home range estimation of forest duikers (100% = life time range).

	Total grid cells	Cells revealed day 1	%	Cells revealed day 2	%	Cells revealed day 3	%
Blue duiker:							
B7 - summer	19	17	89	18	95	19	100
- autumn	18	17	94	18	100	18	100
- winter	15	13	87	14	93	15	100
- spring	15	11	73	13	87	15	100
B22	13	7	54	13	100	13	100
B23 - summer	15	9	60	14	93	15	100
- autumn	17	8	47	14	82	17	100
B24	14	8	57	12	86	13	93
Red duiker:							
R9	32	19	59	29	91	32	100
R21	9	5	56	7	78	9	100
R22	13	4	31	9	69	13	100
R23	34	17	50	23	68	31	92
R24	13	11	85	11	85	13	100
R20	25	6	24	6	24	16	64
R8	19	8	50	16	84	17	90

Table 4.3 Stationary and activity state of forest duikers during daylight (14h), with extrapolation over 24h (blue duikers n=7, red duikers n=8).

	Number of tracking sessions	Daylight activity				24h activity			
		<u>stationary</u> hours	%	<u>mobile</u> hours	%	<u>stationary</u> hours	%	<u>mobile</u> hours	%
Blue duikers:									
Umdoni Park	5	4.6	33.1	9.4	66.9	14.6	60.8	9.4	39.2
KNSR-A	4	7.0	50.0	7.0	50.0	17.0	70.8	7.0	29.2
Red duikers:									
Charters Creek	6	3.4	24.2	10.6	75.8	13.4	55.8	10.6	44.2
KNSR-A	2	9.7	69.3	4.3	30.7	19.7	82.1	4.3	17.9

Daily activity patterns of the two duiker species are shown in Figures 4.1 and 4.2. Both species were most active shortly after dawn and just before dusk. In winter, blue duiker bi-modal activity peaks (early morning and late afternoon) shifted in unison with a later dawn and earlier dusk, rather than possessing an elevated midday trough to accommodate fewer daylight hours (Figure 4.3).

Home range size

As there is no standard measure of home range (Anderson 1982) the results from all five models are listed in Table 4.4; different estimates may be useful for comparative purposes. It is tempting to ascribe the slightly smaller home ranges at Umdoni to better habitat, however, apart from small sample sizes, intra- and inter-study area variability deems unlikely any real biological differences in size. The difference in mean blue duiker home range sizes between Umdoni (0,65ha) and KSNR (0,74ha) was not statistically significant (Mann-Whitney U test, $p > 0.05$; Table 4.4).

Mean red duiker home range size at KSNR (11,6ha) was significantly larger (Mann-Whitney U test, $p < 0.01$) than that at Charter's Creek (7,3ha, Table 4.4). The exceptionally large summer home range estimate for R9 was excluded from the statistical test as this young female was a 'floater' and had not established the permanent home range reflected in the winter tracking session.

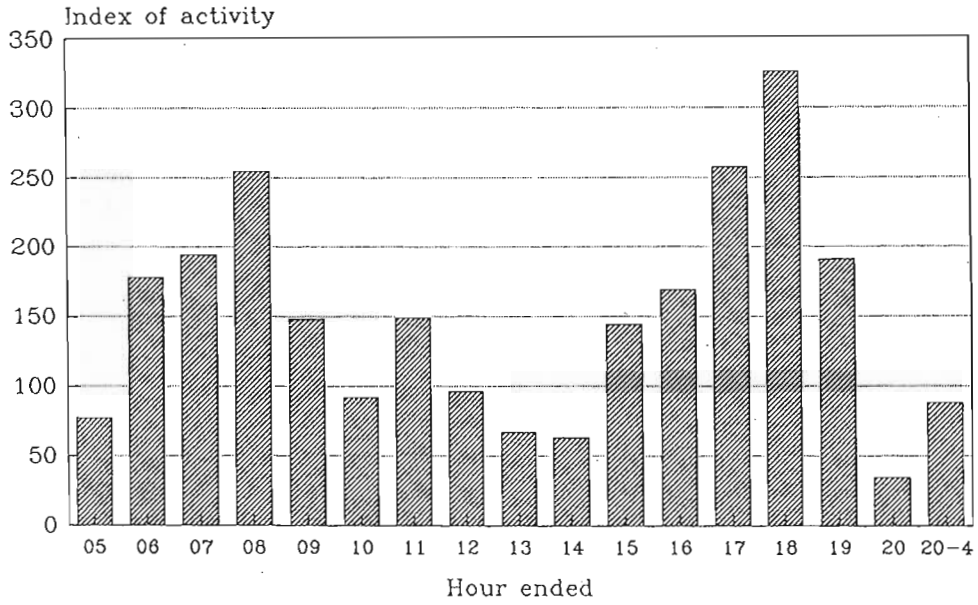


Figure 4.1 Accumulative activity pattern of blue duikers in all study areas.

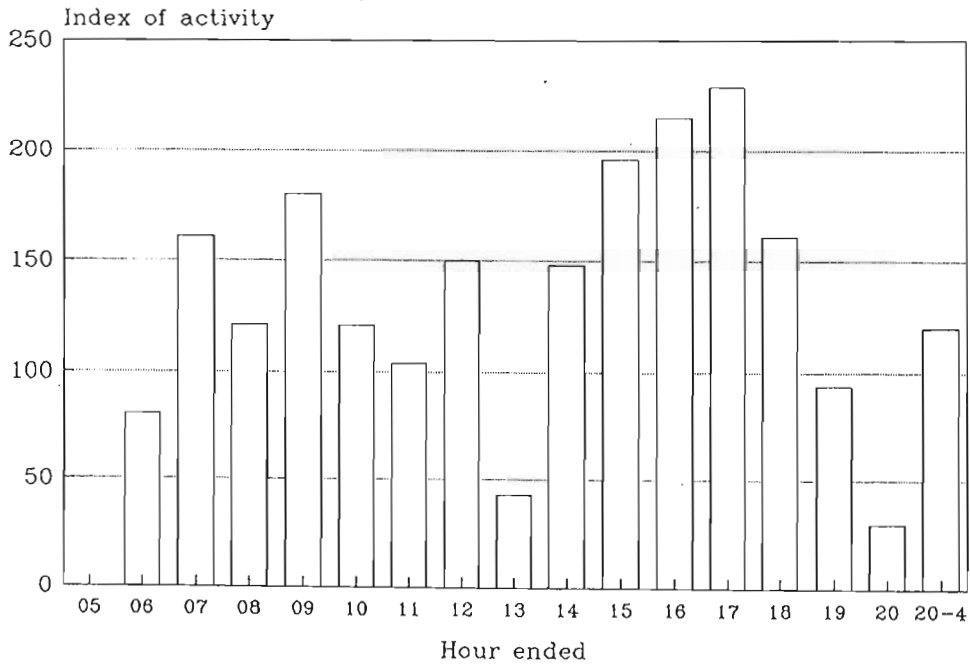


Figure 4.2 Accumulative activity pattern of red duikers in all study areas.

Home range fluctuations

Two blue duiker home ranges [B7 (Umdoni) and B23 (KSNR)] with seasonal plots overlain, showed that though home range boundaries were dynamic (changing slightly during the year) core areas were permanent and remained fixed (Figure 4.4). Seasonal data sets for red duikers were not obtained.

Home range overlap

Blue duikers showed exclusive family home ranges with no overlap between neighbours (Figure 4.5), for this species home range and territory are synonymous. Red duiker home range overlap varied greatly (up to 100% in some cases) indicating the absence of territoriality (Figure 4.6).

Home range core areas

Core areas in the home range of both duiker species were usually associated with bedsites. In blue duiker home ranges core areas were fixed all year with no overlap between neighbours (Figure 4.5) while home ranges and core areas of red duikers overlapped extensively (Figure 4.6).

Table 4.4 Home range estimates of forest duikers using different home range models.

		grid cell <u>count</u>	minimum convex <u>polygon</u>	concave <u>polygon</u>	95% <u>ellipse</u>	harmonic mean <u>transformation</u>	
		(n)	(ha)	(ha)	(ha)	(ha)	
Blue duikers							
Umdoni:							
B7	summer	20	0.80	0.66	0.52	1.77	0.76
	autumn	18	0.72	0.70	0.60	1.98	0.99
	winter	19	0.76	0.70	0.58	1.86	0.74
	spring	16	0.64	0.54	0.42	1.56	0.60
B18		10	0.40	0.14	0.14	0.97	0.16
B5		14	0.56	0.52	0.44	1.65	0.66
	mean	16	0.64	0.54	0.45	1.63	0.65
KNSR:							
B23	summer	15	0.60	0.48	0.32	1.64	0.67
	autumn	17	0.68	0.90	0.54	2.77	0.90
B24		14	0.56	0.34	0.32	1.24	0.53
B22		13	0.52	0.48	0.20	1.73	0.70
B2		14	0.56	0.32	0.30	1.16	0.83
B1		14	0.56	0.32	0.28	1.23	0.82
	mean	15	0.58	0.47	0.33	1.63	0.74
Red duikers							
KNSR:							
R1		12	3.0	3.63	3.00	14.37	5.43
R8		19	4.75	8.25	3.25	23.44	15.20
R20		25	6.25	9.5	6.38	26.7	14.14
	mean	19	4.67	7.13	4.21	21.5	11.6
Charter's Creek:							
R21		9	2.25	1.13	1.13	6.08	1.25
R22		15	3.75	2.63	2.0	9.04	3.53
R9	Summer	66	16.5	19.75	14.0	41.23	18.98
	Winter	29	7.25	7.75	5.62	18.48	8.97
R23		30	7.50	7.13	5.75	15.73	9.24
R24		11	2.75	1.75	0.75	7.8	1.84
	mean	28	6.96	6.69	4.87	16.39	7.3

Temporal separation

Temporal separation is suggested between some individuals and not others; R9 (female) and R24 (male), R23 (male) and R21 (female), and R23 (male) and R24 (male), seem to avoid each other whereas R9 (female) and R21 (female), and R9 (female) and R23 (male) appeared to show more tolerance of each other (Figure 4.7). However, these results need be interpreted with great caution; the interactions between individuals of this dense population is very complex and only a few tagged animals were monitored with no possible measure of the influence on their movements of unmarked animals.

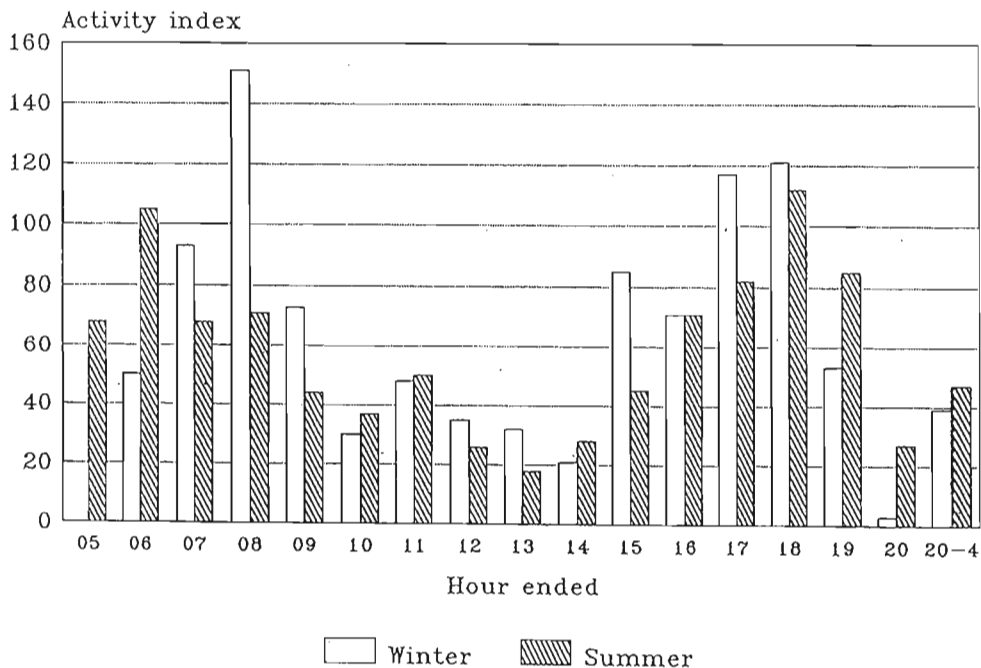


Figure 4.3 Seasonal changes in activity pattern of blue duiker B17.

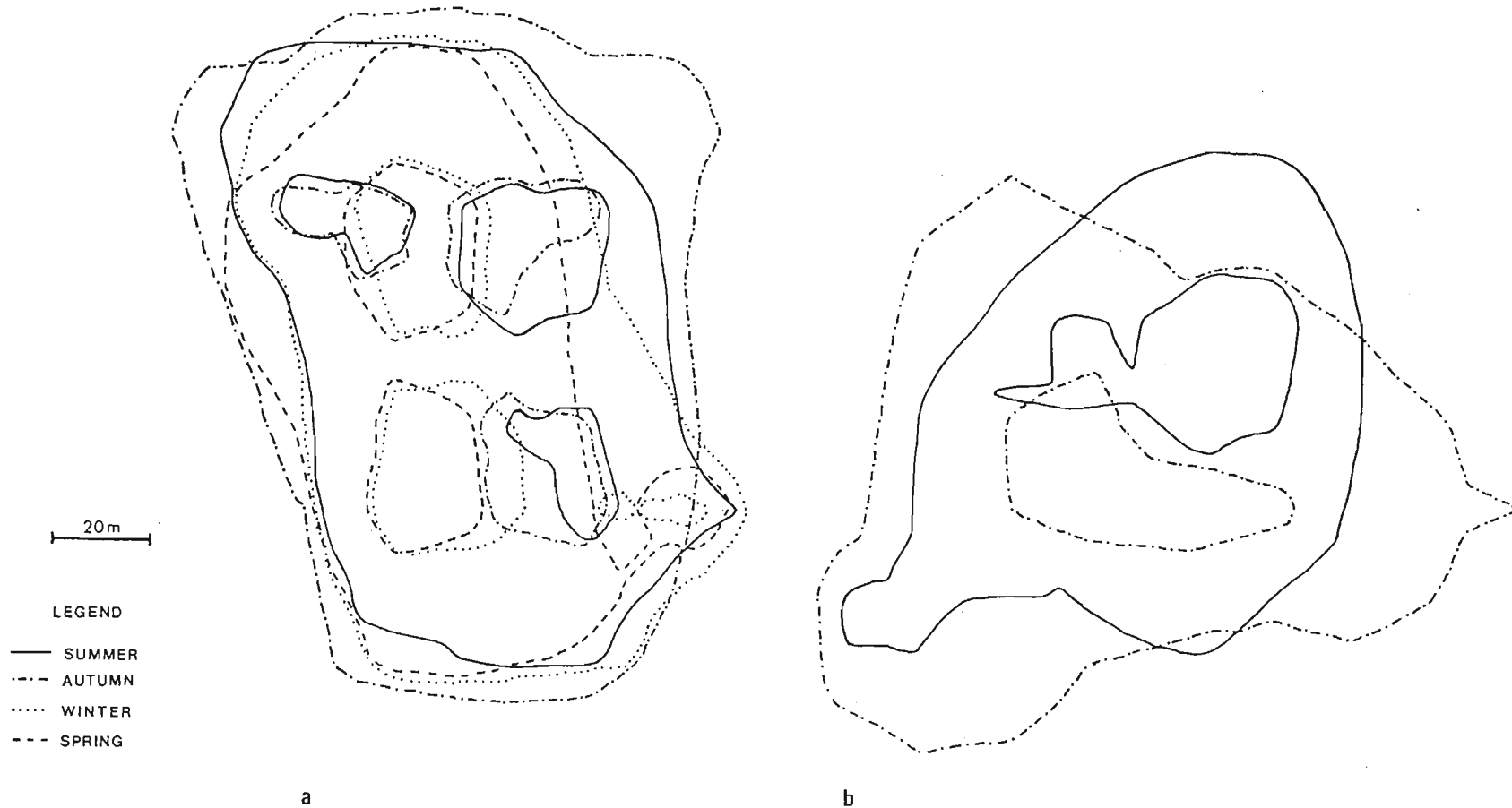


Figure 4.4 Seasonal home ranges of blue duikers,
 (a) B7 in Umdoni, and (b) B23 in KSNR.

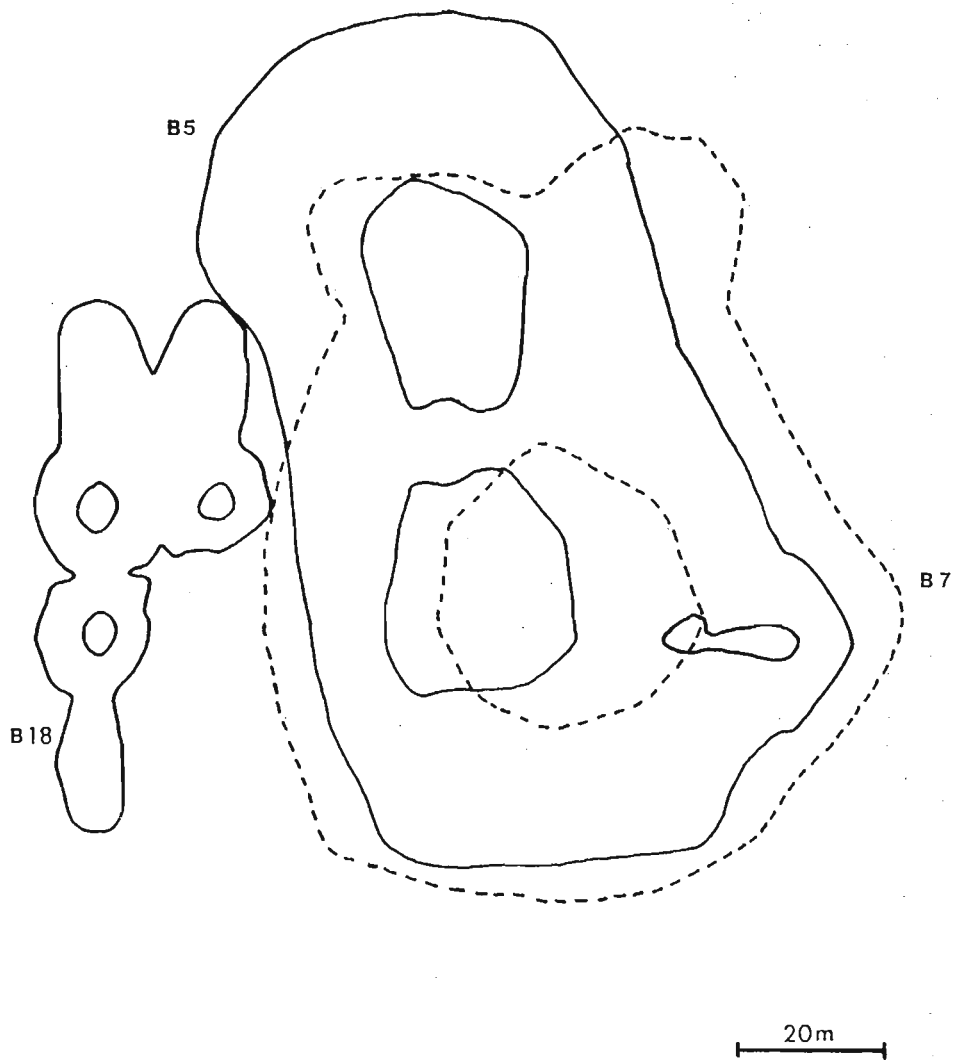
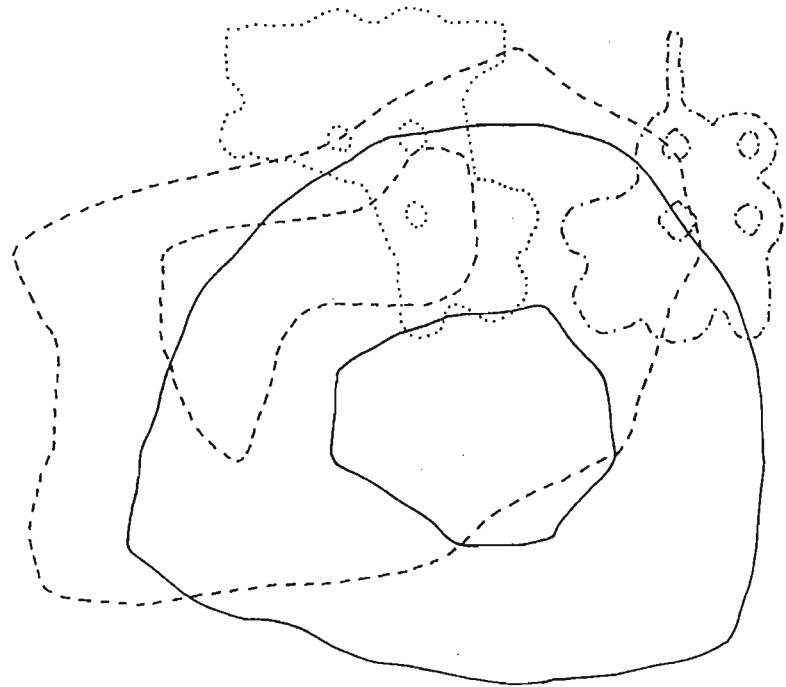
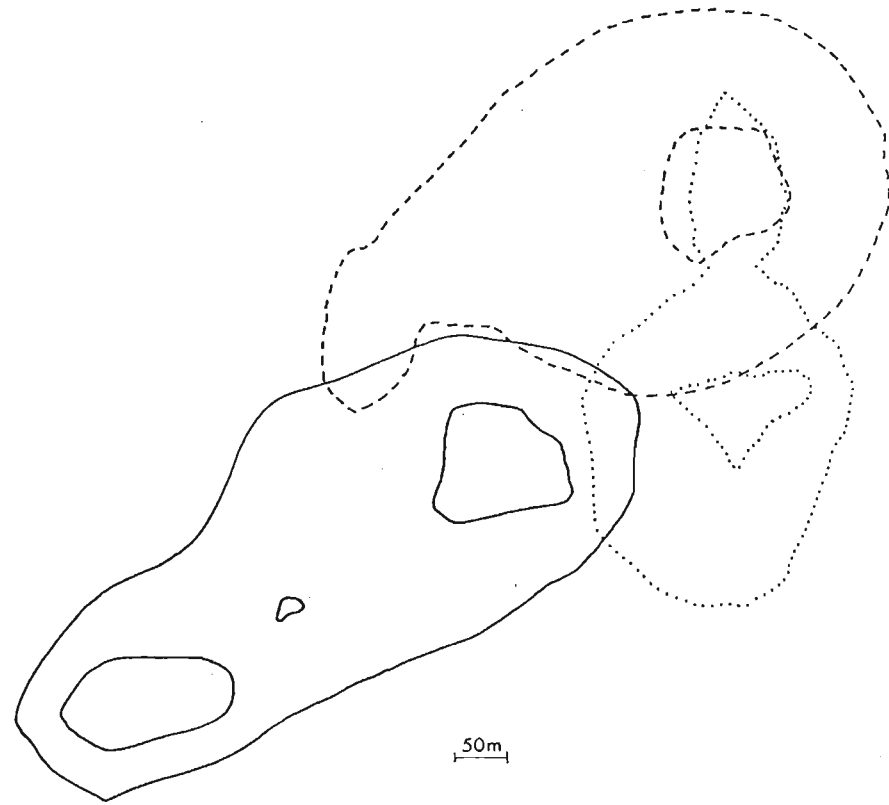


Figure 4.5 Adjacent blue duiker home ranges, family members B7 and B5 do not overlap with neighbour B18.



a

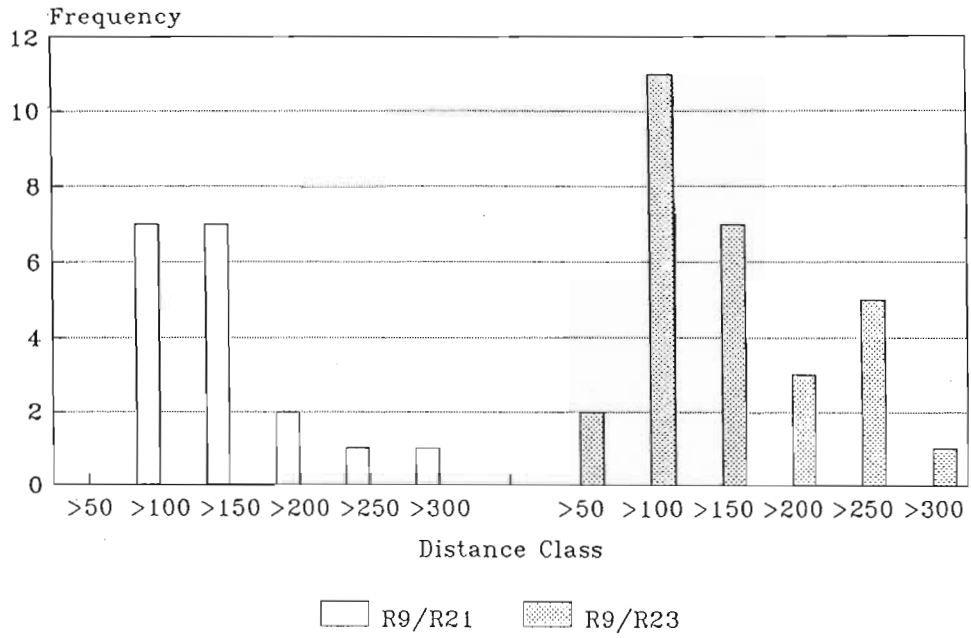
- R9
- · - · - R21
- R23
- R24



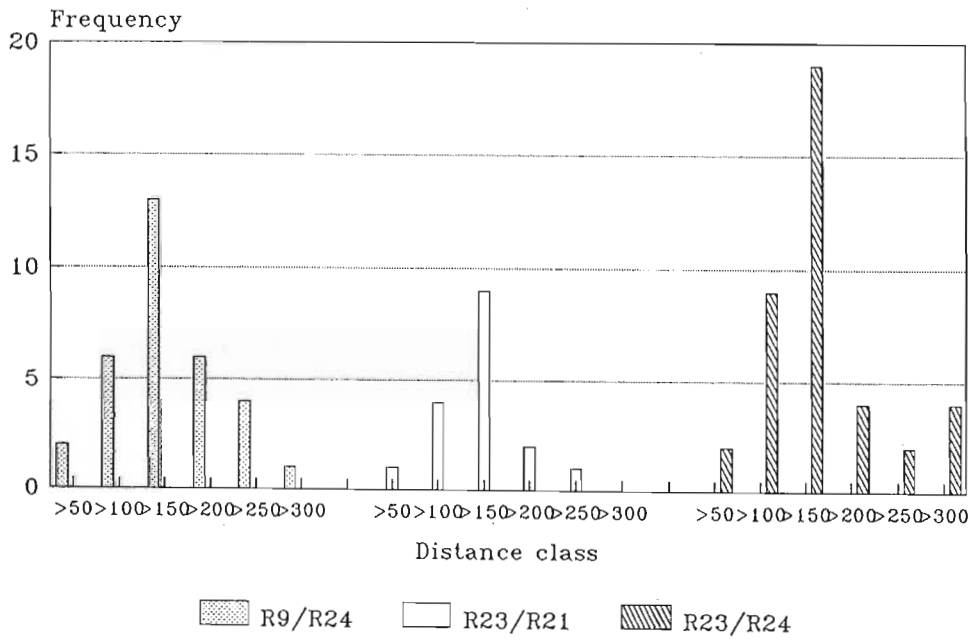
b

- R1
- R8
- R20

Figure 4.6 Overlap of red duiker home ranges and core areas in (a) Charters and (b) KSNR.



a



b

Figure 4.7 Frequency histograms of inter-individual distances at simultaneous fixes, (a) indicates no temporal spacing and (b) indicates temporal spacing.



Figure 4.8 Permanent home ranges and core areas of two blue duiker pairs in KSNR.

Discussion

The high proportion of static behaviour in both duiker species is a function of a ruminant digestive physiology and a relatively small body size. Large, bulk feeders spend more time foraging (Owen-Smith 1988) than forest duikers which are able to quickly fill a small rumen, maintain home range boundaries, and then retreat to a bedsite to ruminate.

In habitats of higher quality (Umdoni and Charter's Creek, Chapter 5) with concomitant high duiker densities (Chapter 3) activity was relatively greater (Table 4.3). Blue duikers, with exclusive home ranges (territories), are probably under great pressure to patrol and maintain territorial boundaries when population densities are high. At maximum density demand for territories is greatest and high contest rates will evoke increased defensive activity. In addition, palatable food plants are assimilated more efficiently and quickly, and require less rumination time. Consequently, in habitats of high quality, which infers more palatable foods, more time will be available for activities other than rumination, particularly scent marking and territorial defense.

Red duikers, whose home ranges overlap extensively (Figure 4.6), cannot secure food resources within a defended territory. Thus, with high red duiker densities more time is needed to forage for good, but relatively scarce, food. As food quality and quantity changes, time available for other activities shifts. The proportionately higher level of mobility in red duikers may be a function of resource scarcity or increased interaction between individuals participating in social activities.

Activity patterns show the diurnal habit of both duiker species, contrary to some reports of nocturnal activity (Williams 1967, Kingdon 1982, Smithers 1983). Diurnal activity is shown by blue duikers in central Africa (Dubost 1980). Nocturnal activity that occurs is associated with animals switching bedsites following disturbance.

The shift in activity patterns in unison with dawn and dusk suggests proximate photoperiodic control. The ultimate cause of activity phasing is likely determined by predation, food availability, inter- and intra-specific interactions, and home range maintenance. Shorter duration of midday inactivity in winter accommodated the seasonally consistent periods of crepuscular activity. Dubost (1980) related slight increases in the midday activity of central African blue duikers in the dry season to reduced food resources. However, in both studies, midday activity was probably related to territory maintenance and/or feeding to maintain the rumen microflora.

Seasonal variations in location and size of home range is common amongst African ungulates; the nature and extent of such variations depend on changes in environmental conditions (food, water) and on attributes of the animal (species, sex, age; Leuthold 1977). McNab (1963) and Harestad and Bunnell (1979) implicate bioenergetic requirements as the primary determinant of home range size whereas Mace *et al.* (1983) suggest that body size predicts home range size far more precisely than do energetic needs. Damuth (1981) points out that no single functional relationship with body size should be expected, rather home range

size represents a compromise between individual metabolic requirements and social pressures.

Numerous studies provide evidence of habitat quality and population density affecting home range size (Sanderson 1966, Hendrichs 1975, MacDonald 1977, Odendaal and Bigalke 1979, Boshe 1984). Changes in these two parameters initiated little response, in terms of changing home range size, from blue duikers. Red duikers followed an inverse trend where the extent of home range decreased with an increase in population density and/or resource availability.

Home range size in territorial blue duikers was similar in two forest communities of quite different habitat qualities and population densities. Umdoni has high conspecific densities (Chapter 3), a broad food base (Chapter 6), and good habitat (Chapter 5) while KSNR-A is inferior in each of these attributes. Yet, in KSNR-A there was no expected compensatory increase in home range size of the resident blue duiker population.

The defence of an area involves cost in time and energy, so for territoriality to have evolved there must be compensatory advantages to the holder to increase its inclusive fitness; when costs of defending resources exceed benefits gained from them through defence, territorial behaviour will not evolve (Mace et al. 1983). Territory defendability depends on the ability of the animal to monitor the area (Mitani and Rodman 1979), energetic costs and territory size (Davies and Houston 1984).

In the case of inferior forest communities a prudent strategy for the blue duiker would be to inhabit smaller patches of high

quality but of defensible size, which satisfy requirements year-round, rather than to extend the boundaries to meet with neighbours. Larger, adjacent territories are counterproductive, since inclusive unexploitable areas merely increase defence costs and reduce benefits. In KSNR-A and KSNR-B, inferior forest communities, blue duikers probably occupy well spaced, discrete pockets of good habitat. Consequently, home range sizes here are the same as those at Umdoni though densities and habitat differ. Dubost (1980) estimated blue duiker home range area in central Africa to be 2,8 to 3,5ha, however, the method used to calculate these areas is not given and so no meaningful comparisons are possible.

In the non-territorial red duikers home range, size was influenced by population density and habitat quality. Home range size decreased with an increase in population density (Chapter 3) and habitat quality (Chapter 5).

Female ungulates, with infants lying out, restrict home range size while the infant cannot accompany them (Ewer 1968, Leuthold 1974, Odendaal and Bigalke 1979). Forest duikers' with small home ranges and lengthy inactive periods in secluded bedsites are probably able to integrate hiding infants without changing daily routine or reducing home range size. It is unlikely that the small home range of red duiker female R21 is a response to the presence of an infant. She was neither visibly pregnant nor lactating at the time of capture, and her home range approximates that of male R24.

Not all parts of the home range are of equal significance to its inhabitants (Leuthold 1974, Samuel *et al.* 1985). Forest duikers

home ranges contain one or more core areas, each usually associated with a bedsite (Chapter 5), where the animals spend a great proportion of time. Time away from the bedsite is usually associated with foraging and, in the case of blue duikers, territory maintenance. Foraging areas (Chapter 5) were not identified by the 25% isopleth, since the proportion of time spent foraging was much less than time spent at the bedsite.

Jarman (1974) related social organisation of antelopes to their ecology and recognised five feeding strategies with associated social behaviour. Class A included small antelopes which are highly selective browsers feeding on plant parts of high nutritive value such as flowers, twig tips or fruits. Species in this class are solitary or form pairs or pair families (which do not vary in size seasonally). The home range, usually a territory, is small, occupied all year, and located in one vegetation type.

Leuthold (1977) classified social organisations of African ungulates according to their use of and relations to space (home range, territories), and the types and sizes of the social groups normally formed.

Blue duikers fit well into Leuthold's (1977) classification, SO-type 3b, where permanent pairs occupy exclusive home ranges. In this class the social unit is a pair, with or without immature offspring, living in a fixed territory. Both sexes take part in territorial activities such as defence and marking. Jarman's (1974) class A aptly describes the blue duiker except for the diet which is less specialised than expected (Chapter 6).

Blue duiker females B5 and B7 and male B4 inhabited the same territory early in the project. B5 soon moved to another territory approximately 100m away and B7 and B4 were sole occupants until B7 calved in February 1987. Male B18 was tracked in an adjacent territory until November 1986 when it was discovered that he had moved about 150m away. On recapture to remove the radio-collar, it was noted that he had been severely horned in the ribs and had almost certainly been displaced. Pairs B1/B2, and B22/B23 were observed in their respective territories for 12 months.

Red duikers, with non-exclusive home ranges, best encompass Jarman's (1974) class B and Leuthold's (1977) class S0-type 1e. In the latter class social units are ill defined; no lasting associations exist between individuals, females and young may form quite large temporary herds while males tend to be solitary except for transient associations with other males and/or female herds. The former class includes selective browsers of highly nutritive food items in home ranges which do not change during the year and utilise one vegetation type. Group size ranges from one to 12, females usually accompany other females and single males are probably always territorial.

Both sexes of red duikers were solitary, and no lasting associations were apparent except in females with young. Adults, generally solitary, sometimes formed loose, transient associations with other individuals. Food selection is not highly specialised (Chapter 6) as hypothesized.

Extensive home range overlap in red duikers indicates that spatial separation does not occur. Observations of scent-marking and

interaction between individuals suggest hierarchical ranking (Jarman 1974). A pronounced tolerance was noted in temporarily associated males in the absence of females. Interest shown in a female inevitably evoked a chase if more than one male was present.

Ewer (1968) stated that it was not uncommon to find that while home ranges overlap core areas do not. Core areas of red duiker home range overlapped extensively. In the absence of spatial separation, temporal spacing, of which tenuous evidence was present, probably reduced the frequency of encounters and conflict situations.

Postscript:

Water is often regarded as a limiting resource in duiker habitat (Fitzsimons 1920, Blamey and Jackson 1956, Kingdon 1982, Smithers 1983). With one exception, however, none of the home ranges in this study had perennial surface water, while radio tracking in all study areas never once disclosed sallies to water sources. Forest duikers are therefore independent of free water and their distribution within a forest community is not influenced by its absence.

CHAPTER 5

HABITAT

Introduction

Most definitions of animal habitat consider the habitat to be the place where the animal is typically found (Shugart 1984). The great variety of African ungulates, related to the almost infinite diversity of habitats, exhibits a wide range of specialisation with some ungulate species restricted to dense forest (Leuthold 1977).

Shelter and food are two critical dimensions of an animal's habitat. For woodland herbivores these two parameters are often tightly interwoven and therefore difficult to examine independently. In the case of forest duikers the constituent vegetation of the habitat plays a double role of providing cover and food, or aptly put as "home and table" by Jacob (1981 vide Oldeman 1983), where the main dietary component is freshly fallen leaves (Chapter 6). Permanent home ranges of forest duikers (Chapter 4) provide and define these two essential resources spatially and temporally.

Habitat quantification in terms of cover requires the identification of inherent features that are vital to the animal. Cover is important at numerous levels. These range from a distal or primary level of canopy cover to a more proximate or tertiary level of the bedsite. In addition to canopy cover, radio tracking

data (Chapter 4) identified three special features characteristic of forest duiker habitat, each strongly associated with vegetation layers, viz. foraging areas, shrub-cover, and bedsites.

✓ Foraging areas are usually open glades beneath a high, closed canopy. Here, not only is the animal able to forage easily in all directions but, it can flee rapidly to shrub-cover if the need arises. Shrub-cover provides the animal with a refuge in which it can seek shelter while continuing mobile activities.

Blue duikers are mobile for 7-9h daily, red duikers for 4-11h (Chapter 4). Duikers lie-up, usually in a bedsite, for up to 19h a day while they rest, sleep, ruminate and/or engage in static behaviour. Infants of both species hide-up rather than accompany adults in the first few weeks of their life, behaviour that also requires appropriate cover.

✗ An inherent feature of the bedsite, therefore, is that the constituent vegetation provides protection and seclusion necessitated by long, static periods. Bedsites comprise dense, usually scrambling, understorey thicket. Cover characteristics of a bedsite are not as rigid for adult red duiker which frequently lie-up in fairly open areas.

✓ Foraging areas and shrub-cover, when translated into a vertical profile of the forest, prescribe, in general terms, that the stratum below 2,5m, the shrub layer, is important in terms of cover, while vegetation > 2,5m to emergents, the tree layer, is the primary food source. Within and between forest community comparisons of these two strata, when correlated with density of

their resident duiker populations, target important habitat attributes.

The forest floor is generally devoid of ground cover (vegetation below 1m). When present, it impeded foraging activities of the duiker or was impenetrable. Suni Neotragus moschatus respond to a marked increase in ground cover by shifting their ranges (Lawson 1986). Ground cover provides relatively little food for duikers, no shelter and is of little importance in the habitat generally. Consequently it was omitted from sampling exercises.

Lianas, a prominent forest component, were present in all the forest communities studied. Their cohesive association with erect vegetation in all strata made it impossible, without destructive sampling methods, to evaluate separately their contribution to the functional attributes of the habitat.

High species diversity, a central theme in many conservation biology studies, is frequently interpreted as an indicator of the well-being of an ecological system (Magurran 1988). Apart from being informative and useful, "diversity" facilitates comparison of the structure of one ecological community against another. In the case of forest duikers, especially the blue duiker, high plant species (and structural) diversity is probably a compulsory prerequisite for the habitat because a relatively small area of forest must provide all life requirements.

Objectives were to accurately describe the salient features of optimum habitat for the management and conservation of forest duikers.

Methods

The increase in number of study areas midway in the project (Chapter 2) meant that not all study areas were sampled with each method described.

Canopy cover

Fixed-point photography was used to monitor canopy cover seasonally in three forest communities (Umdoni, Charter's Creek, and KSNR-A). Twenty permanent photographic stations, spaced at 20m along a randomly located transect line, were established in each forest community.

Canopy cover was calculated by the point-intercept method. Postcard size (14x9cm) black and white photographs of the canopy at each station were placed under a like-size, transparent 10x10mm dot-grid with 108 dots. An intercept (score) was recorded when a dot covered or touched any vegetation on the photograph. Number of intercepts expressed as a percentage of the total gave an estimation of canopy cover.

Seasonal variation in canopy cover between forest communities was compared by means of a contingency table. The null-hypothesis was that seasonal variation in canopy cover is the same in each forest community. Analysis of variance was performed on transformed data to evaluate the extent of seasonal variation in canopy cover within each forest community.

Plotless sampling

Distance or plotless sampling techniques obtain a rapid estimate of density in vegetation types where individual plants are well defined and distinctly spaced, such as forests (Ludwig and Reynolds 1988). Plotless sampling is considerably more efficient than quadrat sampling when individuals are widely scattered. The nature of forest habitat lends itself to plotless sampling techniques.

The point-centre quarter (PCQ) method (Mueller-Dombois and Ellenberg 1974) was used to determine dominant species, stem densities, and basal areas of the tree and shrub strata in five forest communities. Plant identifications were confirmed by the Natal University herbarium and those with a deciduous habit were noted.

Sampling points, at 20m intervals, were along random transects which followed a pre-selected compass bearing. For the tree layer, sampling point to tree (quarter-distance) and circumference at breast height (CBH) were measured while for shrubs only quarter-distance was measured. CBH was used to calculate basal area and perform a size-class analysis of the tree layer. The accurate measurement of CBH in the lower stratum was thwarted by a preponderance of multistemmed and/or scandent shrubs. Quarter-distance was consistently measured as sampling point to the mid-point of the rooted stem. Sample size was considered adequate when the ratio of standard error of the mean to the mean was less than 0,1 (Greig-Smith 1983).

Size structure of the tree layer was determined by ranking basal areas into five size classes. Size-structure variation between forest communities was examined by means of an analysis of variance of transformed basal area measurements.

Spatial patterns

Spatial patterning, an important ecological trait, can be divided into three basic categories: random, clumped or uniform. The influence on diikers of spatial patterning in the tree and shrub strata was examined in four forest communities.

An index of dispersion, I , based on quarter-distance data (from PCQ measurements) was used to test spatial patterning (Ludwig and Reynolds 1988). Dispersion I has an approximate expected value of 2 for a random pattern, less than 2 for a uniform pattern, and greater than 2 for clumped patterns. This method also allowed for the computation of a 'z' value which, when compared to a table of critical values for the standard normal distribution, could provide a level of significance of any departure from randomness. The equations follow:

$$(i) \quad I = (N + 1) \frac{\sum (x_i^2)^2}{[\sum (x_i^2)]^2}$$

where N = the number of sample points, and,
 x_i = quarter distance from the i th sampling point.

$$(ii) \quad z = \frac{I - 2}{\sqrt{4(N-1)/(N+2)(N+3)}}$$

where I = index of dispersion, and,
 N = number of sample points.

Diversity

Species diversity is composed of two components, the first is the number of species in the community, often referred as species richness, and the second, species evenness, which relates to how the number of individuals are distributed among the species (Ludwig and Reynolds 1988). A given value of a diversity index may result from various combinations of species richness and evenness and on its own fails to indicate the relative importance each of species richness or species evenness.

Rarefaction allows the comparison of species numbers or richness between communities where sample sizes are unequal (Hurlbert 1971, Ludwig and Reynolds 1988). Rarefaction curves for each forest community were computed from PCQ data with the following equation:

$$E(S_n) = \sum \left\{ 1 - \left[\frac{(N-n_i)}{N} \right]^n \right\}$$

where $E(S_n)$ = the expected number of species in a sample of n individuals

N = total population, and,

n_i = the number of individuals of the i th species.

Sample size $n=90$ (determined by the smallest sample, Umdoni) was used as a standard to compare the five forest communities (illustrated by a dashed vertical line in Figs 5.3 and 5.4).

Diversity was measured with the Shannon index, H' (Shannon and Weaver 1949), since its wide use in ecology allows direct comparison with other studies. Evenness was measured with the modified Hill's ratio (Hill 1973, Ludwig and Reynolds 1988) where the value for evenness approaches zero as a single species becomes more and more dominant in a community.

Tree:shrub ratio

As mentioned above, large trees (>15cm), though important as primary cover, are indispensable as a food source. Conversely, shrubs (height<2,5m), though providing some food, have a major role in furnishing secondary cover. Logically, not only should these two components, trees and shrubs, be present at certain threshold levels but a correct balance between them is probably a major determinant of habitat quality. To recognize the boundaries of this balance numerous relationships were investigated.

To identify the influence of the balance of trees and shrubs, the ratios of tree to shrub densities were correlated with duiker populations. Also, big tree (>15cm) density estimates, expressed as a percentage of shrub density, were plotted against duiker densities. Size-class percentage applied to total tree density gave an estimation of big tree density.

Numerous biotic and abiotic environmental constraints determine the upper limits of tree volume per unit area (Spurr and Barnes 1980). The allocation of available space between size classes will vary in each forest community. If space is a limiting factor one would expect tree density to vary inversely with the mean size of the trees. To study this spatial relationship, mean tree basal area was plotted against stem density for each forest community.

Bed-sites

Density of blue duiker bedsites, known (radio tracking) and potential (value judgements), were estimated in two forest

communities, Umdoni and KSNR-A, with the random pairs method (Mueller-Dombois and Ellenberg 1974). Sampling points were at 20m intervals along random transects through the forest. Bedside size was calculated from the circumference of the bedside vegetation clump at 1m.

Results

Canopy cover and dominant trees

Canopy cover of the forest communities ranged between 68,4 and 90,6% (Table 5.1). The null-hypothesis that seasonal variation in canopy cover is the same in each forest community was supported ($p=0.87$; Table 5.1). However, in KSNR-A spring canopy cover was significantly different from the other seasons ($p < 0.01$; Table 5.1).

Table 5.1 A comparison of seasonal variation in canopy cover within and between three forest communities.

Forest community	Summer %	Autumn %	Winter %	Spring %	Anova p=
Charter's Creek	82,7	79,0	76,8	82,9	0.96
KSNR-A	90,6	87,7	80,9	68,4	<0.01
Umdoni Park	87,0	90,3	85,2	78,4	0.59
Anova p=	0.28	0.10	0.25	0.27	

Chi-square = 2.49, df = 6, p = 0.87

The ten dominant tree species in each forest community are listed, with an indication of the incidence of deciduousness, in Table 5.2.

Vertical structure

Tree stem density, the main constituent of primary cover, was high at KSNR-B and KSNR-C, intermediate at Umdoni and KSNR-A, and low at Charter's Creek. Stem density of the shrub layer, which contributes to both secondary and tertiary cover, was low at

Table 5,2 Ten dominant tree species in five forest communities showing relative dominance as a percentage,

Charters		KSNR-A		KSNR-B		KSNR-C		Umdoni	
Species	%	Species	%	Species	%	Species	%	Species	%
<u>*Celtis</u>		<u>*Millettia</u>		<u>*Millettia</u>		<u>Protorhus</u>		<u>Schefflera</u>	
<u>africana</u>	30,6	<u>grandis</u>	27,2	<u>grandis</u>	22,9	<u>longifolia</u>	34,3	<u>umbellifera</u>	27,3
<u>Chaetacme</u>		<u>*Sapium</u>		<u>Bequaertiendron</u>		<u>*Millettia</u>		<u>Strelitzia</u>	
<u>aristata</u>	22,2	<u>integerrimum</u>	13,9	<u>natalense</u>	16,6	<u>grandris</u>	10,1	<u>nicolai</u>	11,0
<u>Euclea</u>		<u>Strelitzia</u>		<u>Drypetes</u>		<u>Strychnos</u>		<u>*Croton</u>	
<u>schimperi</u>	6,7	<u>nicolai</u>	11,8	<u>arguta</u>	12,1	<u>henningsii</u>	6,9	<u>sylvaticus</u>	10,3
<u>*Ekebergia</u>		<u>*Croton</u>		<u>Protorhus</u>		<u>Drypetes</u>		<u>Syzygium</u>	
<u>capensis</u>	5,9	<u>sylvaticus</u>	9,1	<u>longifolia</u>	9,8	<u>arguta</u>	6,2	<u>cordatum</u>	8,9
<u>Acacia</u>		<u>Bequaertienden-</u>		<u>*Croton</u>		<u>Bequaertiendron</u>		<u>Harpephyllum</u>	
<u>robusta</u>	3,4	<u>dron natalense</u>	6,5	<u>sylvaticus</u>	8,5	<u>natalense</u>	6,0	<u>caffrum</u>	6,8
<u>Apodytes</u>		<u>Baphia</u>		<u>Gardenia</u>		<u>Brachylaena</u>		<u>Bequaertiendron</u>	
<u>dimidiata</u>	3,3	<u>racemosa</u>	5,2	<u>ameona</u>	3,9	<u>discolor</u>	5,3	<u>natalense</u>	6,6
<u>Trichilia</u>		<u>Tricalysia</u>		<u>Xylothea</u>		<u>*Croton</u>		<u>Linociera</u>	
<u>emetica</u>	2,8	<u>lanceolata</u>	4,9	<u>kraussiana</u>	3,6	<u>sylvaticus</u>	3,9	<u>peglerae</u>	5,9
<u>Scutia</u>		<u>Vepris</u>		<u>Vepris</u>		<u>Vepris</u>		<u>Protorhus</u>	
<u>myrtina</u>	2,4	<u>undulata</u>	3,9	<u>undulata</u>	3,4	<u>undulata</u>	3,3	<u>longifolia</u>	5,2
<u>Brachylaena</u>		<u>Protorhus</u>		<u>Tabernaemontana</u>		<u>Cassine</u>		<u>Brachylaena</u>	
<u>discolor</u>	2,1	<u>longifolia</u>	3,5	<u>elegans</u>	2,7	<u>papillosa</u>	3,3	<u>discolor</u>	3,3
<u>Deinbollia</u>		<u>Mimusops</u>		<u>*Combretum</u>		<u>*Ekebergia</u>		<u>Chaetacme</u>	
<u>oblongifolia</u>	1,8	<u>obovata</u>	2,8	<u>molle</u>	1,7	<u>capensis</u>	2,9	<u>aristata</u>	3,0
Total	81,2		88,8		85,2		82,2		88,3
*Deciduous									
species	36,5		50,2		33,1		16,9		10,3
Duiker density ha ⁻¹									
blue	-		1,1		0,9		1,6		3,2
red	1,6		0,2		0,3		0,6		-

Charter's Creek, intermediate at Umdoni and KSNR-B, and high at KSNR-A and KSNR-C (Table 5.3).

Size structure

Size structure, confirmed by mean basal areas, showed that Umdoni and Charter's Creek sites had a higher proportion of large trees than the intermediate levels at KSNR-A and KSNR-C and the low level at KSNR-B (Table 5.3). A graphic comparison of the five tree communities appears in Figure 5.1. Statistical analysis showed differences in size-structures to be significant (Anova $p < 0.01$).

Table 5.3 Survey characteristics of and blue duiker densities in five forest communities.

	<u>Umdoni</u>	<u>KSNR-A</u>	<u>KSNR-B</u>	<u>KSNR-C</u>	<u>Charters</u>
Size-classes (%):					
Diameter >20cm	6,8	0,7	1,0	2,0	2,0
15-20cm	3,0	5,2	1,7	2,3	5,5
sub-total	9,8	5,9	2,7	4,3	7,5
10-15cm	3,0	5,2	1,3	5,0	8,0
5-10cm	20,3	23,5	14,0	14,7	28,5
>5cm	66,9	65,4	82,0	76,0	56,0
Total	100,0	100,0	100,0	100,0	100,0
n	133	136	300	300	200
Stem densities (ha^{-1}):					
Trees	1765	1993	2572	2941	1070
Shrubs	1784	2451	1933	2731	1333
Tree to shrub ratio	1:1.01	1:1.23	1:0.75	1:0.93	1:1.25
Big tree % of shrub density	9,7	4,8	3,6	4,9	6,0
Mean basal areas (cm^2):	225,7	132,9	81,8	128,7	200,6
Duiker densities (ha^{-1}):					
Blue duikers (Table 1.)	3,2	1,1	0,9	1,6	0,0
Red duikers (Table 1.)	0,0	0,2	0,3	0,6	1,6

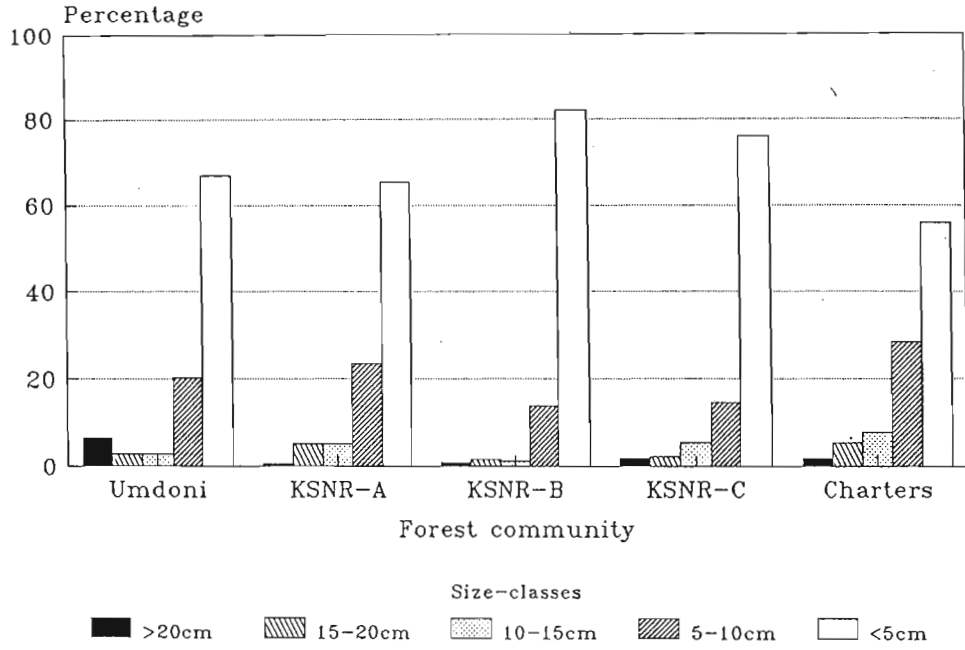


Figure 5.1 Size-classes of the tree layer in five forest communities.

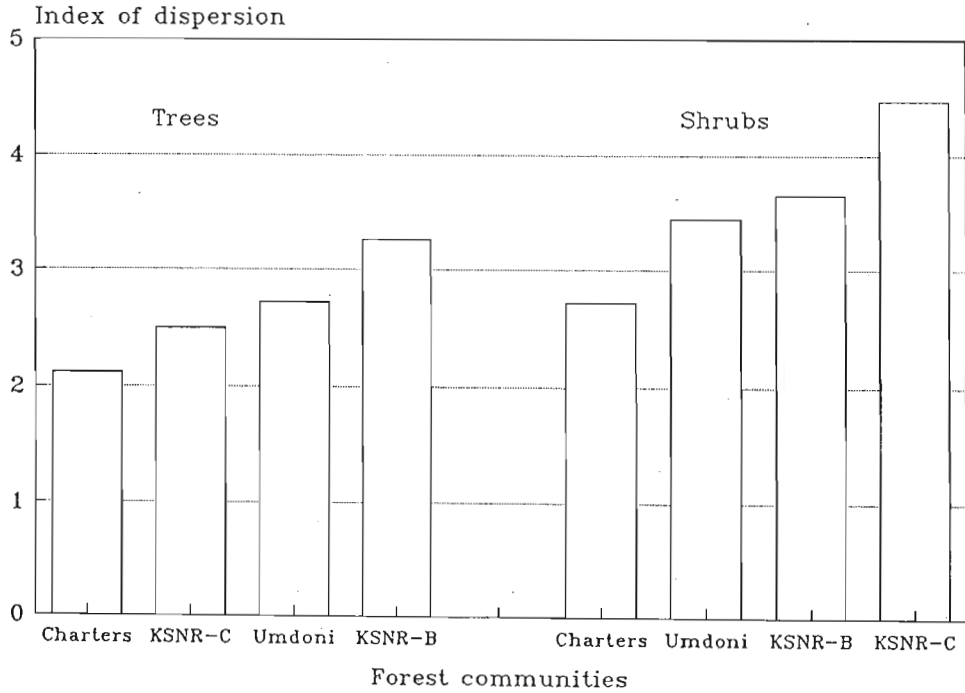


Figure 5.2 Dispersion indices of trees and shrubs in four forest communities.

Spatial patterns

All but one of the forest communities studied reflected a clumped distribution showing a significant departure from randomness in the tree and shrub layers. The tree layer in Charter's Creek showed a random distribution while the extent of aggregation varied noticeably between the rest of the forests.

In KSNR-B tree clumping was more intense than at KSNR-C and Umdoni. Whereas KSNR-C displayed strong clumping of the shrub layer, KSNR-B and Umdoni were intermediate while little clumping occurred at Charter's Creek (Table 5.4, Fig 5.2).

Table 5.4 Spatial patterns of the tree and shrub layers in four forest communities (MQD = mean quarter distance, I = index of dispersion, z = critical value for standard normal distribution).

	n	Trees				Shrubs			
		MQD	I	z	p	MQD	I	z	p
Umdoni	140	2,37	2,72	4,34	<0.01	2,39	3,45	8,76	<0.01
KSNR-B	300	1,97	3,26	11,01	<0.01	2,27	3,66	14,53	<0.01
KSNR-C	300	1,80	2,50	4,38	<0.01	1,90	4,47	21,61	<0.01
Charters	200	3,05	2,12	0,89	>0.05	2,70	2,72	5,20	<0.01

Diversity

Tree species richness was similar in all but one forest community, KSNR-B, which was depauperate in species (Table 5.5, Fig 5.3). The KSNR-C shrub layer had a much higher level of species richness than the equivalent levels recorded elsewhere (Table 5.5, Fig 5.4).

The Charter's Creek tree community displayed a high level of both diversity ($H' = 3.13$) and evenness ($E = 0.75$). The three tree communities in KSNR differed substantially among themselves; KSNR-C showed high diversity ($H' = 2.83$) with low evenness ($E = 0.38$), KSNR-A demonstrated intermediate diversity ($H' = 2.73$) with high evenness ($E = 0.69$), while, KSNR-B was low in both diversity ($H' = 2.22$) and evenness ($E = 0.38$). Umdoni was intermediate in both diversity, $H' = 2.76$, and evenness, $E = 0.52$ (Table 3.5).

Tree:shrub ratios

Areas of parity in ratios of trees to shrubs showed higher blue duiker densities than areas where the ratio favoured either element (Table 5.3). A similar trend was exhibited by the red duiker population in KSNR forest communities whereas at Charter's Creek proportionately fewer trees were associated with high red duiker densities suggesting that tree:shrub ratio may be of limited importance there (Table 5.3).

Duiker densities and the ratio of large trees to shrubs showed a positive affiliation (Fig 5.5) supporting the hypothesis that balance between these strata is an influential determinant of habitat quality. Too few data points precluded statistical analysis but the trends, particularly in the case of blue duikers, is clear.

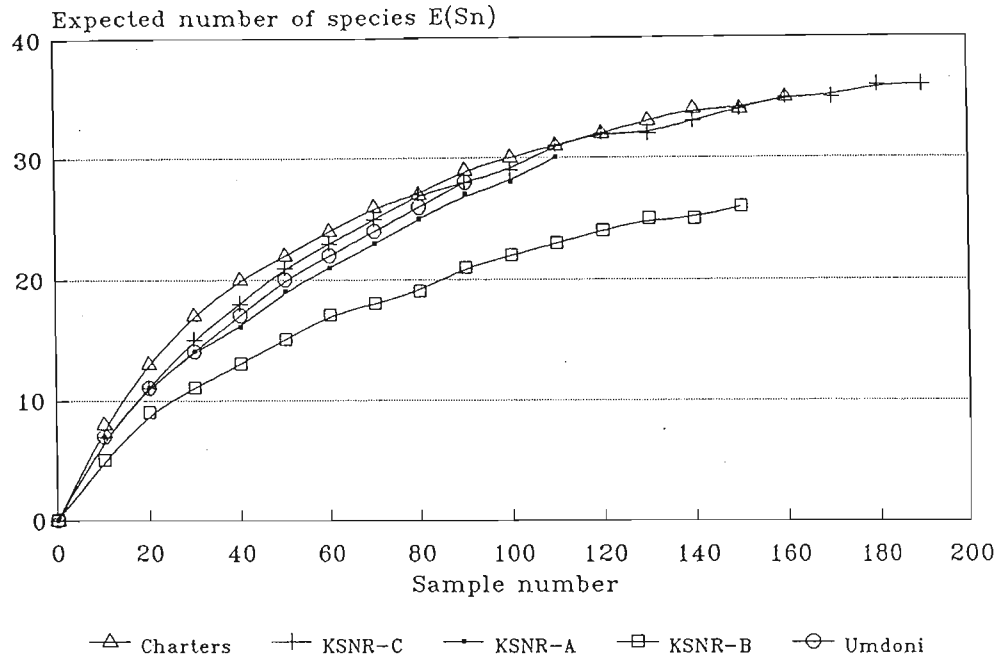


Figure 5.3 Rarefaction curves of the tree layer in five forest communities.

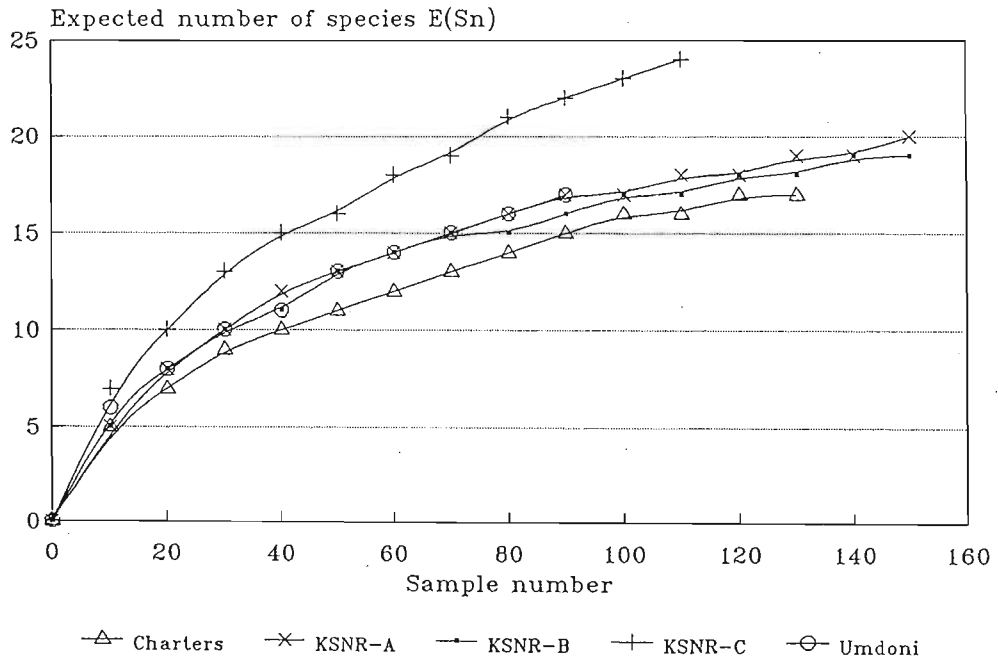


Figure 5.4 Rarefaction curves of the shrub layer in five forest communities.

Table 5.5 Diversity measures of five forest communities. ($E(S_n)$ = expected number of species when $n=90$, H' = Shannon index, E = modified Hill's ratio for evenness).

	$E(S_n)$	H'	E
Tree layer:			
Charters	29	3.13	0.75
KSNR-A	28	2.73	0.69
Umdoni	28	2.76	0.52
KSNR-C	27	2.83	0.38
KSNR-B	21	2.22	0.38
Shrub layer:			
KSNR-C	22	1.97	0.42
KSNR-A	17	2.61	0.65
Umdoni	17	2.14	0.62
KSNR-B	16	2.01	0.44
Charters	15	2.03	0.62

Spatial constraints on forest vegetation were indicated by the convincing negative relationship between tree size (mean basal area) and stem density of the tree stratum (Fig 5.6). Though statistical analysis was prevented by the limited number of data points clear trends are evident.

Bedsites

Bedsite density at Umdoni, 157 ha^{-1} , was not significantly different from that at KSNR, 182 ha^{-1} , ($p > 0.05$). However, the area of bedsite vegetation clumps at Umdoni ($26,6 \text{ m}^2$, $n=58$, $SE \pm 4.2$) was significantly larger ($p < 0.01$) than those in KSNR ($11,7 \text{ m}^2$, $n=58$, $SE \pm 2.0$). The proportion of habitat area, therefore, available for bedsites is between 42% ($157 \times 26,6 / 10\ 000$) and 21% ($182 \times 11,7 / 10\ 000$).

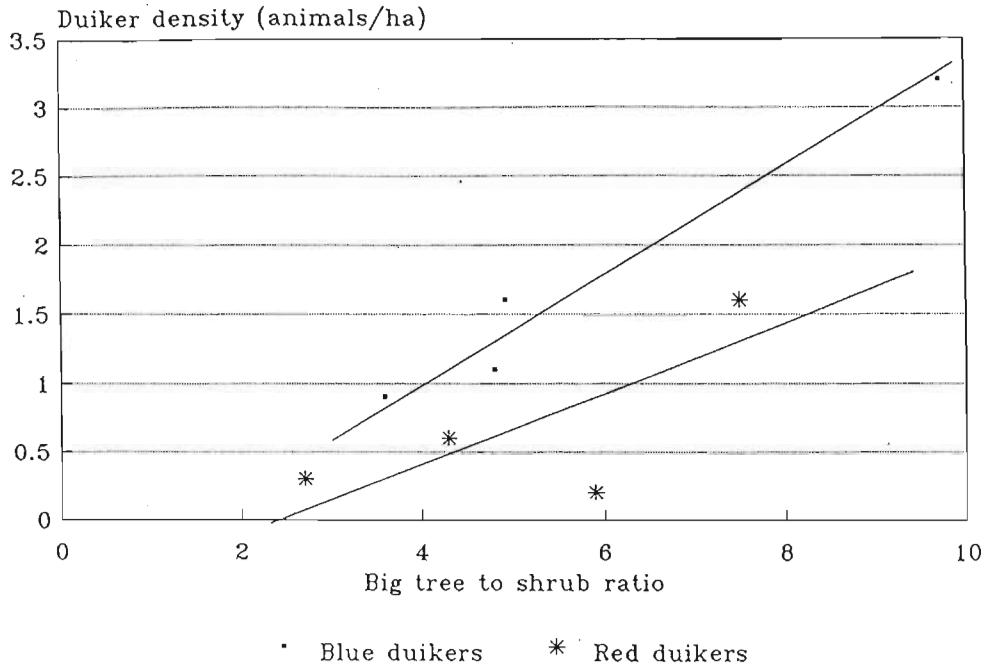


Figure 5.5 Duiker densities plotted against big tree (>15cm) to shrub ratio.

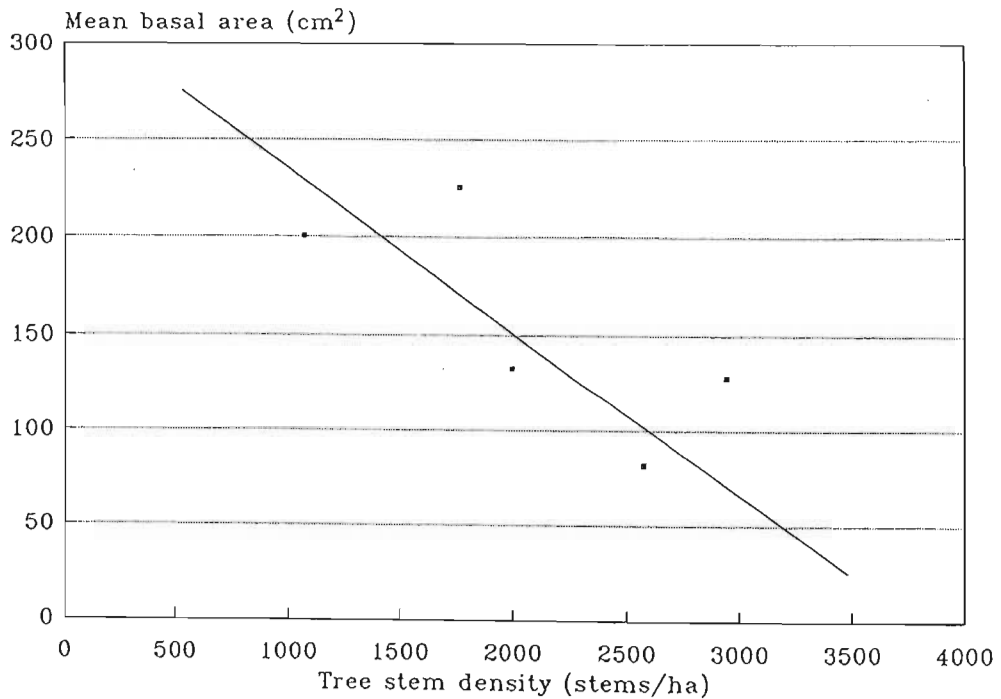


Figure 5.6 Mean basal areas plotted against stem densities.

Discussion

The evaluation of key environmental features of each forest community is impossible without some measure of "duiker success". Duiker densities are used as the benchmark against which numerous attributes were appraised in terms of their contribution to habitat quality.

Canopy cover and deciduousness

x Blue duikers are obligate forest animals (Dubost 1980, Heymans and Lejoly 1981), seldom venturing far from overhead cover, and when doing so, traversing coverless areas rapidly. Time spent away from effective cover exposes animals to both lateral and overhead predation. Blue duiker colouration, although blending well with surroundings beneath the canopy, is conspicuous outside the forest.

x The larger red duiker forages outside the forest canopy, especially on post-burn flushes of forbs in adjacent grassland. Never far from forest and perpetually alert, they flee at the slightest threat of danger. Both species are entirely dependent on primary cover.

Seasonal fluctuations in primary cover at Umdoni and Charter's Creek were characterised by low amplitudes whereas in KSNR-A fluctuations were more significant. The dominant trees in the KSNR-A community contain a high incidence of deciduousness, in particular Millettia grandis, Sapium integerrimum, and Croton sylvaticus which accounts for the marked seasonal changes.

Deciduousness not only reduces habitat quality by impairing primary cover through the creation of large gaps in the canopy and also the leaves of these trees generally have low palatability (Chapter 6). The inverse relationship between the incidence of deciduous dominant trees and duiker densities identifies a determinant factor in habitat quality.

Tree:shrub ratios

Equilibrium between shrub and tree layers has an important influence on habitat quality which declines where the tree:shrub ratio is unequal. The importance of an equal balance is exemplified by the positive association between blue duiker densities and the proportion of big trees to shrubs. Duiker habitat requirements prescribe an obligate balance between food resources and shelter, a deficiency of either reduces habitat quality.

However, this relationship only applies within certain threshold levels. Blue duiker densities at Charter's Creek predicted from Figure 5.5 approximate $1,8 \text{ animals ha}^{-1}$. This is not the case, however; blue duikers are absent from Charter's Creek notwithstanding an acceptable big tree to shrub ratio. The relatively low tree and shrub stem densities determine minimum threshold levels for blue duiker.

A similar prediction for red duikers at Umdoni would approximate $1,5 \text{ animals ha}^{-1}$, but they are absent. Red duikers were an

important part of the Umdoni fauna earlier this century (Osborn 1967) however, and have only become extinct there since the 1970's (Roseveare pers. comm.). It is unlikely therefore that habitat quality was the demise of the red duiker at Umdoni.

The critical role of the shrub layer in influencing habitat quality is exhibited by the near-extinct blue duiker population in Hluhluwe Game Reserve (HGR). Formerly, up to the 1950's, blue duiker sightings were frequent in the forests of HGR (Brooks and Macdonald 1983) but in a recent survey (Bowland 1987) no evidence of these animals, despite sporadic sighting reports, was found. The condition of the shrub layer in earlier years cannot be ascertained from the literature but in recent years it has been severely degraded by the activities of larger herbivores, in particular the bushpig Potamocheorus porcus. Although now below threshold levels for blue duikers, the shrub layer is still adequate for the substantial numbers of red duikers present there.

Vertical structure and spatial patterning

Spatial heterogeneity of plants has been implicated as a major factor in herbivore species survival, in particular where an individual may be expected to spend its entire life in one habitat (Shugart 1984). Two principal ecological factors important to forest duikers are the ability to forage unrestricted in a cluttered understorey for scattered food and the facility to flee rapidly (Dubost 1979). Thus, stem density has a direct influence on foraging and flight behaviour of forest ungulates and as such can be a limiting factor. The distribution of Peter's duiker

Cephalophus callipygus and blackstriped duiker C.dorsalis has been markedly and negatively influenced by vegetation density (Dubost 1979).

Unfavourable features of high stem densities can be tempered by spatial patterning of vegetation which can render forest architecture favourable to duikers. Clumping of vegetation often determines the suitability of forest for animal survival and reproduction (Leigh et al. 1982). Dubost (1979) found that blue duikers avoid dense areas, and prefer areas with large open patches beneath the canopy.

Of the three KSNR forest communities, KSNR-C, with very high densities of both trees and shrubs, contained, contrary to expectations, the densest populations of both red and blue duikers. A contributory factor to this phenomenon is the intense aggregation of the shrubs and the moderate clumping of trees. These conditions improved the habitat in contributing to a highly desirable mosaic of foraging areas, shrub-cover, and bedsites beneath continuous primary cover.

Diversity

In relatively small, permanent home ranges (Chapter 4) the scale of clumping of the vegetation may mean that adjacent areas may have very different resources. One home range may be quite inferior to another in terms of the resource it provides. Under these circumstances diversity is vital to supply food and cover year round within the home range.

Plant species, usually deficient in one or more essential nutrients, are high in indigestible cell wall materials, and contain secondary compounds that can interfere with the digestion of essential nutrients or be toxic to the consumer (Chapter 6). Primary consumers must generally mix and match food of different plant parts and species each day to obtain the required complementary amounts of essential nutrients (Milton 1982).

Umdoni, KSNR-C, and Charter's Creek, all with high duiker densities, had relatively high levels of species richness in the tree layer, the prime food source. The diversity index of this stratum in these forest communities ranged between intermediate and high, unlike KSNR-B which had inferior plant species diversity and species richness and concomitant low duiker populations. Plant species and structural diversity is, thus, a critical feature of duiker habitat quality.

Forest gap dynamics

A forest gap refers to a patch in a forest created by the death of a canopy tree. Gaps become localised sites of regeneration and subsequent growth, and are important in the formulation of a dynamic climax forest (Shugart 1984).

The number of trees occupying a site has important implications not only for duikers but for the trees themselves. Except at low densities, tree mortality, greatest at seedling stage, is caused by competition for light, water, nutrients, and other site

resources. As plants die, remaining individuals become larger, but smaller plants are continually eliminated from the population. There is a strong negative correlation between plant size and density of the stand; larger stems are associated with fewer stems per unit area (Spurr and Barnes 1980).

An unfavourable state, for duikers and trees, of too many large trees relative to smaller ones is curtailed naturally by gap dynamics of the forest. In forests with closed canopies gaps lead to a mosaic of patches in different stages of successional maturity. The regularity and severity of forest disturbances are major determinants driving the structural and compositional dynamics of the forest community. Most forest tree species are dependent on gap occurrence for regeneration and consequently for their continued persistence in climax forest (Doyle 1981).

The mosaic of different structural phases of forest growth contributes to favourable conditions for duikers. However, two processes inherent in gap dynamics may have a negative influence on habitat quality for duikers.

First, the lack of recruitment of some canopy species in mature tropical forests is well documented (Aubreville 1938 vide Hartshorn 1978, Richards 1966). Aubreville (1938) found climax tropical forests of West Africa to be spatially dynamic, but it was difficult to predict the dominant species of a particular climax community, a trend also evident in this study. He found dominants showing no regeneration in one community were regenerating in another where they would eventually displace its dominants. The scale of this cycle, however, is probably too

extensive to operate within the boundaries of the isolated KSNR forest community. Protorhus longifolia, a canopy dominant and important food source, shows no regeneration. Two questions thus arise. Will the species that displaces P.longifolia maintain, improve or degrade the quality of the habitat? What are the chances of P.longifolia completing the cycle by recolonising the isolated KSNR forest community subsequently? (Chapter 7).

Second, the cycle driven by gap dynamics in forest species regeneration collapses with the intrusion of exotic invasive species, in particular Cardiospermum grandiflorum, Cestrum laevigatum, Chromolaena odorata, Lantana camara, Pinus elliotii, Psidium guajava, and Solanum spp. (Macdonald and Jarman 1985). Where no eradication programmes are implemented or they are applied irregularly the forest will be steadily degraded and only offer inferior duiker habitat (Chapter 7).

Study area characteristics

Umdoni

Of the five forest communities studied, Umdoni had the highest blue duiker density (Chapter 3) about two-fold that of the best area in KSNR viz. KSNR-C. Evidence indicated that blue duiker habitat throughout Umdoni was of high quality. It is not unrealistic in this case to infer all available habitat occupied with two individuals per territory (0,65ha, Chapter 4), and so the resultant estimate of 3,08 animals ha⁻¹ approximates the 3,2 animals ha⁻¹ estimated from transects (Chapter 3).

Numerous features contribute to the high quality of the habitat at Umdoni. Canopy cover with minor seasonal fluctuations and low incidence of deciduousness is a very positive attribute of primary cover. The intermediate clumping of both primary and secondary cover in Umdoni contributed to a well balanced mosaic of foraging areas, shrub-cover, and relatively large bedsites. The vertical profile of the habitat is favourable in that similar intermediate densities of trees and shrubs are present. High species richness, intermediate levels of diversity and evenness, and high proportion of large trees contributed to a wide food base.

KSNR

Habitat throughout KSNR, as indicated by duiker densities, varied in quality. KSNR-C supported the highest densities of both red and blue duikers. Favourable features of this community stem from a low incidence of deciduousness in primary cover, an even ratio of trees and shrubs, and a species rich tree layer. High stem densities can reduce habitat quality but the marked aggregation of the dense shrub layer formed a mosaic of desirable cover attributes (uncluttered foraging areas, shrub-cover, and bedsites).

Forest duiker densities were lowest in KSNR-A and KSNR-B. Both communities had a relatively high incidence of deciduous dominant trees with KSNR-A showing a significant seasonal fluctuation in canopy cover. Habitat quality was further reduced by an unequal balance of trees and shrubs where high stem densities, with intermediate levels of clumping, and a strong presence of less

palatable tree species contributed to cluttered foraging areas with a narrow food base.

Charter's Creek

The higher quality of red duiker habitat at Charter's Creek probably arises from three features. The random distribution of very large trees and the diverse, species rich tree layer offer extensive, uncluttered foraging areas with a wide food base at a scale somewhat greater than KSNR. Also, the forest at Charter's Creek is at an earlier successional stage, a condition which increased habitat quality for suni (Lawson 1986), may also be favoured by red duikers.

CHAPTER 6

FOOD AND FEEDING

Introduction

An ecological study of any animal will inevitably centre on its feeding strategies. The trend in feeding strategies purported to have evolved among ungulates, described by the Jarman-Bell Principle, is that smaller species select high quality, highly digestible food whereas large species are less selective and ingest vast quantities of low quality food (Bell 1971, Jarman 1974); and there is a continuum from the small, solitary, concentrate feeders to large, gregarious non-selective roughage feeders (McNaughton 1987).

Feeding ecology is constrained significantly by allometric relationships, gut volume scales linearly with body mass while maintenance metabolism scales as a fractional power of body mass (Demment 1982, McNaughton 1987). McNaughton (1987) states that small herbivores, therefore, with high specific metabolic rates and high ratios of metabolic requirement to gut capacity, must become increasingly selective. Most contemporary literature supports McNaughton's (1987) view and classifies forest duikers as very selective browsers taking only growing shoots, flowers, and fruit (Jarman 1974, Field 1975, Jarman and Sinclair 1979, Spinage 1986).

Habitat utilization and diet are primary determinants of an animal's feeding behaviour. Forest duikers, secretive in habits and confined to dense vegetation, necessitated the collection of much indirect, rather than direct, information.

Observations of duikers feeding in the forest, confirmed by limited rumen content analysis in the laboratory, showed that forest duikers are forest floor gleaners, their diet comprising mainly freshly fallen mature leaves, with fallen fruit and large seeds being eaten readily when available. Browsing of live plant material constituted a minor fraction of feeding behaviour, contrary to the Jarman-Bell Principle.

Potential food availability monitored seasonally (as leaf fall) in the forest, when equated with duiker energy demands determined in the laboratory (Faurie 1990) suggested a superabundance of food. However, the unpalatability of some leaves was evident since the animals often rejected them, either by sniffing and ignoring them, or by spitting them out after the first bite.

Vast differences in food quality occur not only between plant species but also between plant parts within a species, which means that a considerable portion of plant material is simply inedible to many herbivores. Plant tissues mainly comprise indigestible substances (e.g. cellulose, lignin) and contain widely variable concentrations of nutrients (e.g. amino acids, vitamins, minerals) and secondary compounds (e.g. attractants, repellents, toxic chemicals, including tannins and polyphenols; Milton 1982). It follows that herbivore numbers may be controlled by food quality rather than by plant abundance. However, it must be appreciated

that herbivore population densities are determined by a complex of interacting non-linear processes which defy simple one-factor explanations (Crawley 1983).

At KNSR forest duiker densities varied little from 1981 to 1988, but finer focus showed significant localised differences in density within the forest mozaic (Chapter 3). The question then arose, is this disparity in duiker densities linked to patchy food resources with marked qualitative and quantitative differences?

The aims of this part of the study, therefore, were:

1. to determine the diet, food habits, of red diukers and blue diukers by means of feeding observations and rumen content analysis,
2. to quantify food availability (by relating leaf fall to duiker consumption) and to establish if food may be a limiting resource ,
3. to investigate the influence of food quality on duiker densities and distribution.

Methods

Food habits

Feeding observations

Feeding observations of wild forest duikers were conducted during periods of high activity (Chapter 4) in foraging areas (Chapter 5). Forest duikers do not habituate readily, necessitating observations from a portable hide.

Although the ingestion of fallen leaves and fruit was easily detected (from the hide using 8x40 binoculars), it was seldom possible to positively identify the tree species from which the food item came.

Rumen content analysis

The rare status of forest duikers (Smithers 1986) prevented culling to supply samples for rumen analysis. Consequently rumen contents were collected incidentally from individuals found recently dead (dog-kills, road-kills, predation and unknown causes). The resultant small sample (blue duikers n=12, red duikers n=19), from widespread localities, disqualified any detailed macro- or micro- quantitative analysis (Field 1972, Westoby et al. 1976, Irby 1977, Rees 1978, Staines et al. 1982) and restricted the scope of the analysis to percentage relative occurrence and percentage frequency of occurrence of easily discernible plant parts.

Diets may vary locally (and considerably) in relation to availability of preferred foods (Jackson 1974 vide Jackson 1977), a point exemplified by forest duikers occupying small home ranges (Chapter 4) contained in a broader, heterogeneous vegetation type (Chapter 5).

Rumen contents, preserved at the earliest opportunity in formolacetic acid (FAA), were washed and mixed thoroughly in and through a 5-mm sieve. Allen-Rowlandson (1986) found that mesh size (6,35 vs 3,18 mm) did not really affect the determination of the dietary composition of common duiker or bushbuck, and he conducted his analyses equitably, and quickly, with the larger (6,35mm mesh) sieve. Differential digestibility may cause difficulties where rapid digestion of soft parts bias results in favour of coarse material (Jackson 1977). But, by concentrating on the larger, and thus the most recently ingested fraction of ingesta this problem can be restricted (Allen-Rowlandson 1986).

The washed-fraction volume was estimated by water displacement in a 3l litre graduated beaker. For every 100ml of washed-fraction a 25ml sub-sample was analysed. Sub-samples, suspended in water, were spread evenly in a flat dish (50x30cm) with transect lines drawn at 2cm intervals on its bottom.

The line-intercept method was used to estimate the relative occurrence of each of six plant part categories: dicotyledon leaves (1), fruit/seeds (2), and inflorescences (3); leaves of the monocotyledon families gramineae (4) and liliaceae (5); and fungi (6). Plant parts were identified by eye or by using a hand-lens; those that touched or crossed a transect line were recorded

as an intercept. Though point-analysis methods may introduce bias when large items (e.g. fruit or nuts) are encountered (Robel and Watt 1970, Jackson 1977), this problem is avoided by the analysis of recently ingested food where large items in each food category are proportionately represented (Allen-Rowlandson 1986).

Food availability

To monitor food availability throughout the year, leaf fall was quantified seasonally in three study areas; KSNR-A, Umdoni, and Charter's Creek. Thirty 0,5m² leaf traps made from plastic piping and shade cloth, suspended on three wooden stakes at 40-50 cm to prevent removal of trapped leaves by duikers, were placed at 10m intervals along a permanent transect through the forest. Leaf traps were usually emptied after 10 to 14 days. A running estimate of leaf fall over 31 days in KSNR confirmed that 10 to 14 days was adequate sampling time (Figure 6.1).

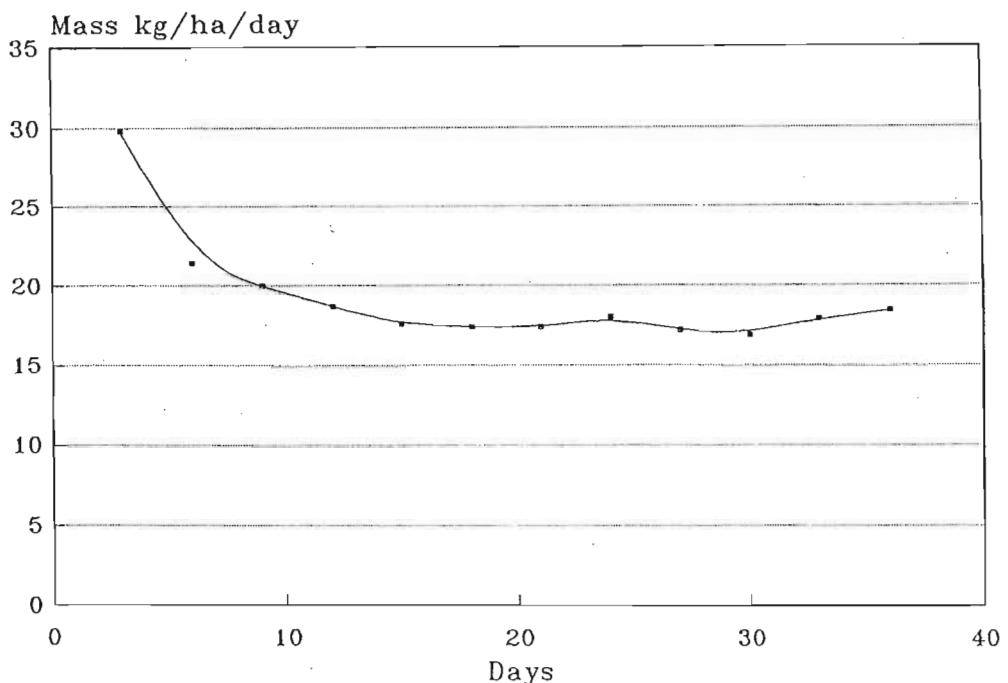


Figure 6.1 A running estimate of leaf fall to determine minimum trapping time.

Trap contents, stored in paper bags, were dried to constant mass at 60°C and then sorted. Plant debris or trash, heavily invertebrate-browsed leaves, fruit, flowers, seeds, and leaves with length or width <1cm were discarded. Fruit, flowers, and seeds, though eaten by duikers were excluded from sampling because of their low and sporadic occurrence in leaf traps. The remaining leaves, grouped by species, were identified and weighed. Seasonal leaf fall was then expressed in terms of $\text{kg ha}^{-1} \text{ day}^{-1}$ and the percentage contribution by each tree species was calculated.

Statistical tests comparing leaf fall data were limited to a contingency table of seasonal estimates for each study area. Transformations of raw leaf fall data did not normalise distributions in all cases. The null-hypothesis stated that there was no difference in seasonal leaf fall between forest communities.

Leaf fall, and thus potential food availability, was quantified in the low duiker density area (KSNR-B) and the high duiker density area (KSNR-C) simultaneously in autumn and spring. Freshly fallen leaves in each area from the ten dominant tree species, determined by the PCQ method (Chapter 5), were analysed for nutrients and secondary compounds. These were presented to captive duikers in food preference tests (see below).

Food quality

Forest duiker population densities, which varied by forest patch in KSNR (KSNR-B and KSNR-C, Chapter 3), gave the opportunity to investigate the role of food quality on duiker habitat selection.

Food preference tests

Tree basal area is a good index of available leaf area (Whitaker *et al.* 1974), and thus contribution to leaf fall. Consequently, preference tests were limited to the ten dominant tree species, determined from basal areas, in two forest communities in KSNR, KSNR-B and KSNR-C (Chapter 2) with their respective high and low duiker densities. Preference ratings, indicative of palatability, were used to evaluate the significance of these major contributors to leaf fall, as determinants of disparate duiker densities in the two forest communities.

Lawson (1986) reported that suni, with a similar feeding habit to forest duikers, preferred fresh leaves to fallen. Thus fresh and fallen leaves of dominant trees were preference-tested to identify the effect of changes in important leaf constituents (nutrients and toxins) of abscised leaves on palatability.

Freshly fallen leaves, collected early morning from raked areas in the forest, and fresh mature leaves, picked simultaneously from the same tree species, were presented to captive duikers. Five fresh and fallen leaves of no more than three tree species were given to the duikers at each experiment. Each leaf species was offered at least three times. Two blue duikers and four red duikers were tested independently during early mornings when the animals forage naturally (Chapter 4).

Duikers usually investigated all leaves promptly, by sniffing them. Preferred leaves were eaten readily; after 15 min the remaining, less preferred leaves were removed. Based on this

behaviour a point system was devised whereby the 30 leaves presented (5 fresh and 5 fallen of three species) were scored in order of ingestion. The first 5 leaves eaten scored 6 points each, the second five 5 points each, the third five 4 points each, and so on. Uneaten leaves scored zero. Mean score per leaf for each tree species was calculated, and tree species were ranked accordingly.

Student's t tests were performed on the paired observations; preference scores of fallen leaves were tested for difference against those of fresh leaves for each duiker species, and preference scores of blue duikers were tested against those of red duikers for fresh and fallen leaves.

Food content analysis

Freshly fallen leaves of the ten dominant trees in KSNR-B and KSNR-C were analysed for water, gross energy, crude protein, crude fibre, nitrogen, condensed tannin content and trace minerals. To facilitate comparison similar measurements for fresh mature leaves of some of the dominant trees were taken from Faurie (1990). Mann-Whitney U tests were performed on the two data sets to identify differences in the contents of fresh and fallen leaves.

Freshly fallen leaves, stored in paper packets, were weighed within three hours of collection before being dried to constant mass: percentage water content was determined.

Gross energy of the fallen leaf samples was determined by bomb calorimetry. Crude protein (Kjeldahl) and fibre content was determined by the Cedara Feed Laboratory, Department of Agriculture. The Vanillin/HCl assay was used by the Centre for Wildlife Research, University of Pretoria to determine condensed tannin content.

Stepwise multiple regression analysis was used to identify which leaf parameters, if any, significantly influenced preference scores. Similar statistical tests were performed to determine relationships between changes in leaf contents of fresh and fallen leaves, and changes in preference scores of fresh and fallen leaves for each tree species. Thereby leaf characteristics influencing palatability could be identified.

A comparison of leaf content weighted averages, based on percentage relative dominance, of the ten dominant trees in KSNR-B and KSNR-C was used as an index of nutrient availability or food quality and tannin levels in each area. A Kolmogorov-Smirnov two group test was used to determine the extent of food quality differences between the two communities.

Results

Rumen content analysis

The results of analysing the contents of 12 blue duiker and 19 red duiker rumens are shown in Tables 6.1 and 6.2. Mature dicotyledon leaves and fruit were present in all rumens whereas the occurrence of dicot flowers, monocotyledon leaves, and fungi was more sporadic. Though high standard error to mean ratios in the relative occurrence analysis demand cautious interpretation of results, it appears that there is a strong negative correlation (blue duikers $r=-0.89, p<0.05$; red duikers $r=-0.96, p<0.05$) between the two major dietary components viz. dicotyledon leaves and fruit.

Food availability

The mean dry mass of leaf fall was lowest in Umdoni, intermediate in KSNR, and highest in Charter's Creek. The null hypothesis that seasonal variation in leaf fall was equivalent in each forest community was rejected ($p>0.05$, Table 6.3).

Table 6.1 Percentage relative occurrence and percentage frequency of occurrence of plant parts in the rumen of blue duikers.

Rumen no.	Washed fraction ml	Dicotyledon			Monocotyledon leaves		fungi %
		leaves %	seeds/fruit %	flowers %	grass %	lilies %	
1	45	99,0	1,0	-			
2	35	97,8	1,6	0,6			
3	35	85,8	12,2	0,5			1,5
4	15	85,7	14,3	-			
5	45	84,2	7,3	8,1			0,4
6	35	79,7	20,3	-			
7	75	77,6	14,2	2,6		0,4	5,2
8	100	71,2	28,3	-			0,5
9	60	57,7	42,3	-			
10	25	57,4	31,8	4,0			6,8
11	50	32,4	24,5	42,4	0,7		
12	65	9,6	81,5	8,3	0,6		
<hr/>							
mean	48,8	69,8	23,3	5,5	0,1	0,03	1,2
SE	6,5	7,4	6,1	3,3	0,1	0,03	0,6
n		12	12	7	2	1	5
% frequency of occurrence		100,0	100,0	58,3	16,7	8,3	41,7

The main contributors to leaf fall for a great proportion of the year at Umdoni are B.discolor, P.longifolia, S.umbellifera, and S.cordatum (Table 6.4). C.aristata, D.obovata, M.grandis, and S.integerrimum contributed substantially to the total most of the year in KSNR-A while F.natalensis and P.longifolia exhibited greater seasonal production (Table 6.5). At Charter's Creek, B.discolor, G.occidentalis, and S.myrtina were prominent all-year producers of leaf fall whereas C.africana, C.aristata, and T.emetica shed leaves on a more seasonal basis (Table 6.6).

Table 6.2 Percentage relative occurrence and percentage frequency of occurrence of plant parts in the rumen of red duikers.

Rumen no.	Washed fraction (ml)	Dicotyledons			Monocotyledon leaves		fungi %	Animal matter %
		leaves %	seeds/fruit %	flowers %	grass %	lilies %		
1	110	95,2	1,6	1,3			1,9	
2	160	94,0	1,4	4,1	0,5			
3	320	90,8	8,1	0,3			0,8	
4	160	90,2	9,6			0,2		
5	50	88,2	9,4		2,4			
6	100	85,0	10,0	0,1	0,1		4,8	
7	30	84,8	14,9	0,3				
8	35	83,8	14,5		0,9		0,8	
9	270	75,5	17,5		0,1	3,4	3,5	
10	60	74,8	17,9		7,3			
11	160	74,5	24,3				1,2	
12	75	71,9	27,2		0,4		0,5	
13	70	69,4	19,5	10,1		1,0		
14	260	41,2	38,0	1,7	0,3	18,8		
15	140	39,7	36,0	2,6				21,7
16	75	36,7	59,1		4,2			
17	240	25,1	73,9	0,5	0,5			
18	95	17,3	81,8	0,9				
19	260	9,3		0,2	2,4	88,1		
mean	140,5	65,7	24,5	1,2	1,0	5,9	0,7	1,1
SE	20,0	6,2	5,3	0,5	0,4	4,5	0,3	1,1
n		19	18	11	11	5	7	1
% frequency of occurrence		100,0	94,7	57,9	57,9	26,3	36,8	5,3

Autumn leaf fall estimates in KSNR-B, which contained low duiker densities, were less than those in KSNR-C while in spring leaf fall was similar in the two forest communities (Table 6.7). The ten dominant trees in the two areas implicated 14 canopy species (Table 6.8) which exhibited different species composition in each area. P.longifolia dominated the KSNR-C community while M.grandis, B.natalense, and D.arguta were common trees in KSNR-B.

Table 6.3 Seasonal leaf fall ($\text{kg ha}^{-1} \text{ day}^{-1}$) in three forest communities: Umdoni, KNSR-A and Charters.

	<u>Umdoni</u>	<u>KNSR-A</u>	<u>Charters</u>
1986 spring	6,50		
summer	11,34		
1987 autumn	8,29	8,34	13,91
winter	7,80		
spring			15,90
summer		8,15	12,98
1988 autumn		8,68	
winter			11,45
spring			10,24
1989 winter		15,65	
mean	<u>8,48</u>	<u>10,21</u>	<u>12,90</u>
Chi-Square = 17,78; DF = 8; P = 0,023			

Food preference tests

Both duiker species preferred fresh leaves over fallen (blue duiker $t=-2.7, p<0.01$; red duiker $t=-3.7, p<0.01$). They differed significantly in preference rankings of fallen leaves ($t=-1.89, p<0.05$) but not in fresh leaves ($t=-1.09, p=0.15$; Table 6.9). G.amoena was favoured by both; P.longifolia, X.kraussiana, and V.undulata showed high palatability in blue duikers whereas V.undulata, B.natalense, and M.grandis were most preferred by red duikers (Table 6.9).

Table 6.4 Percentage contribution of woody tree species to leaf fall at Umdoni.

<u>Species</u>	<u>Spring</u> <u>1986</u>	<u>Summer</u> <u>1986</u>	<u>Autumn</u> <u>1987</u>	<u>Winter</u> <u>1987</u>
<u>Antidesma venosum</u>			1,2	3,5
<u>Apodytes dimidiata</u>	2,5	3,0	6,7	2,0
<u>Bequaertiodendron natalense</u>	6,7	4,5	3,5	4,3
<u>Brachylaena discolor</u>	14,6	19,5	19,5	6,5
<u>Bridelia micrantha</u>	1,3			
<u>Canthium obovatum</u>	2,2	1,0	1,6	3,4
<u>Croton sylvaticus</u>	1,9	1,0	0,2	7,7
<u>Cryptocarya woodii</u>		1,1	0,4	
<u>Dalbergia obovata</u>	1,3	1,7	5,4	12,4
<u>Deinbollia oblongifolia</u>	0,6			
<u>Drypetes arguta</u>	1,9		0,4	0,5
<u>Euclea natalensis</u>	0,6			0,3
<u>Grewia occidentalis</u>				0,2
<u>Harpephyllum caffrum</u>				0,1
<u>Loranthus sp.</u>			1,0	
<u>Monanthotaxis caffra</u>	0,6			0,1
<u>Oricia bachmannii</u>	1,0	1,5	2,1	0,6
<u>Peddiea africana</u>	1,0	0,4	0,2	0,2
<u>Protorhus longifolia</u>	35,9	33,5	17,4	13,5
<u>Rapanea melanophoeos</u>	2,5	4,2	3,7	6,6
<u>Rawsonia lucida</u>			4,5	
<u>Rhus chirindensis</u>	0,6		0,6	0,8
<u>Sapium integerrimum</u>	0,3		0,2	1,5
<u>Schefflera umbellifera</u>	1,6	3,0	15,5	12,5
<u>Strychnos spinosa</u>	0,6	3,1	1,7	
<u>Syzygium cordatum</u>	15,6	16,6	6,6	13,8
<u>Uvaria caffra</u>	0,3	0,7	0,2	1,2
<u>Zanthoxylum capense</u>		0,8		0,3
unidentified	6,4	4,4	7,4	8,0
	100,0	100,0	100,0	100,0
Dry mass of leaf fall (kg ha ⁻¹ day ⁻¹)	6,50	11,37	8,29	7,80

Table 6.5 Percentage contribution of woody tree species to leaf fall at KNSR-A.

Species	Autumn 1987	Summer 1987	Autumn 1988	* Winter 1989
<u>Antidesma venosum</u>				0,5
<u>Beguaerti dendron natalense</u>	0,4	1,1	1,1	3,8
<u>Bersama lucens</u>			0,3	0,2
<u>Brachylaena discolor</u>	3,6	2,5	4,2	2,9
<u>Canthium inerme/obovata</u>	0,2	0,1	1,6	1,3
<u>Chaetacme aristata</u>	9,0	16,0	14,3	5,0
<u>Combretum molle</u>	5,8	1,0	9,1	5,0
<u>Croton sylvaticus</u>	6,0	6,0	7,3	1,5
<u>Cryptocarya woodii</u>	0,5	0,3	0,1	
<u>Dalbergia obovata</u>	10,9	1,4	11,6	11,3
<u>Drypetes arguta</u>	1,9	1,8	3,5	1,1
<u>Euclea natalensis</u>		1,4	0,1	0,4
<u>Ficus natalensis</u>	2,4	1,3	1,5	12,5
<u>Grewia occidentalis</u>	0,5		1,4	0,3
<u>Heteropyxis natalensis</u>			0,5	
<u>Loranthus sp.</u>	3,9	3,2	3,2	1,8
<u>Millettia grandis</u>	7,9	11,9	11,3	19,6
<u>Monanthes caffra</u>	0,1		0,1	1,5
<u>Peddiea africana</u>		0,1	0,4	
<u>Protorhus longifolia</u>	7,6	33,0	6,6	1,3
<u>Rawsonia lucida</u>	1,0			
<u>Rhus chirindensis</u>	2,5	1,1	2,0	7,7
<u>Sapium integerrimum</u>	19,5	9,3	11,6	14,0
<u>Tricalysia lanceolata</u>	1,3	1,4	1,0	0,6
<u>Uvaria caffra</u>	0,4			0,5
<u>Vepris undulata</u>	2,9	2,1	2,8	1,8
<u>Zanthoxylum capense</u>			0,3	0,2
unidentified	11,7	5,0	4,1	5,2
	100,0	100,0	100,0	100,0
Dry mass of leaf fall (kg ha ⁻¹ day ⁻¹)	8,34	8,15	8,68	15,65

* Leaf fall was sampled along two different transects in Spring 1988 at KNSR-B and KNSR-C (see Table 6.7)

Table 6.6 Percentage contribution of woody tree species to leaf fall at Charter's Creek.

<u>Species</u>	<u>Autumn</u> <u>1987</u>	<u>Spring</u> <u>1987</u>	<u>Summer</u> <u>1987</u>	<u>Winter</u> <u>1988</u>	<u>Spring</u> <u>1988</u>
<u>Adenia gummifera</u>	1,1		0,6		0,3
<u>Antidesma venosum</u>	0,3	2,9		0,6	0,8
<u>Brachylaena discolor</u>	7,9	25,2	14,6	9,4	39,4
<u>Bridelia cathartica</u>		0,1		0,2	
<u>Canthium inerme</u>	0,8	1,2	3,2	1,7	2,1
<u>Casearia gladiiformis</u>	5,7	4,1	4,3	5,3	2,6
<u>Celtis africana</u>	45,4	0,5	1,6	37,0	3,4
<u>Chaetacme aristata</u>	2,7	8,4	16,5	3,1	11,5
<u>Clerodendrum glabrum</u>	1,6	1,6	0,7	1,0	
<u>Deinbollia oblongifolia</u>		2,4	0,7	0,6	2,0
<u>Diospyros natalensis</u>		0,4	0,6	0,2	0,1
<u>Ekebergia capensis</u>		2,3	1,2	1,5	0,7
<u>Embellia ruminata</u>	0,1	0,4	0,5		0,3
<u>Euclea natalensis</u>	1,5	2,0	0,2	0,3	0,4
<u>Grewia occidentalis</u>	7,8	11,9	10,1	13,4	5,4
<u>Harpephyllum caffrum</u>	0,4	3,2	1,8	0,3	2,7
<u>Kraussia floribunda</u>	2,5	0,9	0,5		
<u>Landolphia kirkii</u>	0,7	1,8	2,5	0,6	1,4
<u>Monanthotaxis caffra</u>		1,1	0,2		0,2
<u>Pavetta sp.</u>		0,7	0,3		0,1
<u>Peddiea africana</u>	0,3		0,2	0,3	0,9
<u>Phyllanthus reticulatus</u>			0,2	1,5	
<u>Ptaeroxylon obliquum</u>	0,1		0,3		0,1
<u>Rhoicissus tomentosa</u>	0,2			0,5	
<u>Rhus chirindensis</u>	8,7	3,2	1,8	9,0	4,1
<u>R. macowanii</u>			0,2	0,2	
<u>Sclerocarya caffra</u>	0,3		1,8		
<u>Scutia myrtina</u>	6,6	13,6	10,9	6,2	11,1
<u>Strychnos mitis</u>	2,5		1,3	2,3	0,5
<u>Tricalysia sonderana</u>			0,6		0,2
<u>Trichilia emetica</u>	0,1	2,2	15,7	0,9	3,8
<u>Uvaria caffra</u>		0,5			0,2
<u>Zanthoxylum sp.</u>		0,2	0,2	0,5	0,1
unidentified	2,7	9,2	6,7	3,4	5,6
	100,0	100,0	100,0	100,0	100,0
Dry mass of leaf fall (kg ha ⁻¹ day ⁻¹)	13,91	15,90	12,98	11,45	10,24

Table 6.7 Leaf fall ($\text{kg ha}^{-1} \text{ day}^{-1}$) and duiker densities (animals ha^{-1}) in two KNSR forest communities.

	<u>KNSR-C</u>	<u>KNSR-B</u>
Leaf fall: 1988 Autumn	9,21	6,35
Spring	15,40	13,30
Duiker Densities: blue	1,6	0,9
red	0,6	0,3

Table 6.8 The ten dominant tree species in two KNSR forest communities with respective duiker densities.

	Relative dominance	
	<u>KNSR-C</u>	<u>KNSR-B</u>
	%	%
<u>Protorhus longifolia</u>	34,3	9,8
<u>Milletia grandis</u>	10,1	22,9
<u>Strychnos henningsii</u>	6,9	
<u>Drypetes arguta</u>	6,2	12,1
<u>Bequaertiodendron natalense</u>	6,0	16,6
<u>Brachylaena discolor</u>	5,3	
<u>Croton sylvaticus</u>	3,9	8,5
<u>Vepris undulata</u>	3,3	3,4
<u>Cassine papillosa</u>	3,3	
<u>Ekebergia capensis</u>	2,9	
<u>Gardenia amoena</u>		3,9
<u>Xylothea kraussiana</u>		3,6
<u>Tabernaemontana elegans</u>		2,7
<u>Combretum molle</u>		1,7
Duiker densities (animals/ha)		
Blue duiker	1,6	0,9
Red duiker	0,6	0,3

Table 6.9 Ranked forest duiker preference scores of dominant tree species.

	Freshly fallen leaves				Picked leaves			
	<u>Blue</u>	Rank	<u>Red</u>	Rank	<u>Blue</u>	Rank	<u>Red</u>	Rank
<u>G.amoena</u>	4,2	1	3,5	1	4,1	4	4,7	1
<u>P.longifolia</u>	3,7	2	2,2	9	5,5	1	3,1	11
<u>X.kraussiana</u>	2,5	3	1,7	11	4,4	3	3,5	6
<u>V.undulata</u>	2,5	4	3,4	2	1,1	12	2,9	12
<u>B.natalense</u>	2,2	5	3,0	3	2,3	9	3,5	5
<u>M.grandis</u>	2,1	6	3,0	4	1,7	10	3,2	9
<u>C.molle</u>	1,8	7	1,6	13	3,7	6	4,7	2
<u>D.arguta</u>	1,7	8	2,4	7	3,9	5	3,3	7
<u>B.discolor</u>	1,4	9	2,3	8	4,9	2	3,8	3
<u>E.capensis</u>	1,1	10	2,6	6	2,4	8	3,2	8
<u>T.elegans</u>	1,1	11	2,7	5	1,3	11	2,3	13
<u>S.henningsii</u>	0,7	12	1,6	12	3,7	7	3,2	10
<u>C.sylvaticus</u>	0,0	13	2,2	10	0,0	13	3,8	4

Statistical tests

	1.picked and fallen leaves for each duiker species		2.blue and red duiker preference scores	
	<u>Blue</u>	<u>Red</u>	<u>Fallen</u>	<u>Fresh</u>
T	-2,6719	-3,709	-1,886	-1,0911
df	12	12	12	12
p	0,01	<0,01	0,04	0,15

Food content analysis

Leaf content analyses involved 13 species, Cassine papillosa was found not to be shedding leaves when sampling and, therefore, was excluded from further analyses. Water, gross energy, crude protein, nitrogen, crude fibre, condensed tannins, Cu, Mn, and Zn content of fallen leaves of dominant trees in KSNR-B and KSNR-C are presented in Table 6.10. The only meaningful relationship between leaf content and duiker preference was a positive correlation between tannin content and blue duiker preference scores (Table 6.11).

Table 6.10 Contents of fallen leaves and duiker preference scores of dominant trees in two KNSR forest communities.

Species	Water %	Gross energy kcal g ⁻¹	Crude protein %	N %	Crude fibre %	Condensed tannins %	Preference scores		Zn ppm	Cu ppm	Mn ppm
							blue	red			
<i>Protorhus longifolia</i>	45,2	4,79	5,86	0,94	21,07	17,0	3,7	2,2	17	3	617
<i>Millettia grandis</i>	23,9	4,37	16,60	2,66	31,11	9,3	2,1	3,0	34	3	278
<i>Bequaertiodendron</i> <i>natalense</i>	40,8	4,64	8,11	1,30	31,34	19,2	2,2	3,0	15	6	496
<i>Drypetes arguta</i>	42,2	4,62	11,03	1,76	6,33	20,0	1,7	2,4	53	6	1738
<i>Croton sylvaticus</i>	53,3	3,85	14,23	2,28	24,35	3,5	0,0	2,2	33	15	704
<i>Strychnos henningsii</i>	47,4	4,68	20,62	3,30	24,94	5,9	0,7	1,6	22	23	3521
<i>Vepris undulata</i>	35,8	4,62	16,24	2,60	25,20	5,1	2,5	3,4	52	12	971
<i>Brachylaena discolor</i>	46,5	4,23	8,29	1,33	24,88	4,9	1,4	2,3	128	13	1332
<i>Gardenia amoena</i>	56,5	4,32	17,07	2,73	20,65	22,6	4,2	3,5	26	16	2508
<i>Xylothea kraussiana</i>	53,9	4,15	15,93	2,55	25,06	10,9	2,5	1,7	30	7	1235
<i>Cassine papillosa</i>	-	-	-	-	-	-	-	-	-	-	-
<i>Ekebergia capensis</i>	62,3	4,19	10,80	1,73	16,99	8,7	1,1	2,6	65	8	549
<i>Tabernaemontana</i> <i>elegans</i>	56,1	4,20	11,19	1,79	25,01	6,1	1,1	2,7	24	7	1632
<i>Combretum molle</i>	20,9	4,31	10,72	1,71	20,65	14,2	1,8	1,6	36	6	537
mean	44,98	4,38	11,43	2,05	22,89	11,3	1,9	2,5	41	10	1240

Table 6.11 Probability values in stepwise multiple regressions of: A. fallen leaf contents on preference scores (Table 6.10), and B. changes in leaf contents between fresh and fallen leaves on subsequent changes in preference scores (Table 6.12).

	<u>Blue duiker</u> (p)	<u>Red duiker</u> (p)
A. water	0,86	0,88
energy	0,49	0,70
protein	0,69	0,88
nitrogen	0,68	0,88
fibre	0,25	0,60
tannin	0,008*	0,47
Zn	0,90	0,99
Cu	0,85	0,74
Mn	0,97	0,66
B. water	0,37	0,002*
energy	0,23	0,68
protein	0,27	0,002*
tannin	0,63	0,26

* Significant positive correlation between the dependent variable (preference scores) and independent variables (leaf contents).

Water, gross energy, and protein content showed significant differences between fresh and fallen leaves while changes in tannin content were not significant (Table 6.12). None of the leaf content changes was implicated in changes in blue duiker preference scores whereas changes in water and protein content seemed to influence red duiker choices (Table 6.11). Overall food quality in KSNR-B and KSNR-C was not significantly different (Table 6.13).

Table 6.13 Leaf content weighted averages, based on relative dominance, of the ten dominant trees in two KNSR forest communities.

	<u>KNSR-B</u>	<u>KNSR-C</u>
Water content %	39,37	42,8
Gross energy kcal g ⁻¹	4,44	4,59
Crude protein %	12,37	10,29
Nitrogen %	1,99	1,69
Crude fibre %	24,43	22,75
Condensed tannins %	13,56	13,16
Zn ppm	30,84	33,76
Cu ppm	6,52	7,04
Mn ppm	612,37	971,01

Statistical test

Kolmogorov-Smirnov two group test Chi-Square=5,6; DF=2; p=0,06

Discussion

According to the Jarman-Bell Principle, small, mammalian ruminants tend to feed on small, energy-rich, dispersed food sources at relatively low density (seeds, fruit, flowers, new growth), while large species feed less selectively on more abundant, less nutritious foods high in plant fibre (mature foliage, grass). Thus, large ruminants tolerate a lower minimum diet quality than small species, and forest duikers, classified as small, solitary, high-concentrate feeders, are placed at the lower limit of the continuum (Jarman 1974, Spinage 1986, McNaughton 1987).

A high-concentrate feeder, nowhere clearly defined, generally implies that the animal is solely dependent on fruit, flowers, and growing shoot tips for high, easily digestible energy input (Bell 1971, Jarman 1974, Demment 1982, Spinage 1986). The requirement for easily assimilated and highly nutritious foods is usually linked with the relatively high metabolic demands of a small body (Bell 1971, Milton 1982, Van Soest 1983).

Feeding observation data, confirmed by rumen content analysis, showed mature dicot leaves as the single most important dietary item of forest duikers. Leaf particles in the washed rumen fraction were usually mature leaves, with few young leaves and shoot tips providing evidence of a high-concentrate feeder.

However, the strong negative correlation between fruit (a scarce and unreliable food source in the dry, lowland coastal forests) and freshly fallen leaves (a potential year-round, abundant food

source) indicated that fruit has a higher preference rank. Forest duikers are able to vary their food habits throughout their distribution, and in the highly productive tropical rain forests of central Africa, the blue duiker is a prominent, albeit a diminutive, member of a mammalian frugivore community (Gautier-Hion *et al.* 1980, Dubost 1984).

Browsers in general are very selective feeders; specialised tongue and muzzle morphology, and dentition allow them to feed delicately and selectively (Bell 1971, Owen-Smith 1982, Spinage 1986). Their principal foods, forbs and woody dicot foliage (Owen-Smith 1982, Allen-Rowlandson 1986), are those of concentrate feeders. Crude protein, an approximate index of food quality (Owen-Smith 1982, Houston 1982), in the forest duiker diet appears at best equivalent, if not lower than that of browsers (Table 6.14). Diet quality in all ruminant browsers, ranging from 5kg dikdik *Madoqua* sp. to 250kg kudu *Tragelaphus strepsiceros*, is high and appears not to scale with body size.

Table 6.14 Mean crude protein (as percent of dry matter) of browse (after Owen-Smith 1982).

	early growing	late growing	early dormant	late dormant
Forbs	17	15	17	12
Woody dicot foliage	18,0	13,5	15,5	12,0
Freshly fallen leaves (Table 6.9)	11,4	11,4	11,4	11,4

The proportion of time spent foraging is related to the spatial dispersion of acceptable food items in the vegetation, if food

items are continuously distributed little time is devoted to searching and feeding (Owen-Smith 1988). Small ruminants with high specific metabolic rates and high ratios of metabolic requirement to gut capacity, must become increasingly selective as plant standing crop increases until at the extreme, in forests, they are reduced to searching for very rare plant material capable of sustaining them in a general environment with a plentiful supply of unsuitable foods (McNaughton 1987).

Eating time depends on the rate of food collection relative to body mass. If this rate varies in direct proportion to body mass then, since large ruminants eat less food per day per unit body mass than small ones, very large animals should be able to satisfy their nutritional needs within a shorter feeding time than required by smaller species (Owen-Smith 1988). Further, with high selectivity, an important characteristic of high-concentrate feeders, bite size and travel time per bite become important constraints, since slight increases in selectivity reduce intake drastically (McNaughton 1987). Therefore, to achieve the required intake rate from a dispersed, rare source, small ruminants should be more active than large animals.

However, megaherbivores are constantly on the move, 50-75% of the day, and mainly foraging; while medium size herbivores, active for 35-60% of the day (Owen-Smith 1988), exceed the activity periods of forest duikers, at 18-44% (Chapter 4). In terms of cost-benefit constraints, forest duikers, in less productive forests at southern limits of their distribution, opt for a readily accessible lower quality diet which needs long rumination time (Crawley 1983) rather than a more costly high-concentrate diet

which requires more careful and extended foraging. Forest duikers are able to achieve this because, though their metabolic rates are high, they are much lower than expected from allometric equations (Faurie 1990).

Forest duiker feeding behaviour, therefore, appears anomalous in terms of some general concepts in African ungulate feeding strategies. First, their diet, like that of suni (Lawson 1986), differs from that predicted for small ungulates, and second, their time budget is not that of a high-concentrate feeder searching for rare food items.

Definitions of food quality vary but generally depend on the complex interplay between nutritional composition of plants and their digestibility (Houston 1982, Owen-Smith and Novellie 1982, Demment and Van Soest 1985, McNaughton and Georgiadis 1986). Although nutritional quality is believed to be of primary importance, it is speculated that forage selection patterns are largely the result of avoidance of secondary compounds (Bryant and Kuropat 1980, Waterman et al. 1988, Waterman 1983).

Diet quality is implicated as a population regulating mechanism (Westoby 1974, Milton 1982, Crawley 1983, Waterman et al. 1988). Plants vary considerably in nutritional quality and primary consumers must generally mix and match foods of different species each day to obtain the necessary complimentary amounts of various essential nutrients (Freeland and Janzen 1974, Bryant and Kuropat 1980, Milton 1982).

Leaf fall in all study areas ($6-15\text{kg ha}^{-1}\text{day}^{-1}$) far exceeded the daily requirement of duikers ($200-400\text{g}$ dry mass, Faurie pers. comm.) per unit area. The main contributors to leaf fall not only differed greatly between forest communities but seasonally within each community. Forest duikers with relatively small home ranges, particularly blue duikers, must survive on the species mix in their patch, which contains a wide variety of leaf species. They are unable to fully utilise a single species diet (Faurie 1990).

Preference tests disclosed that forest duikers eat the leaves of many of the dominant trees in the two forest communities (KSNR-B and KSNR-C) studied in detail, though some were preferred over others. Correlations between leaf contents and palatability indicated that low water and protein levels reduced food quality for red duikers while high condensed tannin levels improved quality for blue duikers.

Condensed tannins are found in the leaves and stems of all vascular plants where they can be important as a defence mechanism against herbivore feeding (Swain 1979). Evidence strongly suggests browsing vertebrates avoid feeding on plant tissues that contain high concentrations of secondary compounds, particularly tannins (Bryant and Kuropat 1980, Waterman 1983, Cooper and Owen-Smith 1985).

Mammals differ in their capacities to process particular chemicals, and the quantity of a particular food eaten is limited by the degradation rate of its secondary compounds (Freeland and Janzen 1974). In preference tests forest duikers consumed leaves with condensed tannin content up to 22%; they may have been able

to do this because there was no build up of secondary compounds from their captive diet of antelope cubes. Faurie (1990), too, found no correlation between condensed tannin concentration and leaf preference, highly preferred species had tannin concentrations exceeding 18% while in rejected species concentrations were less than 2%.

Most woody vegetation produces secondary compounds (Swain 1979) and forest duikers, confined to relatively small permanent home ranges (Chapter 4), are clearly adapted to deal with high levels of this common food ingredient. At KSNR-C, a high duiker density area, the weighted average of condensed tannins of dominant trees, the major food source, was 13,56%.

The ability of tannins to influence food choice may be over emphasized (Waterman 1983) and there is evidence that tannins may in fact be beneficial to mammalian herbivores in that they assist in protein uptake (Mole and Waterman 1987, Waterman *et al.* 1988).

It was hypothesized that food quality, and/or condensed tannins, might be the primary determinant of disparate duiker densities in KSNR-B and KSNR-C. However, there is no significant difference in food quality between the two areas and the major factor controlling duiker densities appears to be habitat quality (Chapter 5).

CHAPTER 7**CONSERVATION CONSIDERATIONS AND MANAGEMENT RECOMMENDATIONS**

Introduction

A condition crucial to the conservation of all wild plants and animals is to maintain their habitats (Prescott-Allen 1982). Botkin (1984) states that there is no such thing as conserving a species; there is only the conservation of ecosystems and their constituent populations. Therefore, in the conservation and management of any species we need to take an ecosystem (holistic) view (Soule and Simberloff 1986); in the case of forest duikers, conservation of indigenous, evergreen forests should be given at least equivalent status as the animals themselves. My recommendations include both the forest duikers and their habitat.

Recommendation 1: Land acquisition

Acquire indigenous, evergreen forests or the control of these forests, for the protection or introduction of forest duikers, whenever the opportunity arises regardless of size or condition of forest. Though reserves should be as large as possible, a few dispersed, small sites can contain at least as many species as a single site of equal area (Soule and Simberloff 1986).

Recommendation 2: Forest ecology

Forest biomes, less known than any other, and biologically the richest ecosystems on Earth, are being disrupted and depleted more rapidly than any other biome (Myers 1984 and 1986). The need to conserve them is urgent. In terms of long term forest duiker conservation requirements, two perspectives of forest ecology need immediate attention; the role of invasive, exotic vegetation and the impact of air pollution.

Forests are characterised by a mosaic of patches of different sized trees belonging to a diverse number of species at various stages of maturity (Whitemore 1978, Brokaw 1982). This diversity is driven by the gap dynamics of fallen trees. Many canopy tree species depend, at one or all stages in their life histories, on growth in a gap to reach maturity (Brokaw 1982); the canopy continually changes, in terms of species diversity and structure, as trees grow up, die, and are replaced (Whitemore 1978). This dynamic equilibrium may be divided into three growth phases: the gap phase (seedlings and saplings), the building phase (pole forest), and the mature phase (Whitemore 1978).

Gap size has an important influence on species composition and spatial arrangement in the forest. Requirements for canopy openings vary among forest tree species, different degrees of canopy opening lead to different species compositions at particular sites.

Two broad alternatives may initiate the building phase of the forest growth cycle; either existing seedlings and saplings

commence upward growth or new trees establish from seeds germinating in the gap. Shade-tolerant seedlings and saplings most often grow up to maturity in small gaps, where subtle changes in microclimate caused by the gap stimulates apical growth (Longman 1978). Whereas many young shade-tolerant trees die as a result of drastic changes in microclimate that follow the formation of a big gap.

Instead, big gaps are usually colonised by light-demanding species absent from the undergrowth of tall forest, equipped to exploit open sites. Light-demanding species, often called pioneers, can only establish in the open, usually have small seeds which are continually and prolifically produced and are efficiently dispersed by wind or animals (Whitemore 1978).

Shade-tolerant species, characterised by large seeds with substantial food reserves, are able to establish in deep shade, produce seeds periodically in response to climate stimuli, and have either a brief or no dormancy. Seedlings often persist, growing slowly or not at all, in dense undergrowth shade, marking time until a gap occurs above them (Whitemore 1978).

Several biotic and abiotic factors (invasive exotic plants, air pollution) may reduce the potential of indigenous colonisers at the gap site. Indigenous forests are prone to intrusion from exotic invasive plants (Chapter 5, MacDonald and Jarman 1985) at the critical building phase in the growth cycle. Interference at this phase inhibits regeneration of forest species and probably has far reaching consequences in terms of canopy tree species composition.

In view of the undesirable impact of exotic vegetation on forest regeneration cycles it is essential that invasive vegetation eradication programmes be conducted on a regular basis, no matter how light the infestation. The practice of allowing this alien vegetation to build up is clearly undesirable; it should be removed at the seedling stage where its affect is most marked.

Eradication programmes of alien vegetation should extend beyond nature reserves. Natal Parks Board, the Provincial conservation authority, should promote and co-ordinate vigorous eradication programmes in areas under the control of the private sector, the farming community, and government and local authorities.

Air pollution, defined as materials in the troposphere in excess of normal quantities, imposes widespread effects on forest vegetation. Owing to its regional character, and sometimes global extent, air pollution has become an important ecological factor (Treshow 1968). Numerous northern hemisphere countries report an increase in the disease rate among forest trees where air pollution is implicated in nutrient imbalances exacerbated by acid rain (Hutchinson and Meema 1987).

A distinct feature of air pollution is that a single pollutant seldom acts alone (Materna 1984, Legge and Krupa 1986) and ecosystems as well as their components and processes are affected in multiple ways (Goldstein and Legge 1986). Pollutants influence, directly or indirectly, usually in a negative way, all stages in the life cycles and maintenance processes of forest eventually leading to the decline of the forest community (Smith 1981,

Materna 1984, Legge and Krupa 1986, Heck and McLaughlin 1986; Table 7.1).

Gaseous pollutants, acid deposition, and particulates directly influence assimilatory apparatus of plants, soils and climatic conditions (Materna 1984, Legge and Krupa 1986). Indirect influence on an ecosystem is due to the interference in the functioning of individual components (Materna 1984).

Table 7.1 Interaction of air pollution and temperate forest ecosystems under conditions of intermediate contaminant load (after Smith 1981).

Forest soil and vegetation: activity and response	Ecosystem consequence and impact
1. Forest tree reproduction, alteration or inhibition.	1. Altered species composition
2. Forest nutrient cycling, alteration a. reduced litter decomposition b. Increased plant leaching, soil leaching and soil weathering c. disturbance of microbial symbiosis	2. Reduced growth, less biomass
3. Forest metabolism, alteration a. decreased photosynthesis b. increased respiration	3. Reduced growth, less biomass
4. Forest stress, alteration a. phytophagus insects, increased or decreased activity b. microbial pathogens, increased or decreased activity c. foliar damage increased by direct air pollution influence	4. Altered ecosystem stress a. increased or decreased insect infestations b. increased or decreased disease epidemics c. reduced growth, less biomass altered species composition
5. Severe morbidity, excessive foliar damage	5. Dramatic change in species composition, reduced biomass, increased erodability, nutrient attrition, altered microclimate and hydrology
6. Mortality	6. Forest simplification or destruction

The effects of pollutants are not necessarily obvious, trees may experience loss in growth or productivity without visible injury symptoms (Legge and Krupa 1986) or any appearance of foliar abnormalities (Heck and McLaughlin 1986).

The pH of precipitation in KSNR is usually between 3,0 and 4,5 (Grobler pers. comm.). To what degree is the forest at KSNR being affected by the acid rain? Is the absence of P.longifolia juveniles part of a natural cycle (Chapter 5) or is it caused by air contamination (Table 7.1)? What other unknown exigencies threaten the long term viability of forest communities?

The most important facet of forest duiker conservation is the ultimate viability of habitat. Knowledge of forest ecosystem dynamics in Natal is very limited and needs immediate attention. Priority should be given to research on forest ecosystem dynamics, particularly the threats posed by invasive, exotic vegetation, air and soil contaminants, the effect of the local fragmentation on long term processes and cycles such as replacement of dominant tree species (Hubbell and Foster 1986, Wilcove et al. 1986).

Recommendation 3: Coexistence of two forest duiker species

In 1983 the red duiker at KSNR population showed a 28% increase on estimates for 1982 (Fig 7.1). In 1982, 19 blue duikers were translocated from KNSR reducing the population by about 15%. The subsequent increase in red duiker population density suggested intense inhibition of the red duiker population by interspecific competition from blue duikers.

To investigate the extent of competition between two similar species experimentally would involve animal removals and habitat manipulative procedures, clearly undesirable in a high profile nature reserve.

In 1984 red duiker population densities declined slightly notwithstanding the removal of 43 blue duikers in 1983, suggesting that factors, other than interaction with blue duikers, were operative. How are resources partitioned between the ecologically equivalent forest duikers?

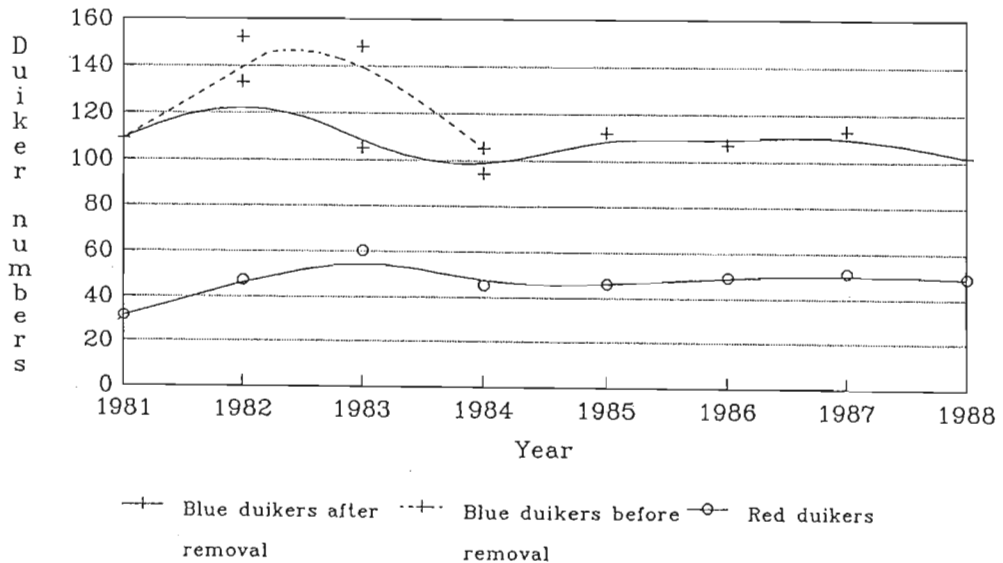


Figure 7.1 Forest duiker numbers in KSNR.

Syntopic forest mammals are shown to adopt various strategies in partitioning resources. Gautier-Hion et al. (1980), in a central African rain forest, compared the food habits of three frugivorous taxa (primates, squirrels and ruminants) and found common trends in resource partitioning within each group. In each taxon, ecological separation was realized according to habitat (mainland or riparian forest), different foraging levels, partitioning of the nycthemeral cycle, and different trends of frugivory. But, despite this separation there was much potential interspecific competition since many plant species (parts) were limiting and eaten by members of two or three taxa at the same time.

Emmons (1980) studied 9 species of sympatric rain forest tree squirrels. Her findings on resource partitioning included:

- (1) two species restricted to two different special habitat types,
- (2) differential use of the vertical vegetation column divided seven species into four arboreal and three ground foraging forms.
- (3) species occupying a given foraging level and habitat differed in body size by approximately Hutchinson's ratio (body size acted to partition fruit resources by size and hardness),
- (4) quantitative differences in diet between some species, and,
- (5) four large species had short active periods.

High species richness of squirrels was permitted by constant fruit production and high plant species diversity in the African rain forest.

Dubost (1984) analysed the gut contents of seven species of sympatric forest ruminants of northeastern Gabon. He found that

fruit size eaten was directly proportional to body mass and that fruit size classes were taken in proportion to availability. The great diversity of the fruit species eaten resulted in little dietary overlap among the ruminants. Peter's duiker C.callipygus and the bay duiker C.dorsalis, sympatric species of similar body mass (about 20kg) and diet (mainly fruit), separate temporally with the former being diurnal and the latter nocturnal (Feer 1988).

However, resource partitioning, if any, between the two forest duiker species in the less productive forests at KSNR is difficult to identify. Generally, the two species are ecologically equivalent. Diets are similar, both ingest primarily freshly fallen leaves of a variety of species (Chapter 6). No temporal separation exists, both species are diurnal (Chapter 4). No aggression was noted between the species either in captivity or in the wild. Local differences in habitat quality influenced both species in a similar manner, localized variations in population densities between forest patches followed similar trends in both species (Chapter 3)

However, a subtle difference in spatial utilization is evident, body size differences may require slightly different foraging and predator avoidance tactics. Though home range overlap between the species is extensive, the red duiker is capable of foraging beyond the forest margin.

In terms of management there appears no need to manage them as competitive species, rather manage them as a single unit (forest duikers). The relocation of red duikers to areas within their

current or former range should not be disqualified by the presence of blue duikers.

Recommendation 4: Interaction with other species

Lawson (1986) showed that the presence of high numbers of nyala had an adverse affect, through habitat degradation, on suni population densities. Sensitivity to habitat modification is also exhibited by blue duiker in particular. At Hluhluwe Game Reserve their numbers have declined to marginal levels where understory vegetation has been trampled or removed during the foraging activities of ungulates, particularly bushpig (Bowland 1987). At Mkambathi Nature Reserve, Transkei, eland and kudu removed all vegetation below the 2m browse line in forest to the detriment and exclusion of blue duikers.

At KSNR, zebras frequently use the forest either for shade or as a corridor between grasslands. The effect on the forest understorey is negligible while zebra numbers remain below about 20 animals; above this number the impact on forest understorey becomes very noticeable. The impact of larger ungulates on forest should be monitored and where necessary controlled by removal, in all managed areas where forest duikers have high conservation status.

Recommendation 5: Genetic aspects of duiker conservation

Political, cultural, and economic, rather than biological, factors often determine the location and size of reserves (Soule and Simberloff 1986). Consequently, in Natal reserves are scattered

throughout the province with most of them in perfect isolation from each other. Thus, many plant and animal species are conserved in small, isolated populations separated by vast, unnegotiable barriers.

The smaller the number of individuals in a population the greater will be the dangers of losing genetic variation through inbreeding and consequent loss of fitness (Ballou and Ralls 1982, Soule 1984, Ralls et al. 1986). Inbreeding is often a consequence of confinement, the limited extent of many nature reserves restricts the size of populations and hence some degree of inbreeding happens, the amount of inbreeding increasing in response to a decline in population size (Soule 1984).

Proximal fitness, i.e. the maintenance of structure and function of a population (fecundity and viability), permits a population to survive and successfully reproduce under particular conditions. Loss of proximal fitness will lead to decreasing abundance and ultimately local extinction of the species. Ultimate fitness, the capacity of a population to change in an adaptive way, requires that the gene pool contain raw material that permits natural selection to operate (Soule 1984).

The isolated nature and relative small size of many forest duiker populations require that genetic principles be taken into account by conservation authorities to preserve proximal and ultimate gene pool fitness. This requires the exchange of individuals among populations. Population geneticists advise that translocations need not be large or frequent; one successful transfer per

generation suffices to completely mix two populations regardless of their sizes (Soule 1984).

Small populations can persist for many years, with some showing strong effects of inbreeding (Soule 1984). A cytogenetic study would not only provide baseline data on the vulnerability of duiker gene pools to inbreeding, i.e. population vulnerability analysis (Gilpin and Soule 1986), but also confirm the genetic identity of the animals and so prevent mixing of taxonomic groups (subspecies, ecotypes; Comrie-Greig 1979).

Evidence for genetic deterioration in forest duikers is circumstantial. Reports on the blue duiker in southern Natal indicate that populations have dwindled for no obvious reasons (Allen-Rowlandson 1986, Wichmann pers. comm.). At Weza State Forest and on the farm Sea View and surrounding farms (Port Edward), despite constancy in environmental conditions (habitat, hunting, dog predation), blue duiker populations have declined since the 1960's. The decline, whether or not from the genetic deterioration of these isolated populations, provides a starting point for cyto-genetic investigations of blue duikers.

A comparative cytogenetic study of red duikers at KSNR, a small closed population, and those at Charter's Creek, a large open population, should reveal the relative degree of inbreeding, if any, prevalent in the KSNR population.

Limitations in current knowledge make it very difficult to determine what the minimum number of individuals is to keep the population viable in the long term, i.e. the Minimum Viable

Population (Gilpin and Soule 1986). The perennial question, "How much is enough?" (Soule and Simberloff 1986, Soule 1986a), can be circumvented by a properly planned translocation programme (Comrie-Greig 1979).

Many biological factors need to be taken into account when considering translocations in particular and conservation biology on a broader scale and literature on the subject should be thoroughly consulted (Comrie-Greig 1979, Soule and Wilcox 1980, Schonewald-Cox et al. 1983, Soule 1986b).

Recommendation 6: Translocation of forest duikers

Long term conservation needs of isolated forest duiker populations necessitate the translocation of animals (Recommendation 5). Translocation programmes should, to enhance success, accommodate the specific behaviour of the animals. Some guidelines are offered for forest duikers:

- release duikers into vacant areas to reduce the chance of confrontation with resident animals, particularly in the case of blue duikers which are territorial,
- translocate pairs from more than one source after ensuring taxonomic compatibility, and,
- keep strict and detailed records of translocations e.g. date, sex, numbers, source population/s.
- identify, with gum tattoos, translocated individuals to prevent inadvertant repatriation in subsequent translocations.

Recommendation 7: Captive propagation

Promote the propagation and maintenance of forest duikers in captivity to compensate for the diminishing number of wild populations. Forest duikers are relatively easy to transport and keep in captivity (Appendix A). Offer forest duikers for sale to reputable international, national and local institutions, especially those active in breeding programmes.

These recommendations for forest duiker conservation incorporate numerous divisions of the life sciences, e.g. genetics, zoology, botany, and ecology, which clearly indicates that a multi-disciplinary team approach is necessary. The primary objectives of such an holistic approach should centre on indigenous, evergreen forest ecosystems, not on single components, such as forest duikers, in isolation. The long term conservation of indigenous, evergreen forests requires a well coordinated research effort.

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APPENDIX A

THE CAPTURE, HANDLING, IMMOBILISATION AND TRANSPORTATION
OF FOREST DUIKERS

Introduction

Management of wildlife frequently necessitates the capture and translocation of animals. Problems, in terms of injuries and fatalities, can arise if inadequate techniques are used. Capture operations need to be carefully planned and the animals subjected to as little stress as possible. Methods outlined below were successfully employed on forest duikers.

Methods

Capture

Duikers were captured with 2m high nets (mesh size = 40mm for blue duikers and 100mm for red duikers) supported on trees or stakes in the forest and set according to Mathias and Bourquin (1984) and Flamand and Lawson (1986). Forest and forest clumps were searched for recent signs of duiker (spoor and droppings).

Two factors affected the siting of the nets:

1. the driving technique, one-man or beating line (Mathias and Bourquin 1984),
2. the nature of the vegetation, forest clumps or continuous forest.

The one-man driving technique, successful in continuous forest, was more economic in terms of manhours than a beating line. It involved the surveillance of a likely capture site, denoted by high duiker activity in an open glade, for two to three days from a portable hide. Duikers movements were recorded, in particular the routes to and from the surveillance area. Regular routes soon became apparent and nets were located such that they would intercept a duiker pursued from the hide.

The one-man technique proved impractical for the capture of duikers in forest clumps, where a beating line was more effective. Nets, facing the forest clump to be driven, were sited along the margins of adjacent vegetation rather than 'fencing in' the clump to be driven as suggested by Mathias and Bourquin (1984).

When using a beating line under continuous canopy, nets were sited along the perimeter of open glades, paths or roads and on the side away from but facing the direction of the drive.

Nets were usually set in position the day prior to capture, furled overnight, then set silently before first light on the day of capture. All drives were conducted as soon after light as possible to avoid the heat of the day.

Darting attempts with a custom-built capture rifle (Lawson et al. 1987) proved unsuccessful:

1. the small target provided by the blue duiker required an unobtainably close firing range,
2. it is difficult to draw a bead on a cryptic target in subdued light beneath the forest canopy,
3. vegetation structure of the habitat allowed no clear flight path for the arcing trajectory of the dart.

Immobilization

Animals caught in the nets were immobilised with a mixture of Fentanyl (dosage approx. $0,4\text{mg kg}^{-1}$) and 2% Rompun solution (dosage approx. $0,06\text{mg kg}^{-1}$). Given intra-muscularly M5050 (dosage approx. 12mg kg^{-1}) was a very effective antidote. The response of some duikers to an alternative less expensive antidote, Nalorphine ($0,7\text{mg kg}^{-1}$), was undesirable in that it induced a prolonged semi-conscious state with intermittent spasms and exaggerated lolling of the head. Care was taken to prop sedated duikers upright on the ventral surface (brisket) rather than allowing them to recline laterally on their sides. This prevented uncontrolled rumen fluid from entering the lungs.

Translocation

Animals netted but not immobilised should be removed from the nets according to Mathias and Bourquin (1984) and transferred to crates (Fig A.1) immediately. Critical dimensions of the wooden crates should permit animals to execute comfort movements, i.e. lie down, stand up, or turn around easily. Crate height should be such that although animals can stand at full height they cannot jump around and sustain injuries. Crates should be prepared before the capture with bedding (hay, dry leaves, or wood shavings) and an abundant food supply: antelope cubes, cubed apples and carrots, and fresh leaves of indigenous trees.

During capture operations crated animals should be left in a quiet, shady spot in the forest. Provide water immediately in non-tippable dishes. Allow the animal 3-4h to settle down after capture to become familiar with its crate before travelling. Long journeys (500kms+) require at least a 24h settling period.

Travel should be at night when it is cool and the animals normally sleep. If day time travel is unavoidable, stop and water the animals every 2-3h especially on hot days. Pregnant females may abort during travel but this appears to have little effect on their general well being. Diarrhoea is best treated by sprinkling slaked lime on the food.

In this study three consignments of blue duikers, two (6 and 14 animals) to Sun City, Boputhatswana and one (6 animals) to Bulawayo, Zimbabwe, suffered no losses.

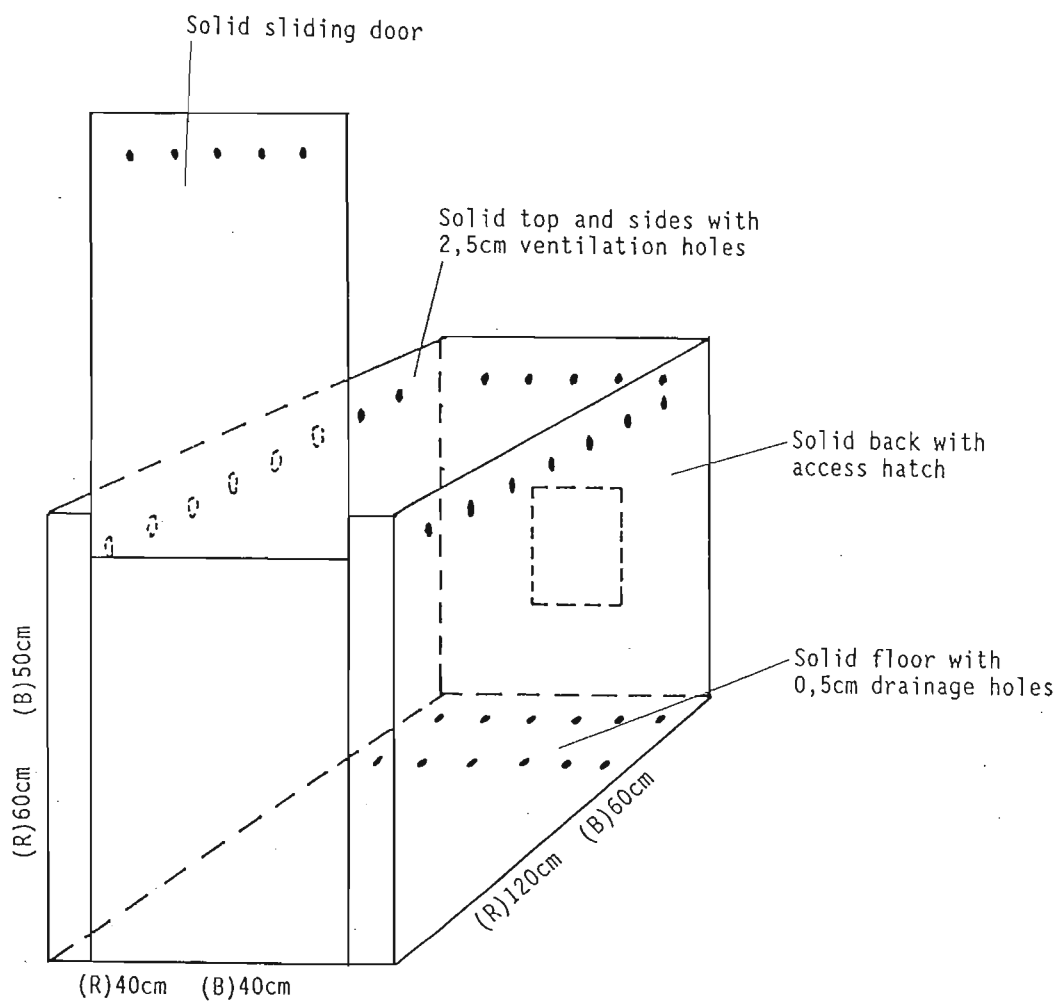


Figure A.1 Crate design for transportation of red (R) and blue (B) duikers.

Conditioning to captivity

Recently caught duikers, if released immediately into an enclosure will, by trying to escape, persistently run into the enclosure walls. Not only does this situation produce a very stressed animal but repeated injury is inevitable. Daily maintenance and observations of the animal are impossible.

A method, involving three steps, was developed to condition wild duikers to a captive environment. The rationale behind the method is simple; confine the animal to small, secure, and comfortable quarters, as it becomes familiar with its environment, in particular the close proximity of people, increase its living space.

Step 1

Accommodation

House wild duikers for 10-21 days in "keeping" crates. Transport crates (Fig A.1) are easily converted into "keeping" crates by adding a hinged grid door to the front. Grid doors, made of 1 cm weldmesh, permit animals to see out and so become accustomed to people nearby. Spend time with crated animals, offer food (leaves, apples, carrots) through the grid door. Close the solid door whenever animals become agitated.

Housekeeping

Crates must be cleaned out every day and fresh bedding provided. Transfer animals to prepared spare crates by placing the two crates end on, doors facing, and pushing the animal into the clean crate from the back through the access hatch. Do not clean crates with animals inside. Moving animals daily is an important part of the conditioning process as they become familiar with routine and being touched. Keep food and water dishes clean.

Food and water

Sometimes animals do not eat for the first two or three days in captivity and lose on average 8% (6,1 - 15,9) of their body mass. Lost weight is usually regained by the third or fourth week as animals adjust to their new environment. The captive diet should be introduced gradually by replacing natural vegetation with cubed (2cm^3) fruit and vegetables (apples, carrots, sweet potatoes), antelope or horse cubes, and mulberry leaves when available. Fresh water should always be present.

Keeper's behaviour

Restrict loud noise near the animals. Talk to the animals quietly while tending to them, they will be aware of your whereabouts and are less likely to be startled. Adopt a rigid daily routine, the animals then know what to expect.

When an animal in its keeping crate is at ease at the close presence of the keeper, readily feeds and accepts a scratch, begin step 2.

Step 2

"Tame" animals in their "keeping" crates, with grid doors removed, should now be introduced in pairs (male plus female or two females) to a nested enclosure (2m x 2m) with solid walls inside the main enclosure (Fig A.2). Animals in pairs appear less stressful than animals alone. Not all individuals are compatible, check for aggression after pairing. Rematch incompatible individuals.

Keeping crates substitute for natural bed-sites in the forest where animals readily take refuge. Rather than flee blindly into enclosure walls now, animals hide in the crates when alarmed. Once the animals have settled in the nested enclosure (2+ weeks) the final step may commence.

Step 3

Allow duikers access, from the nested enclosure, to the main enclosure (\pm 7m x 7m; Fig A.2). Keeping crate and nested enclosure retain their function as refuge and bedsite.

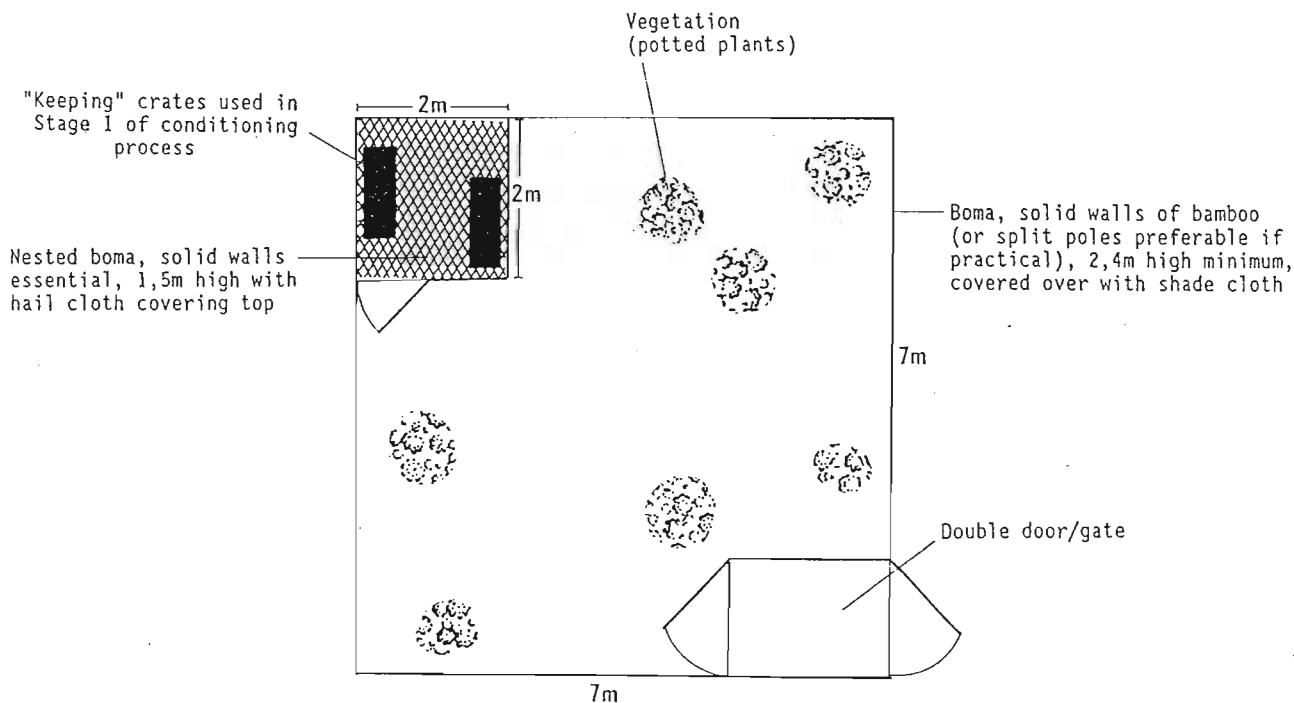


Figure A.2 Annotated plan of a nested enclosure system used in conditioning forest duikers to captivity.

Provide waterproof shelter, fresh water supply, and vegetation (shrubs, potplants) in the enclosure. Netting over excludes raptors and mammalian predators (feral cats).

Each duiker has a unique temperament; some tame quickly, soon take food from the hand and enjoy a scratch; others, partially tame, remain aloof, but manageable; a few remain wild, are constantly agitated, and are best released into the wild.

Confinement of duikers in "keeping" crates appears an extreme measure but in the forest duikers are usually only active for about 8 out of 24h. With plenty of food and water, a secure and comfortable bed-site they seem content in their "keeping" crates, a more acceptable situation than animals continually crashing into enclosure walls.

Red duikers and blue duikers were tamed, kept, and bred in captivity with success using this method.

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APPENDIX B

Table B.1 Dietary items of forest duikers recorded in the southern African subregion (R=red duiker; B=blue duiker; Source number refers to authority listed below).

<u>Family</u>	<u>Species</u>	<u>Duiker</u>	<u>Source</u>	<u>Leaves</u>	<u>Fruit/ Seeds</u>	<u>Flowers</u>	<u>Shoots</u>
canthaceae	<u>Isoqlossa woodii</u>	B	2	*			
	<u>Justicia protacta</u>	R	6	*	*		
macardiaceae	<u>Harpephyllum caffrum</u>	B	9		*		
	<u>Protorhus longifolia</u>	B	9	*	*		
nonaceae	<u>Monodora junodii</u>	R	10			*	
pocynaceae	<u>Carissa macrocarpa</u>	B	9	*	*		
	<u>C.tetramera</u>	R	10		*		
	<u>Diplorhynchus</u>						
	<u>condylocarpon</u>	B	7	*			
rubiaceae	<u>Cussonia</u>						
	<u>sphaerocephala</u>	R	9	*			
	<u>Schefflera</u>						
	<u>umbellifera</u>	B	9	*			
alanitaceae	<u>Balanites maughamii</u>	R	10	*			
ignoniaceae	<u>Kigelia africana</u>	R	9,10			*	
elastraceae	<u>Cassine crocea</u>	R	10		*		
commelinaceae	<u>Commelina africana</u>	R	6	*	*		
compositae	<u>Brachylaena discolor</u>	R,B	2,9	*			*
	<u>Chromolaena odoratus</u>	R	9				*
benaceae	<u>Euclea natalensis</u>	R	1		*		
	<u>Diospyros sp.</u>	B	1	*			
uphorbiaceae	<u>Antidesma venosum</u>	R,B	9	*	*	*	
	<u>Bridelia micrantha</u>	B	9		*		
	<u>Sapium integerrimum</u>	R,B	6,9	*	*		
	<u>Spirostachys africana</u>	R	10	*			
lacourtiaceae	<u>Casearia gladiiformis</u>	R	9				*
	<u>Dovyalis caffra</u>	R	10		*		
	<u>D.longispina</u>	R	9,10	*	*		
	<u>D.zeyheri</u>	R	10		*		
graminae	<u>Dactyloctenium</u>						
	<u>australe</u>	R	4	*			
acaceae	<u>Apodytes dimidiata</u>	R,B	9		*		
cythidaceae	<u>Barringtonia racemosa</u>	R	9		*		
guminosae	<u>Acacia sp.</u>	R	8				*
	<u>A.robusta</u>	R	9		*		
	<u>Albizia adiantifolia</u>	R	9	*			
	<u>Bauhinia galpinii</u>	R	4	*		*	
	<u>Dalbergia armata</u>	B	2,9	*	*		*
	<u>Dichrostachys cinerea</u>	R	6,8	*	*		
	<u>Erythrina lysistemon</u>	B	9			*	
	<u>Trifolium sp.</u>	B	9		*		
liaceae	<u>Asparagus fulcatus</u>	R	6	*	*		
	<u>A.virgatus</u>	R	1	*			
	<u>Chlorophytum modestum</u>	B	9				*
maniaceae	<u>Strychnos innocua</u>	R	6	*	*		
	<u>S.spinosa</u>	R	6,9	*	*		
liaceae	<u>Ekebergia capensis</u>	R	9	*	*		

Table B.1 continued

<u>Family</u>	<u>Species</u>	<u>Duiker Source</u>	<u>Leaves</u>	<u>Fruit/ Seeds</u>	<u>Flowers</u>	<u>Shoots</u>
Coniariaceae	<u>Cissampelos torulosa</u>	R	1	*		
Ficusaceae	<u>Ficus</u> sp.	R,B	2,5,8			*
	<u>F.natalensis</u>	B	9	*		*
	<u>F.stuhlmanii</u>	R	9	*		
	<u>F.vogelli</u>	B	9	*		
	<u>Syzygium cordatum</u>	B	2,9,11			*
Oleaceae	<u>Olea africana</u>	B	2			*
	<u>O.capensis</u>	B	3			*
	<u>Oxalis</u> sp.	R	4			*
Podocarpaceae	<u>Podocarpus</u> sp.	R	1			*
Rhamnaceae	<u>Ziziphus mucronata</u>	R	1,9			*
Rubiaceae	<u>Canthium obovatum</u>	B	9	*		*
	<u>Gardenia cornuta</u>	R	6,10	*		*
Salvadoraceae	<u>Azima tetraantha</u>	R	6	*		*
Sapotaceae	<u>Bequaerti dendron</u>					
	<u>magalismsontanum</u>	R	4			*
	<u>B.natalense</u>	B	9	*		
	<u>Mimusops</u> sp.	B	2			*
Solanaceae	<u>Sideroxylon inerme</u>	R	10			*
	<u>Solanum</u> sp.	R	8			*
	<u>S.mauritianum</u>	B	9			*
Strelitziaceae	<u>Strelitzia nicolai</u>	B	2,9			*
Urticaceae	<u>Grewia</u> sp.	R	6	*		*
Ulmaceae	<u>Celtis africana</u>	R	9	*		
	<u>Chaetacme aristata</u>	R	1			*
Urticaceae	<u>Urera tenax</u>	B	2	*		

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