THE SOCIAL AND SPATIAL ORGANISATION OF THE GREATER KUDU
(*Tragelaphus strepsiceros* Pallas 1766)
IN THE ANDRIES VOSLOO KUDU RESERVE,
EASTERN CAPE.

by

T.S. ALLEN-ROWLANDSON

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requirements for the degree of
Master of Science
at
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CORRIGENDUM

P	39	14 lines up and elsewhere. 'known age' should be 'known-age'.
P	55	and elsewhere. All figures following mean values in Tables 4.2, 4.3, 5.5, 5.6, 7.1, 7.3, 7.7, and 8.1, and elsewhere in the text (unless stated otherwise) are standard deviations.
P	61	line 13. Addition as underlined: 'Reproductive organs from 208 shot kudu (119 males, 89 females) were collected during the hunting seasons (June, July and August) of 1976 to 1979, and were supplemented by eighteen mortalities (eight males, ten females) on the Reserve'.
P	61	Addition to the end of paragraph 4 (line 22). 'Males were classified as having attained puberty or sexual maturity if spermatozoa were detected in these smears. The age at attainment of puberty was provided by the youngest age class to contain spermatozoa in at least 50 % of all individual smears. (Due to the highly seasonal distribution of samples, this age must be a maximum value.) Since mating was never witnessed in the field, distinction between puberty (or physiological maturity) and sexual (or behavioural) maturity (Asdell 1964), was not possible, and when discussing male kudu both terms have been used synonymously to mean physiological maturity.'
P	61	Addition as underlined to 5th line from bottom. 'Cows with follicle diameters larger than 5 mm were arbitrarily regarded as having attained puberty (the seasonal distribution of samples and high conception rates of older females prevented detailed examination of follicular development) while females with corpora lutea were classified as mature.'
P	64	Table 5.2 . 'Age at puberty and first parturition of captive female kudu' should read 'Age at puberty/sexual maturity and first parturition of captive female kudu'.
P	65	Line 5. Addition as underlined. 'Seventy of the 83 examined uteri (from all female kudu) contained a foetus.'
P	65	7 lines up and Table 5.5 . 'mean birth mass of 15,257 kg' should read 'mean birth mass of 15,3 kg'.
P	66	Table 5.3 . For 'Mature' under Remarks of kudu no. 78 read 'Pubertal/Mature?'
P	74	5.4.6 Calving intervals. Delete the first paragraph commencing with 'Placental scars were not detected in .... ' etc..
P	104	line 5. Addition as underlined '(t = 2,389, d.f. = 24, p < 0,05)'
P	120	Methods Addition to be inserted after 1st sentence. 'Female ages, based on tooth eruption and wear patterns, were assessed from dental impressions taken on capture and recapture.'
P	212	lines 13 and 14. Addition as underlined. 'Spermatogenesis was evident .... throughout life after puberty.'

ACKNOWLEDGEMENTS

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ABSTRACT

The social and spatial organisation of the greater kudu was studied in the Eastern Cape, South Africa.

Methods of capture, marking and age determination in the field, were investigated. The density and structure of the population, individual movements and social relationships were determined. Aspects of reproduction examined included age at puberty, age-specific fecundity, calving intervals and seasonality. Temporal changes in the spatial and social organisation are discussed in relation to environmental conditions, reproduction and population structure. Factors influencing the fecundity, dynamics and grouping patterns within the population are considered.

Chapter 1

INTRODUCTION

The greater kudu, *Tragelaphus strepsiceros* has received little attention from biologists since its discovery in 1766, so that knowledge of its biology is limited. Much of the available scientific information, which includes reproductive data and ageing criteria, has resulted from game eradication programmes (Wilson 1965, 1970; Simpson 1966, 1968, 1971, 1972a) or physiological studies (Skinner & Huntley 1971; Skinner 1971). Walther (1964) conducted a comprehensive study of the behaviour of the greater kudu in captivity, but detailed behavioural studies in the wild are lacking. Studies on free-ranging kudu have largely been confined to diet and feeding strategies (Conybeare 1975; Owen-Smith 1979), and limited aspects of social and spatial organisation (Simpson & Cowie 1967; Simpson 1972b; preliminary results of Owen-Smith 1975; Underwood 1978).

The kudu is an inconspicuous antelope often inhabiting areas with densely structured vegetation. This habitat selection is undoubtedly one of the main reasons for the lack of detailed study, since prolonged observations in such areas are difficult to maintain.

1.1 Taxonomy

The classification of the greater kudu, following Ansell (1971) is:-

Family : Bovidae
Subfamily : Bovinae
Tribe : Tragelaphini
Genus : Tragelaphus
Species : strepsiceros

Ansell (1971) recognises four subspecies; *T. s. strepsiceros* from South Africa to Zambia, Malawi and Mozambique; *T. s. bea* in Tanzania, northern Mozambique and Kenya; *T. s. chora* in Somalia, Ethiopia, and eastern Sudan and *T. s. burlacei* (Ansell 1969) in Chad and Central African Republic.

Most authors agree on the number of Tragelaphine species, but opinions at the levels of genus, tribe and subfamily are at variance (Leuthold 1979). Ansell (1971) presents the Tragelaphines as follows:

Tribe : Tragelaphini
Genus : Tragelaphus
Subgenus : Boocercus -
Tragelaphus euryceros : Bongo
Subgenus : Tragelaphus
Tragelaphus buxtoni : Mountain nyala
Tragelaphus spekei : Sitatunga
Tragelaphus angasi : Nyala
Tragelaphus scriptus : Bushbuck
Tragelaphus strepsiceros : Greater kudu
Tragelaphus imberbis : Lesser kudu
Genus : Taurotragus
Taurotragus oryx : Eland
Taurotragus derbianus : Giant eland

Several authors consider that the Tragelaphines should form a separate subfamily, Tragelaphinae (Walther 1964; Leuthold 1979), while hybrids between eland and kudu (Jorge, Butler & Benirschke 1976) and between bongo and sitatunga (Tijskens 1968) are considered by Van Gelder (1977) as reasons for including all Tragelaphines in the single genus *Tragelaphus*.

Unless otherwise stated, the term kudu in this study refers to the greater kudu, *Tragelaphus s. strepsiceros*.

Detailed morphological descriptions of the greater kudu can be found in Dorst & Dandelot (1970) and Ansell (1971).

1.2 Distribution

The geographic ranges occupied by the four subspecies of greater kudu (Ansell 1971) illustrate the wide distribution of this species, which has also been documented by Sidney (1965) and Bigalke (1968). Numerous authors have provided details of more localised distributions in; southern Africa (Smithers 1966; du Plessis 1969; Zaloumis & Cross 1974); Zambia (Ansell 1960a); Botswana (Smithers 1971); Rhodesia (Fraser 1958; Child & Savory 1964); Mozambique (Smithers & Tello 1976); South Africa (Knobel 1958); Transvaal (Kettlitz 1955, 1962); Natal (Vincent 1962; Mentis 1974); Cape Province (Bigalke & Bateman 1962); and the Eastern Cape (Hewitt 1931). Dorst & Dandelot's (1970) distribution map is incomplete since it omits the distribution of indigenous populations in the Cape Province.

The preferred habitat of the greater kudu has often been described as densely structured vegetation (offering plenty of cover), and usually in areas of broken terrain (Bigalke & Bateman 1962; Smithers 1966; Dorst & Dandelot 1970; Zaloumis & Cross 1974; Smithers & Tello 1976). However, as illustrated by its wide distribution, the greater kudu is a highly adaptable species capable of exploiting a diverse range of habitats (Brynard & Pienaar 1960; Kettlitz 1962; Pienaar 1974; Ferrar & Walker 1974; Evans 1979) often showing little preference for any one local vegetation type (Pienaar 1963; Hirst 1975).

1.3 Purpose of this study

As indicated above, limited scientific data concerning the biology of the greater kudu were available when this study commenced in 1976. Further, all previous studies have been conducted in habitats that differ markedly from those in the Eastern Cape, and thus the data were not directly applicable to populations in this region. The purpose of this study is therefore to provide a thorough knowledge of the social biology of the kudu in the recently established Andries Vosloo Kudu Reserve. Such knowledge is vital to the development of a sound understanding of the population biology of this species, and will enable existing, theoretically based, management policies to be replaced by ones based on factual, scientific grounds.

Chapter 2

STUDY AREA

2.1 Introduction

All field observations were conducted on the Andries Vosloo Kudu Reserve, (A.V.K.R.), approximately 40 km north-east of Grahamstown, Eastern Cape, ($33^{0}8$'S, $26^{0}39$'E, Fig. 2.1). The Reserve was established when the Department of Nature and Environmental Conservation purchased two farms in 1973. Another adjacent farm was acquired in 1977, extending the Reserve to 6,500 ha of Fish River Valley Bushveld.

The perimeter fence is 1,4 m high and restricts the movements of young kudu and several other large mammal species. Adult kudu can clear these fences with ease, and most species are unaffected by a few remaining internal stock fences.

2.2 Topography

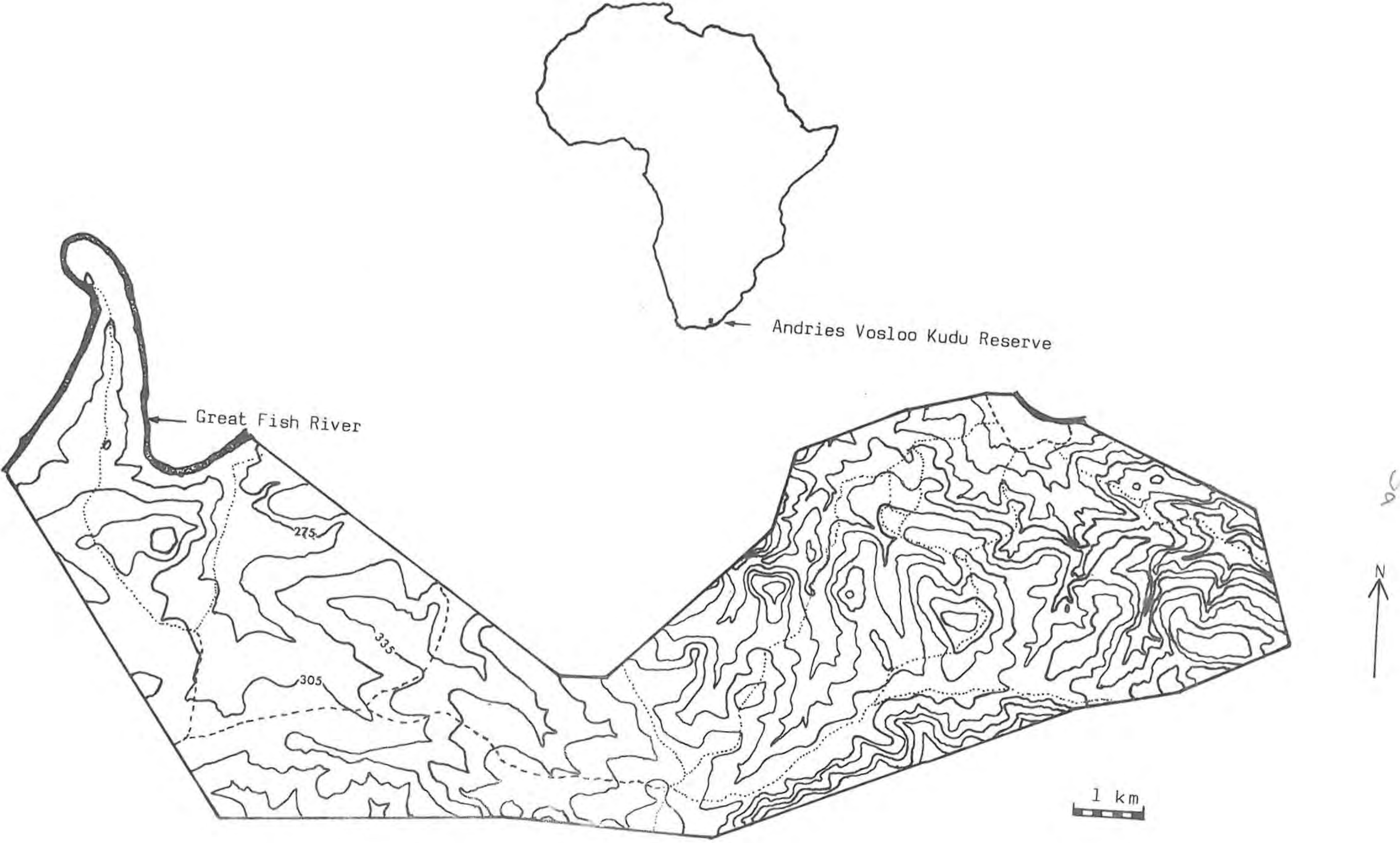
The eastern section of the Reserve rises from 160 m.a.s.l. at the boundary with the Great Fish River, to over 500 m.a.s.l. (Fig. 2.1). The undulating terrain of the western section rarely exceeds 350 m.a.s.l. Here the north-eastern boundary runs parallel to an abrupt ridge, while the southern boundary traverses a south facing slope. "Kentucky Kop" (387 m.a.s.l.) dominates this area and in the north the Reserve is bounded by the Great Fish River (244 m.a.s.l.) for nearly 10 km (Fig. 2.2). This area with its flatter terrain facilitates travel, field observations and radio telemetry, and most of the field observations were undertaken here (Fig. 2.2).

2.3 Climate

Rainfall in the Fish River Valley area is variable but minimal during the winter months. Mean monthly values recorded throughout 1967-1979 on an adjacent farm, "Bucklands", (all rainfall data are from this farm), indicate that the wettest months are February and March, with a secondary peak in August (Fig. 2.3). The maximum and minimum values for each calendar month during this thirteen year period are shown in Fig. 2.4. The mean annual rainfall is 514 mm p.a.

Rainfall figures for the duration of the study are illustrated in Fig. 2.5. Annual precipitation was 507 and 599 mm p.a. for 1978 and

FIG. 2.1 The location and main topographical features of the Andries Vosloo Kudu Reserve (A.V.K.R.).


Andries Vosloo Kudu Reserve
Great Fish River
275
335
305
1 km
N

5a

FIG. 2.2 The topographical features and place names of the study area in the A.V.K.R.

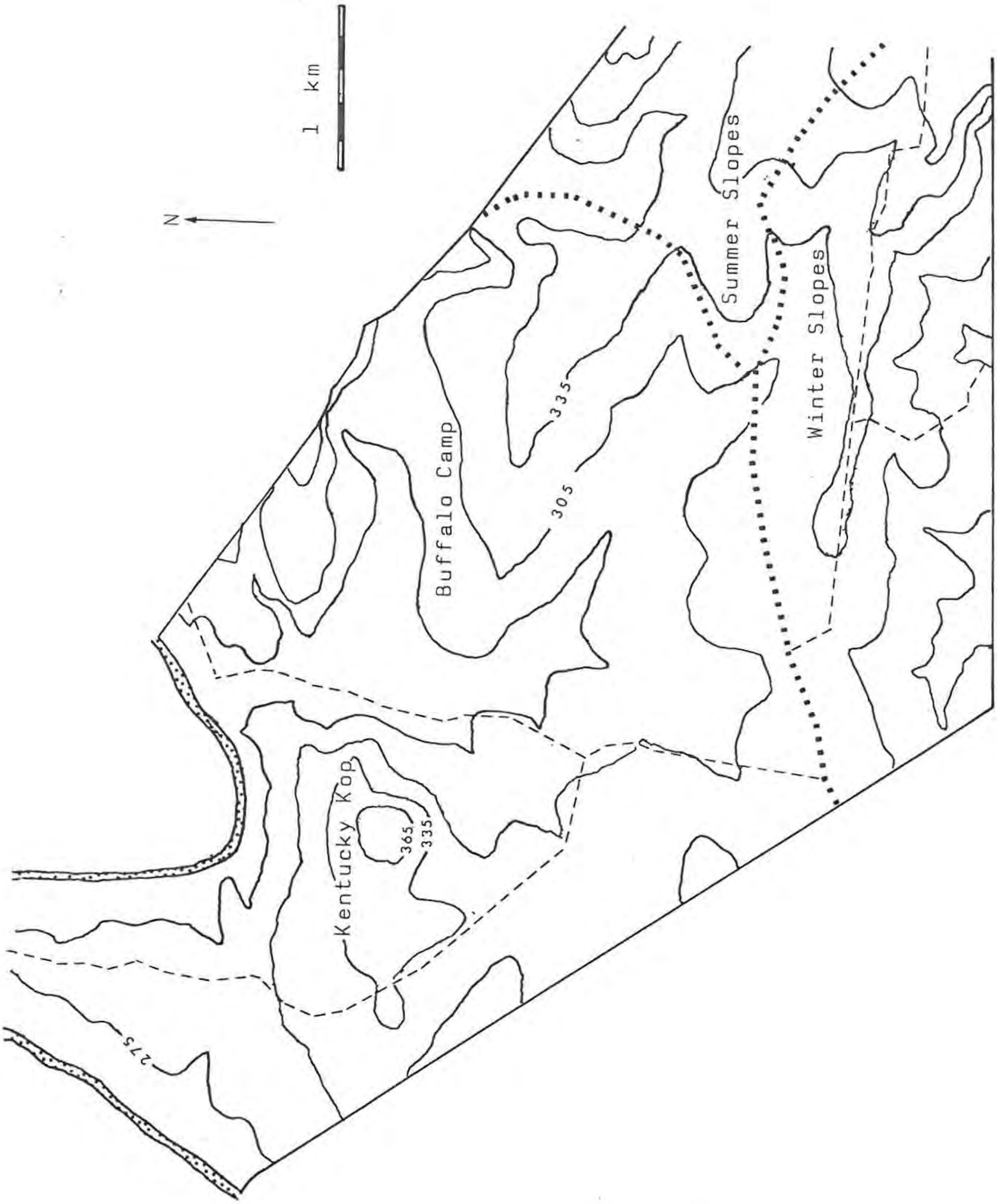
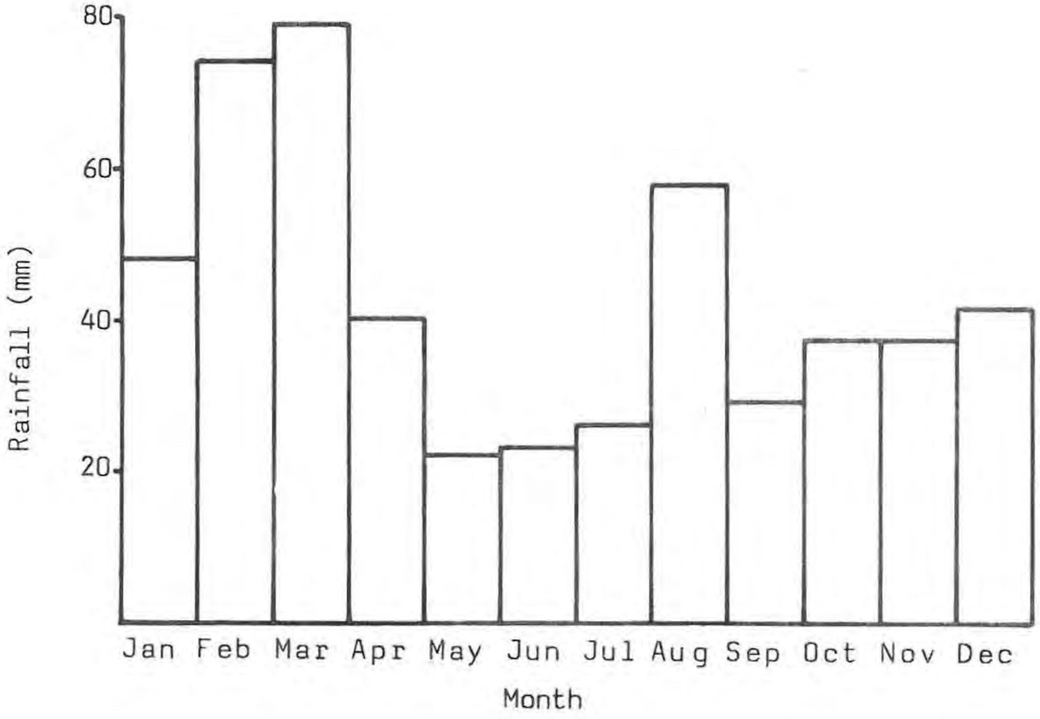

1 km
N
Summer Slopes
Winter Slopes
Buffalo Camp
335
305
Kentucky Kop
365
335
275

FIG. 2.3 The mean monthly rainfall at Bucklands (1967-1979).

FIG. 2.4 Maximum (□) and minimum (■) monthly rainfall at Bucklands (1967-1979).


80
60
40
20
Rainfall (mm)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

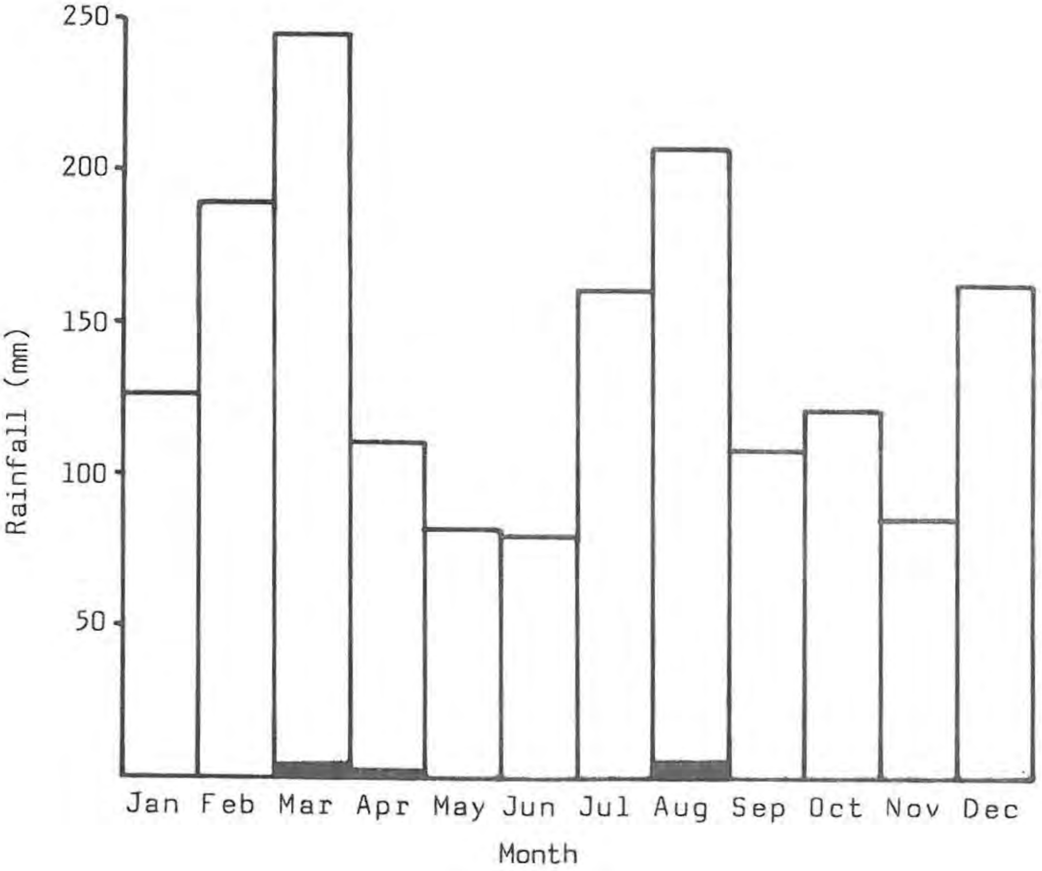
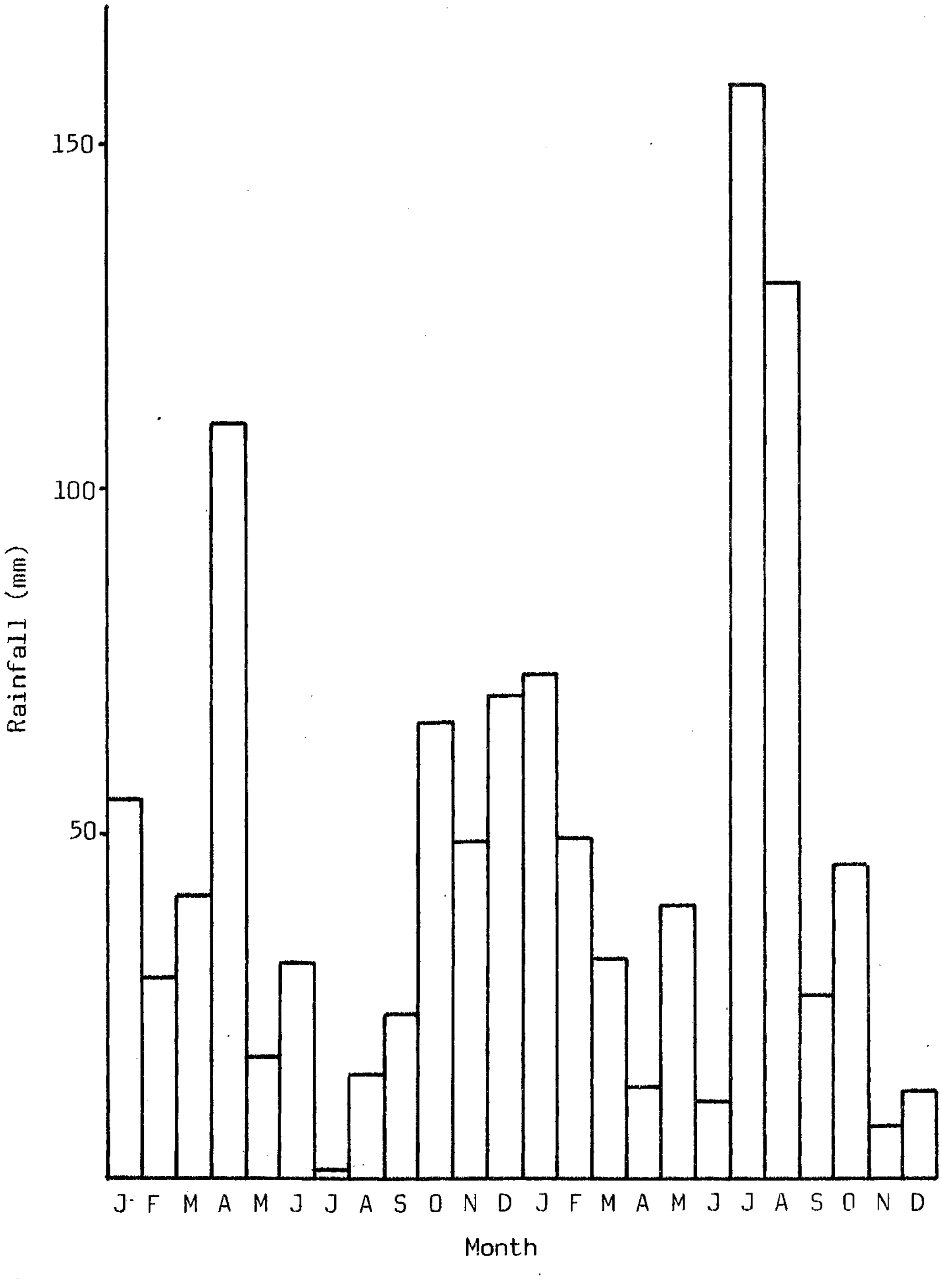

250
200
150
100
50
Rainfall (mm)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

FIG. 2.5 Rainfall recorded each month between Jan 1978 and Dec 1979 at Bucklands.


150
100
50
Rainfall (mm)
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
Month

1979 respectively. Some flooding of poorly drained low-lying regions of the Reserve occurred during the abnormal rains of July and August 1979 (288 mm).

Monthly mean maximum and minimum temperatures, recorded in Grahamstown (1922-1950) are shown in Fig. 2.6. Unfortunately, extensive records from the Reserve (or surrounding farms) are not available. It is believed that the Fish River Valley becomes several degrees hotter than Grahamstown during the summer months.

2.4 Vegetation

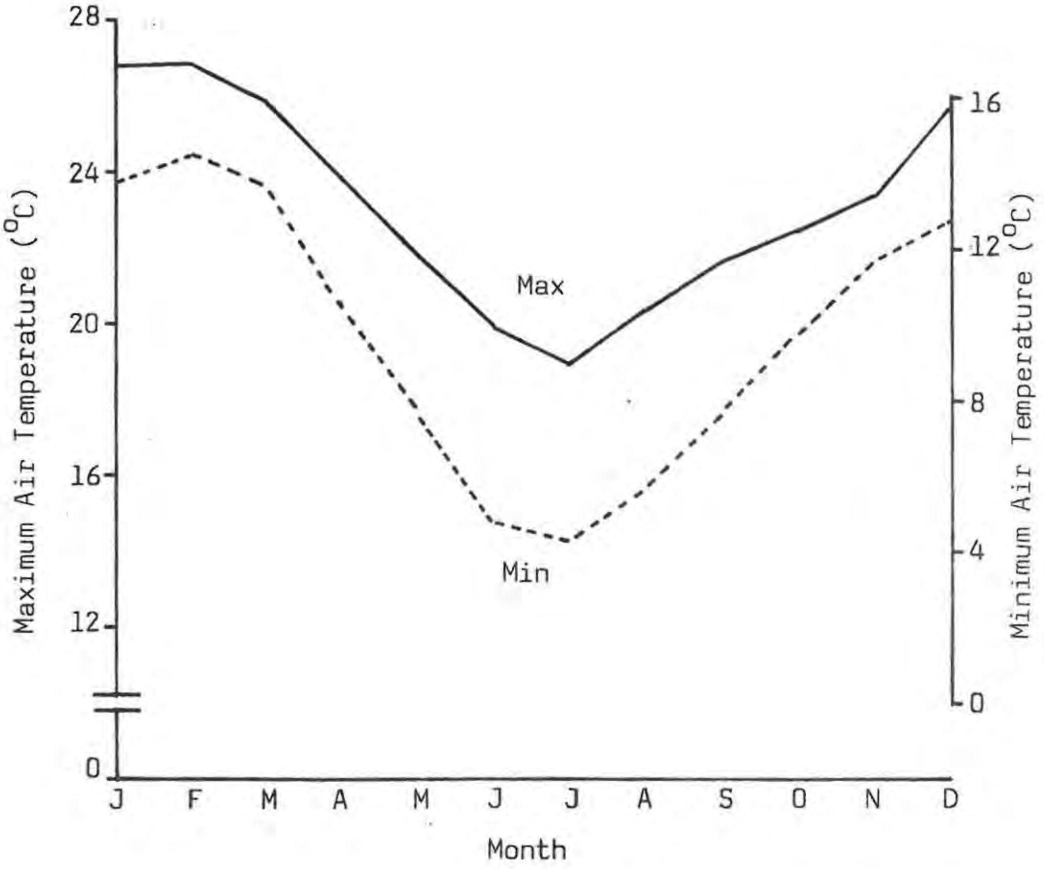
The vegetation on the Reserve consists of valley bushveld, which Acocks (1975) described as Fish River scrub. Jessop (undated report) subjectively classified the vegetation into eight principal communities and noted the heterogeneous nature of the veld, which ranges from near desert conditions, almost pure grass veld, succulent and non-succulent bush, to non-succulent forest. The most densely structured communities, which are influenced by altitude and aspect (Jessop, undated), are found in the eastern section. The remainder of the Reserve is more open and accessible, and therefore field observations were largely confined to the central and western portions. Jessop's (undated) descriptions of these areas are presented below.

Much of the western half of the Reserve is covered by *Euphorbia bothae* scrub (Plates 2.1d, 8.1a, c, d, f, g and h). Numerically dominant species in this community are *E. bothae*, and *Portulacaria afra*, while *Schotia afra*, *Grewia* spp., *Euclea undulata*, *Crassula* spp., *Ptaeroxylon obliquum*, *Phyllanthus verrucosa*, *Maytenus polyacantha* and *Pappea capensis* are also common. Bush clumps are interspersed with grasses including *Eragrostis obtusa*, *Sporobolus nitens*, *Aristida congesta*, and *Digitaria eriantha*. Among the bush clumps which are usually 1-2 m high, *Panicum deustrum* and *P. maximum* are quite common.

Dense *Portulacaria* bush (Plate 2.1e) provides greater lateral cover than *Euphorbia bothae* scrub. Most of the plants found in the latter community are also present, but species that are particularly common in *Portulacaria* bush include *Jatropha capensis*, *Grewia robusta*, *Phyllanthus verrucosa*, *Brachylaena elliptica*, *Tarchonanthus camphoratus*, *Putterlickia pyracantha*. Common tree species in this community include

FIG. 2.6 Monthly maximum and minimum air temperatures for Grahamstown 1922-1950.

10a


28
24
20
16
12
0
Maximum Air Temperature (°C)
16
12
8
4
0
Minimum Air Temperature (°C)
Max
Min
J
F
M
A
M
J
J
A
S
O
N
D
Month

Pappea capensis and Euclea undulata while grasses present are Panicum spp., Eragrostis obtusa, Digitaria eriantha and Setaria neglecta.

Portulacaria bush has been degraded to Euphorbia bothae scrub where heavy grazing has occurred (Acocks 1975). Climatic, topographic or edaphic factors (all the soils are derived from the underlying Ecca shales and sandstones), may also influence the distribution of the scrub community (Jessop, undated).

Thirdly, non-succulent bush predominates the central region of the Reserve (Fig. 2.7, Plates 2.1a, b, c and f, 8.1b and e). The principal species here include Maytenus polyacantha, Putterlickia pyracantha, Euclea undulata, Rhus undulata and R. refracta. Ptaeroxylon obliquum and Olea africana are also present, as are the grass species Eragrostis obtusa and Setoria neglecta. Jessop (undated) suggests that this vegetation is a product of stock management practices and that where grazing/browsing pressures were reduced Portulacaria bush would occur. The few stands of P. afra present in this community are heavily browsed.

Finally the river valleys and water courses (intermittent) support Acacia karroo, Acalypha glabrata, Combretum caffrum, Olea africana, Ziziphus mucronata and Schotia afra. Beneath these trees Azima tetracantha, Scutia myrtina, Ehretia regida, Carissa bispinosa, C. haematocarpa and Maytenus heterophylla often form a dense undergrowth.

The relative distribution of these four communities in the western half of the Reserve is shown in Fig. 2.7.

2.5 Large Mammal Status

Kudu are extremely common throughout the Reserve and population estimates are high (Chapter 4). Censuses of other large mammals have not been conducted on the Reserve and approximate totals are only known for herbivores that have recently been re-introduced. These include 20 buffalo (Syncerus caffer), 16 eland, and 10 red hartebeest (Acelaphus buselaphus). A declining springbok population (Antidorcas marsupialis) of less than 50 is confined to the Buffalo Camp, together with the buffalo and hartebeest. Several blesbok (Damaliscus dorcas phillipsi) are present, while bushbuck are localised and occur at low densities.

Steenbok (Raphicerus campestris) and grey duiker (Sylvicapra grimmia) occur and the latter, are common in denser areas of bush. Warthog (Phacochoerus aethiopicus) have been successfully re-introduced and may

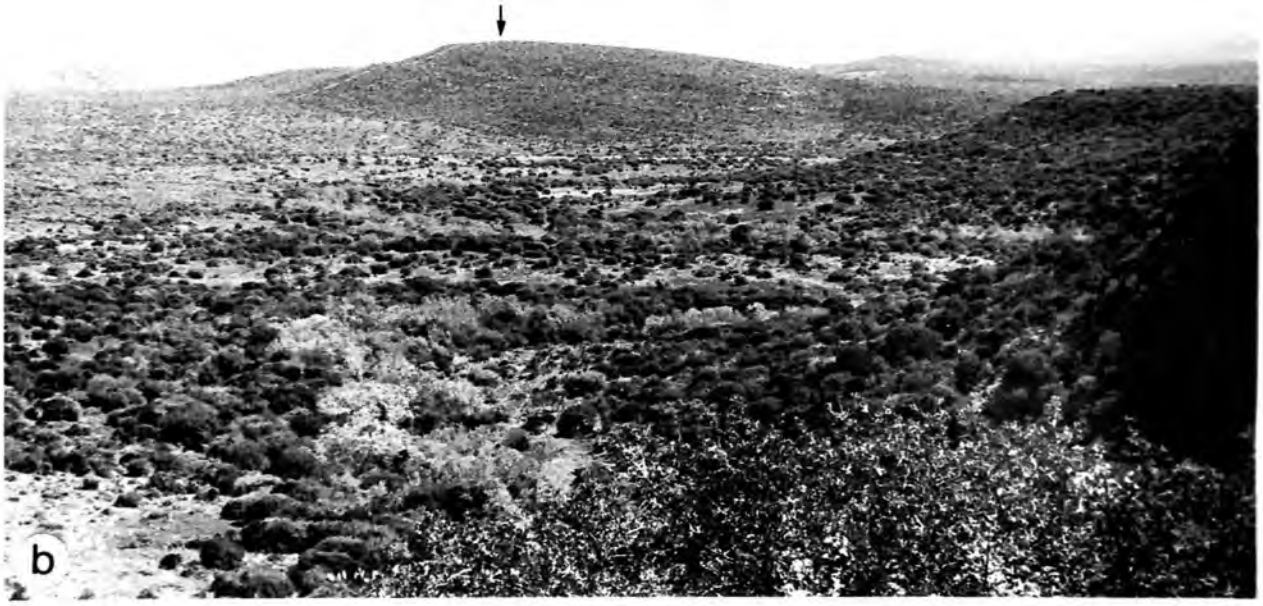
PLATE 2.1 The major vegetation communities in the study area.

a) The non-succulent bush community in the Buffalo Camp, A.V.K.R. Note the dense riverine vegetation in the centre of the photograph and the position of the radio-tracking base station on Kentucky Kop (arrowed).

b) The non-succulent bush community in the Buffalo Camp, A.V.K.R. Photograph taken from a frequently visited vantage point on the Reserve. The position of the radio-tracking base station on Kentucky Kop is arrowed.

c) The non-succulent bush community in the Buffalo Camp. Note riverine vegetation and Kentucky Dam. Photograph taken from the radio-tracking base station on Kentucky Kop.


a


b


c

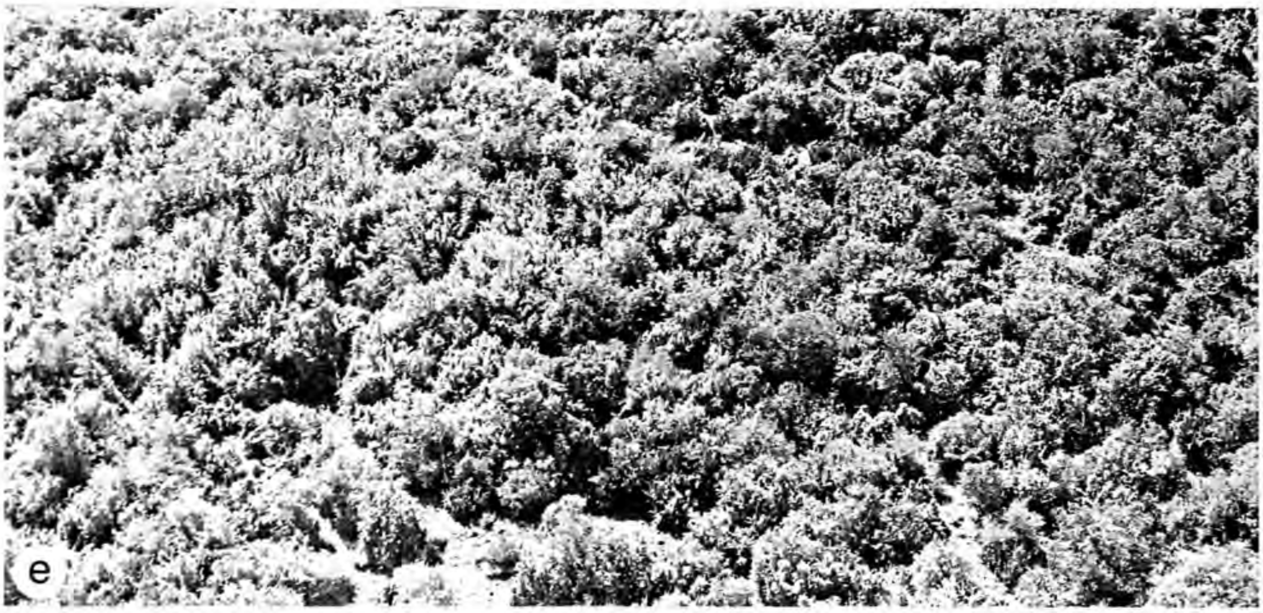
PLATE 2.1 continued.

d) The *Euphorbia bothae* scrub community on Kentucky Kop, A.V.K.R. Note the almost impenetrable nature of this community, and the conspicuously painted horns of a released 3 year old male kudu.

e) An aerial view of the densely structured *Portulacaria* bush community on the Winter Slopes, A.V.K.R.

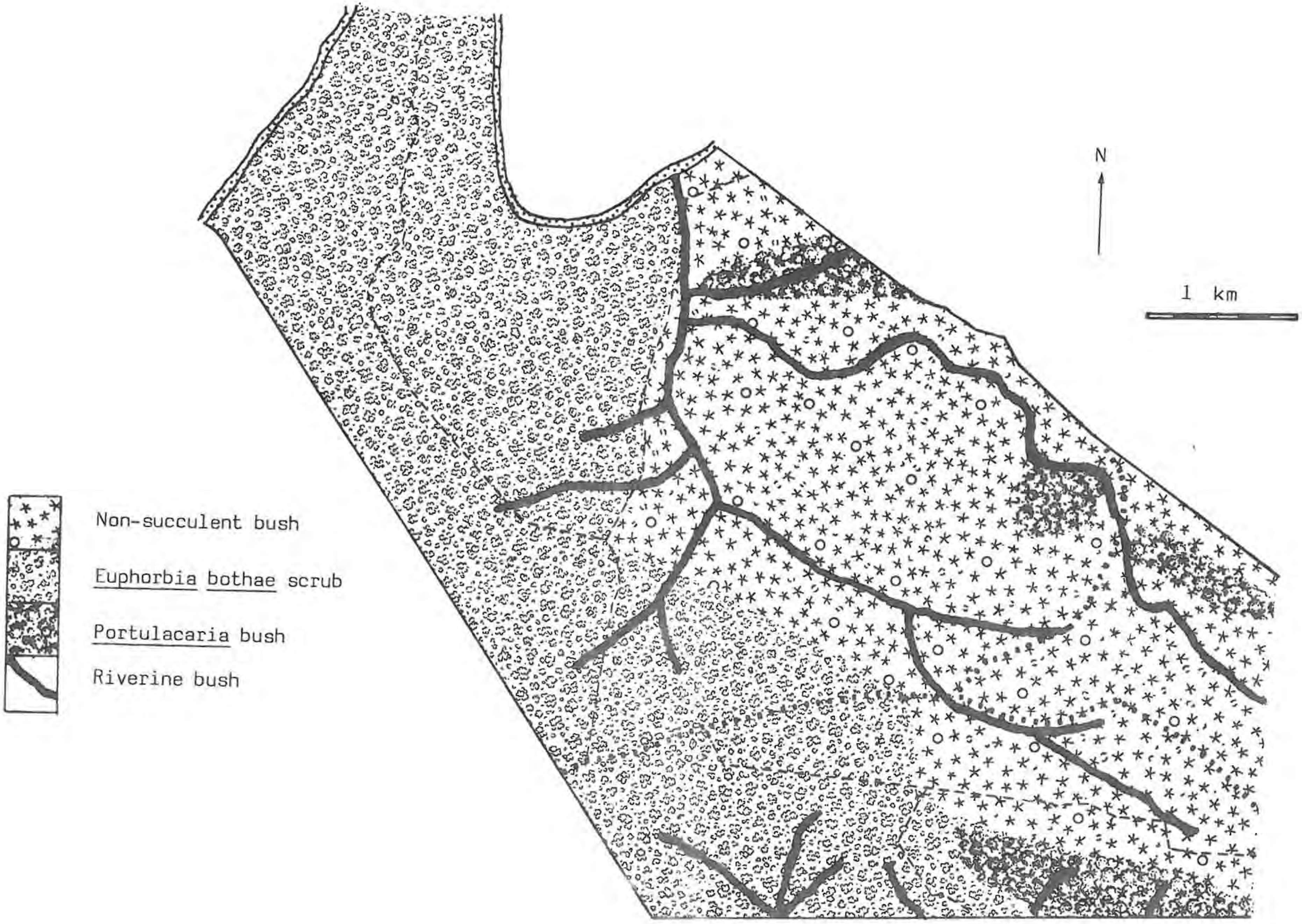
f) The non-succulent bush community on the Summer Slopes, A.V.K.R. Note the riverine vegetation in the centre of the photograph.


d


e


f

FIG. 2.7 The major vegetation communities in the western half of the A.V.K.R.


N
1 km
Non-succulent bush
Euphorbia bothae scrub
Portulacaria bush
Riverine bush

now total over 50 animals, while bushpig (*Potomachoerus porcus*), aardvark (*Orycteropus afer*) and aardwolf (*Proteles cristatus*) are rarely seen. Chacma baboons (*Papio ursinus*) and vervet monkeys (*Cercopithecus aethiops*) are common, while the largest predator on the Reserve is the black-backed jackal (*Canis mesomelas*).

Kudu are predominantly browsers (Wilson 1965, 1970; Jarman 1971; Hofmann & Stewart 1972; Hofmann 1973; Conybeare 1975; Wilson, Hirst & Ellis 1977; Owen-Smith 1979; Liversidge pers. comm.; pers. obs.) and undoubtedly compete with buffalo, eland, bushbuck, springbok, steenbok and duiker (and possibly baboons and vervet monkeys) for certain plant species (Wilson 1966; Pooley 1968; Littlejohn 1968; Dorst & Dandelot 1970; Bigalke 1972; Huntley 1972; Hofmann 1973; de Graaff, Schulz & van der Walt 1973; Field 1975).

Chapter 3

CAPTURE, MARKING AND RADIO-TRACKING OF KUDU

3.1 Introduction

The ability to recognise individual kudu is a prerequisite to the monitoring of individuals' movements, group composition and dynamics, and in assessing growth and age determination. Recognition of tragelaphids based on natural markings has been accomplished by Jacobsen (1974), Leuthold (1974, 1979), Waser (1975a, 1975b), Allsopp (1978) and Owen-Smith (pers. comm.). This is impossible on the Reserve because kudu are rarely seen totally unobscured by vegetation. This problem has been solved by using coded collars. Only the head and neck of the kudu need be visible to ensure positive identification.

This method necessitates capture of the subjects, and numerous techniques for ungulate capture have been described (Pienaar 1973a, 1973b; Harthoorn 1976). Two methods have been employed on the Reserve, namely netting and drug immobilization.

3.2 Materials and methods

3.2.1 Capture

3.2.1.1 Netting

Attempts to net kudu occurred in June 1977 and January 1978. Sites were selected in Euphorbia bothae and Portulacaria bush where the nets could be camouflaged and where kudu densities were known to be high.

Game nets (150 mm mesh size) were hung 2-3 m above the ground from a strand of high-strain 14 guage wire 300 m long (Plate 3.1c). The nets were supported by poles and trees and were fastened to the wire strand by clips of light guage wire. The lower portion of the nets were arranged so that their base draped over the ground, forming an apron (Pienaar 1973b).

Nets were most commonly arranged in a straight line, but with short (5-10 m) projections set at right angles to prevent kudu running parallel to the main line. They were usually erected and insepected in the late afternoon, and each beat commenced at 7 a.m. the following morning. Approximately forty beaters were employed to drive kudu over distances of 1-2 km towards the net. As animals approached the nets, they were flushed into them by additional members of the capture team hidden less than 20 m away. A section of net dropped on to the animal on impact, and the apron on the ground entangled the animals' legs. Kudu were quickly secured by tying the fore and hind limbs together with a rope.

If few or no animals were caught, the nets were checked, the apron reversed, and a second drive would immediately commence from the opposite direction. After two such drives the nets were moved to a new locality. The supporting wire was left in position to facilitate reassembly at that site several days later if required. In addition to beaters, a helicopter was also used in the netting attempts of January 1978.

3.2.1.2 Drug immobilization

Drug immobilization techniques were adopted in January 1978, April 1978 and April 1979. Due to the terrain and dense nature of the bush inhabited by kudu, darting from the air was essential.

The immobilizing agents selected for kudu capture during the first operation were etorphine hydrochloride ("M 99", Reckitt) and xylazine hydrochloride ("Rompun", Bayer). Detailed pharmacological descriptions of these drugs have been given by Harthoorn (1973, 1976).

Etorphine was used at a concentration of 4 mg per ml of buffered solvent, and xylazine at 100 mg per ml of solvent. Drugs were administered intramuscularly in the hind quarters, by automatic projectile syringes (darts) fired from a CO_2 long-range "Capchur" (Palmer) gun at a range of 5-15 m. Syringes had a capacity of either 3 ml or 5 ml and were fitted with barbed needles 2,8 cm long.

Antidotes administered were cyprenorphine hydrochloride ("M 285") and nalorphine hydrochloride ("Lethidrone") at concentrations of 10 mg per ml and 10-20 mg per ml respectively. These were given intravenously into the recurrent tarsal vein.

Dart wounds were treated with a commercial wound aerosol spray and animals suffering from any cuts and lesions were given intramuscular injections containing approximately 5 g of long acting penicillin ("Compropen").

A Hughes 300 helicopter and commercial pilot were employed and during aerial darting the ground team maintained visual contact with the helicopter. Once a kudu was darted, the helicopter followed the animal from a height of approximately 300 m. This enabled the ground team to pursue the helicopter in a truck. As soon as the kudu was immobilized, the marksman left the helicopter to attend to the darted animal. The ground team was directed to the kudu by means of two-way ground-to-ground radios. The team brought the materials needed for collaring and data collection. Inaccessible kudu were therefore immobilized for longer periods than accessible ones. Animals were placed in sternal recumbency to prevent bloating or inhalation of rumen contents.

In subsequent capture programmes (April 1978 and April 1979) communication between marksman and ground crew was facilitated by ground-to-air two way radios. Additional drug combinations were employed, namely fentanyl citrate (Janssen) with xylazine hydrochloride, and fentanyl citrate with etorphine and xylazine hydrochlorides. Fentanyl was administered in an aqueous solution of 25 mg per ml. An additional antidote, diprenorphine hydrochloride ("M 5050" Reckitt) was used at a concentration of 8 mg per ml of buffered solvent.

During all capture programmes, field data were recorded on standardized forms. The following were noted: drug dosage, antidote and recovery time, body measurements (e.g. body length, horn length, girth, etc.), for growth rates, dental measurements and impressions for age determination studies, condition and parasite loads (assessed subjectively), physiological parameters (rectal temperature, respiration rate), kudu sighting position and release point, and group size and composition. All kudu were collared (see below) but only a small number could be weighed due to problems of cartage and erection of the heavy tripod and scales in the field.

3.2.2 Marking

Captured kudu were marked with conspicuous collars. Most collars were made from 15 cm wide 3-ply transmission belting. Cow collars were 60-75 cm long, while bull collars ranged from 80 cm to 125 cm.

The initial collar used (designed by Brooks, pers. comm.) is shown in Plate 3.1a. A strip of colourful "Sterkolite" (a tough polyvinyl plastic material reinforced with nylon thread) was secured to the central portion of belting by contact adhesive and by pop rivets. At either end of the belting 11 x 8 cm numbers, letters, or symbols cut from 5 mm thick white plastic sheets, were fastened with 6 mm nuts and bolts. Bolt heads protruding from the inside surface of the collar were covered to prevent injury to the animal's neck.

Most of the kudu marked during the capture programmes of June 1977 and January 1978 were fitted with such collars. Young kudu bulls, and radio-collared individuals were fitted with more temporary "Sterkolite" collars (Plates 3.1b and e, 3.2e) as described by Smuts (1972, 1974a).

The original collar was redesigned for the subsequent marking programmes. Belting was retained but plastic codes were replaced by templates of letters and symbols cut from "Sterkolite". These were then either glued directly on to the black belting (giving a black symbol) or glued to an underlying, contrasting colour of "Sterkolite", and then fastened on to the belting (Plate 3.1a). Potential confusion of collars in the field was reduced by using only the following symbols:-

C, F, H, I, J, L, M, N, O, S, T, V, W, X, Y, Z,
2, 3, 4, 5, 6, 7, 8, 9, 10, 21
■ □ ▲ ▽ ● ○ ◆ ◇

A single symbol only was used (with the exception of 10 and 21) and carefully considered colour combinations further reduced any similarity.

All collars were fastened on to the animal by three 6 mm nuts and bolts, together with two galvanised washers. Numbered ear tags were fastened on all captured animals. A circular orange plastic ear tag 3,5 cm in diameter ("Rhotag", Millborrow) was secured on to the left ear, while a steel tag ("Ketchum" tamperproof cattle tag) was clipped on to the other ear (Plate 3.1d). Both tags carried the same number, while the author's address was engraved on the metal tag. Later, only steel tags were employed for the return of shot animals.

Finally, the horns of kudu were painted with white and/or yellow rubberized road paint to facilitate rapid recognition in thick bush (Plate 3.1e and f).

PLATE 3.1 Materials used to mark kudu.

a) Collars used for marking kudu. The initial and modified designs are shown on the left and in the centre respectively. Both had been fitted to kudu for one year. Comparing these with the new collar on the right, demonstrates the durability of these collars.

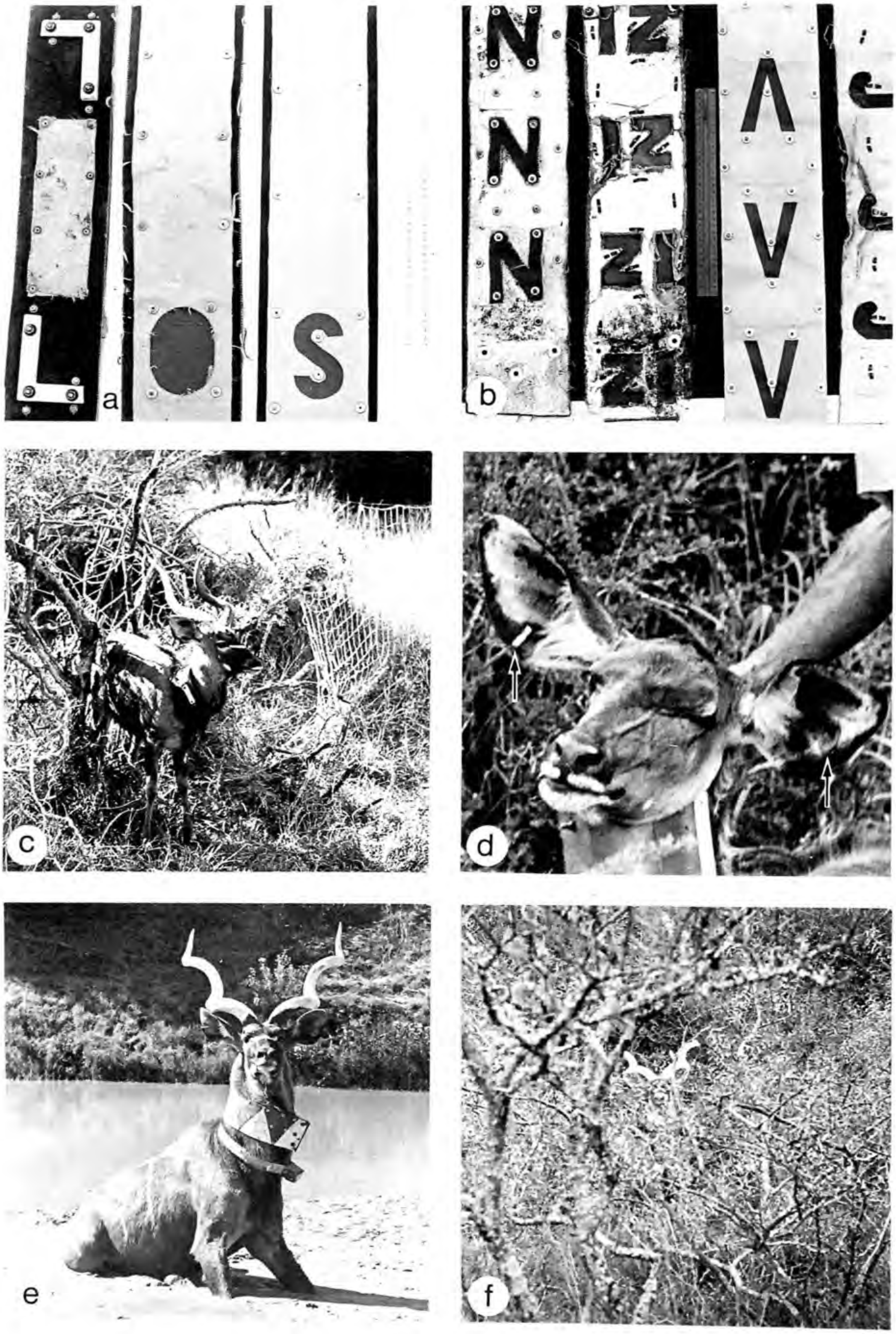
b) "Sterkolite" collars used for marking kudu. The third collar from the left is new; all others had been worn for exactly one year.

c) The release of a 2 year old male kudu captured in nets. Note the conspicuous collar and painted horn.

d) Metal (left) and plastic (right) ear tags used for marking captured kudu.

e) An adult male kudu recovering from immobilization. Note radio and "Sterkolite" collars and the painted horns.

f) An example of the value of conspicuous horns in detecting collared male kudu.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3.2.3 Radio-telemetry

The radio-tracking equipment used in this study was designed and constructed by the National Electrical Engineering Research Institute, C.S.I.R. Transmitters had an estimated life of either 12 or 24 months, and emitted a pulsed signal (two/second) in the 84 MHz band. These were sealed in resin and enclosed in a collar constructed from belting (Plate 3.2a) which was secured with pop rivets. The weight of each radio-collar was approximately 600 g.

The portable receiver (Plate 3.2c and d) had twenty channels 20 KHz apart, and each channel could be changed by 5 KHz to obtain an audible tone. Signal strength could be metered visually and/or audibly.

Two types of receiving antennae were employed. A four element vertically polarized Yagi antenna was mounted or hand held at each of the three fixed base stations (Plate 3.2b) while signals were recorded from several other known reference points using other Yagis or a loop antenna with a diametrically mounted telescopic antenna (Plate 3.2c and d). Wherever possible, tracking stations were positioned where bearings intersected at 90^{o}, and where subjects were less than 2 km away, since both these practices improve the accuracy of the system (Heezen & Tester 1967; Tester 1971).

To obtain a bearing, the Yagi was rotated until maximum signal strength was realized, and a compass bearing taken. If maximum signal strength occurred over a wide arc, then both bearings were recorded and the angle bisected. The loop antenna provided a much wider arc of maximum signal strength, and signal direction was obtained using the null position.

Positions of radio-tagged kudu were determined by triangulation on a 1:18,000 topographical map. Simultaneous bearings for each animal were not possible, but readings were taken within one hour of each other.

3.3 Results and discussion

3.3.1 Capture

3.3.1.1 Netting

A total of eighteen animals were caught in nets during the fourteen day exercise in June 1977 (7 females, 2 males and 3 female

PLATE 3.2 Radio-tracking equipment.

a) One of the intact CSIR radio-collars used in this study, and an empty harness; the transmitter had fallen from the collar (left).

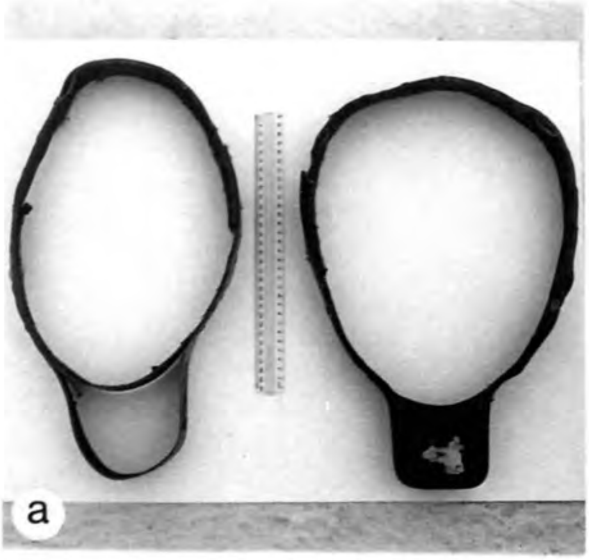
b) A four element, vertically polarized Yagi receiving antenna at the base station on Kentucky Kop.

c) The portable CSIR receiver and loop antenna used in this study.

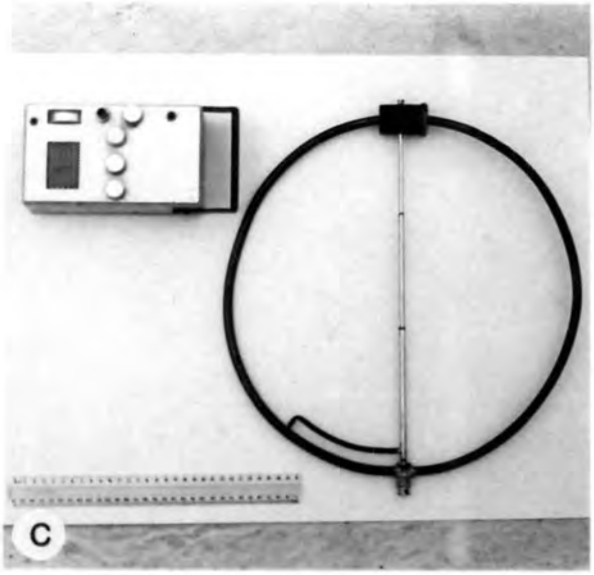
d) The receiver and loop antenna in operation.

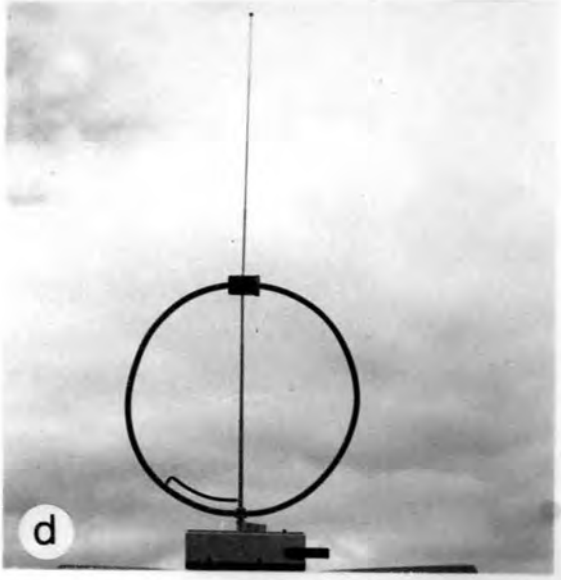
e) A "Sterkolite" and radio-collar fitted to an immobilized adult female kudu.

f) The same female recaptured exactly one year later. Note the eroded resin and exposed components of the transmitter.


a


b


c


d


N
e


N
f

and 6 male calves). Several other kudu hit the nets but were only temporarily secured, emphasising the importance of having personnel stationed near the nets.

One disadvantage of using this technique for kudu concerns their grouping and flight behaviour. Kudu tend to run in single file, usually with an adult cow leading, and with any bulls present at the rear of the line. Capture of the first animal often initiated avoidance and flight responses by the remainder of the group.

One kudu bull had to be destroyed during this operation because its right horn pierced the thorax and punctured the right lung. This death represents a mortality of 6%.

Attempts to drive kudu into nets using beaters and/or a helicopter were generally unsuccessful. Animals could not be herded, nor could the helicopter alter their direction of flight. After two drives in different areas, the exercise involving the helicopter was abandoned.

3.3.1.2 Drug immobilization

Drug immobilization from the air resulted in the capture of 107 kudu (49 males, 58 females). Thirty animals were caught in January 1978, 51 in April 1978 and the remaining 26 in April 1979. Details of drug combinations used and the associated induction times are given in Tables 3.1 and 3.2. The mean induction time was 8,7 minutes ± 4.0 minutes (n = 107).

One hundred of these animals were immobilized with the contents from a single dart. When two darts were necessary, both were checked on recovery. On eight occasions the first dart failed to detonate, and the induction time was therefore determined as the time from re-darting to collapse. These times are included with successful captures from one dart only, and provide a mean induction time of 7,9 minutes ± 2,7 minutes (range 1,4-15,2 minutes, n = 100, Table 3.1).

Seven kudu were effectively darted twice. Mean intervals between first and second injections, and second injection and recumbency are given in Table 3.2

Most animals (42 males, 48 females) were immobilized with the analgesic-neuroleptic combination of etorphine and xylazine

TABLE 3.1 Single doses and induction times of one hundred free-ranging kudu immobilized with combinations of etorphine hydrochloride (M99), fentanyl citrate and xylazine hydrochloride (Rompun).

Sex	No. of kudu	M99 (mg)	Rompun (mg)	Fentanyl (mg)	Mean induction time (mins) ± S.D.	Range
Males	2	6	200	-	11,9	8,7-15,2
	13	5	150-300	-	8,7 ± 3,2	4,0-13,5
	23	4	150-250	-	7,9 ± 2,8	1,4-15,1
	5	3	100-150	30	6,9 ± 1,4	5,4-9,1
	2	3	200-250	-	6,0	5,5-6,5
Sub total	45	(3-6)	(100-300)	(0-30)	8,1 ± 2,9	1,4-15,2
Females	1	6	200	-	7,0	-
	4	4	150-200	-	9,2 ± 2,0	7,5-11,7
	41	3	100-200	-	7,6 ± 2,5	3,7-13,6
	8	2	125	30	8,2 ± 3,3	4,1-13,5
	1	-	100	60	9,1	-
Sub total	55	(0-6)	(100-200)	(0-60)	7,8 ± 2,5	3,7-13,6
TOTAL	100	(0-6)	(100-300)	(0-60)	7,9 ± 2,7	1,4-15,2

TABLE 3.2 Double doses and induction times of seven free-ranging kudu immobilized with combinations of etorphine hydrochloride (M99), fentanyl citrate and xylazine hydrochloride (Rompun).

Sex	Contents of initial dart	Contents of 2nd dart	Time interval between administration of 1st & 2nd darts	Time interval between administration of 2nd dart and immoblization	Induction time (mins)
♀♀	3mg M99 100mg Rompun	3mg M99 100mg Rompun	12,9	4,5	17,4
	3mg M99 100mg Rompun	3mg M99 100mg Rompun	12,0	11,2	23,2
	60mg Fentanyl 100mg Rompun	60mg Fentanyl 100mg Rompun	14,0	3,2	17,2
♂♂	4mg M99 200mg Rompun	2mg M99 30mg Fentanyl 125mg Rompun	22,0	4,9	26,9
	4mg M99 150mg Rompun	4mg M99 150mg Rompun	11,0	5,9	16,9
	4mg M99 150mg Rompun	3mg M99 100mg Rompun	14,0	4,7	18,7
	3mg M99 30mg Fentanyl 150mg Rompun	60mg Fentanyl 100mg Rompun	10,1	6,9	17,0
n=7			13,7 ± 3,9	5,9 ± 2,6	19,6 ± 3,9

hydrochlorides (Tables 3.1 and 3.2), as recommended by Harthoorn (1976), Pienaar (1973a) and Smuts (1973). Xylazine counteracts the excitatory effects induced by etorphine, and although no published results are available for comparison, the low induction times recorded here illustrate the efficacy of this combination.

Most subadult and adult males were immobilized with 4 or 5 mg etorphine, irrespective of size (Fig. 3.1) and induction times did not differ significantly between the two doses (t = 0,78; d.f. = 34). Therefore in most instances the extra cost of the additional 1 mg etorphine was not warranted. Ebedes (1971a, cited in Harthoorn 1976) used 4-5 mg etorphine to immobilize male kudu, but Pienaar (1973a) and Smuts (1973) also recommend a dose of 4 mg etorphine for kudu bulls. Heard (pers. comm.) suggested that costs could be further reduced by replacing 1 mg etorphine with 30 mg of the much less expensive fentanyl. Five bulls were therefore administered 3 mg etorphine and 30 mg fentanyl, and no statistically significant differences in induction time between these and animals immobilized with 4 mg etorphine were apparent (t = 0,66; d.f. = 26).

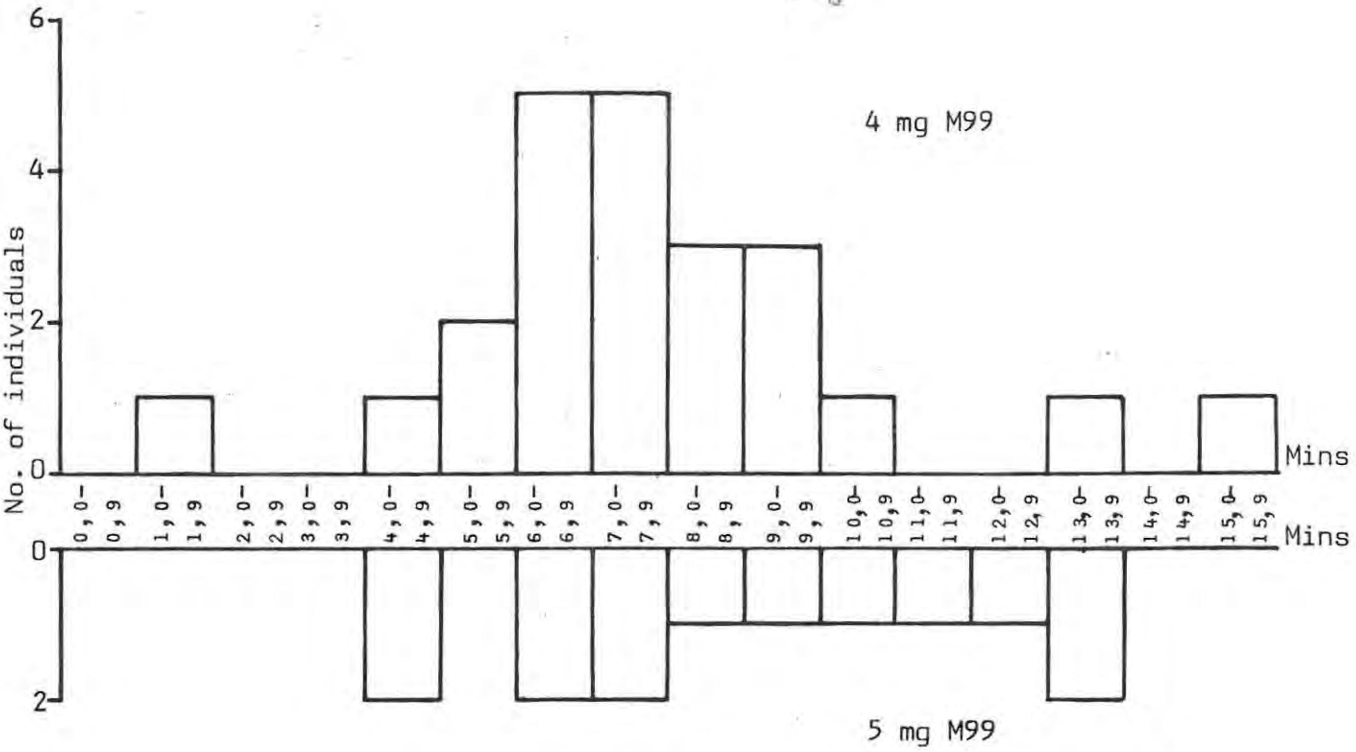
The yearling males were successfully captured with 3 mg etorphine, while two adult bulls were each given 6 mg etorphine after a number of animals had to be darted twice (see below).

Most cows (70%) were immobilized with 3 mg etorphine. Only four received 4 mg each when darts originally intended for bulls had to be used. On eight occasions cows were darted with 2 mg etorphine and 30 mg fentanyl, and no statistical differences between these induction times and those from animals darted with 3 mg etorphine were found (Fig. 3.2, t = 0,62; d.f. = 47).

One cow was successfully captured with 6 mg etorphine for the same reason as the two males mentioned above, while two others were immobilized using 60 mg fentanyl and 100 mg xylazine. One collapsed after 9,1 minutes (Table 3.1) but the second cow was re-darted (after 14,0 minutes) with an identical combination and was immobilized 3,2 minutes later (Table 3.2). Smuts (1973) recorded longer induction times using 50 mg fentanyl and 200-350 mg xylazine, but shorter times recorded here were probably due to higher doses of fentanyl, and perhaps through more rapid absorption during the animals' flight.

FIG. 3.1 Induction times of male kudu immobilized with 4 mg etorphine (n = 23), and 5 mg etorphine (n = 13). All animals also received between 150-300 mg xylazine.

FIG. 3.2 Induction times of female kudu immobilized with 3 mg etorphine (n = 41), and 2 mg etorphine and 30 mg fentanyl (n = 8). All animals also received between 100-200 mg xylazine.


4 mg M99
5 mg M99
No. of individuals
6
4
2
0
0
2
Mins
Mins
0,0-0,9
1,0-1,9
2,0-2,9
3,0-3,9
4,0-4,9
5,0-5,9
6,0-6,9
7,0-7,9
8,0-8,9
9,0-9,9
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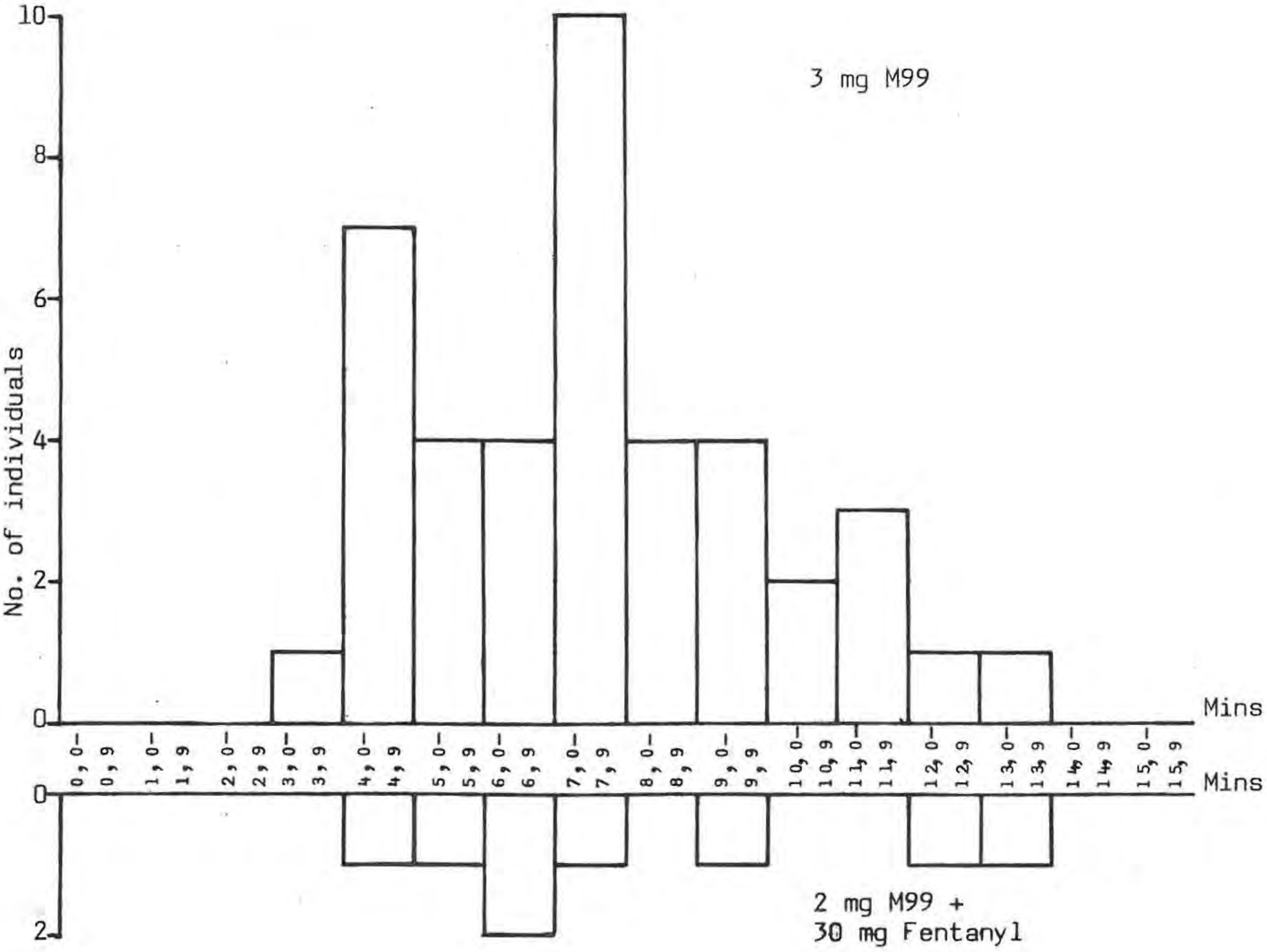
14,0-14,9
15,0-15,9


3 mg M99
2 mg M99 +
30 mg Fentanyl
No. of individuals
10
8
6
4
2
0
0
2
Mins
Mins
0,0-0,9
1,0-1,9
2,0-2,9
3,0-3,9
4,0-4,9
5,0-5,9
6,0-6,9
7,0-7,9
8,0-8,9
9,0-9,9
10,0-10,9
11,0-11,9
12,0-12,9
13,0-13,9
14,0-14,9
15,0-15,9

The decision to leave or re-dart an animal was based on experience. The onset of immobilization was usually apparent when the animals adopted a high-stepping or "hackney" gait, copious salivation, and later, paralysis of the tongue and "star-gazing". These characteristic signs have previously been described by Harthoorn (1976) and Smuts (1973).

To economise on flying time, animals were re-darted if none of these symptoms were apparent 10 minutes after initial darting. Nine kudu were re-darted in January/April 1978 owing to detonator failure.

Induction times in these instances were recorded from the time of the second (effective) injection to recumbency, and the results are included in Table 3.1.

Seven other kudu were darted and followed for at least 10 minutes with no visible signs of reaction, before they were lost in thick riverine vegetation. It is highly probable that the immobilizing drugs were not injected into these seven animals.

Reasons for detonator failure are unknown. Every precaution was taken to ensure that the charges were kept completely dry (Harthoorn 1976). New detonators purchased for the last darting operation were free from failure. Gasaway, Franzman & Faro (1978) found that detonator failure was responsible for 75% of all dart malfunctions.

One animal darted twice (in April 1978) showed a partial response to the first dart, and as a result was only re-darted after 22 minutes, collapsing 4,9 minutes later (Table 3.2). This partial reaction may have resulted from slow absorption by subcutaneous injection or injection into fat (Woodford, Eltringham & Wyatt 1972). All six animals re-darted in April 1979 showed partial response after the first dart, and in each case, all the contents had been injected. This suggests that the etorphine used on these kudu was less effective than the previous batches. Mean induction times for January and April 1978, and April 1979 were; 7,3, 8,2 and 11,4 minutes respectively. No statistical difference was apparent between January 1978 and April 1978, but highly significant differences were found between January 1978 and April 1979 (t = 4,2; d.f. = 54; $p<0,001$) and between April 1978 and April 1979 (t = 3,2; d.f. = 75;

$p<0,01$). This verifies that the etorphine used in April 1979 was less potent. To compensate for this, a number of animals were successfully captured with an initial dose of 6 mg etorphine in April 1979.

The detonator failure and reduction in the potency of etorphine caused serious disruptions to the capture programmes. Both produced a considerable increase in flying time and were thus very costly.

Darts bouncing off the target occurred twice in January 1978 (both darts lost), sixteen times in April 1978 (eight retrieved, four of these empty) and five times in April 1979 (all lost). Dräger, Patterson and Breton (1976) experienced the same problem using identical equipment. Reasons for these deflections are not known, but the high velocity of the dart may have been partially responsible (Woodford, Eltringham & Wyatt 1972). Such failures constitute considerable financial loss in terms of both drug wastage and lost darts.

Sixteen darted animals were not found, (13% of all darted kudu). In some instances the drugs had probably not penetrated into the animals. However, several animals were lost when they entered riverine vegetation, where virtually closed canopies prevented visual contact from the air. Attempts to divert darted kudu from such areas usually failed, as did extensive ground and air searches. Published reports concerning the incidence of lost animals are rare, but considering the nature of valley bushveld, some losses are inevitable.

Several lost animals were seen a few days after darting. They were recognised either by the protruding dart, or by old collars due for replacement. This suggests that some immobilized animals completely recovered without receiving the antagonist, (one such recovery was actually witnessed). These latter kudu were lost in April 1979 when there was no incidence of detonator failure.

Recovery time was recorded as the interval between antidote injection and the animal standing up. Mean recovery times using various antagonists (and ranges given per mg narcotic) are shown in Table 3.3. The mean recovery time for 105 kudu was 2,8 ± 3,0 minutes.

Cyprenorphine and diprenorphine hydrochlorides were usually administered at the recommended ratios of 2,5 mg and 2 mg per mg

TABLE 3.3 The response of one hundred and five free-ranging kudu to the antagonists cyprenorphine hydrochloride (M285), diprenorphine hydrochloride (M5050) and nalorphine hydrobromide (Lethidrone).

No. of kudu	Narcotic	Antagonist	Range of antagonist per mg of narcotic	Mean recovery time (mins) ± S.D.	Range
35	M99	M285	2,5-4,0	3,2 ± 3,2	0,8-13,0
50	M99	M5050	1,3-2,7	2,9 ± 3,3	0,8-15,9
14	M99 Fentanyl	M5050 Lethidrone	1,7-2,7 0,3-0,5	1,4 ± 0,6	0,5-2,8
3	M99	Lethidrone	10-30	1,4 ± 0,4	1,1-1,8
1	M99 Fentanyl	M5050	3,0 0,2	6,8	-
1	Fentanyl	M5050	0,1	2,2	-
1	Fentanyl	Lethidrone	0,63	3,3	-
n=105				2,8 ± 3,0	0,5-15,9

etorphine respectively. Animals darted twice had both darts checked to determine the amount of injected narcotic before appropriate doses of antidote were given. Fourteen animals had recovery times longer than 4 minutes and some of these were given supplementary injections (accounted for in Table 3.3). On some of these occasions the hypodermic needle may have gone through both walls of the vein and delivered the antidote intramuscularly.

Differences in recovery times using cyprenorphine and diprenorphine to counteract etorphine were not significant. Ebedes (1971a, cited in Harthoorn 1976) obtained similar results. However, marked postural and locomotory differences were witnessed in this study. Animals injected with cyprenorphine rose slowly and remained motionless for several seconds, often showing poor co-ordination before wandering away (Plate 3.3a-d). Conversely, animals given diprenorphine were more alert, and reacted to all stimuli in a perfectly co-ordinated way (Plate 3.3e-f). These differences may be due to the residual sedation often caused by cyprenorphine which has some agonist activity, whereas diprenorphine is a pure antagonist (Harthoorn 1976).

Nalorphine produced the most rapid recovery times, (Table 3.3, divergent sample sizes and periods of immobilization precluded statistical analyses), and the subsequent actions of kudu receiving this antidote were identical to those injected with diprenorphine. Thus in areas where large predators are common, it is suggested that nalorphine be used to counteract etorphine, in spite of the additional cost this would entail.

Diprenorphine is preferable to cyprenorphine, especially in areas where an animal could injure itself if still sedated (e.g. hilly terrain etc.). Cyprenorphine may be more suitable where animals are to be held captive.

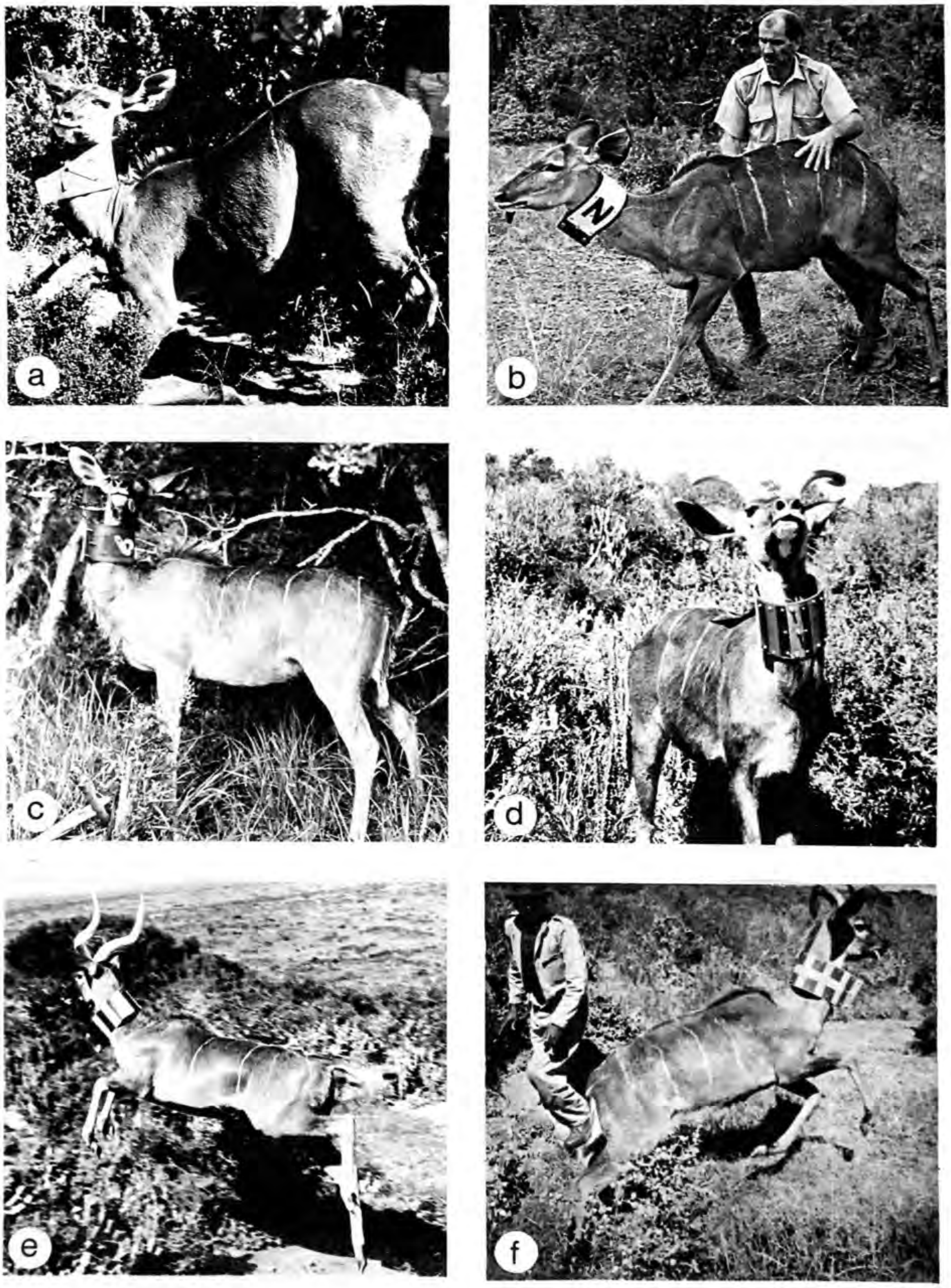
The mean time interval between darting and recovery was 41,7 minutes (S.D. = 11,3 minutes, range 13-73 minutes, n = 98). Animals were therefore recumbent for approximately 30 minutes (10 minutes following time), during which time they were marked and measured.

Two animals died during the darting operations. The first was a young cow (± 15 months old) darted in the flank with 3 mg

PLATE 3.3 Collared kudu recovering from narcosis.

a-d) Recovery resulting from the administration of the antagonist cyprenorphine hydrochloride. Most animals rose slowly and remained motionless for several seconds.

e-f) Once standing, kudu that had received the antagonist diprenorphine hydrochloride showed immediate co-ordination.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etorphine and 200 mg xylazine. First signs of ataxia were after 2,8 minutes, and the animal was immobilized within 4,2 minutes of darting. The antidote, 8 mg diprenorphine was administered 50 minutes after darting and the kudu died less than 5 minutes later. It was in good condition and had only run approximately 1 km before collapsing. The rectal temperature of this cow, 39,5°C, was below the average value (40,3°C ± 1,0, range = 37,7-42,7, n = 99). The respiration rate was 7 per minute relative to a mean of 8,9 (± 4,1 per minute, range = 4-25 per minute, n = 104). The cause of death could not be ascertained from a field post mortem.

The other fatality occurred when a mature cow, running at full speed, fell into a two metre deep gulley. The animal failed to respond to the antidote and was humanely killed. A post mortem revealed massive abdominal haemorrhaging and several broken ribs.

A third animal, a collared cow, was seen dead from the air. Intensive searches from the ground have failed to retrieve the carcass, so the cause and time of death are unknown.

These fatalities during capture represent a mortality of less than 3% compared to 6% when using nets. This low mortality is largely due to the wide safety margin (or effective margin; Harthoorn 1976) of etorphine hydrochloride. Other advantages gained by using the highly effective combination of etorphine and xylazine hydrochlorides include, a) low induction times which are important when darting from the air; b) rapid and complete reversal with one of several antagonists which minimises post-capture mortality due to predation; and c) capture operations can be completed more rapidly which might also reduce disturbance (e.g. 51 kudu immobilized and released in eight days compared with 18 kudu caught in nets over 14 days). Finally, capture by darting permits a much greater degree of selectivity in terms of both area and individuals, and is particularly advantageous in open habitats and when recapture is necessary.

For these reasons the drug immobilization technique is highly recommended for kudu capture in valley bushveld and similar areas. Some mechanical failures using the present injection system are to be expected (Woodford et al. 1972; Gasaway et al. 1978) and the manufacturers should make every effort to alleviate these problems.

3.3.2 Marking

One hundred kudu were marked with collars and released. Wherever possible animals were colour-coded according to the area where they were first seen, as shown in Table 3.4. Kentucky Kop was predominantly a white area, the Buffalo Camp a yellow region, etc.

White and yellow collars were found to be the most conspicuous in the field. Orange and red tended to blend with the natural colouring of the animals, while green and blue collars tended to merge in with the vegetation and were difficult to see in shadows and failing light.

Nineteen animals were recaptured during April 1979 and no signs of injury from collars were apparent. All old collars were replaced, and in most instances the new and old collars were identical. Collar colours were only changed if the collar did not conform to the predominant colour of the area. This usually meant that a darker coloured collar was replaced by a white or yellow one. This practice may have been responsible for the increased number of sighting of certain individuals (e.g. one green collared cow, caught in nets in June 1977 was only seen in April 1979, when she was recaptured. The old collar was replaced with a white one and the animal has since been seen four times in the same locality).

These old collars and ones returned by farmers from shot kudu, showed little deterioration. Some had been in service for 23 months, and all could still be recognised in the field (Plate 3.1a). "Sterkolite" collars showed the greatest degree of wear (Plate 3.1b), while a number of plastic symbols had broken on original machine belting collars. Least wear was seen in modified collars made from belting and "Sterkolite" (Plate 3.1a). It is believed that these collars would be serviceable for 2-3 years in most habitats.

All recaptured kudu had retained their ear tags. Although these were of no aid to field identification, they may be of considerable value in future recapture programmes, if collars have deteriorated beyond recognition, or in the return of samples from shot kudu (calves were not collared).

TABLE 3.4 The colours of collars fitted to one hundred kudu captured in the six divisions of the Andries Vosloo Kudu Reserve.

Predominant colour of collar	Kentucky Kop	Buffalo Camp	Summer Slopes	Winter Slopes	Marginal	Eastern Section	TOTAL
Males							
White	11	-	-	-	2	-	13
Yellow	8	9	-	-	-	1	18
Orange	3	-	1	1	-	1	6
Red	-	1	-	3	-	1	5
Blue	1	1	-	1	-	-	3
Green	1	1	-	-	-	-	2
Sub total	24	12	1	5	2	3	47
Females							
White	9	3	1	-	2	-	15
Yellow	5	12	1	-	-	-	18
Orange	1	-	5	-	-	-	6
Red	1	3	1	3	-	-	8
Blue	2	-	1	2	-	-	5
Green	1	-	-	-	-	-	1
Sub total	19	18	9	5	2	-	53
TOTAL	43	30	10	10	4	3	100

Marked males were often initially detected by their conspicuously painted horns, (Plate 3.1f), but identification could only be made when the collar was visible. The paint was only effective for a maximum of four months.

3.3.3 Radio telemetry

Details of the operational history of the sixteen radio-transmitters are given in Table 3.5. Two of these exceeded their estimated life, while the expected expiry date of the remaining fourteen transmitters is April 1980.

Transmitter failure could only be ascertained when a radio-collared animal was seen in the field and simultaneously, no signals were received on the relevant channel. This situation occurred on four occasions and all four male transmitters ceased functioning within five months of collar attachment. The cause of failure was established for two of these since the transmitter package had fallen out from the harness portion of the collar (Plate 3.2a). Reasons for this occurring in bulls only are not known. Sparring or overt fighting may be responsible, but damage to other (e.g. "Sterkolite") collars has not been witnessed. Whatever the cause, it is imperative that transmitter attachment to the harness should be significantly improved. The radio package should also be enclosed more thoroughly, since one female collar had exposed components, (where the resin had eroded) after one year (Plate 3.2f) and although the radio was still operating, continued erosion would certainly have lead to transmission failure.

No signals were detected from another four transmitters in November 1979 when field work was terminated. Some of these animals may however, have moved out of the range of reception which was approximately 6 km with a Yagi in flat terrain, and $1^1/_2$ km when using the loop antenna.

The accuracy of the equipment was assessed on eight occasions when animals were sighted shortly after their positions had been determined by radio-tracking. The mean difference between each set of these positions was 400 ± 138 m (range 110-570 m). These values represent maximal errors, since the subjects could have moved either while radio fixes were taken (fixes could not be taken

TABLE 3.5 Operational history of C.S.I.R. radio transmitters.

Channel	Sex	Estimated life (months)	Date fitted	Date of last signal	Duration (months)	Remarks
C	♀	12	Jan '78	Mar '79	15	
D	♂	12	Jan '78	Feb '79	14	
A	♂	24	Apr '78	Sep '78	5	radio malfunction
B	♂	24	Apr '78	Jul '78	3	radio malfunction
E	♀	24	Apr '78	-	-	still transmitting
F	♂	24	Apr '78	May '78	1	radio malfunction
G	♀	24	Apr '78	-	-	still transmitting
H	♀	24	Apr '78	-	-	still transmitting
I	♀	24	Apr '78	-	-	still transmitting
J	♂	24	Apr '78	*	-	still transmitting
A	♀	12	Apr '79	Jul '79	?	emigration/malfunction?
B	♂	12	Apr '79	May '79	?	emigration/malfunction?
F	♂	12	Apr '79	Apr '79	?	emigration/malfunction?
K	♂	12	Apr '79	Apr '79	1	radio malfunction
L	♂	12	Apr '79	Nov '79	-	still transmitting
M	♂	12	Apr '79	Jul '79	?	emigration/malfunction?

* = Animal found dead in May '79 - radio still transmitting in laboratory.

simultaneously and occasionally two bearings failed to intercept), or during the time interval between the termination of the radio bearings and the actual location of the animals.

To overcome problems concerning accuracy several biologists have homed in on radio-tagged animals, and recorded the position of their subjects only when visual contact has been made (Cumming 1971). Such a technique was not possible on the Reserve, since the range of visibility on the ground may be reduced to less than 10 m.

While the techniques employed in this study may be of limited accuracy, errors of ± 400 m are relatively small for such a large and potentially mobile ungulate. The results obtained from radio-tracking individual kudu will be discussed in Chapter 7.

Chapter 4
FIELD METHODS

4.1 Determination of sex

Greater kudu exhibit pronounced sexual dimorphism. Males possess spiral horns and a fringe of hair on the throat, and in adults there are conspicuous intersexual differences in body size and colouration. Adult males have a mass of approximately 300 kg and are almost 50% heavier than adult females, stand about 200 mm higher at the shoulder and typically have a greyish brown pelage while cows are a reddish brown colour (Dorst & Dandelot 1970; Ansell 1971; Jarman 1974; Walker 1975).

These differences permit accurate sex identification of subadult and adult kudu in the field. No attempt was made to sex animals under one year of age.

4.2 Age classification

4.2.1 Males

As antelope horns grow throughout life, relative ages can be obtained from horn shape and size (Simpson 1966; Spinage 1967; Kerr & Roth 1970; Roettcher & Hofmann 1970; Rowe-Rowe & Mentis 1972). All males seen on the Reserve were classified using this technique as outlined below.

Initially, in the absence of known age material, reference was made to Simpson's (1966) classification. This was found inadequate, however, since only two classes described animals older than 30 months.

As the study progressed it was established that kudu in the Fish River Valley area have a short restricted calving season (Chapter 5), thereby producing distinct yearly age calsses. Examination of horn growth of captive and collared kudu over several years permitted the allocation of absolute age to some of these classes.

Several kudu calves were caught, reared and housed in an enclosure on the Reserve to facilitate ongoing studies concerning age determination dietary preferences, growth and reproduction. One captive male, (Rudolf) has been photographed and measured periodically since its capture in 1976. Plate 4.1a-1 shows the horn development of this animal over the last four years.

PLATE 4.1 The horn development of a captive, known-age male kudu. ("Rudolf").

a) at 8 months

b) at 10 months

c) at 14 months

d) at 18 months

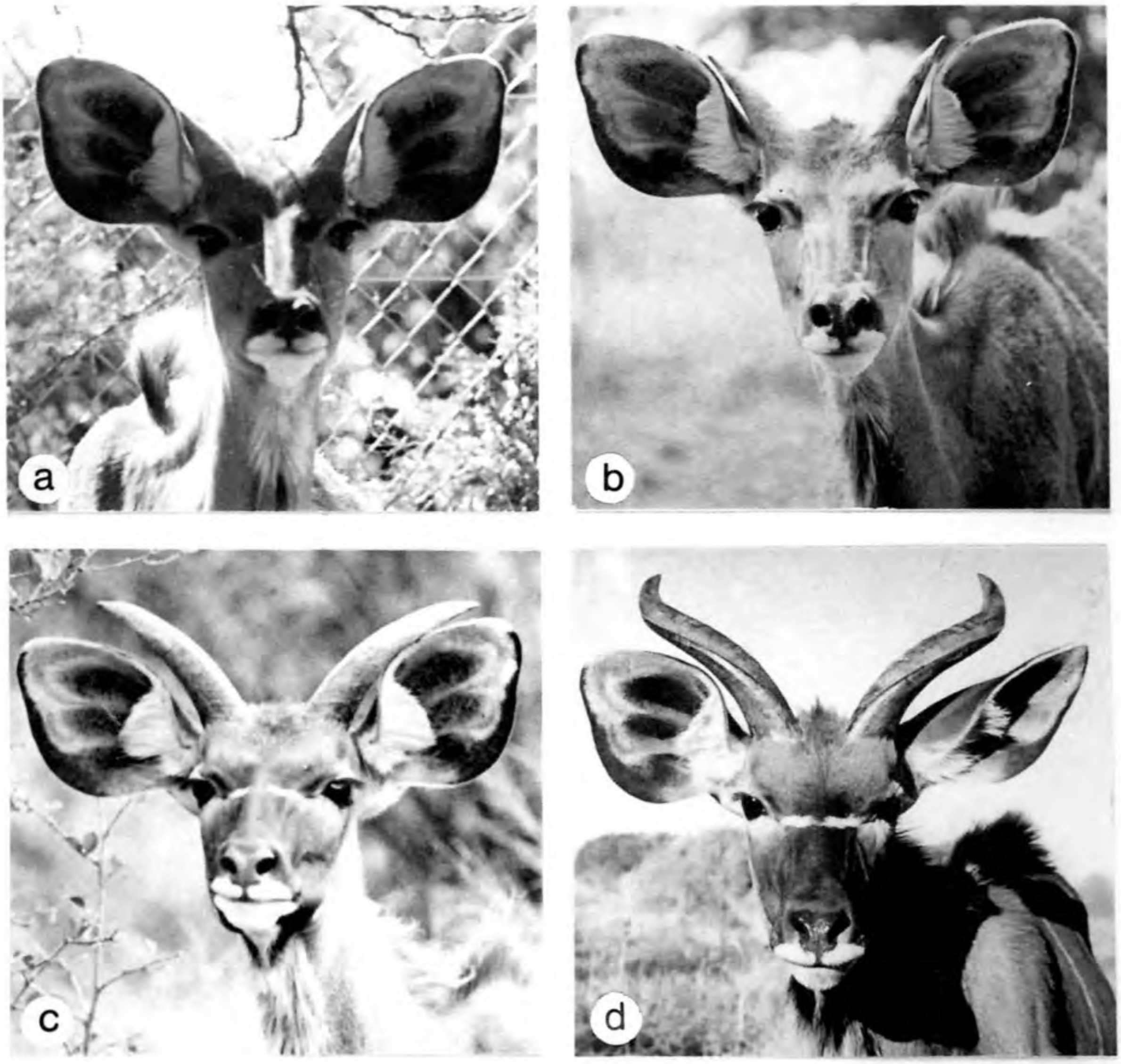

a
b
c
d

PLATE 4.1 continued.

e) at 21 months

f) at 23 months

g) at 31 months

h) at 33 months


e


f


g


h

PLATE 4.1 continued.

i) at 37 months

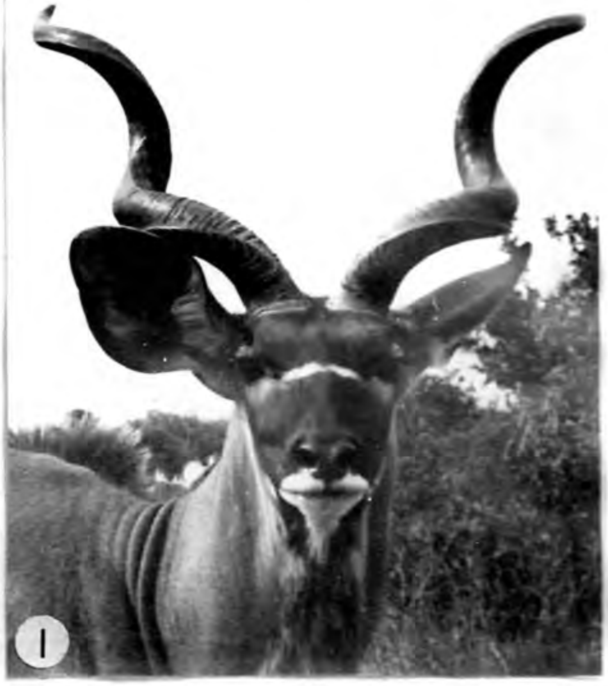
j) at 42 months

k & l) at 46 months


i


j


k


l

In addition, five marked bulls caught in 1978 were recaptured in April 1979. Capture intervals were 12 months (4 kudu) and 16 months (1 kudu). All animals were measured and photographed on both occasions (Plate 4.2a-l), allowing horn growth to be determined over a known period of time.

From the known-age bull data it was possible to allocate age classes to all recaptured males. Rudolf was 14 months old in Plate 4.1c. Male 92, caught in April 1978 (Plate 4.2a) belonged to the same class, and was allocated an arbitrary age of 16 months on the basis of horn length and known calving season. Recaptured exactly one year later, male 92 was then approximately 28 months old (Plate 4.2b). Male 106 was 28 months old at first capture (April 1978) (Plate 4.2c) and on recapture was approximately 40 months old (Plate 4.2d). Male 30 was 36 months old when captured in January 1978 (Plate 4.2e) and males 70 and 75, 40 months in April 1978 (Plate 4.2g and 4.2i respectively). All three males were approximately 52 months old on recapture (Plate 4.2f, h and i). Although four year old males were caught in 1978 (Plate 4.2i) none were recaptured in 1979. Male 95, at least five years old when first caught, was recaptured in 1979 (Plate 4.2k and l respectively).

Difficulties were experienced when trying to apply age classes to males beyond the age of five, because - a) horn growth is allometric; b) horn wear may exceed horn growth in five year plus animals, producing shorter horns (Simpson 1971, 1972a); and c) considerable individual variations in horn configuration may occur, especially in older males (Simpson 1971; Leuthold 1979).

Male 95 illustrates two of these points. Horn growth was only 2,5cm. The narrow horn configuration, an extreme example of variation, could not readily be placed into any one class (Plate 4.2k and l).

In the field males were not classified beyond five years old. Owen-Smith (pers. comm.) detected subtle differences that distinguished five and six year olds, but such differences are difficult to observe over long distances and were therefore ignored.

Although these age categories are based on a small sample size (n = 7), they are corroborated by - a) close examination and classification of 139 males shot over the last four hunting seasons

PLATE 4.2 Horn growth of free-ranging male kudu measured over known intervals of time.

a) Male 92 captured in April 1978. Approximately 16 months of age, horn length = 31 cm.

b) Male 92 recaptured in April 1979. Approximately 28 months old, horn length = 73 cm.

Horn growth over 12 months = 42 cm.

c) Male 106 captured in April 1978. Approximately 28 months of age, horn length = 77 cm.

d) Male 106 recaptured in April 1979. Approximately 40 months old, horn length = 97 cm.

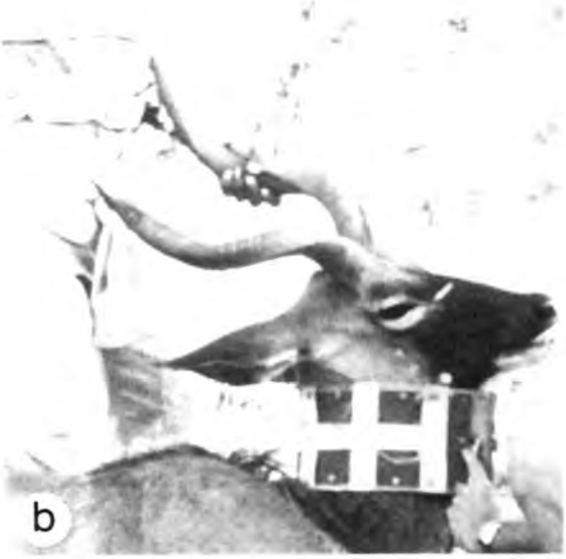
Horn growth over 12 months = 20 cm.

e) Male 30 captured in January 1978. Approximately 36 months of age, horn length = 94 cm.

f) Male 30, recaptured in April 1979. Approximately 52 months old, horn length = 111 cm.

Horn growth over 16 months = 17 cm.


a


b


c


d


e


f

PLATE 4.2 continued.

g) Male 70 captured in April 1978. Approximately 40 months of age, horn length = 101 cm.

h) Male 70 recaptured in April 1979. Approximately 52 months old, horn length = 113 cm.

Horn growth over 12 months = 12 cm.

Note that the radio transmitter has fallen from the harness on this male.

i) Male 75 captured in April 1978. Approximately 40 months of age, horn length = 106 cm.

j) Male 75 recaptured in April 1979. Approximately 52 months old, horn length = 117 cm.

Horn growth over 12 months = 11 cm.

k) Male 95, captured in April 1978. A physically and socially mature bull, at least 5 years of age, horn length = 125 cm.

Note the thickened neck on this animal.

l) Male 95 recaptured in April 1979. At least 6 years old, horn length = 127,5 cm.

Horn growth over 12 months = 2,5 cm.


g
S


h
S


i


j


k
J
J


l
J
J

(see below), b) records from numerous known-aged kudu currently being studied by Owen-Smith (pers. comm.; pers. obs.), and c) young known-aged animals from Rhodesia (Simpson 1966).

To facilitate documentation in the field, January was regarded as the birth month of all kudu on the Reserve (Chapter 5). Thus, in January all kudu progressed from one age class to the next, and were described as, for example, three year olds for the whole of the calendar year. This assessment was valid since all age classes were distinct for one to five year old males. It also obviated problems associated with possible seasonal variations in horn growth, as found in impala by Roettcher & Hofmann (1970).

Although horns may be 2-3 cm long in six to seven month old males, and 15 cm long before the animals become a year old, these horns are often obscured by the ears, (Plate 2.1a and b), and are very difficult to detect at a distance. Other secondary characteristics, such as development of the throat fringe and a darkening of the coat, only occur in the second year. As a result, males under one year of age were not sexed, and recorded as calves.

4.2.2 Females

No similar ageing criterion was available for females, so they were subjectively classified according to body size. Several disadvantages were apparent using this method, namely:

a) a gradation in size was required in any one group before ages could be allocated, i.e. calves, yearlings, subadults and adults.

b) sizes could only be assessed with any degree of accuracy for adjacent animals.

c) kudu were often obscured by closed vegetation.

d) the size of an animal could not be determined while it was lying down.

Growth is almost complete when a female reaches two years of age (pers. obs.) and no attempt was made to separate animals after this age. Only two classes were therefore recorded; one year old subadult females, and older females. (Animals under one year were not sexed.)

The consequences of using such a restricted classification are discussed in Chapter 6.

4.3 Culled material

Samples from 237 kudu shot on neighbouring farms were taken during the hunting season (June-August) of 1976-1979. Body measurements (after Ansell 1965) and lactation details were recorded whenever possible. The head, reproductive organs and rumen sample were collected from each numbered carcass.

Skulls were subsequently cleaned and eyes injected with 10% formalin for ongoing age determination studies. Testes and uteri (for assessment of fertility, puberty and calving season, etc.), were preserved in 10% formalin while rumen samples were stored in formol-acetic-alcohol.

Samples were not culled at random and were therefore not suitable for population dynamics studies.

4.4 Field observations

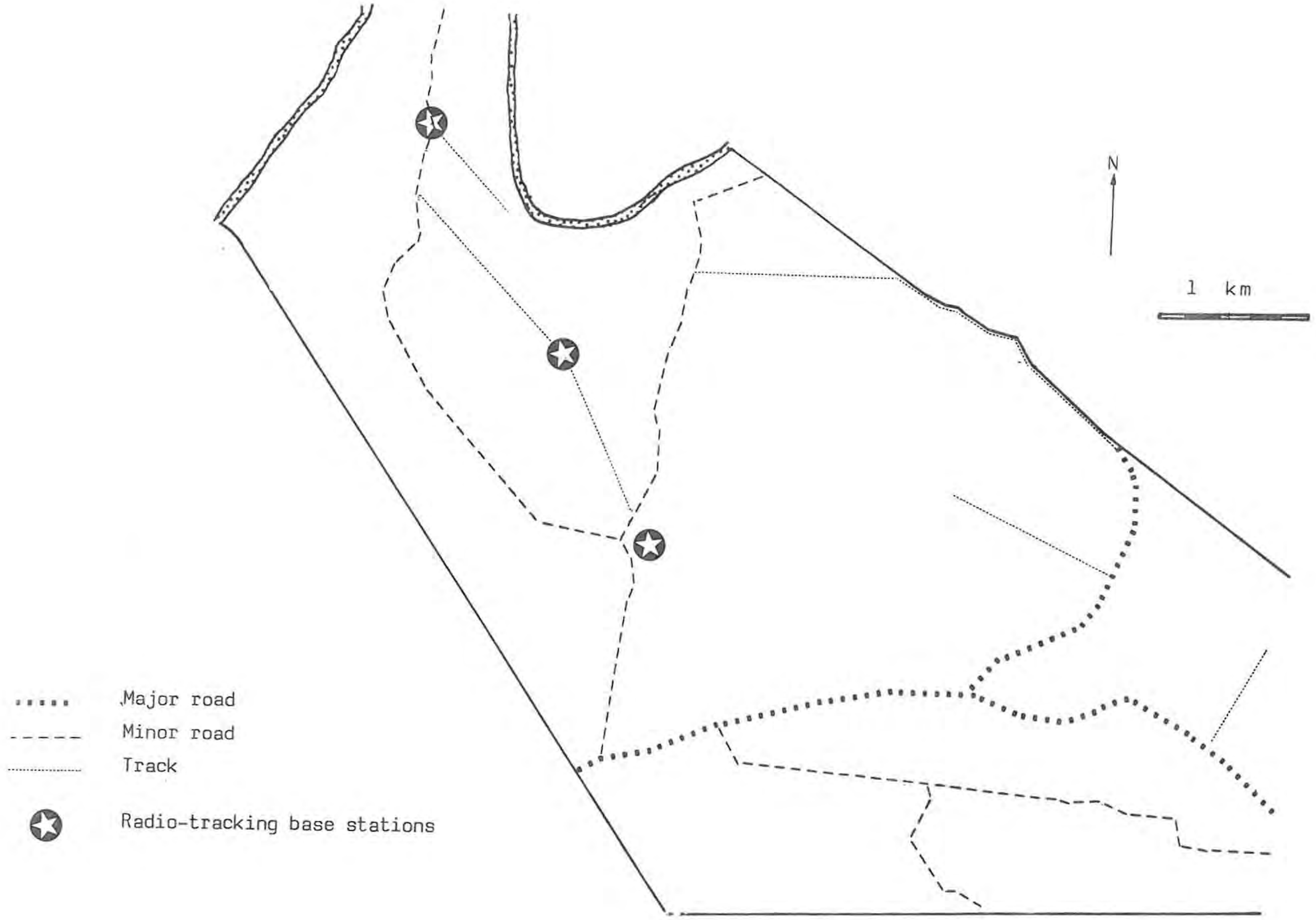
4.4.1 Ground sightings

Detailed field observations commenced in December 1977, and except for March and April 1978 were conducted monthly until November 1979. All observations were made or confirmed by the author, thereby ensuring that any errors in sex/age classification were constant.

The majority of sightings were made on foot, and selected vantage sites with a good range of visibility were visited frequently. Observation routes taken in a vehicle and on foot are shown in Fig. 4.1 and route direction was often altered to ensure that sites were visited at varying times of the day.

Observations were made to a distance of over 1 km with 7 x 50 mm binoculars and a mounted 60-power telescope. The locality, date, time of day, sex, age, activity and group size and composition (where possible) of each sighting were noted, and provided data on population structure, habitat preferences and group patterns. Sightings of collared kudu, recorded on individual maps (1:36 000) and data sheets, were used to determine kudu range sizes, group dynamics and population size (see below). Local distribution could not be determined by field observations from the ground since all areas were not covered with the same degree of regularity or intensity. A total of 4836 kudu were seen from the ground during 22 months of

FIG. 4.1 Observation routes most frequently used during the field study in the A.V.K.R.


N
1 km
Major road
Minor road
Track
Radio-tracking base stations

observation. Sightings of more than 200 kudu/5-6 days in a given month were made on fourteen occasions (64%); fewer animals were seen during the hot summer months (Fig. 4.2).

4.4.2 Aerial sightings

Sightings of kudu were also recorded during three aerial surveys. Two of these (in April 1978 and April 1979) were conducted from a Hughes 300 helicopter with one observer, while the other (in December 1978) was made in an Alouette II helicopter with three observers. A total of 625 kudu were seen during these three flights (Fig. 4.2), which are described in more detail below.

4.4.3 Resightings of marked kudu

Collared animals were seen on 937 occasions (16% of all observed kudu). Seventeen collared kudu (17%) were not seen subsequent to their release while a further three were only seen from the air. Resighting frequencies are given in Table 4.1 and will be discussed later. Original, personal sightings ensured that only positive identifications (confirmed with binoculars or the telescope) were recorded.

4.5 Population estimation

4.5.1 Aerial counts

Although several biologists have stressed the advantages of sampled aerial counts (e.g. Jolly 1969; Laws, Parker & Johnstone 1975; Caughley 1977), surveys were purposely flown over the entire western section of the Reserve. This was necessary because:

i) sample sizes would have been small (the area of the Reserve is 65 km^2) and kudu movements through disturbance may have influenced results

ii) sightings of any marked kudu present were required (see below).

For each flight the study area was divided into blocks with well defined boundaries such as roads, rivers and fences. Each block was surveyed before proceeding to the adjacent one, and block totals were later summed to give a total for the flight. Duplication was avoided by ignoring groups of identical composition within an area of approximately 25 ha.

FIG. 4.2 Total number of kudu seen each month between Dec 1977 and Nov 1979 (total number of kudu sighted = 5670).

* no data available

□ Ground census

░ Aerial census

▥ During darting operations

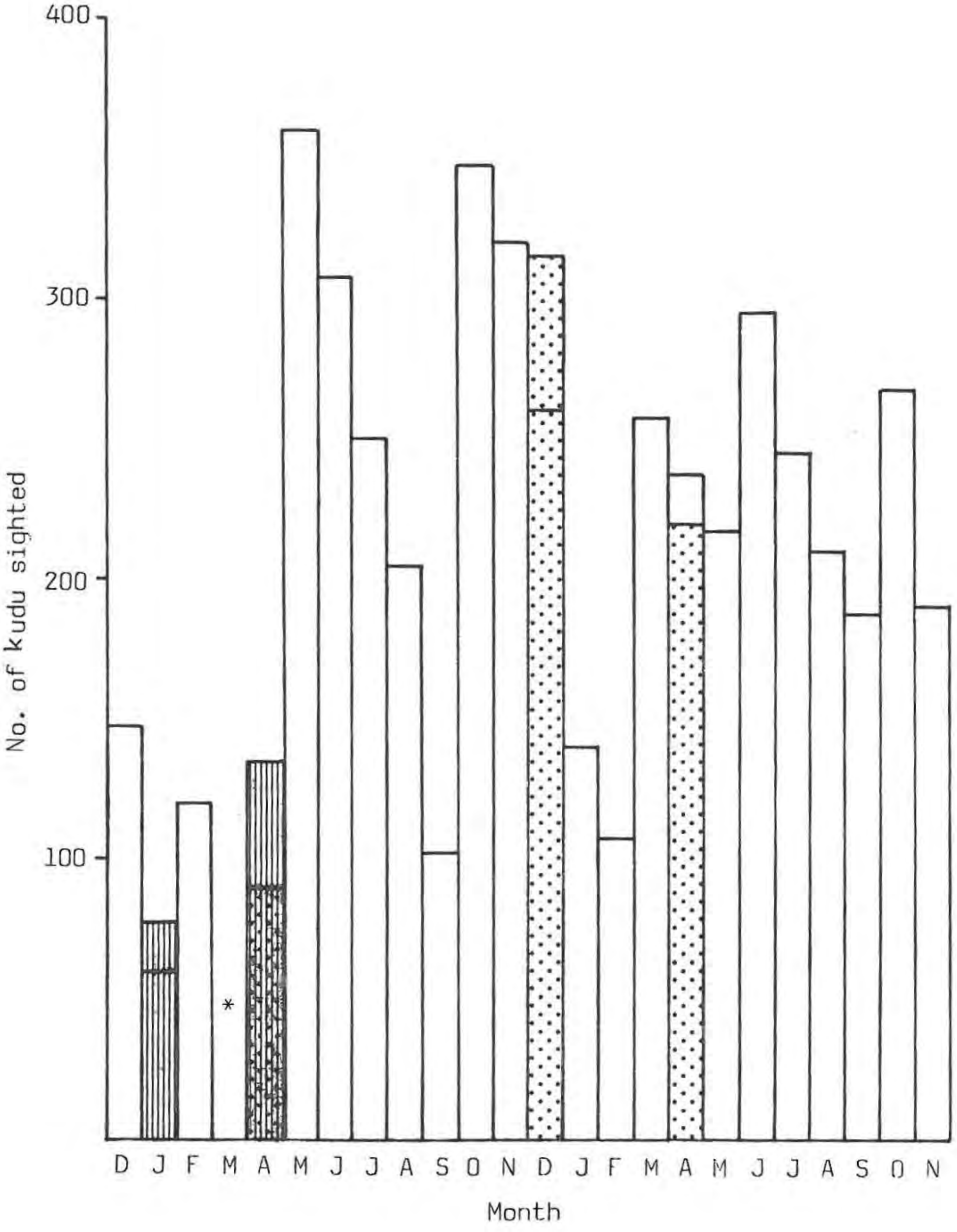

400
300
200
100
No. of kudu sighted
*
D J F M A M J J A S O N D J F M A M J J A S O N
Month

TABLE 4.1 Numbers of individually collared kudu with their resighting frequencies.

Sex	No. collared	% not sighted since marking	Resighted kudu 1-4 times (%)	>5 times (%)
♂♂	47	15	30	55
♀♀	53	19	19	62

Although all blocks were surveyed during the first census, these were not covered extensively due to lack of flying time. Ninety kudu were seen in 48 minutes. Greater coverage of the western section of the Reserve was made during the subsequent flights of 95 and 130 minutes, when totals of 221 and 314 kudu were seen. Thus most kudu were recorded during the longest census. Assuming this to be a total count, then the estimated kudu density was 12 kudu/km^2 for the western section of the Reserve. This should be regarded as a minimum value as aerial censuses are invariably underestimates (Caughley 1974; Laws et al. 1975). Melton (1978a) showed that kudu were undercounted (but not consistently so) from the air in Umfolozi, an area of wooded grassland and savanna.

Positions of all kudu herds seen during the flights were plotted on a map to illustrate relative distribution (Fig. 4.3). Kudu were more easily detected in certain areas (e.g. in the Buffalo Camp, which is non-succulent bush) than in densely structured habitats.

4.5.2 Petersen's estimate

The release of a known number of marked kudu allowed population estimates using the Petersen estimate, i.e.

$$N = \frac{Mn}{m}$$

(where M = total number of marked individuals, m = number of marked animals during a subsequent sampling of n animals, and N = population estimate, Caughley 1977). This method provides accurate results only when:-

a) the probability of seeing an individual is the same for all individuals in the population,

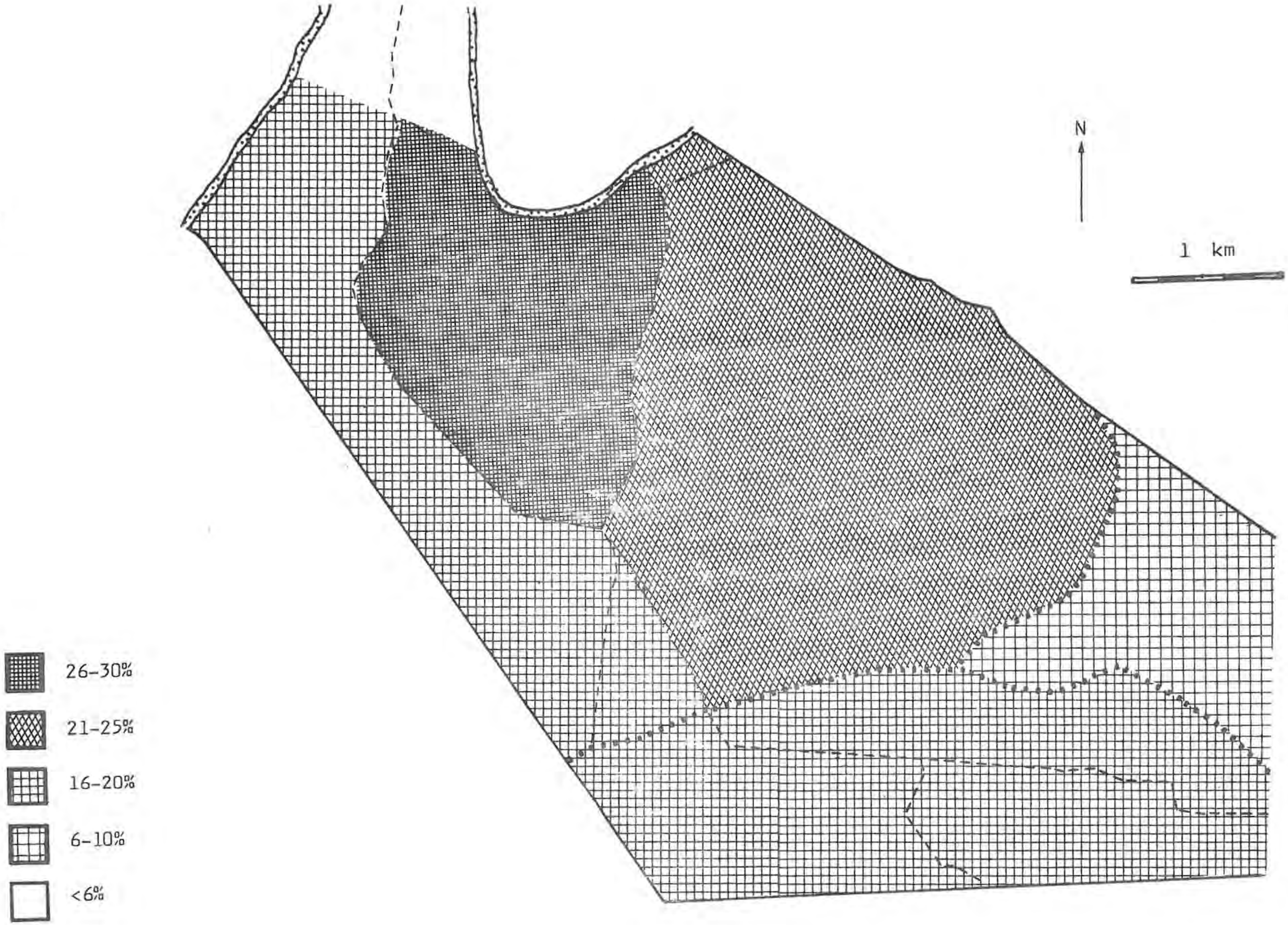
b) there is no population change through immigration and natality between sampling periods,

c) marked and unmarked individuals die or leave the area at the same rate and,

d) no marks are lost (Delany 1974; Caughley 1977).

These conditions were best fulfilled by surveying the Reserve from a helicopter immediately after marking had terminated. The

FIG. 4.3 The relative distribution of kudu sighted during three aerial censuses.


N
1 km
26–30%
21–25%
16–20%
6–10%
<6%

resulting population estimate was 445 kudu for the western section (17 kudu/km^2), which is approximately 41% of the total area. Assuming equal densities on the eastern portion, the total number of kudu on the Reserve was estimated at 1077.

Subsequent estimates, using the data from monthly ground sightings and the aerial surveys were made with two modifications.

i) Method I - Firstly, marked-animal mortalities were subtracted from the total number of animals marked (M) as soon as these were known. Time lags between date of death and subtraction from the total were inevitable when the date could not be determined with any degree of accuracy (e.g. carcass found in the field). These would provide overestimates. Population estimates using this technique are shown in Table 4.2.

ii) Method II - The second method was similar to Method I but marked animals that were never subsequently sighted were also excluded from the total. The estimates obtained from this technique were therefore lower (by 67-172 kudu) in the western section (Table 4.3).

Loss of marked animals through emigration or mortality could not be determined accurately. An approximate estimate of collar loss was computed as follows. Collared animals were regarded as present on the Reserve even if not seen for several months, provided that subseuqent sightings were confirmed. These "assumed" totals of kudu present were then expressed as percentages of the total number of marked kudu calculated from a) Method I and b) from Method II. Fig. 4.4 shows the rapid decline of "assumed" total collars from May 1979 to November 1979, and for this reason population estimates are only given for April 1978 to April 1979 (Tables 4.2 and 4.3).

All kudu numbers derived from the Petersen estimate (either Method) were higher than those obtained from a "total" count. This infers that the latter was an underestimate. However, widely fluctuating estimates were obtained using the Petersen estimate, and should be regarded, at best, as approximate estimates.

Potential sources of error - One characteristic of the Petersen estimate is that overestimates are obtained with time (Bailey 1951, 1952, cited in Caughley 1977). This is illustrated by comparing

TABLE 4.2 Kudu population estimates based on the Peterson Method. Known mortalities of collared individuals have been excluded from the total number of marked animals (M).

Month	Observed no. of marked kudu (m)	Observed no. of kudu (n)	Collared kudu alive (M)	Population estimate of Western section (N)	Extrapolated population estimate for whole Reserve
1978					
Apr Aerial census	19	90	94	445	1077
May	81	360	94	417	1009
Jun	72	307	94	401	970
Jul	43	249	94	544	1316
Aug	38	205	92	496	1200
Sep	23	102	92	408	987
Oct	43	347	91	734	1776
Nov	48	317	91	601	1454
Dec	33	261	91	719	1739
Aerial census	28	314	91	1020	2468
1979					
Jan	26	140	91	490	1186
Feb	17	107	91	573	1386
Mar	38	259	91	620	1500
Apr	30	239	91	724	1752
Aerial census	18	221	91	1117	2703
			Mean value = 1501 ± 519 (n = 15)		

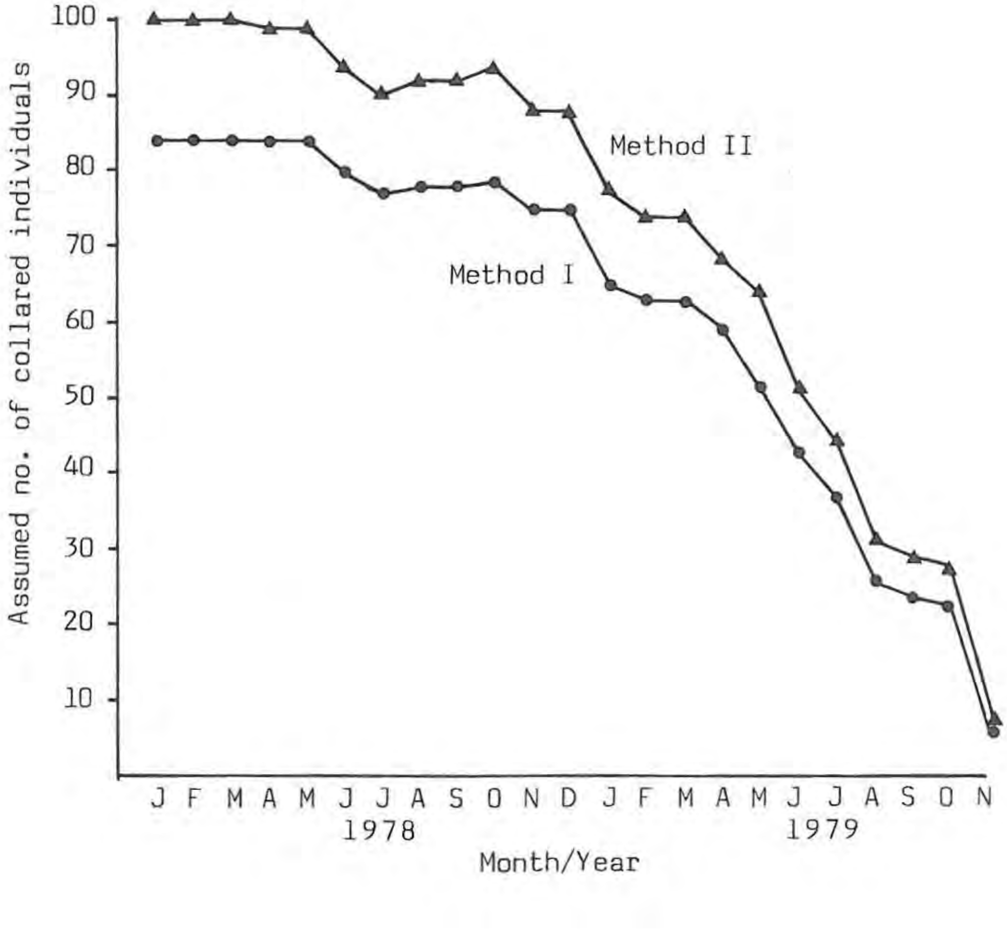
TABLE 4.3 Kudu population estimates based on the Peterson Method. Dead and unsighted collared kudu are excluded from the total of collared animals (M).

Month	Observed no. of marked kudu (m)	Observed no. of kudu (n)	Total no. of marked animals excluding dead and unsighted collared kudu (M)	Population estimate of Western section (N)	Extrapolated population estimate for whole Reserve
1978					
Apr Aerial census	19	90	80	378	915
May	81	360	80	355	859
Jun	72	307	80	341	825
Jul	43	249	80	463	1120
Aug	38	205	78	421	1019
Sep	23	102	78	346	837
Oct	43	347	77	621	1508
Nov	48	317	77	508	1229
Dec	33	261	77	609	1473
Aerial census	28	314	77	863	2088
1979					
Jan	26	140	77	415	1004
Feb	17	107	77	485	1173
Mar	38	259	77	525	1270
Apr	30	239	77	613	1483
Aerial census	18	221	77	945	2287

Mean value = 1272 ± 438

(n = 15)

FIG. 4.4 Changes in the "assumed" number of collared kudu in the A.V.K.R. with time (see text).


100
90
80
70
60
50
40
30
20
10
Assumed no. of collared individuals
Method II
Method I
J F M A M J J A S O N D J F M A M J J A S O N
1978
1979
Month/Year

estimates obtained from ground sightingsin September and October 1978. Any real increase in the population would have resulted from immigration, not natality, over this period (Chapter 5) yet it is highly unlikely that immigration could account for a 70% increase in estimated numbers. Estimates prior to October were much more constant (Tables 4.2 and 4.3).

Digressions from the conditions of the Peterson method would also produce inaccurate results. Under certain conditions, the probability of seeing a conspicuously marked kudu is greater than seeing an unmarked animal - therefore resulting in an underestimation. Conversely overestimations would be made if a greater proportion of marked animals were undetected. During darting in April 1979 several marked kudu attempted to avoid detection by entering extremely dense vegetation or by lying under bushes and small trees (pers. obs.). A similar report of "helicopter shy" marked animals has been published (Brooks, pers. comm. to Melton 1978b). The pronounced population estimation increases obtained during aerial censuses in December 1978 and April 1979 may have been influenced by such differences in behaviour. In addition, 27 marked individuals were seen one to three days before the December flight, but only eight of these (29,6%) were seen during the census, when 28 collars were observed. It is highly unlikely that the other nineteen kudu moved from the Reserve during this time (Chapter 7). Since this flight was the most extensive and involved three observers, it is improbable that these kudu were "missed" by chance, and again it is suggested that at least some marked kudu show avoidance behaviour to a helicopter.

Overestimations also result from births and immigration, and estimates from January 1979 (the peak calving time, Chapter 5), onwards will reflect this.

Although more sophisticated methods of population estimation exist, all rely on repeated marking and recapture exercises. For various reasons, the four marking programmes in this study could not be utilized in any of these refined techniques, and costs of capture prohibited any subsequent, relevant marking exercises.

The limitation of the counting techniques used in this study prevent assessment of population trend (Melton 1978b) and provide only approximate population estimates. Nevertheless, the initial results indicate that the Reserve contains approximately 1100 kudu, or 17 kudu/km^2. This density is considerably higher than any other published values (Table 4.4) and will be discussed in Chapter 9.

TABLE 4.4 Densities of kudu in southern Africa. (Figures in parentheses are local densities, those marked * were calculated by the author.)

Density (kudu/km^2)	Area	Source
0,1*	Willem Pretorius Reserve, S.A.	Bourquin (1973)
± 0,3*	Kruger National Park, S.A.	Pienaar (1963)
0,3*	Kruger National Park, S.A.	Smuts (1974b)
1,0 (2,0-3,0)	Kruger National Park, S.A.	Owen-Smith (1977)
0,6 (0,2-1,7)	Southern Lowveld, Rhodesia	Simpson & Cowie (1967)
(0,4-13,0)	Middle Zambezi Valley, Rhodesia	Jarman (1972)
0,9*	Umfolozi Game Reserve, S.A.	Mentis (1970)
1,5	Victoria Falls National Park, Rhodesia	Dasmann & Mossman (1962b)
2,0*	Addo Elephant National Park, S.A.	Hall-Martin (1978)
(3,9-6,2)	Wankie National Park, Rhodesia	Dasmann & Mossman (1962b)
5,7*	Kyle National Park, Rhodesia	Wilson (1970)
4,5 (14,0)	Chobe, Botswana	Owen-Smith (1977)
17,0	Initial estimate for this study	

Chapter 5
REPRODUCTION

5.1 Introduction

In seasonally reproducing species, cyclic changes in the level of social and spatial organisation are usually most complex and pronounced during the rut (Leuthold 1974, 1977). A knowledge of the timing and duration of this event is therefore of fundamental importance to any study of social organisation.

In addition to providing data concerning the seasonality of breeding, other relevant aspects of reproduction in the kudu were also examined during this study. Such information is essential to a sound understanding of the social and population biology, and the successful management, of this species.

5.2 Materials and methods

Reproductive organs from shot kudu were collected during the hunting seasons (June, July and August), of 1976 to 1979, and were supplemented by mortalities on the Reserve. All samples came from the Fish River Valley area.

Testes and epididymides were removed from the scrotum, the vas deferens was cut level with the caput epididymis, and each testis was weighed to the nearest 0,1 g. Kerr's (1965) smear technique was adopted for the detection of spermatozoa at a magnification of 400 x. Smears were usually prepared and examined within 24 hours of collection, when spermatozoa were still motile.

Each uterus was dissected in the laboratory, all foetuses weighed and where possible sexed. The ovaries of non-pregnant females were sectioned sagittally with a scalpel at approximately 2 mm intervals. Cut surfaces were examined macroscopically for corpora lutea or corpora nigra (Golley 1958) while each mean follicle diameter (the mean of two diameters at right angles, Laws et al. 1975) was recorded. Cows with follicle diameters larger than 5 mm were arbitrarily regarded as having attained puberty (the seasonal distribution of samples and high conception rates of older females prevented detailed examination of follicular development). Lactation details of most shot and all captured females were recorded. Ages of animals under three years were determined by tooth eruption and replacement criteria (Simpson 1966; pers. obs.) or where skulls were unavailable, from body measurements. Rutting and calving times were also recorded during field observations (more than 1000 hours, see Chapter 8).

Additional reproductive data were obtained from replies to a questionnaire sent to 64 zoological gardens.

5.3 Results

5.3.1 Age at attainment of puberty

5.3.1.1 Males

Twenty (95%) of the eighteen-month-old males examined showed spermatozoa in the testes and epididymides. These bulls had a mean paired testes mass of 64,9 g (±10,0 g), while the only prepubertal male of this age had a combined testes mass of 41,6 g. All males less than one year old (n=9) showed no evidence of spermatogenesis. Ninety-six percent of the 28 two year old males examined were producing spermatozoa.

5.3.1.2 Females

Thirteen samples of eighteen-month-old females were examined. Six (46%) were pregnant. Another two females had large corpora lutea (indicating that ovulation had occurred) and three other cows had mature Graafian follicles (larger than 5 mm in diameter). Only two (15%) of these cows were therefore prepubertal. Material from cows under one year of age was unavailable. Ninety-nine percent of all females (n=76) two or more years old were sexually mature.

Similar findings were obtained from records of captive male and female kudu (Tables 5.1 and 5.2).

5.3.2 Fertility

5.3.2.1 Males

Ninety-seven percent of all males older than eighteen months (n=90) were producing spermatozoa (92% were collected from June to August). The three exceptions were two $3\frac{1}{2}$ year old bulls (taken in February and August) with paired testes masses of 24,6 g and 62,6 g, and a 30 month old bull (shot in July) with a testes mass of 60,5 g.

TABLE 5.1 Age at puberty/sexual maturity of captive male kudu.

Age (months)	Source of information
11*	D. Thomson, Gladys Porter Zoo (pers. comm.)
ca 16	H. Klös, Berlin Zoo (pers. comm.)
ca 18	H. Heck, Catskill Game Farm (pers. comm.)
ca 18	A. Petric, Chicago Zoological Gardens (pers. comm.)
ca 18	M. Kaal, Tallinn Zoo (pers. comm.)
18	St. Louis Zoological Park (pers. comm.)
18*	R. Tremper, Roeding Park Zoo (pers. comm.)
ca 21*	P. Vogt, Krefelder Zoo (pers. comm.)
24	F. Kinsey, Denver Zoological Gardens (pers. comm.)
By 18	This study.

* - seen mating

TABLE 5.2 Age at puberty and first parturition of captive female kudu

Age at puberty (months)	Source of information
12	St. Louis Zoological Park (pers. comm.)
ca 16	H. Klos, Berlin Zoo (pers. comm.)
ca 18	H. Heck, Catskill Game Farm (pers. comm.)
ca 18	A. Petric, Chicago Zoological Gardens (pers. comm.)
18	F. Kinsey, Denver Zoological Gardens (pers. comm.)
18	N. Carnes, Los Angeles Zoo (pers. comm.)
18	Busch Gardens, Florida (pers. comm.)
18-24	L. Curtis, Oklahoma City Zoo (pers. comm.)
20	R. Darby, Detroit Zoo (pers. comm.)
By 18	This study

Age at first parturition (months)	Source of information
21	A. Wünschmann, Munich Zoo (pers. comm.)
21-23	J. Block, National Zoological Park Washington (pers. comm.)
22	D. Dekker, Amsterdam Zoo (pers. comm.)
24	L. Curtis, Oklahoma City Zoo (pers. comm.)
24	M. Reed, San Antonio Zoological Gardens (pers. comm.)
24	Grzimek (1962)
25	Carl Hagenback Zoo (pers. comm.)
26	P. Vogt, Krefelder Zoo (pers. comm.)
28	S. Matthews, London Zoo (pers. comm.)
24	This study

One other male, at least 5 years old, had testes of unequal size (77,8 g and 27,6 g). Spermatogenesis was only evident in the larger testis.

5.3.2.2 Females

Seventy of the 83 examined uteri contained a foetus, indicating a crude conception rate of 84 per 100 females. Details of all non-pregnant cows are given in Table 5.3. Two of these females Nos. 177 and 178) were captured and held in captivity, but both died within a month. Neither had follicles larger than 2 mm in diameter, yet both were at least 30 months old. All adult females (2 years +) shot during June, July and August (n=64) were pregnant, as were 46% of the yearlings collected at this time. Only 9% of 33 lactating females were not pregnant but all were examined early in the year.

5.3.3 Seasonality of conception and births

Foetal ages were determined using the Huggett and Widdas (1951) formula,

$$\sqrt[3]{W} = a(t - to)$$

where W is foetal mass, a is the specific foetal growth velocity, t is foetal age and to is a numerical estimate obtained from to = 0,2 x gestation period (for animals with a gestation length of 100-400 days).

As in other similar studies (Mitchell & Lincoln 1973; Skinner & Hall-Martin 1975; Smuts 1975; Anderson 1978) birth mass and a mean gestation period were used to calculate a . Few records of the mass of kudu neonates have been published (Wilson 1965, Vice & Olin 1969) while kudu gestation periods recorded in the literature show considerable variation (Table 5.4). Consequently, the mean birth mass of 15,257 kg and mean gestation period of 251 days used in this study were determined largely from replies to the zoo questionnaires (Tables 5.5 and 5.6). When entered into the Huggett and Widdas (1951) equation, these data yielded an a value of 0,0123.

Foetal age could then be determined since

$$t = \frac{\sqrt[3]{W} + ato}{a}$$

TABLE 5.3 Reproductive data of thirteen non-pregnant female kudu.

No.	Age	Lactating	Presence of corpus luteum	Follicle > 5 mm	Month collected	Remarks
212	17m	No	No	No	Jul	Immature
197	17m	No	No	No	Jun	Immature
204	17m	No	No	Yes	Jul	Pubertal
151	17m	No	No	Yes	Jul	Pubertal
191	17m	No	Yes	-	Jun	Mature
27	17m	No	Yes	-	Aug	Mature
KR 81	21m	No	No	Yes	Oct	Pubertal
KR177	30m	No	No	No	May	Mature?*
KR178	Adult (30m+)	Not recorded	No	No	May	Mature?*
78	Adult (30m+)	Not recorded	No	Yes	Mar	Mature
77	Adult (30m+)	Yes	-	-	Feb	Mature
173	Adult (30m+)	Yes	-	-	Apr	Mature
180	Adult (30m+)	Yes	-	-	Apr	Mature

* Captured and held in captivity prior to translocation, but died within three weeks.

TABLE 5.4 Gestation periods quoted for kudu.

Gestation period	Source of information		
210 days	Stevenson-Hamilton	1912	cited in Kenneth & Ritchie 1953
210 days	Wilhem	1933	
214 days	Jennison	1927	
212 days	Morris & Jarvis	1959	
214 days	Asdell	1964	
ca 7 months	Smithers	1966	
ca212 days	Walker	1975	
8 months	Wilson	1970	
271 days	Dittrich	1972	

TABLE 5.5 Mass at birth of a) captive and b) wild kudu.

Mass (Kg)	Source of information
a)	
ca 11,34	N. Carnes, Los Angeles Zoo (pers. comm.)
11,33	L. Curtis, Oklahoma City Zoo (pers. comm.)
15,87	L. Curtis, Oklahoma City Zoo (pers. comm.)
14,75	S. Matthews, London Zoo (pers. comm.)
14,97	St. Louis Zoological Park (pers. comm.)
13,61	M. Reed, San Antonio Zoological Gardens (pers. comm.)
14,06	M. Reed, San Antonion Zoological Gardens (pers. comm.)
15,87	M. Reed, San Antonio Zoological Gardens (pers. comm.)
ca 15,50	C. Schmidt, Zurich Zoo (pers. comm.)
17,46	J. Block, National Zoological Park, Washington (pers. comm.)
19,05	J. Block, National Zoological Park, Washington (pers. comm.)
ca 15,00	Vice & Olin (1969)
b)	
16,30	Wilson (1965)
14,75	This study
19,00	This study
Mean birth weight 15,257 ± 2,248 (n = 15)	

TABLE 5.6 Gestation periods of captive kudu.

Gestation period (days)	Source of information
217	H. Klös, Berlin Zoo (pers. comm.)
ca 220	N. Ramsey, Y-O Ranch, Texas (pers. comm.)
229	I. Schmidt, Rio Grande Zoological Park (pers. comm.)
231	Carl Hagenbeck Zoo (pers. comm.)
ca 232	St. Louis Zoological Park (pers. comm.)
ca 240	M. Reed, San Antionio Zoological Gardens (pers. comm.)
ca 248	L. Wehr, Milwaukee County Zoo (pers. comm.)
ca 248	T. Asai, Nagoya Higashiyama Zoo (pers. comm.)
ca 248	J. McMorris, San Francisco Zoological Gardens (pers. comm.)
ca 263	N. Carnes, Los Angeles Zoo (pers. comm.)
ca 270	C. Schmidt, Zurich Zoo (pers. comm.)
271	Dittrich (1972)
267	J. Block, National Zoological Park, Washington (pers. comm.)
278	J. Block, National Zoological Park, Washington (pers. comm.)
279	J. Block, National Zoological Park, Washington (pers. comm.)
285	J. Block, National Zoological Park, Washington (pers. comm.)

Mean 251 ± 22 (n = 16)

This age was subtracted from the date when the mother was killed to provide the conception date. The length of the gestation period was added to conception date, thereby producing the predicted birth date of the foetus. The results of these calculations revealed that 97% of all foetuses (n=62) would have been born between December and February, with a peak (52%) in January (Figs. 5.1 and 5.2). All five pregnant yearlings shot in 1976 would have given birth in the latter portion of the calving season, which was less pronounced than those in subsequent years. Predicted calving dates of non-lactating 3 year + females (mean = 13th January ± 14 days, n = 9) did not differ significantly from those of lactating adults (mean = 11th January ± 17 days, n = 22).

Birth dates were also obtained from zoo records (Jarvis & Morris 1961; Brand 1963; Dittrich 1970; and pers. comm. from directors of numerous zoological gardens). Animals kept in the southern hemisphere (Fig. 5.3a) showed a calving peak from January to March (56% of 43 births) while the calving peak of kudu maintained in the northern hemisphere (Fig. 5.3b) occurred during July to September (55% of 410 births). Both peaks were highly significant (χ^2 = 16,33, d.f. = 1, p<0,001 and χ^2 = 151,2, d.f. = 1, p<0,001 respectively).

5.3.4 Foetal sex ratio

Of the 51 foetuses sexed, 30 were males and 21 females (143 males : 100 females). This ratio does not significantly differ from parity. No incidence of twinning was recorded.

Kudu born in captivity (numerous zoo records) exhibited a sex ratio closer to unity (91 males : 100 females, n = 490). Twins were also extremely rare (0,1% of 568 births).

5.3.5 Lactation

The udders of 51 adult females shot during June, July and August (1976 to 1979) were examined, and 65% of these were lactating. During August thirteen (62%) of all adult cows were still producing milk. Sixty percent of all pregnant females (irrespective of age, and season, n = 70) were lactating.

The proportion of captured adult cows lactating in June 1977

FIG. 5.1 Parturition dates of kudu in the Fish River Valley area, determined from foetal age.

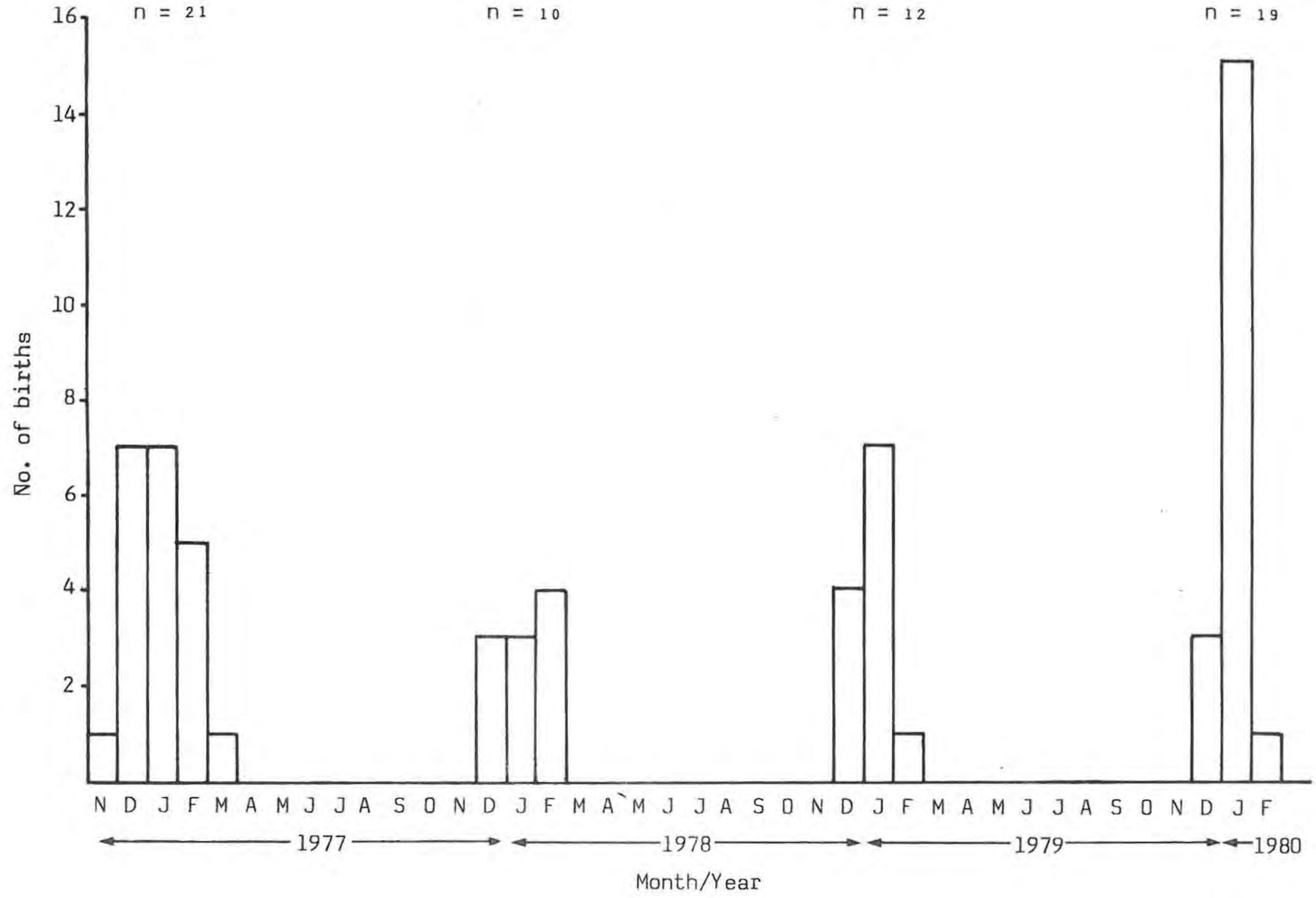

No. of births
16
14
12
10
8
6
4
2
n = 21
n = 10
n = 12
n = 19
N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1977
1978
1979
1980
Month/Year

FIG. 5.2 Accumulated parturition dates of kudu in the Fish River Valley area determined from foetal age. (Data from 1976-1979 summed, n = 62).

72a

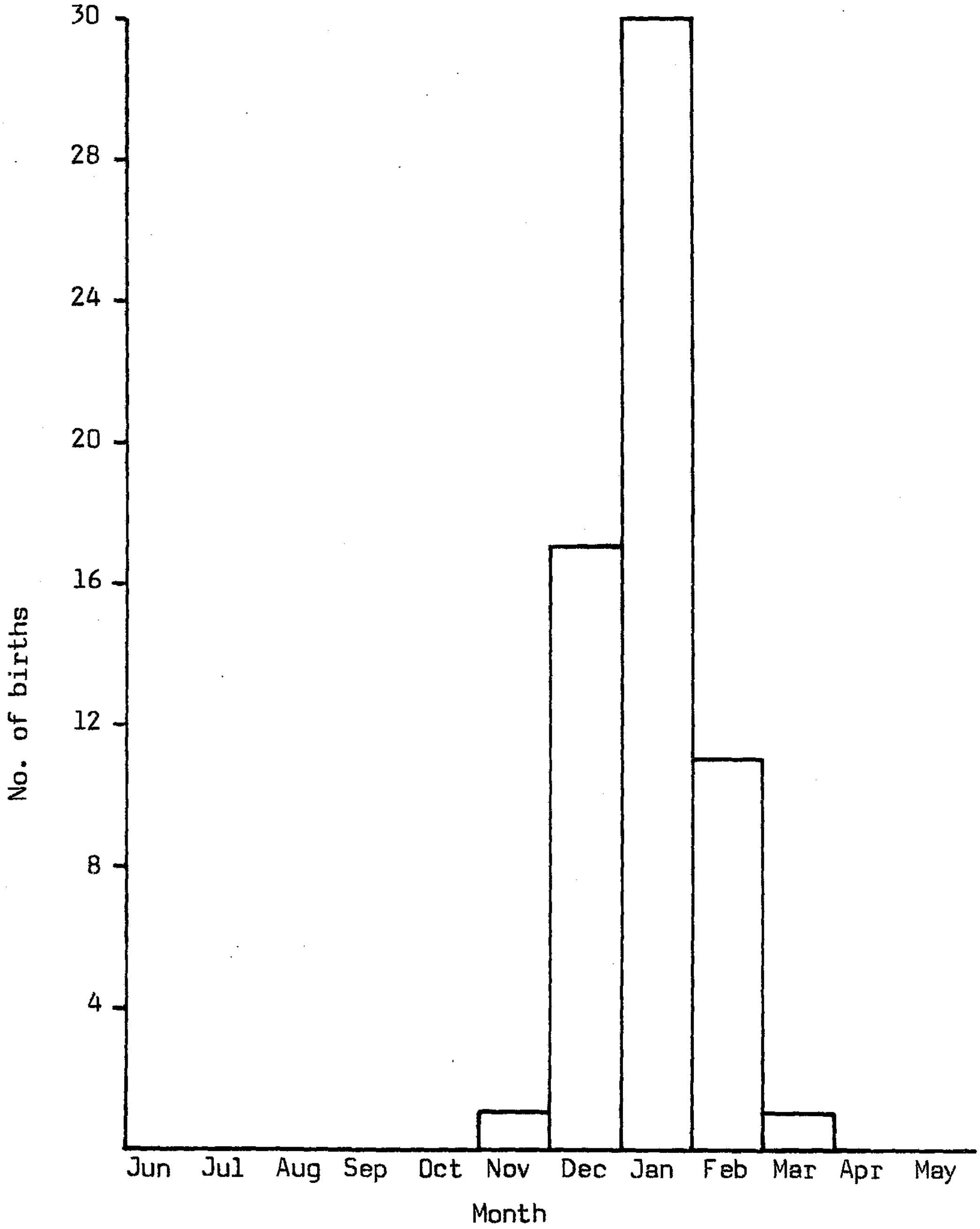
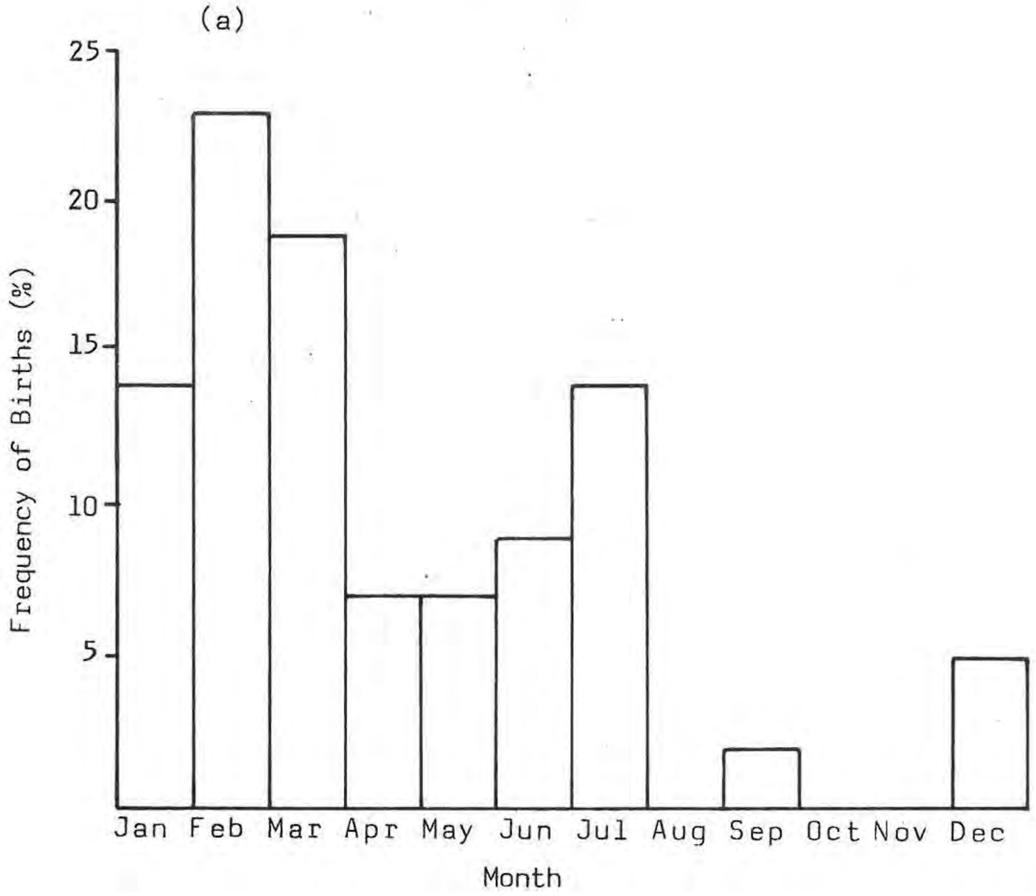
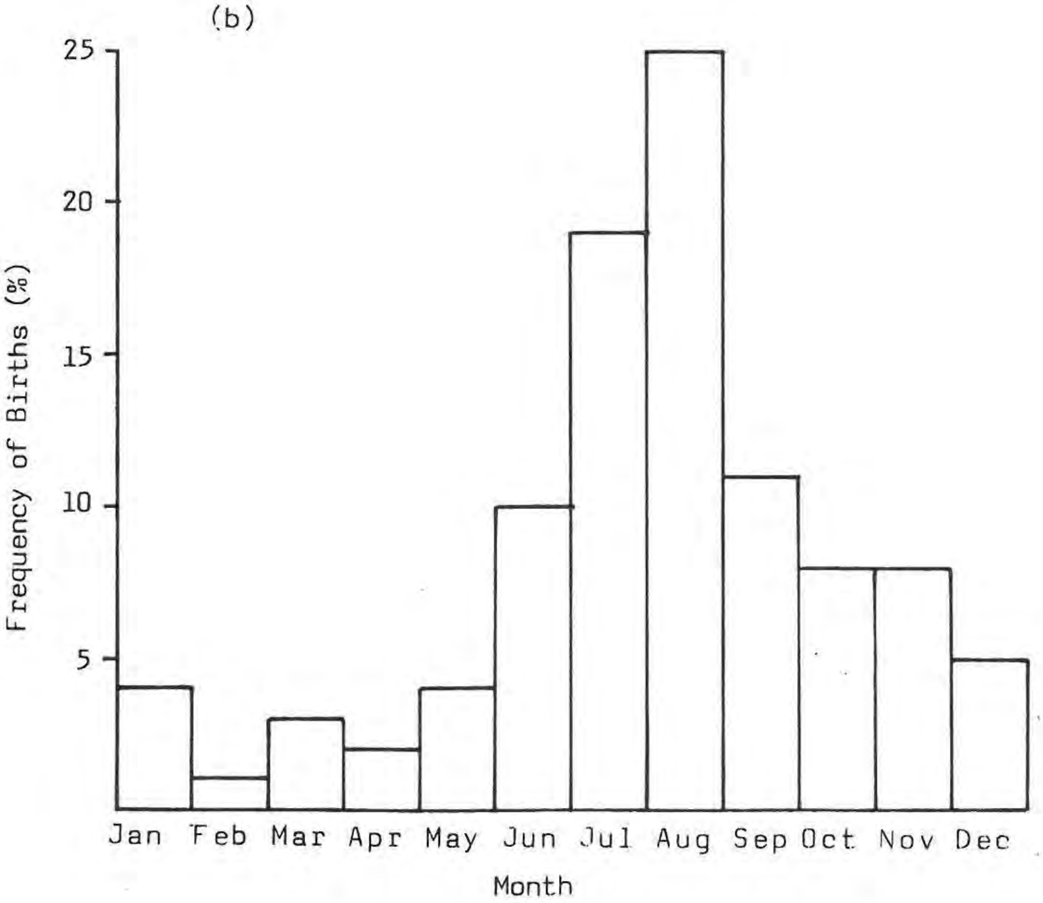

30
28
24
20
16
12
8
4
No. of births
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Month

FIG. 5.3 The percentage distribution of captive kudu births in:

a) the Southern Hemisphere (n = 43)

b) the Northern Hemisphere (n = 410).


(a)
25
20
15
10
5
Frequency of Births (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month


(b)
25
20
15
10
5
Frequency of Births (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

(n = 7), January 1978 (n = 16), April 1978(n = 20) and April 1979 (n = 15) were 71%, 56%, 40% and 80% respectively. Of the seven cows captured in April 1978 and recaptured in April 1979, 43% were lactating on both occasions.

Zoo data indicate that lactation in the kudu lasts for approximately six to eight months (range 3-12 months, numerous zoo records). In captivity at least, yearlings attempt to suckle after another calf has been born (Schmidt pers. comm.) and nursing is not exclusive; calves may suckle from females other than their mother (Dittrich 1968, Lent 1974, Block pers. comm.; Schmidt pers. comm.) but such females are probably related (Wilson 1975).

5.3.6 Calving intervals

Placental scars were not detected in primiparous or multiparous females. Consequently, calving intervals were determined from the proportion of pregnant females shot each year, and from the incidence of lactation in known individuals (see Discussion).

Data from zoos demonstrated that yearly calving intervals are common in captive kudu (46% of 112 intervals under one year, while thirteen replies to the questionnaire (28%) stated "approximately one year", numerous zoo records). Since artificial management practices may influence this length, the shortest mean calving intervals determined from four or more consecutive births are presented in Table 5.7. At the time of the questionnaire (1977) one kudu produced ten calves in ten years at San Antònio Zoo, and was expected to continue to reproduce for several more years (Reed, pers. comm.). The shortest single intervals reported from zoos are given in Table 5.8, while the only confirmed interval between birth and conception was 45 days (Block pers. comm.).

5.3.7 Field observations

Adult male:adult female associations were most frequently observed during April to July (Chapter 8). Copulation was never witnessed in the field, but adult bulls were seen attempting to mount cows on six occasions (April-June). Flehmen was also observed during April (n = 3), May (n = 4) and June (n = 1).

Eighty-two percent (n = 22) of all captured adult females

TABLE 5.7 Shortest mean calving intervals based on four or more consecutive births of nine captive kudu.

No. of consecutive births	Mean calving interval ± S.D. (days)	Source of information
6	346 ± 6	J. Volf, Prague Zoo (pers. comm.)
5	356 ± 23	D. Thomson, Gladys Porter Zoo (pers. comm.)
5	345 ± 16	P. Vogt, Krefelder Zoo (pers. comm.)
5	362 ± 34	M. Kurdi, Paris Zoo (pers. comm.)
4	346 ± 68	S. Matthews, London Zoo (pers. comm.)
4	367 ± 12	D. Dekker, Amsterdam Zoo (pers. comm.)
4	384 ± 6	D. Dekker, Amsterdam Zoo (pers. comm.)
4	367 ± 31	L. Wehr, Milwaukee County Zoo (pers. comm.)
4	372 ± 24	L. Wehr, Milwaukee County Zoo (pers. comm.)
4	373 ± 23	D. Thomson, Gladys Porter Zoo (pers. comm.)
Total 45	363 ± 26	
	ca 365	This study

TABLE 5.8 Calving intervals of less than 300 days.

Calving interval (days)	Source of information
259	R. Darby, Detroit Zoo (pers. comm.)
266	M. Reed, San Antonio Zoo (pers. comm.)
274	M. Kaal, Tallinn Zoo (pers. comm.)
291	A Petric, Chicago Zoo (pers. comm.)
295	R. Tremper, Roeding Park Zoo (pers. comm.)
297	S. Matthews, London Zoo (pers. comm.)
298	T. Asai, Nagoya Higashiyama Zoo (pers. comm.)

examined during April and June were in oestrus, while none of the sixteen adult females examined in January showed this condition.

The carcass of an adult female found in December had the hind limbs of a full term foetus protruding from the vulva; death was probably due to this breech presentation. Another female captured in January had a heavily swollen vulva and a copious discharge inferring that birth was fairly imminent. Four calves with portions of their umbilical cords still attached were caught by hand in January and the first week of February, while mothers and calves were only seen regularly from March onwards (Chapter 8).

5.4 Discussion

5.4.1 Reproduction in the male

Male kudu reach puberty by the age of eighteen months. Since spermatozoa were recorded from the epididymides of these bulls, the onset of puberty must be at a slightly earlier age. Wilson (1970) found spermatozoa in the testes and epididymides of a fourteen month old male kudu, while zoo records (Table 5.1) confirm that males of eighteen months of age are, physiologically, sexually mature. However, under natural conditions, pubertal males are probably prevented from mating by older, more dominant bulls (see Chapter 9) that have reached "sociological" or "sexual" maturity (Laws et al. 1975; Anderson 1978).

Although few samples were collected outside of the hunting season, spermatogenesis was evident throughout the year. Skinner & Huntley (1971) and Skinner (1971) showed that spermatogenic activity fluctuated according to season, peaked in June, but never ceased completely. Skinner & Huntley (1971) also found one infertile adult bull (5% of total examined), while this condition was recorded for 3% of all males during this study. Sexual senescence is not evident in male kudu.

5.4.2 Reproduction in the female

Kudu cows reach puberty by eighteen months of age, while nearly 50% of yearlings produce their first calf when two years old. Similar observations have been reported in Rhodesia (Dasmann & Mossman 1962a; Simpson 1968) and in zoological gardens (Table 5.2). Once females reach two years of age, specific conception rates of 100% are realized and maintained: fecundity is therefore not age-specific (all non-pregnant adults were either shot out of the breeding season or were kept in captivity (Table 5.3) where stress may have influenced their reproductive cycle, Perry 1971; Jenkins & Kruger 1973). Analysis of Simpson's (1968) data collected in Rhodesia indicates that females over 30 months of age have a specific birth rate of 80% and that fecundity decreases with age. There was no evidence of sexual senescence in this study.

The maximum conception rate of kudu in this area implies that cows produce calves at consecutive yearly intervals. That all lactating females shot during the breeding season were pregnant confirms this. Further evidence from the proportions of a) pregnant females lactating during June to August (62%) and b) collared females lactating in April 1978 and April 1979 (43%) appears less conclusive. However, these proportions reflect calf survival rather than parturition rates (the low incidence of lactating females caught in 1978 suggests that calf survival was particularly low during this time, since the conception rate of females shot during the previous rut was 100%). Responses to the questionnaire reveal that calving intervals of one year or less are also common in captive kudu (Tables 5.7 and 5.8).

The high conception rate also indicates that kudu are seasonally polyoestrous, especially if, like the congeneric nyala, they are receptive for a few hours only (Anderson 1978). No prolonged lactational anoestrus is evident, while calving intervals of less than 300 days (Table 5.8) and the recorded interval between parturition and conception of 45 days (Block pers. comm.) indicate that kudu have a post-partum oestrus.

The limited data from yearlings suggest that primiparous females come into oestrus slightly later than multiparous females. A similar trend has been reported in other kudu populations (Simpson 1968), in eland (Underwood 1975) and in red deer (Mitchell & Lincoln 1973). This may account for the high proportion (83%, n = 6) of yearling conceptions in 1976, since most (72%, n = 7) of the non-pregnant yearlings shot in subsequent years were taken at least one month earlier in the season. Alternatively, the high yearling conception rate in 1976 may reflect a possible increased plane of nutrition (as found in other ungulate species; Sadlier 1969a, 1969b;

Mitchell 1973; Mitchell & Brown 1973; Mitchell, McCowan & Nicholson 1976) resulting from the higher rainfall during that year.

5.4.3 Foetal sex ratio

The absence of twin foetuses in this study, and the very low incidence of twins from captive animals demonstrates that twinning is extremely rare in kudu. The foetal sex ratio in this area (143 males : 100 females, n = 51) is similar to the published ratios of 142 males : 100 females (n = 34) and 150 males : 100 females (n = 20), (Simpson 1968). The preponderence of males in each of these ratios is not statistically significant. Sex ratios will be discussed further in Chapters 6 and 9.

5.4.4 Seasonality of reproduction

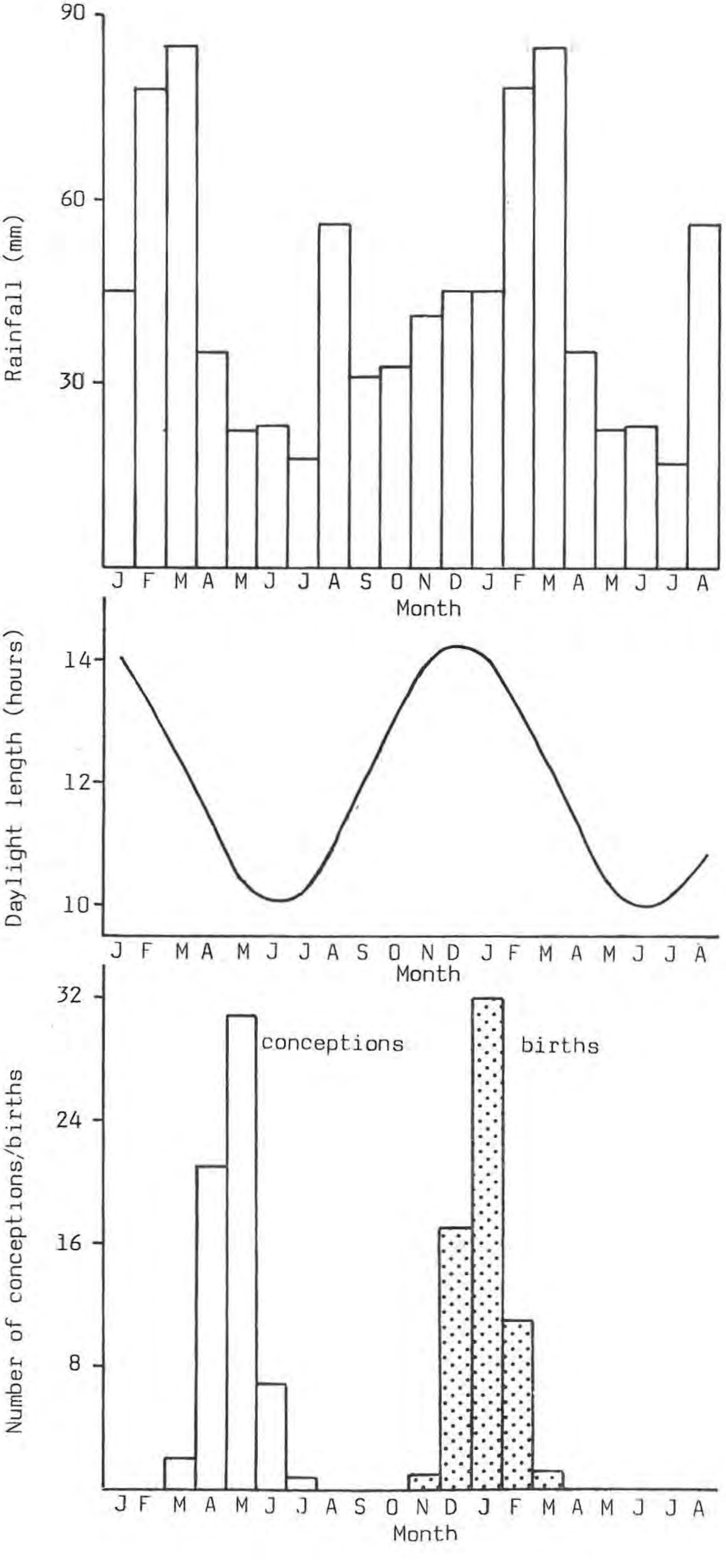
Conception and predicted parturition dates clearly show that breeding in the kudu is strictly seasonal. Although earlier accounts suggested that kudu breed throughout the year (Ansell 1960a, 1960b; Asdell 1964) more recent reports are in general agreement that calving occurs during January to April (Brynard & Pienaar 1960; Dasmann & Mossman 1962a; Pienaar 1963; Wilson 1965; Simpson 1966, 1968; Child 1968b, in Mentis 1972; Fairall 1968; Underwood 1978; Owen-Smith pers. comm.). However, most of these latter studies indicate that calving commences slightly later, and continues for a longer period than in the Fish River Valley area. Moreover, the majority of these reports were based on calf sightings (not actual births): none have employed the Huggett and Widdas (1951) formula to determine foetal age. The two methods therefore merit further attention. The accuracy of the latter technique clearly depends on the initial values of mass and age used to determine the specific foetal growth velocity, $\underline{a}$. Earliest reports of gestation periods cited durations of 210 to 220 days (Table 5.4) but more recent records indicate that the period may be at least one month longer (Table 5.6). Since gestation periods are rarely influenced by environmental conditions (Sadlier 1969a), such variation is probably due to errors in estimation. Durations of 210 to 220 days are similar to those of nyala and lesser kudu (Dittrich 1972; Anderson 1978), both of which are considerably smaller than the greater kudu. As the length of gestation is closely correlated with the mass of the adult (Sadlier 1969a, 1972a, 1973) this further indicates that a longer period is more probable. Parturition intervals of 259 and 266 days (Table 5.8) infer that gestation is unlikely to be much longer than the 251 days used in this study, while entering this value in to the Huggett and Widdas (1951) equation yields an a value similar to those determined for other Tragelaphines (Anderson 1978).

Field observations further demonstrate the accuracy of this technique. Adult male kudu were most frequently seen associating with females during May and June (Chapter 8). With a gestation period of approximately 250 days, most births would therefore be expected in January and February. Foetal data, captured calves, and the proportion of females lactating in January (56%) confirm this.

Calves were not seen in the field until February and March, when they ceased "lying-out" (Gosling 1969) and joined female groups (Chapter 8). It is suggested that in most published accounts concerning the calving season of kudu, authors have failed to take this concealment behaviour into consideration. In such cases, calving dates should be advanced by two months, since this is the usual duration of concealment (Owen-Smith pers. comm,; pers. obs.). These advanced calving peaks and seasons would then show much closer agreement with those determined from this study.

Seasonal breeding in mammals has evolved to ensure that conditions are optimal for the survival of both mother and young, and such conditions are usually referred to as the ultimate cause of the breeding season being at that time (Sadlier 1969a). The most frequently cited ultimate factors influencing ungulate reproduction are rainfall and nutrition (Spinage 1973), although the effects of these variables are usually difficult to separate (Sadlier 1969a). The distributions of kudu births and annual rainfall in the Fish River Valley area (Fig. 5.4) show that most calves are born just prior to the months of maximum and most predictable rainfall in February and March. Nursing, which lasts for at least six months, and when the energetic demands on the mother are greatest (Sadlier 1972a, 1972b; Moen 1973) therefore occurs during the time when plant growth

FIG. 5.4 The distribution of kudu conceptions and births in the Fish River Valley area in relation to rainfall and photoperiod.


90
60
30
Rainfall (mm)
J F M A M J J A S O N D J F M A M J J A
Month
Daylight length (hours)
14
12
10
J F M A M J J A S O N D J F M A M J J A
Month
32
24
16
8
Number of conceptions/births
conceptions
births
J F M A M J J A S O N D J F M A M J J A
Month

and thus the level of nutrition is increased.

Photoperiod is often the proximate factor that initiates seasonal breeding in mammals (Sadlier 1969a; Spinage 1973). Ninety-eight percent of all kudu conceptions occurred during days with decreasing and least photoperiod, suggesting that, like cervids, (Sadlier 1972b) kudu are "short day" breeders. Subtracting the gestation period from zoo births (Fig. 5.3) confirms this (56% of southern hemisphere conceptions from May to July, 55% of northern hemisphere conceptions from November to January). Since peaks in conceptions are separated by exactly six months, the seasonality is due to photoperiod. Fletcher (1974) found that a similar interval separated the breeding times of red deer maintained on either side of the equator.

The significance of seasonal breeding in kudu will be discussed further in Chapter 9.

Chapter 6
POPULATION STRUCTURE

6.1 Introduction

A meaningful examination of the social organisation of the kudu on the A.V.K.R. requires consideration of the population structure. Knowledge of certain population parameters are also essential for the successful management of this species. The population was therefore monitored for two years.

The results, together with pertinent details from studies elsewhere, are discussed below and considered further in Chapters 8 and 9.

6.2 Methods

Whenever possible, kudu were sexed and assigned to one of the following age classes:-

a) calves - all animals under one year of age
b) subadults - one to two year old animals (yearlings)
c) adults - animals two years of age or older.

Adult males were further classified according to horn size and shape (Chapter 4). While kudu bulls are not sociologically mature until at least five years old, the above classification was utilized to permit general comparisons between males and females; the latter cannot be aged accurately in the field once adult status has been reached.

Field observations were conducted monthly from December 1977 to November 1979, except for March and April 1978. Aerial surveys were flown in April and December 1978 and April 1979. Details of all kudu seen were recorded during the darting programmes of January and April 1978. Hence, population structure data were absent only for March 1978.

6.3 Results

Eighty-five percent of all sightings were conducted from the ground, and the population structure derived from these is shown in Table 6.1. All records obtained from aerial flights are presented in Table 6.2, while the population structures obtained from two aerial

TABLE 6.1 The population structure of kudu on the Andries Vosloo Kudu Reserve based on ground sightings recorded from December 1977 to November 1979.

Year	Ad ♂♂	Sub ♂♂	Ad ♀♀	Sub ♀♀	Unsexed Yearling	Calves	Total no. of kudu
1977/ 1978	22,8%	8,0%	62,9%	2,5%	0,5%	3,2%	2475
1979	22,4%	4,6%	59,4%	2,4%	0,0%	11,2%	2361
1977-1979	22,6%	6,3%	61,2%	2,5%	0,3%	7,1%	4836

TABLE 6.2 The population structure of kudu on the Andries Vosloo Kudu Reserve based on sightings from five aerial counts conducted between January 1978 and April 1979.

Year	Ad ♂♂	Sub ♂♂	Ad ♀♀	Sub ♀♀	Unsexed Yearling	Calves	Total no. of kudu
1978-1979	20,1%	6,2%	63,9%		2,9%	6,8%	834

TABLE 6.3 The population structure of kudu on the Andries Vosloo Kudu Reserve determined from two aerial censuses in April 1978 and April 1979.

<table>
<tr><th>Year</th><th>Ad ♂♂</th><th>Sub ♂♂</th><th>Ad ♀♀</th><th>Sub ♀♀</th><th>Unsexed Yearling</th><th>Calves</th><th>Total no. of kudu</th></tr>
<tr><td>April 1978</td><td>17%</td><td>12%</td><td colspan="2">67%</td><td>0%</td><td>4%</td><td>90</td></tr>
<tr><td>April 1979</td><td>15%</td><td>1%</td><td colspan="2">55%</td><td>10%</td><td>19%</td><td>221</td></tr>
</table>

TABLE 6.4 The population structure of kudu on the Andries Vosloo Kudu Reserve based on ground and aerial sightings recorded from December 1977 to November 1979.

<table>
<tr><th>Year</th><th>Ad ♂♂</th><th>Sub ♂♂</th><th>Ad ♀♀</th><th>Sub ♀♀</th><th>Unsexed Yearling</th><th>Calves</th><th>Total no. of kudu</th></tr>
<tr><td>1977/ 1978</td><td>22,7%</td><td>7,9%</td><td colspan="2">65,8%</td><td>0,5%</td><td>3,1%</td><td>3088</td></tr>
<tr><td>1979</td><td>21,7%</td><td>4,3%</td><td>58,9%</td><td>2,2%</td><td>0,9%</td><td>11,9%</td><td>2582</td></tr>
<tr><td>1977-1979</td><td>22,2%</td><td>6,3%</td><td colspan="2">63,7%</td><td>0,7%</td><td>7,1%</td><td>5670</td></tr>
</table>

TABLE 6.5 Subadult and adult kudu sex ratios in the Andries Vosloo Kudu Reserve between 1978 and 1979, calculated to a base of 100 females.

	Number sexed		Ratio	Chi-square value	p value
	♂♂	♀♀	♂♂:100♀♀		
1977					
Dec	51	88	58	9,85	<0,01
1978					
Jan	20	38	52,6	5,58	<0,05
Feb	39	78	50	13,0	<0,001
Apr	26	60	43,3	24,6	<0,001
May	109	240	45,4	49,2	<0,001
Jun	91	208	43,8	45,7	<0,001
Jul	74	166	44,6	35,3	<0,001
Aug	57	137	41,6	32,9	<0,001
Sep	33	66	50	11,0	<0,001
Oct	116	213	54	28,6	<0,001
Nov	90	213	42,3	49,9	<0,001
Dec	82	174	47,1	33,1	<0,001
1979					
Jan	60	80	75	2,85	>0,05
Feb	43	63	68,3	3,77	>0,05
Mar	68	174	39,1	46,4	<0,001
Apr	63	141	37,6	29,8	<0,001
May	57	129	44,2	27,8	<0,001
Jun	66	191	34,6	60,8	<0,001
Jul	56	162	34,6	51,5	<0,001
Aug	46	122	38	34,4	<0,001
Sep	46	116	39,7	30,2	<0,001
Oct	76	162	46,9	31,1	<0,001
Nov	56	118	47,4	16,2	<0,001
Sub total	1425	3139	45,3	644	<0,001
other aerial censuses	194	473	41,0	117	<0,001
TOTAL	1619	3612	44,8	759	<0,001

TABLE 6.6 Comparative sex ratios of adult and subadult kudu in southern Africa, calculated to a base of 100 females.

Number sexed ♂♂	♀♀	Ratio ♂♂:100♀♀	Chi-square value	p value	Source
119	291	41	72,2	<0,001	Dasmann & Mossman 1962b
86	72	119*	1,24	>0,05	Wilson 1965
174	415	42	98,6	<0,001	Wilson 1965
57	75	76*	2,45	>0,05	) Child 1968a in
35	84	42	20,2	<0,001	) Mentis 1972
109	180	61*	17,4	<0,001	Simpson 1968
119	186	64*	14,7	<0,001	Mentis 1970
60	129	47	25,2	<0,001	Wilson 1970
20	80	25	36,0	<0,001	Jarman 1972
46	84	55	11,1	<0.001	Underwood 1978
Total 825	1596	52	245	<0,001	
Total minus shot samples 454	1083	42	257	<0,001	
1619	3612	44,8	759	<0,001	This study

* Shot samples

census exactly one year apart are compared in Table 6.3. Adult and subadult cows could not be readily distinguished from the air, and were simply recorded as females.

Table 6.4 shows the population structure derived from all recorded sightings between December 1977 and November 1979. These values must be regarded as averages since an unknown number of kudu were seen repeatedly.

Sighting frequencies of the population sex and age classes are shown in Figs. 6.1-6.4. These are from regular ground observations except for the aerial census in April 1978 which was included for the continuity of data.

6.3.1 Population sex ratio

The population sex ratios recorded each month are shown in Table 6.5. All the ratios except for January and February 1979 deviate significantly from parity. The ratio obtained from all ground and aerial sightings is 45 males : 100 females (n = 5231).

Other published ratios, analysed in an identical manner, are shown in Table 6.6 for comparison. Most of these ratios differ significantly from the expected 1:1 ratio; those that do not are derived from shot animals or small samples. Removing all ratios from culled kudu (which may not have been shot at random) the overall ratio of 42 males : 100 females is in close agreement with that obtained during this study.

6.3.2 Adult males

Adult males constituted 22% of the population over the two year study period. Numbers fluctuated from 16,5% (February 1978) to 35,5% (February 1979) of the population (Fig. 6.1). Twenty-one percent of the 1139 adult males seen and classified in 1978 and 1979 were two year olds, 30% were three year olds, 24% were four year olds and 25% were males of five years or older.

6.3.3 Adult females

Adult females comprised 61% of the population, and showed less monthly fluctuation than males (from 51% in December 1977 to 67% in April 1978, Fig. 6.2). Fewer cows were seen during summer months

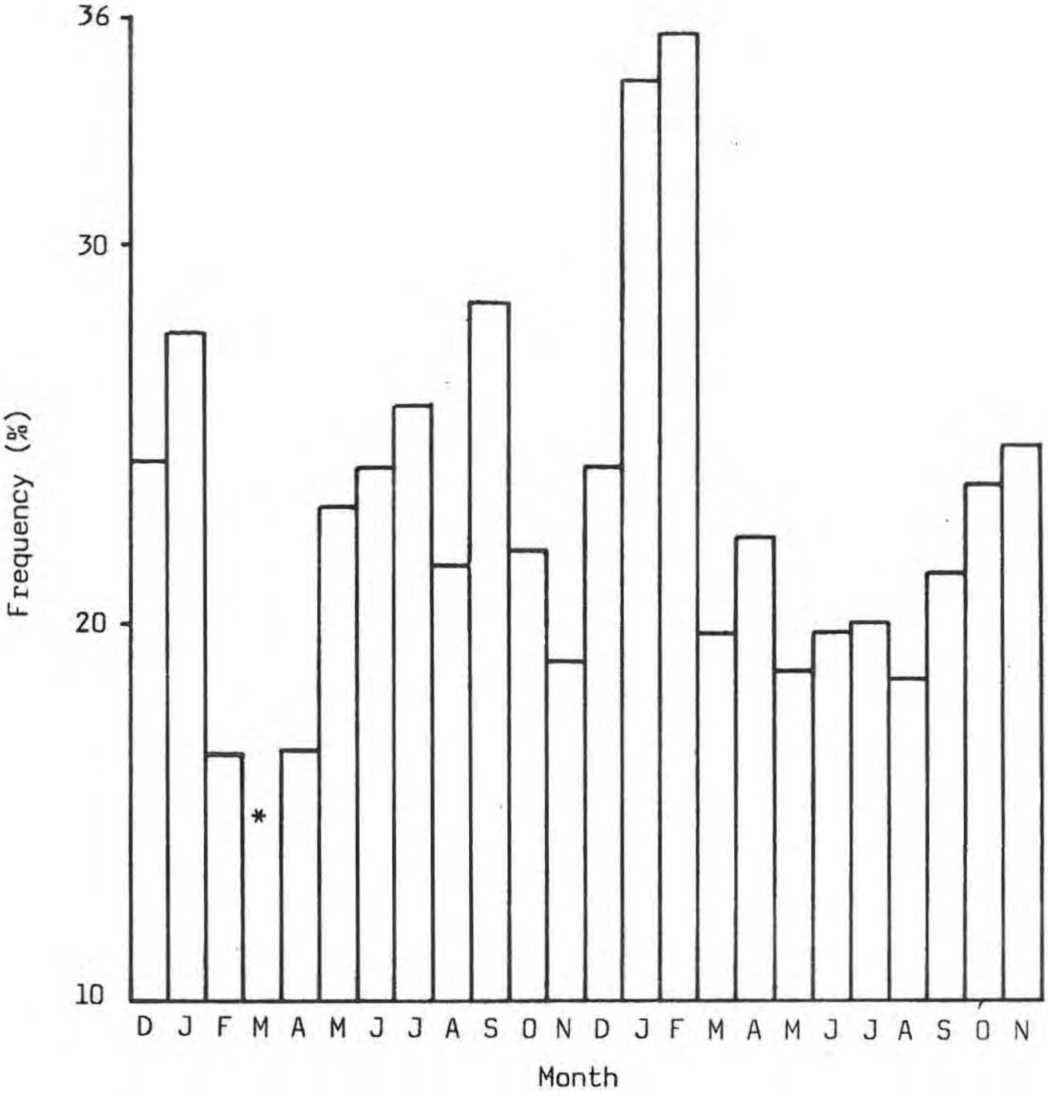
FIG. 6.1 Ground sightings of adult male kudu on the A.V.K.R. between Dec 1977 and Nov 1979 expressed as a % of all kudu sightings per month.

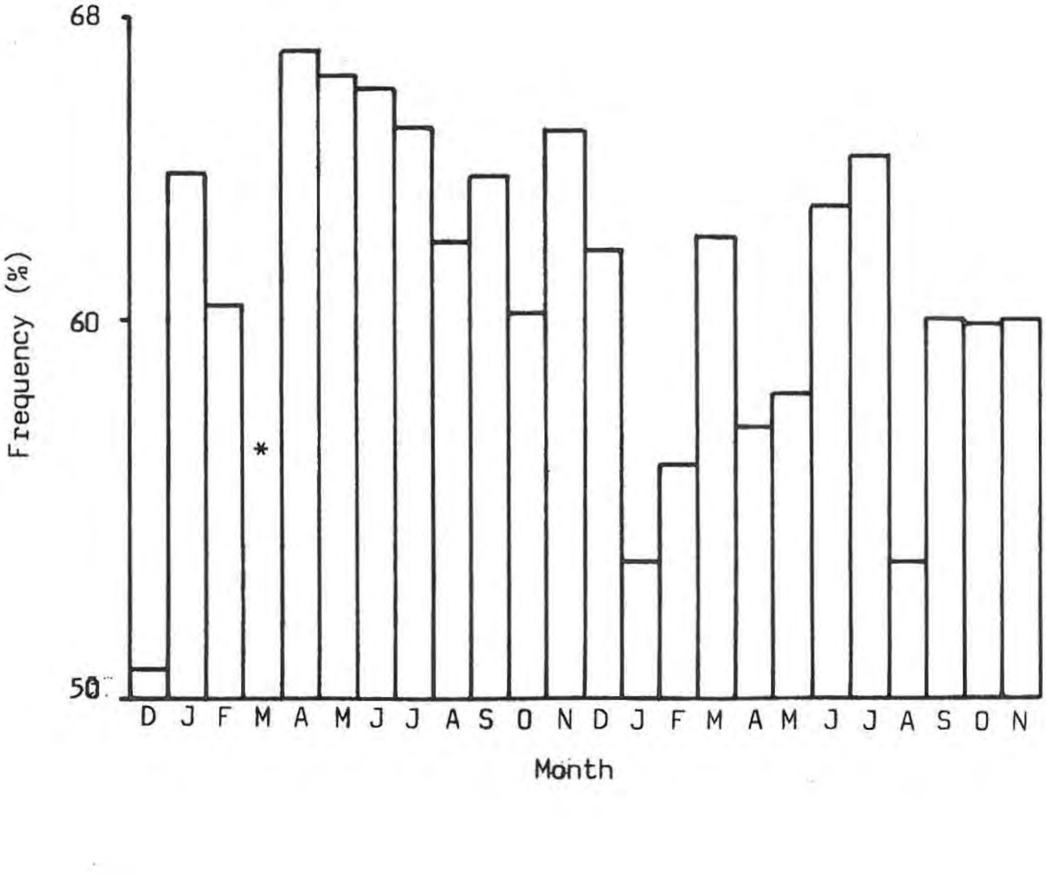
* no data available.

FIG. 6.2 Ground sightings of adult female kudu on the A.V.K.R. between Dec 1977 and Nov 1979 expressed as a % of all kudu sightings per month.

* no data available.

89a


36
30
20
10
Frequency (%)
*
D J F M A M J J A S O N D J F M A M J J A S O N
Month


68
60
50
Frequency (%)
*
D J F M A M J J A S O N D J F M A M J J A S O N
Month

(51% of the population in December 1977 and 54% in January 1978) and during August 1979 (Fig. 6.2).

6.3.4 Subadults

More than twice as many subadult males (6,3% of the population) as subadult females (2,5%) were recorded from the ground (Fig. 6.3). This sex difference is highly significant ($\chi^2 = 82,9$, $p<0,001$). Young cows rarely constituted more than 5% of the population, while subadult males rarely exceeded 10%. Generally, fewer subadult males were seen on the Reserve during the winter months.

6.3.5 Calves

The proportion of calves within the population increased almost fourfold between 1978 and 1979. In both years, most calves were observed during August, followed by a steady decrease towards the end of the year (Fig. 6.4). Monthly ratios of calves per 100 females (adults and subadults) are shown in Table 6.7. Subadults were included in the ratios since they could not always be distinguished from adults. Data from three aerial censuses are included for comparison. Similar results from independent studies are shown in Table 6.8.

6.4 Discussion

The population structure showed little variation between months, and uniformity was maintained for ground and aerial surveys. The latter however, were more extensive and involved fewer known duplicated observations. This suggests the recorded observations constituted a representative sample of the population, and that inaccuracies in sex/age classifications were similar.

6.4.1 Population sex ratio

Since foetal and birth sex ratios do not differ significantly from parity (Chapter 5) the disparate population sex ratio, which is heavily biased towards females, must result from:

a) increased dispersal of males and/or

b) differential sexual mortality.

Male dispersal as a major cause of the imbalance is not supported

FIG. 6.3 Ground sightings of subadult kudu on the A.V.K.R. between Dec 1977 and Nov 1978 expressed as a % of all kudu sightings per month

a) subadult females

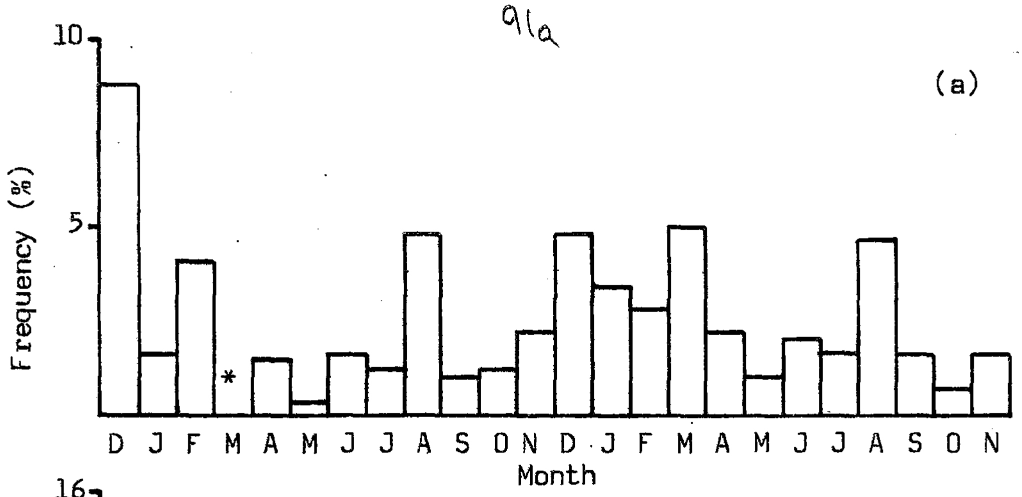
* no data available

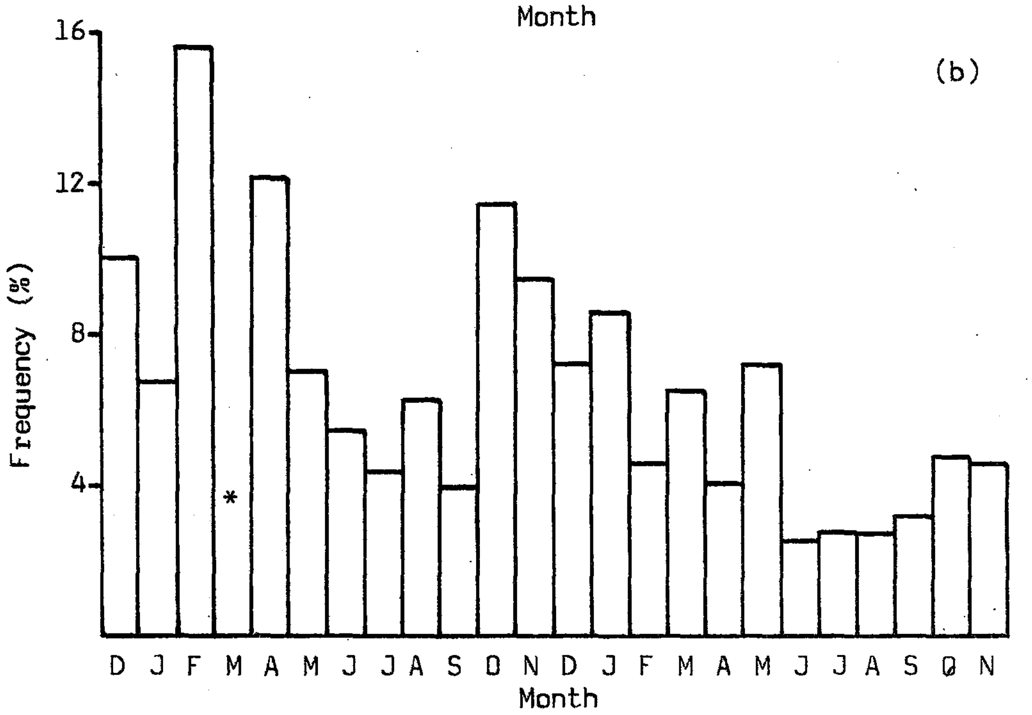
b) subadult males

* no data available

FIG. 6.4 Ground sightings of kudu calves on the A.V.K.R. between Dec 1977 and Nov 1979 expressed as a % of all kudu sightings per month.

* no data available.


(a)
Frequency (%)
10
5
*
D J F M A M J J A S O N D J F M A M J J A S O N
Month


(b)
Frequency (%)
16
12
8
4
*
D J F M A M J J A S O N D J F M A M J J A S O N
Month

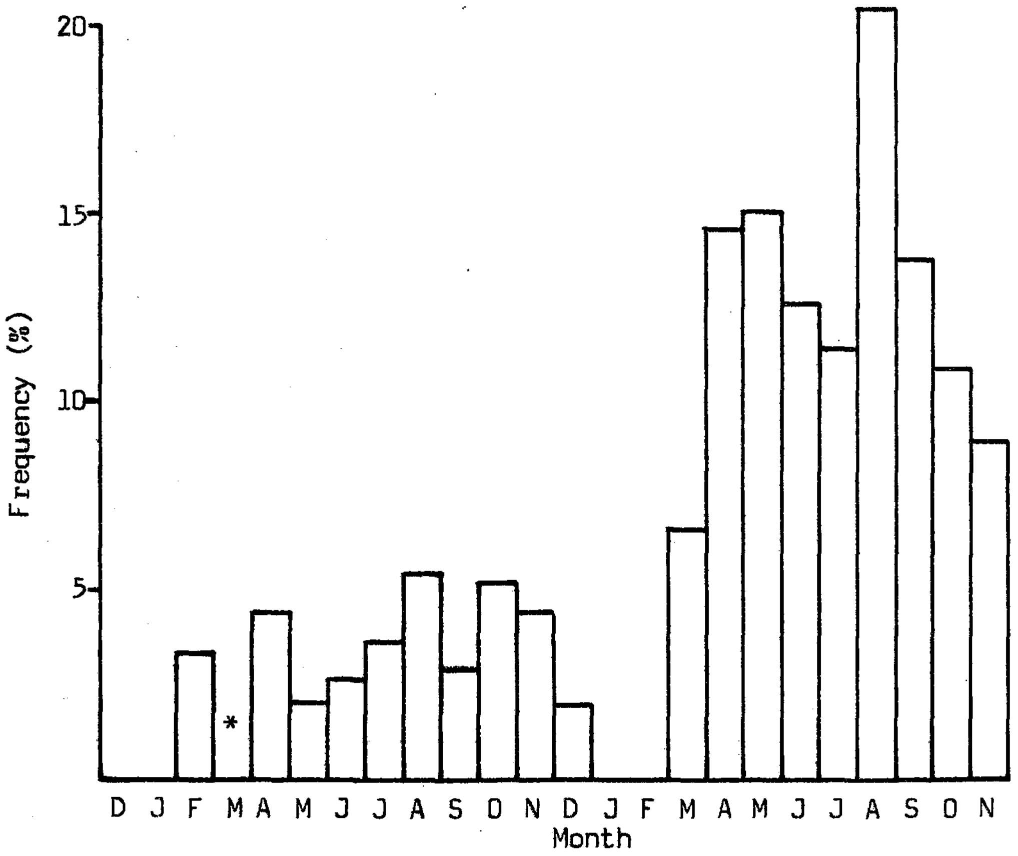

Frequency (%)
20
15
10
5
*
D J F M A M J J A S O N D J F M A M J J A S O N
Month

TABLE 6.7 Monthly calf:cow ratios during 1978-1979, calculated to a base of 100 females (subadult and adult). To facilitate comparisons, data from December 1977 and two darting operations have been omitted.

Month	1978			1979		
	Observed no. of ♀♀	Observed no. of calves	Ratio of calves:100♀♀	Observed no. of ♀♀	Observed no. of calves	Ratio of calves:100♀♀
Jan	38	0	0	80	0	0
Feb	78	4	5	63	0	0
Mar	-	-	-	174	17	10
Apr	-	-	-	141	35	25
Aerial census	60	4	7	122	42	34
May	240	7	3	129	33	26
Jun	208	8	4	191	37	19
Jul	166	9	5	162	28	17
Aug	137	11	8	122	43	35
Sep	66	3	5	116	26	22
Oct	213	18	8	162	29	18
Nov	213	14	7	118	17	14
Dec	174	5	3	-	-	-
Aerial census	217	7	3	-	-	-
Total	1810	90	5	1580	307	19

TABLE 6.8 Comparative kudu calf:cow ratios in southern Africa, calculated to a base of 100 females (subadult and adult).

Observed no. of ♀♀	calves	Ratio of calves:100♀♀	Remarks	Source
415	54	13	Aug '59-Oct '63	Wilson 1965
160	33	21	Shot sample	Simpson 1968
57	28	60	Sept '67	Wilson 1970
72	41	57	May '68	Wilson 1970
67	41	61	Oct '65	Jarman 1972
13	5	38	Aug '66	Jarman 1972
-	-	80	-	Owen-Smith pers comm.
3612	401	11	Dec '77-Nov '79	This study

by data from home range and mobility studies (Chapter 7). Male biased mortality may be due to selective hunting by man (Markgren 1974), selective predation (Mitchell, Shenton & Uys 1965; Hirst 1969; Pienaar 1969; Wright 1960; Schaller 1972; Smuts 1974b, 1976; Joubert & Bronkhorst 1977; Anderson 1978), and/or other natural differential mortality.

Although considerably more males than females are shot each year (143 males : 94 females, pers. obs.), no hunting has occurred on the Reserve for at least ten years. Predation is an unlikely natural cause of the disparate sex ratio, since the largest predator on the Reserve is the black-backed jackal, which is only capable of taking kudu calves (Pienaar 1969). Sex ratios, from areas where large predators are common, are in close agreement with that obtained for the Reserve (Table 6.6), suggesting that predation does not alter the sex ratio to any marked extent.

The imbalanced ratio in the Reserve is therefore probably due to other natural sex differential mortality. The age at which this occurs is not yet known. Field data suggest that it occurs after adolescence but it is evident from Fig. 6.3 that an unknown number of subadult females have been incorrectly classified as adults. Their subjective assessment therefore, renders any subadult male/subadult female comparisons invalid. Few adult skulls of either sex have been found on the Reserve, and kudu were shot non-randomly on surrounding farms. Consequently it has not been possible to calculate life tables and associated mortality rates.

In other ungulates, young bachelor males may be forced, by territorial males, into areas of inferior habitat where they may suffer relatively greater mortality than females through increased nutritional and social stress, and predation pressure (Jarman & Jarman 1973; Jarman 1974; Crowe & Liversidge 1977; Leuthold 1978a). However, kudu are not territorial (Chapter 7, 8 and 9), and therefore, the higher male mortality rate on the Reserve cannot be attributed to harassment and eviction by dominant males.

Approximately equal numbers of adult males of different age classes were seen in the field. Since kudu may live for at least ten years in the wild (Mentis 1972) and for over fifteen years in captivity (Rabb 1960; Crandall 1964, 1965; Petric pers. comm.; Wünschmann pers. comm.; St. Louis Zoo pers. comm.), the proportion of males five years and older (25% of all adult males) appears to be very low in comparison with the other age classes. While this suggests that mortality may be considerably higher in old individuals, no attempt has been made to determine the mortality rates of males aged in the field because age-ratio methods assume that the population is stable (Caughley 1977).

In several ungulate species, increased mortality in prime, dominant males has been attributed to malnutrition, resulting from the depletion of fat reserves during the rut and an inability to recover condition before winter, when food is limiting (Lowe 1969; Geist 1971; Grubb 1974a; De Bie 1976). However, conditions on the Reserve indicate that adult mortality from starvation is extremely unlikely (Chapter 9) and that other, as yet obscure, factors are responsible for the differential sexual mortality.

6.4.2 Changes in population structure

The adult component of the population was relatively constant throughout 1978 and 1979. This is to be expected over a short duration and suggests that immigration and emigration rates were slight or equivalent. Cows leaving their herds to give birth and suckle their concealed young during the summer months (Chapter 8), almost certainly account for the fewer female sightings recorded during this time (Table 6.5 and Fig. 6.2). The slightly lower proportion of adults seen in 1979 is obviously a result of the increased number of calves that year.

Proportionately fewer subadults were seen in 1979 (Fig. 6.3). This is obviously a direct result of the poor calf production of 1978 (Fig. 6.4). The fact that this is evident in males but not reflected in the subadult female segment of the population again illustrates my inability to accurately age females in the field. Similar problems have been experienced by others studying tragelaphids (Anderson 1978; Underwood 1978; Leuthold 1979). Sightings of subadult bulls declined during the winter months in both years. This was probably due to changes in their social relationships at this time (Chapter 8).

The most obvious change in the population structure was the increased number of calves seen in 1979. The similar numbers of calves seen from the air (greater visibility) and from the ground in any one month (Table 6.7) confirm that the calf increase was real and not a result of inadequate sampling in previous years. The incidence of lactation in females captured in April 1978 and April 1979 (41% and 92% lactating respectively) further corroborate this conclusion.

Such an increase may have been due to either higher conception rates and/or a decrease in calf mortality in 1979. A substantially increased conception rate is regarded as highly improbable since female kudu on neighbouring farms have had a specific conception rate of 100% for the last four years (Chapter 5). However, no marked seasonal decrease in the number of calf sightings, (as recorded by Underwood 1978) were witnessed in either year. The gradual decline in calf sightings towards the end of the year, when calves are approaching one year of age is probably due to errors in field classification. This would suggest that either calf mortality was extremely heavy during the early months of 1978 before calves were observed in the field, or that the mortality rate remains fairly constant throughout the first year of life. The latter is considered unlikely since the rate of juvenile mortality in ungulates usually decreases sharply with time from birth (Caughley 1966, 1976; Spinag 1968); neonates and young calves are often more vulnerable to predators (Sadlier 1969a; Spinage 1970; Cook, White, Trainer & Glazener 1971; McDairmid 1974; Miller & Broughton 1974; Carroll & Brown 1977), and are often more susceptible to starvation, exposure and disease at this age (Wilson, Bartsch, Bigalke & Thomas 1974; Wegge 1975; Wilson & Hirst 1977; Guinness, Clutton-Brock & Albon 1978; Staines 1978). However, assuming that calf survival was enhanced in 1979, reasons for this are not obvious.

Whatever the cause of the higher calf numbers in 1979, these are still considerably less than those reported from other areas (Dasmann & Mossman 1962b; Wilson 1970; Jarman 1972; Owen-Smith pers. comm.). This is further illustrated by comparing the cow:calf ratios in Tables 6.7 and 6.8. Adult cow:calf ratios are a product of conception rate and mortality (Attwell 1977). While the ratio obtained from observations on the Reserve contains subadult and adult cows, with the result that calf values are depressed by an unknown amount, the figures in Table 6.8 were derived in an identical manner and are therefore comparable. Even if subadult females constituted 20% of the total female population and were subtracted from the ratio obtained from the Reserve, the calf values would increase only by a similar amount, resulting in a maximum ratio of 44 calves per 100 adult females, for August 1979. This is well below the figures of Wilson (1970), Jarman (1972) and Owen-Smith (pers. comm.) in Table 6.8.

It would therefore appear that calf survival or production has been much lower on the Reserve over the last two years than in other areas of southern Africa. Assuming maximum adult cow:calf ratios of 100:10 in 1978 and 100:44 in 1979, recruitment for the entire Reserve during these periods is estimated at 60 and 264 calves respectively.

Further long term studies of the factors causing fluctuations in calf survival and detailed knowledge of the proportion of calves that survive to reproduce and recruit offspring are clearly vital to a sound understanding of the population biology and successful management of this species.

Chapter 7
SPATIAL ORGANISATION

7.1 Introduction

Jewell (1966, p. 103) defines the term 'home range' as "the area over which an animal normally travels in pursuit of its routine activies". However, as Leuthold (1979) points out, it is often necessary to adopt a more operational definition, when determining the spatial organisation of a species, and in this study 'home range' is simply the entire area within which an individual was recorded. Thus it can be regarded as the area containing all the resources needed by that animal, and its size therefore indicates the nature of these resources. In addition, the extent to which this area is shared by adult males of equal social status is highly informative in an evaulation of the population's level of social orgnaisation.

7.2 Methods

The positions of all collared kudu seen during the monthly field surveys and the aerial censuses were recorded and plotted on individual 1:36 000 topographical maps. Home ranges were calculated by connecting all the outermost points with straight lines and measuring the resultant convex polygon with a planimeter. The date of observation and group composition were also recorded.

Positions of radio-collared kudu were also determined by telemetry (Chapter 3) and home range areas were calculated in an identical manner.

The periphery method of determining home range size (B. Leuthold 1979; Leuthold 1979), does not illustrate any temporal and spatial differences in range utilization. However, the tecnhique was used in this study since widely divergent locations were not observed, and the technique has been extensively used in other field studies (Allsopp 1970; Leuthold 1974, 1979; Waser 1975a; Odendaal 1977; Anderson 1978) and therefore permits direct comparisons.

7.3 Results

7.3.1 Home range size

7.3.1.1 Field observations

Home range sizes were calculated for 59 collared kudu (59% of total) seen at least five times on the Reserve and mean sizes are presented in Table 7.1. The frequency distribution of home range sizes (in four size classes) are given in Table 7.2. Periods of observation (first to last months seen) expressed as a percentage of the maximum possible observation period are illustrated in Fig. 7.1.

7.3.1.2 Radio-tracking

Home range sizes of nine (69%) of the radio-collared kudu, determined from at least five positions per individual, are presented in Table 7.3. Corresponding values based on field observations are also shown, as are home range sizes calculated from both sets of positions. Mean differences in home range size determined from radio-tracking and field observations were not significant for males or females and the individual ranges superimposed showed considerable variation in the extent of overlap (Fig. 7.2).

7.3.1.3 Sex and age differences

a) Males. Two collared subadult males were seen more than five times (Nos. 26 and 42), and had home ranges of 29,2 ha and 14,2 ha respectively. Both males inhabited *E. bothae* bush on Kentucky Kop.

The mean home range size of adult males was 133,6 ha (±85,6 ha, n = 24). Mean home range sizes were also determined for each of the four adult male age classes (Table 7.4). Differences in these range sizes, and also between each of these and the mean value for subadult males, were not statistically significant.

b) Females. The mean female kudu home range size was 96,3 ha (±69,4 ha, n = 33). Subadult female range sizes did not differ significantly from those of adult cows.

Adult male home ranges were generally, but not significantly, larger than those of adult females

TABLE 7.1 Kudu home range sizes (ha) determined from sightings of collared kudu.

n	Sex	Mean home range size (ha)	Mean no. of sightings	Mean period of observation (months)
12	♂	84,4±61,9	7,0*	9,8
14	♂	159,9±93,1	18,9**	15,9
Total				
26	♂	125,0±8,25	13,4	13,1
13	♀	95,7±70,5	6,9*	14
20	♀	96,7±70,5	21,9**	17,8
Total				
33	♀	96,3±69,4	16,1	16,3

* = seen 5-9 times, ** = seen at least 10 times

TABLE 7.2 Frequency distribution of individual kudu home range sizes determined from field sightings.

	Home range sizes (ha)				
Sex	1-99	100-199	200-299	300-399	Total
♂♂	11	11	3	1	26
♀♀	20	9	4	-	33
Total	31	20	7	1	59

FIG. 7.1 Frequency distribution of field observation periods for kudu seen at least five times on the A.V.K.R.

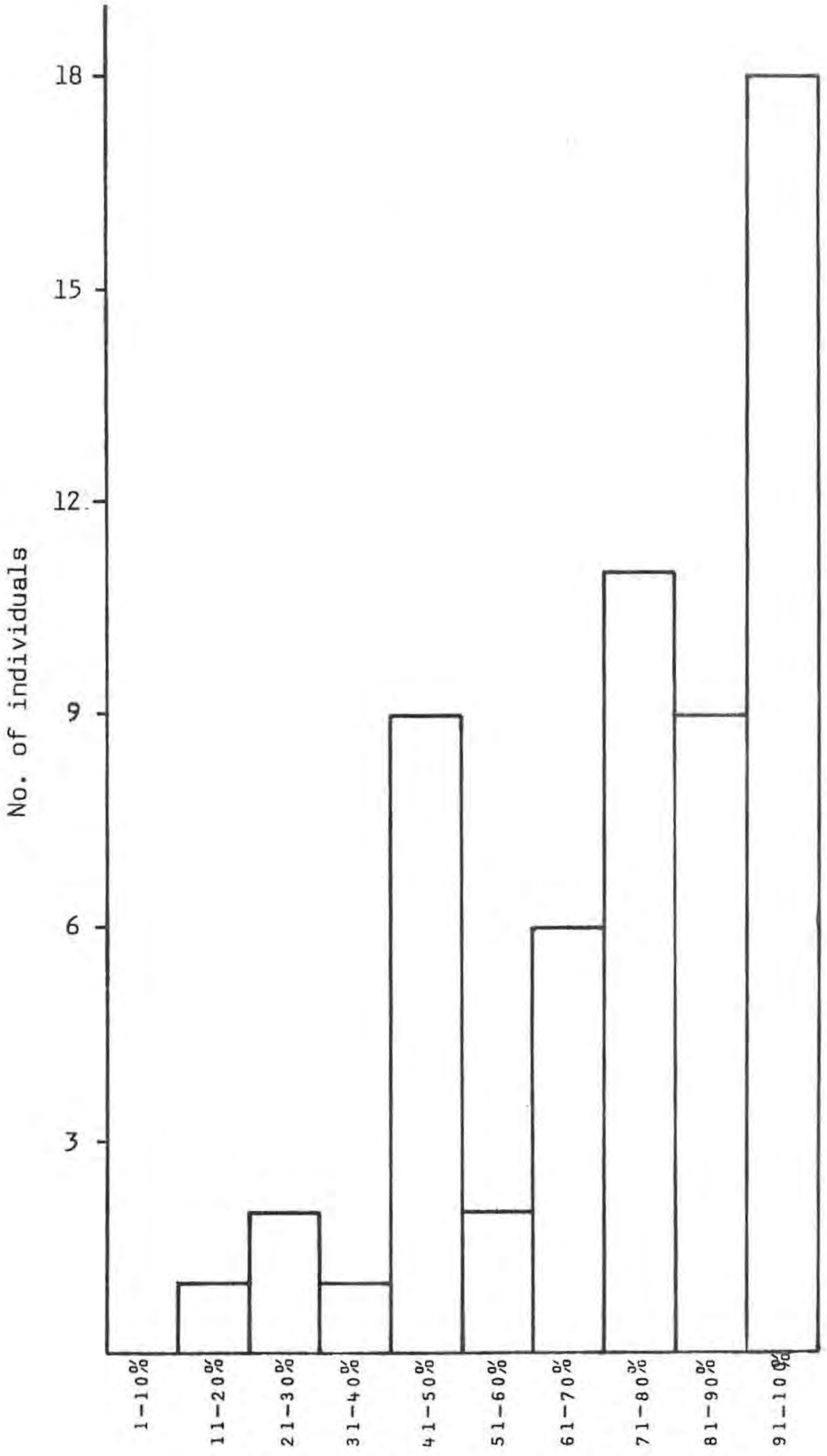

No. of individuals
18
15
12
9
6
3
1-10%
11-20%
21-30%
31-40%
41-50%
51-60%
61-70%
71-80%
81-90%
91-100%
Duration of observation expressed
as a % of the maximum possible period

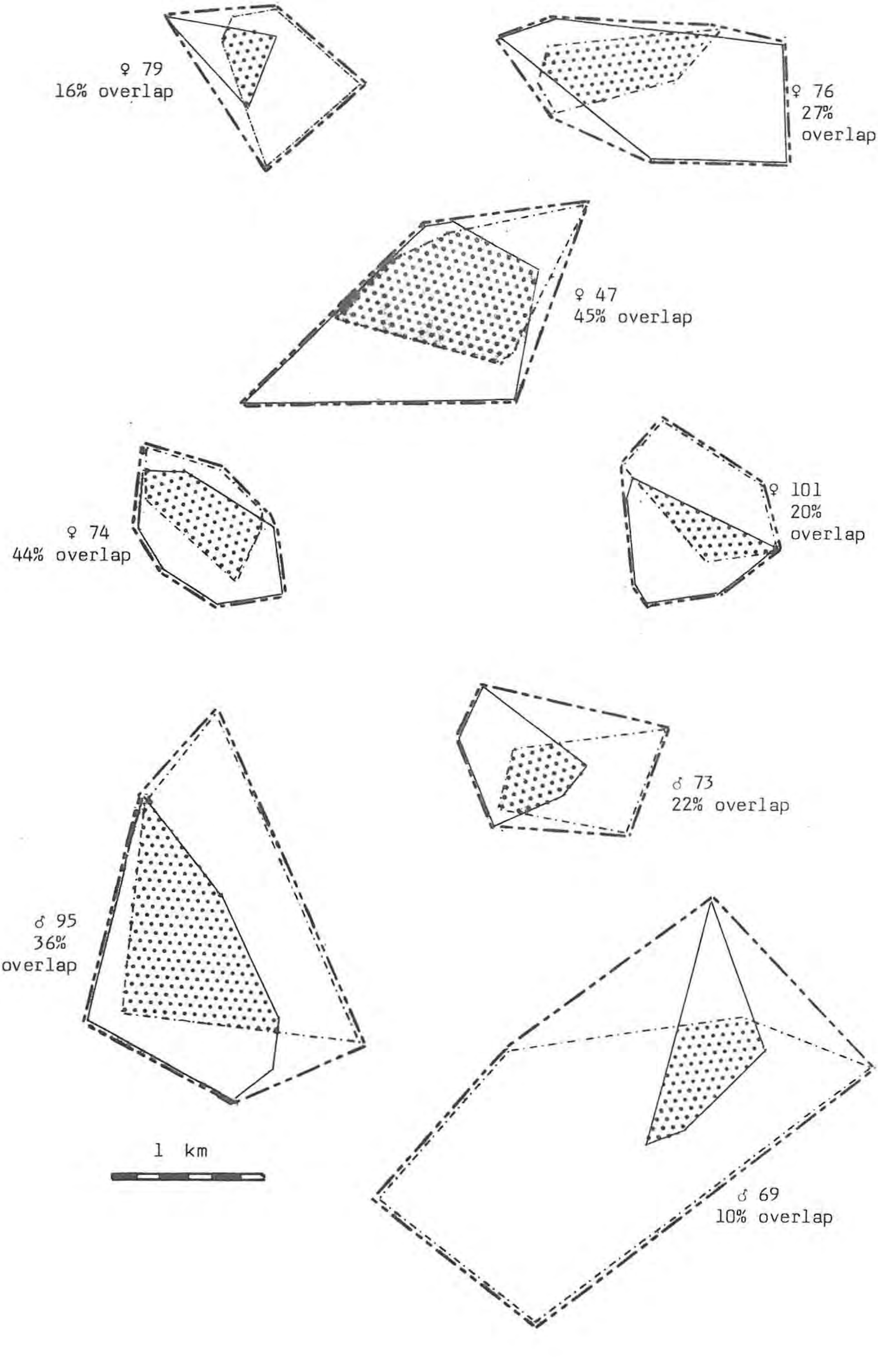
TABLE 7.3 Kudu home range sizes (ha) determined from a) field sightings b) radio-tracking, and c) both methods.

		a		b		c	
Kudu no.	Sex	No. of field sightings	Home range sizes (ha)	No. of fixes	Home range sizes (ha)	Total no. of positions	Home range sizes (ha)
44	♂	2	-	10	124,6	12	151,4
69	♂	6	64,3	5	389	11	499,8
73	♂	15	47,4	7	68,6	22	119,8
95	♂	26	166,9	12	222,4	38	300,2
Mean	♂♂		92,8±64,7		201,2±140,0		267,8±173,5
47	♀	21	180,4	22	109,9	43	212,5
74	♀	46	71,6	16	42,9	62	79,1
76	♀	26	146,8	14	44,2	40	160,8
79	♀	14	23,6	17	60,3	31	85,8
101	♀	35	56,3	16	59,8	51	97,7
Mean	♀♀		95,7±65,4		63,4±27,3		127,2±57,7
Mean	♀+♂		94,6±60,2		124,5±114,2		189,7±135,8

TABLE 7.4 Mean home range sizes of adult male kudu, determined from field observations.

	2-3yr ♂♂	3-4yr ♂♂	4-5yr ♂♂	5+yr ♂♂	Mean
Mean	135,3	129,3	89,1	171,6	133,6
± S.D.	± 73,1	± 73,7	± 34,2	± 157,4	± 85,6
Sample size	9	8	3	4	24

FIG. 7.2 Kudu home ranges determined from field sightings (———), radio-tracking (-··-··-) and from both methods (- — -). The extent of range overlap (░) is expressed as a % of the total range size.


♀ 79
16% overlap
♀ 76
27%
overlap
♀ 47
45% overlap
♀ 74
44% overlap
♀ 101
20%
overlap
♂ 73
22% overlap
♂ 95
36%
overlap
1 km
♂ 69
10% overlap

7.3.1.4 Frequency and duration of sightings

Mean home range sizes of kudu seen a) five to nine times and b) at least ten times are shown in Table 7.1. These differences in area were significant in males ($t = 2,389$, $p<0,05$), but not in females. Similarly, correlations between individual home range size and i) the number of sightings, and ii) the length of observation period were significant in males only (Table 7.5). Home range size increases with time/number of sightings of the three most frequently sighted male and female kudu are illustrated in Figs. 7.3 and 7.4.

7.3.1.5 Seasonal variations

The positions of collared kudu seen at least twenty times were separated according to season (Figs. 7.5 and 7.6). These results indicate that both sexes are more mobile and perhaps utilize more of their ranges during the autumn and winter months. The seasonal distribution of these sightings are shown in Table 7.6.

7.3.1.6 Habitat variations

Mean home range sizes of kudu inhabiting non-succulent bush were significantly larger than those living in *E. bothae* bush, irrespecitve of sex or sighting frequency (Table 7.7). Kudu inhabiting both vegetation types had ranges of intermediate size (mean = 142,2 ± 23,3 ha, n = 4). Insufficient data from other vegetation types prevented further comparisons.

7.3.2 Extent of home range overlap

All ranges of males seen at least five times in the non-succulent bush showed considerable overlap (Fig. 7.7). Ranges of similarly aged bulls inhabiting *E. bothae* bush are illustrated in Figs. 7.8 to 7.10, and again show extensive overlapping, as do the female ranges in Figs. 7.11 to 7.13.

7.4 Discussion

The mean home range sizes of male (1,25 km^2) and female (0,96 km^2) kudu on the A.V.K.R. are considerably smaller than those recorded in other areas (15 km^2 and 4-12 km^2 respectively,

TABLE 7.5 Correlation coefficients for home range size with number of sightings and length of observation period. (All kudu seen at least five times.)

Sex	r for no. of sightings/individual	r for no. of months under observation
♂♂ (n = 26)	0,562 p<0,01	0,415 p<0,05
♀♀ (n = 33)	-0,026 n.s.	0,056 n.s.

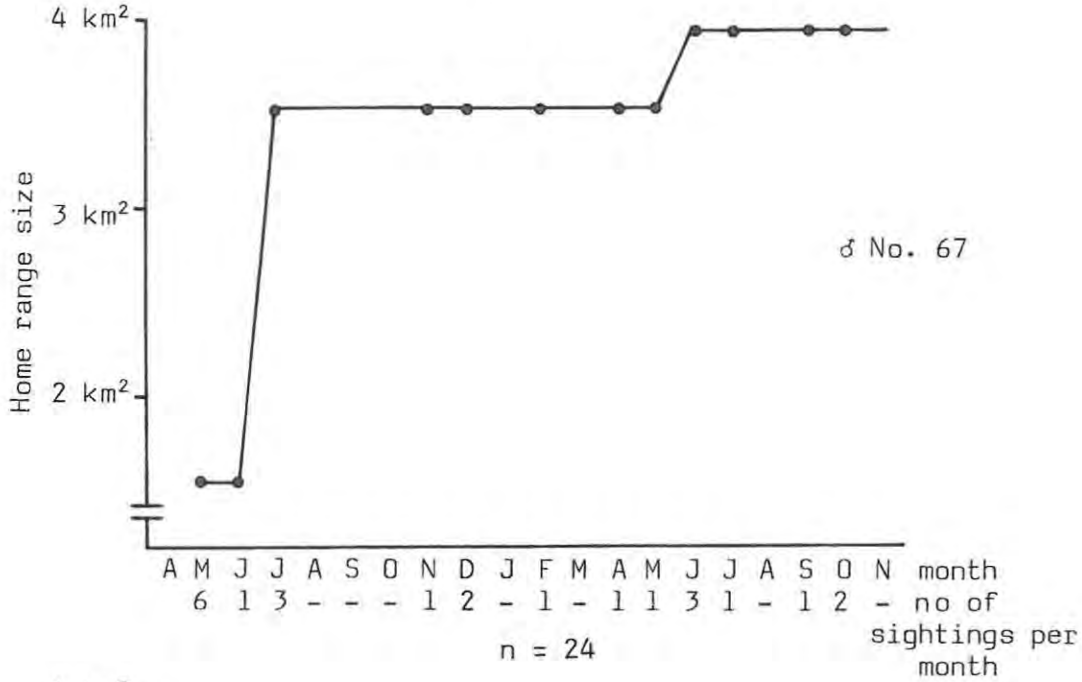
TABLE 7.6 Seasonal distribution of sightings of collared kudu seen at least twenty times on the Andries Vosloo Kudu Reserve.

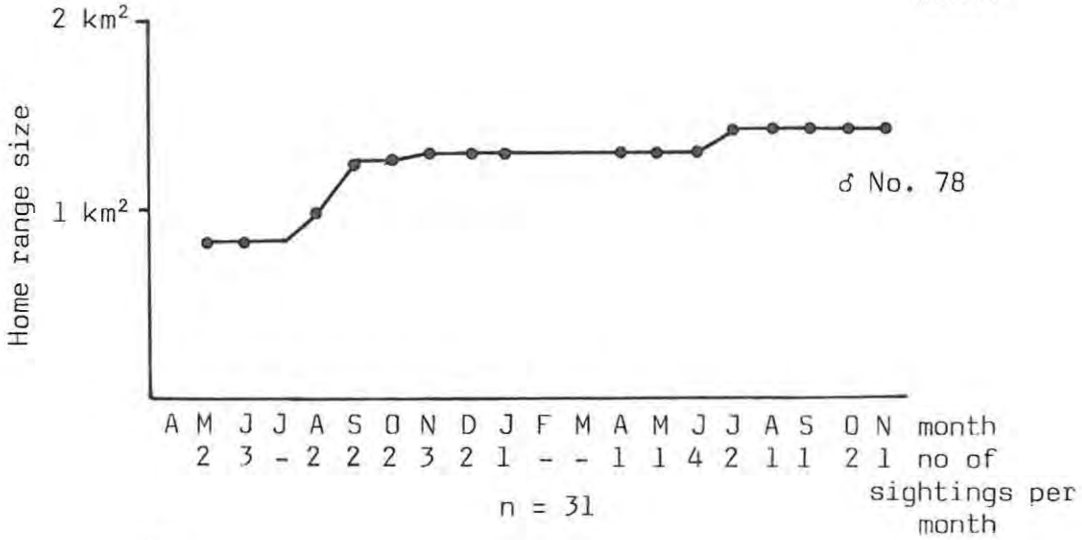
Sex	Mar-May	Jun-Aug	Sep-Nov	Dec-Feb	Total no. of sightings
♂♂	31%	31%	25%	11%	149
♀♀	38%	32%	19%	11%	260
Total	36%	32%	21%	11%	409

TABLE 7.7 Mean home ranges of kudu inhabiting non-succulent and *E. bothae* bush. (All kudu seen at least five times.)

Sex	No. of sightings	Mean home range size in non-succulent bush (in ha)	Mean home range size in *E. bothae* bush (in ha)	t value	p value
♂♂	5-9	85,7±30,3 (n = 2)	39,5±14,4 (n = 7)	3,275	<0,02
	>10	240,1±113,2 (n = 4)	132,8±52,9 (n = 8)	2,298	<0,05
	Total	195,3±124,7 (n = 6)	89,3±61,8 (n = 15)	2,641	<0,02
♀♀	5-9	193,0±16,1 (n = 3)	71,4±55,0 (n = 8)	3,659	<0,01
	>10	128,8±87,4 (n = 9)	53,9±19,3 (n = 9)	2,512	<0,05
	Total	144,9±80,3 (n = 12)	62,1±39,9 (n = 17)	3,675	<0,002
Both sexes		161,7±96,7 (n = 18)	74,9±52,3 (n = 32)	4,137	<0,001

FIG. 7.3 Monthly changes in recorded home range sizes of three male kudu seen at least twenty times.


4 km²
3 km²
2 km²
Home range size
♂ No. 67
A M J J A S O N D J F M A M J J A S O N month
6 1 3 - - - 1 2 - 1 - 1 1 3 1 - 1 2 - no of sightings per month
n = 24


2 km²
1 km²
Home range size
♂ No. 78
A M J J A S O N D J F M A M J J A S O N month
2 3 - 2 2 2 3 2 1 - - 1 1 4 2 1 1 2 1 no of sightings per month
n = 31

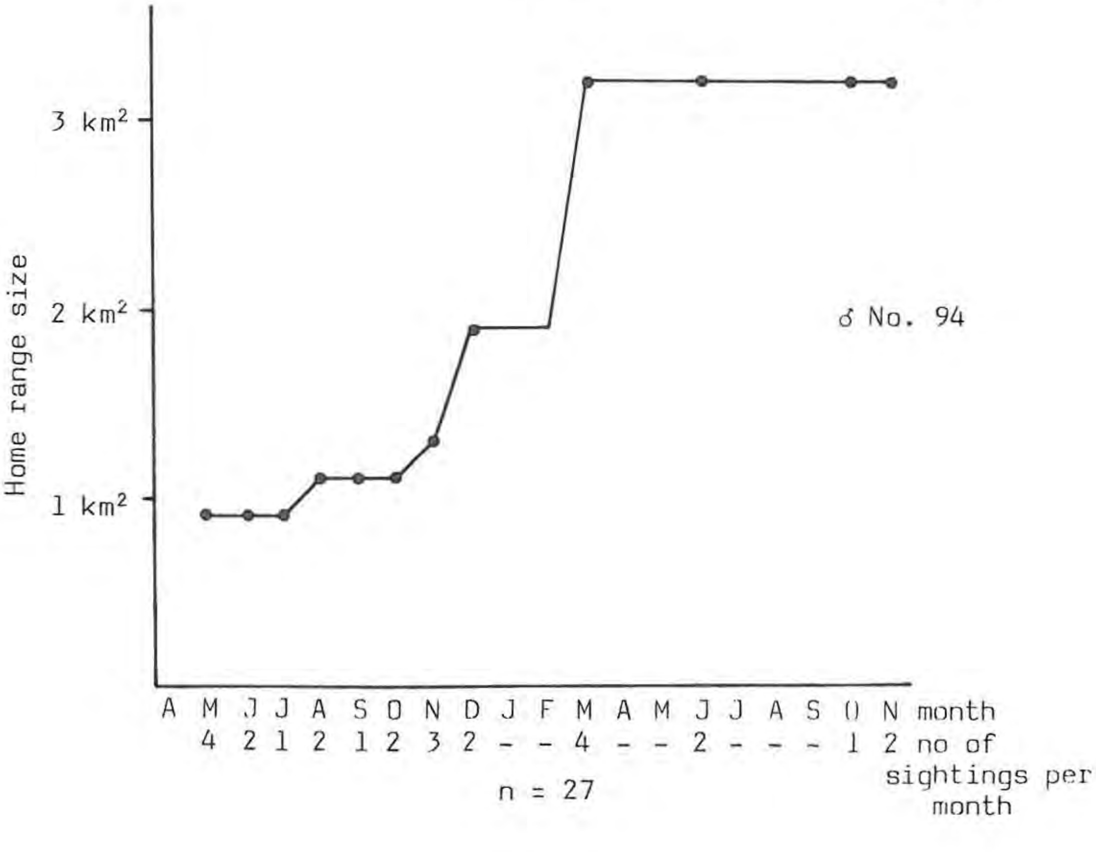
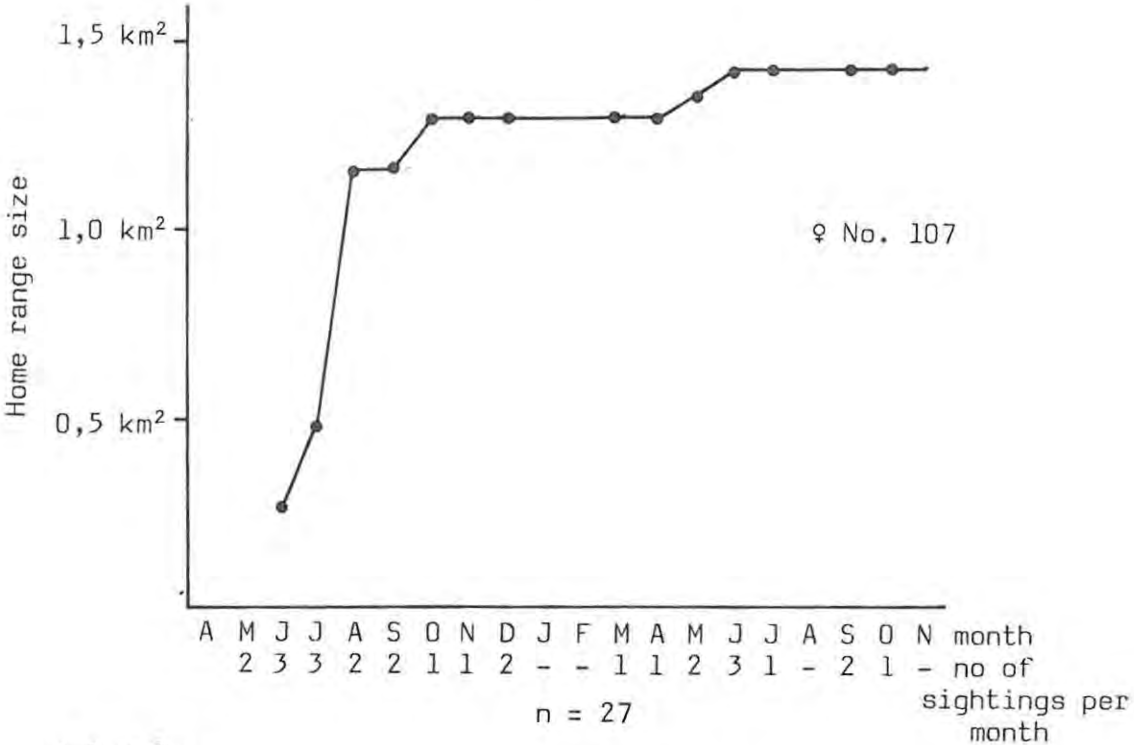
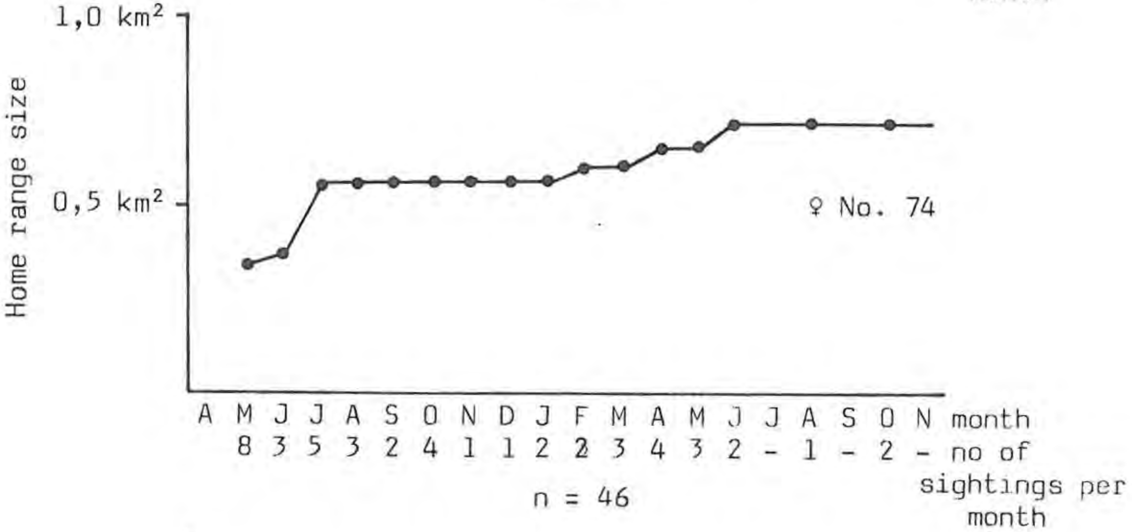

3 km²
2 km²
1 km²
Home range size
♂ No. 94
A M J J A S O N D J F M A M J J A S O N month
4 2 1 2 1 2 3 2 - - 4 - - 2 - - - 1 2 no of sightings per month
n = 27

FIG. 7.4 Monthly changes in recorded home range sizes of three female kudu seen at least twenty times.


1,5 km²
1,0 km²
0,5 km²
Home range size
♀ No. 107
A M J J A S O N D J F M A M J J A S O N month
2 3 3 2 2 1 1 2 – – 1 1 2 3 1 – 2 1 – no of sightings per month
n = 27


1,0 km²
0,5 km²
Home range size
♀ No. 74
A M J J A S O N D J F M A M J J A S O N month
8 3 5 3 2 4 1 1 2 2 3 4 3 2 – 1 – 2 – no of sightings per month
n = 46

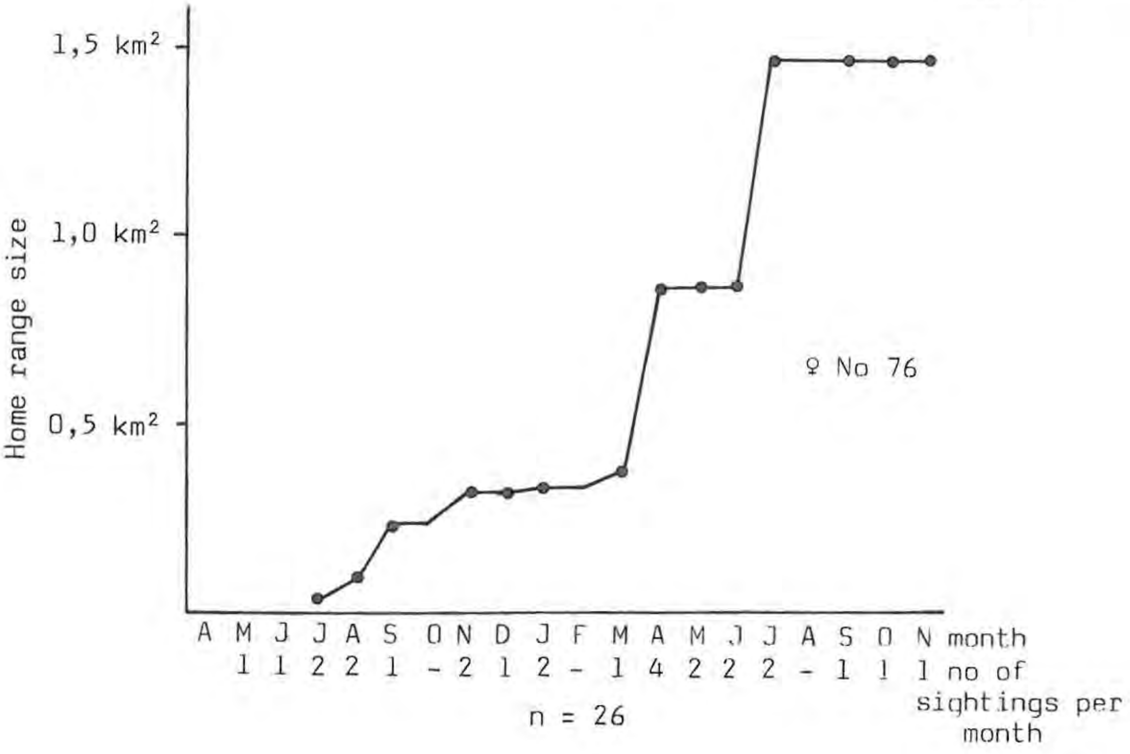

1,5 km²
1,0 km²
0,5 km²
Home range size
♀ No 76
A M J J A S O N D J F M A M J J A S O N month
1 1 2 2 1 – 2 1 2 – 1 4 2 2 2 – 1 1 1 no of sightings per month
n = 26

FIG. 7.5 Seasonal variations in recorded home range sizes of kudu inhabiting non-succulent bush. Each kudu was seen a minimum of twenty times.

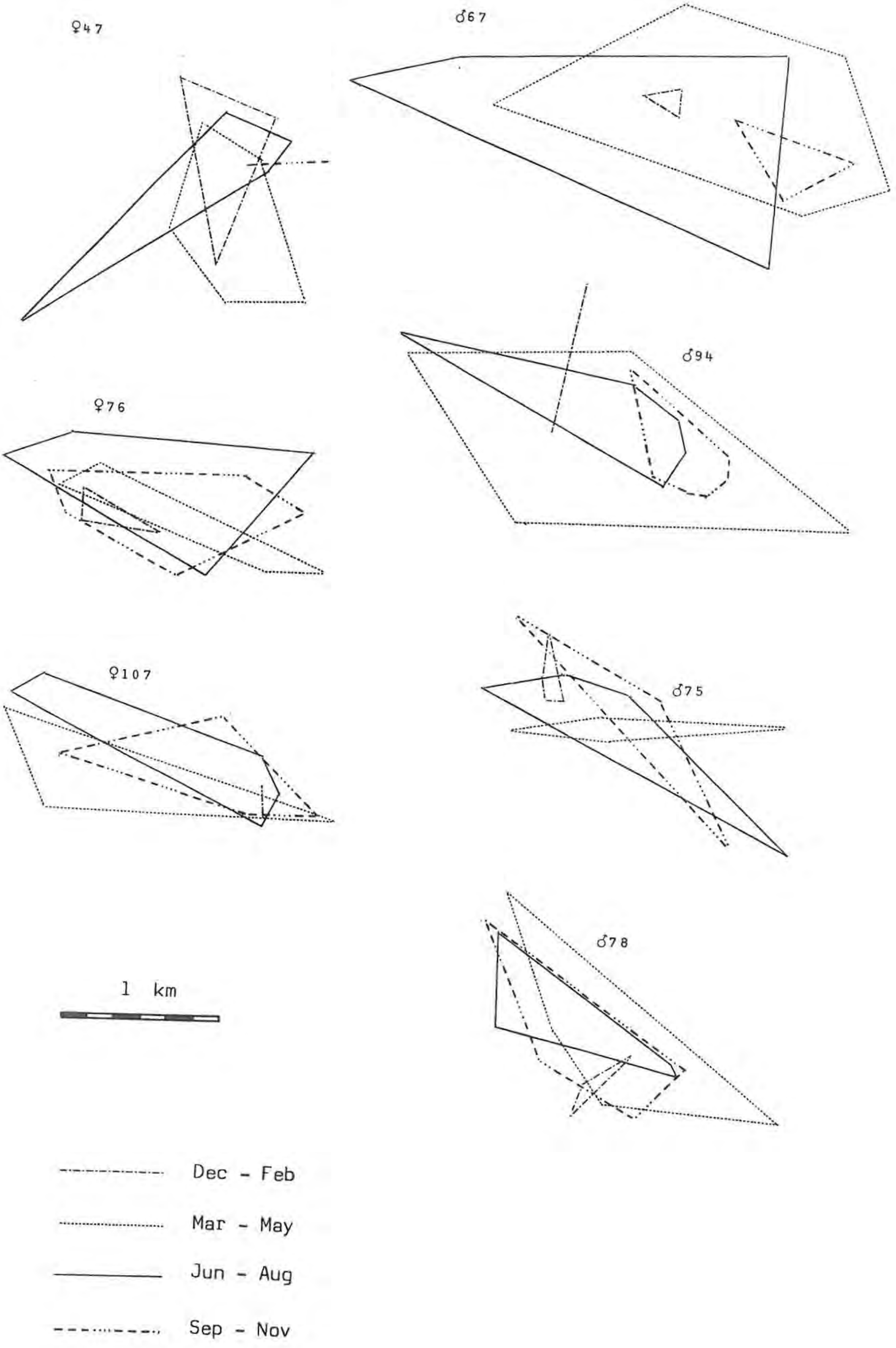

♀47
♂67
♀76
♂94
♀107
♂75
♂78
1 km
Dec - Feb
Mar - May
Jun - Aug
Sep - Nov

FIG. 7.6 Seasonal variations in recorded home range sizes of kudu inhabiting *E. bothae* bush. Each kudu was seen a minimum of twenty times.

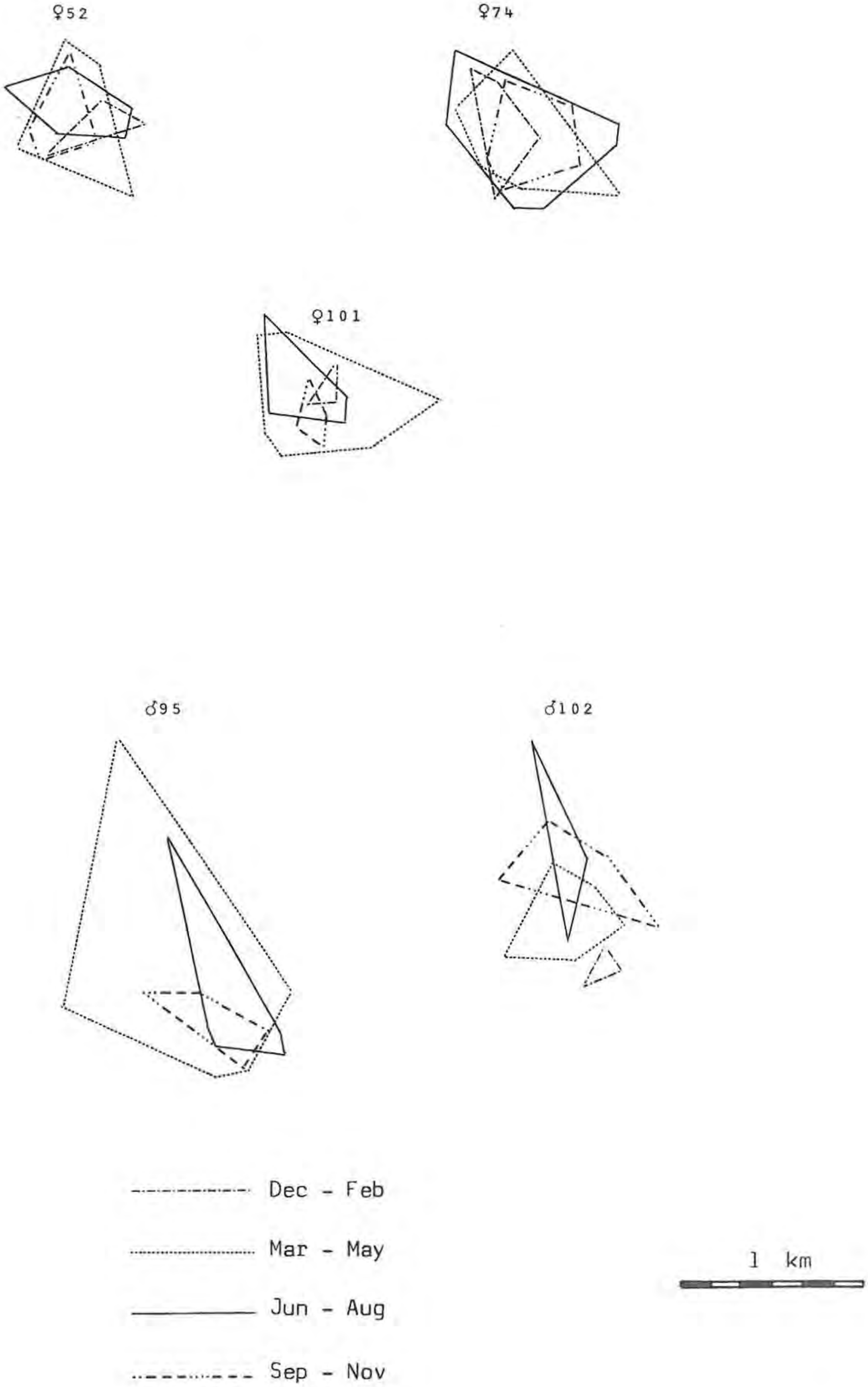
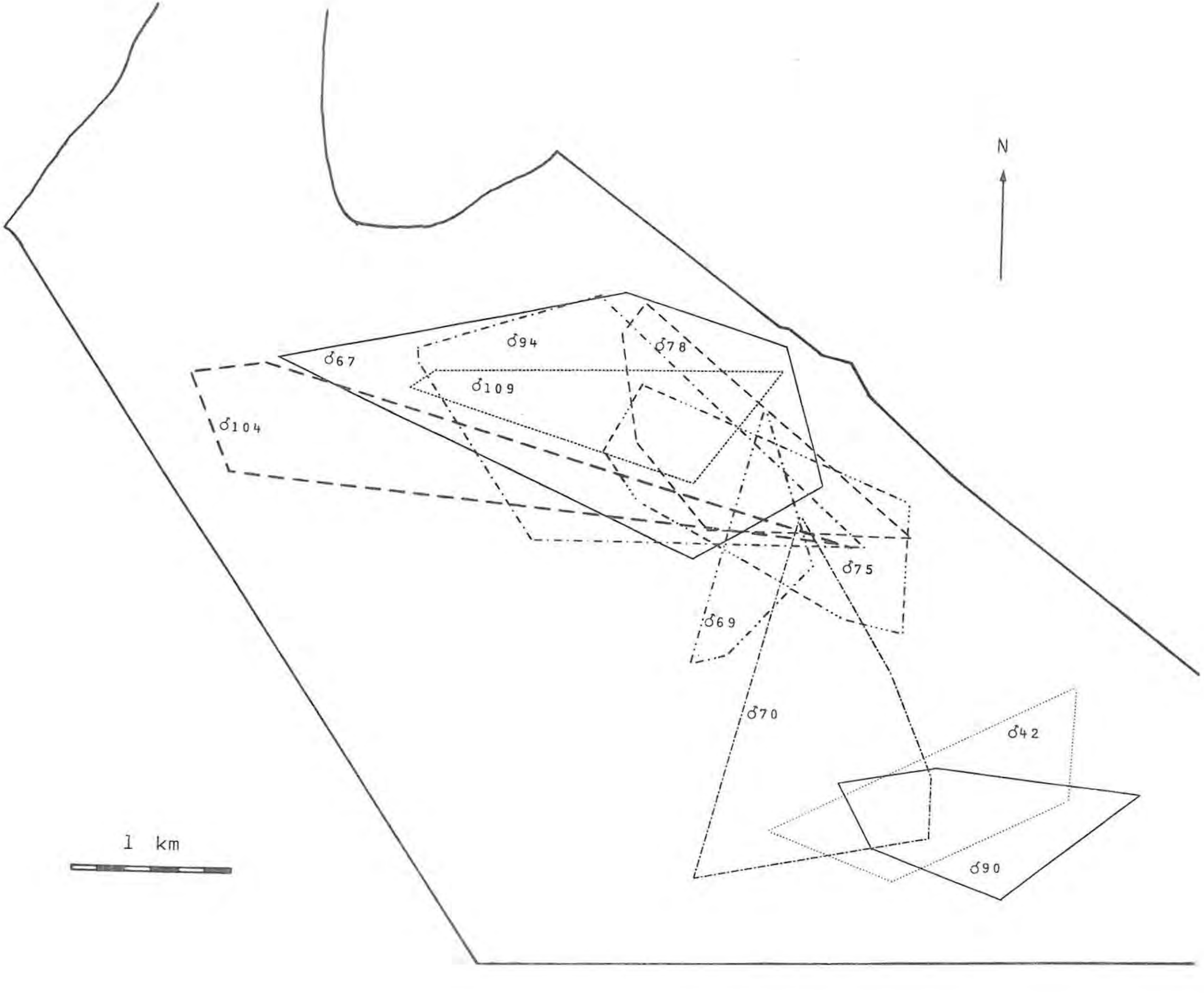

♀52
♀74
♀101
♂95
♂102
Dec - Feb
Mar - May
Jun - Aug
Sep - Nov
1 km

FIG. 7.7 Home ranges of all collared male kudu seen at least five times in non-succulent bush.



111a

FIG. 7.8 Home ranges of collared subadult and 2 year old male kudu inhabiting _E_. _bothae_ bush. All animals were seen at least five times.

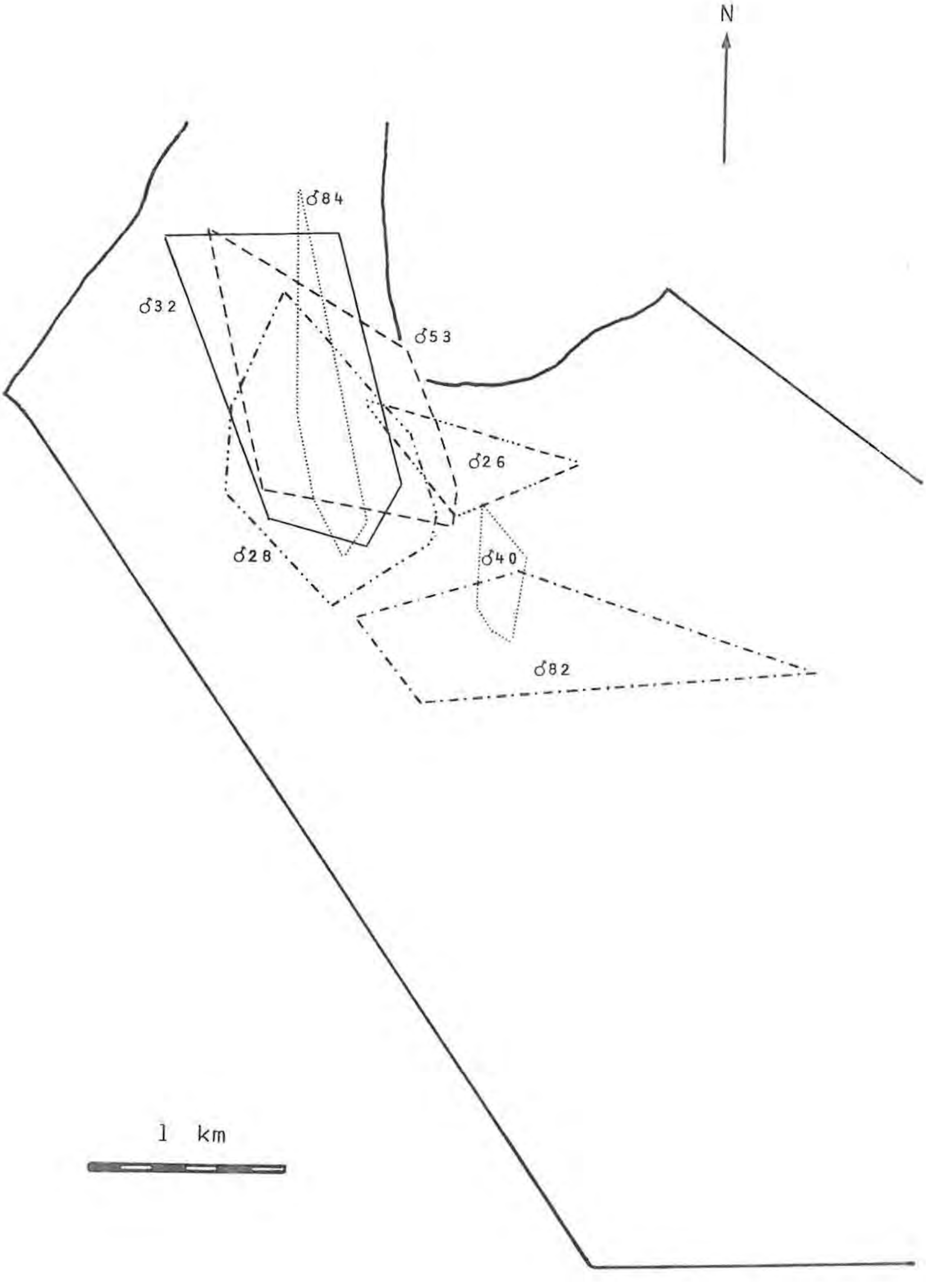
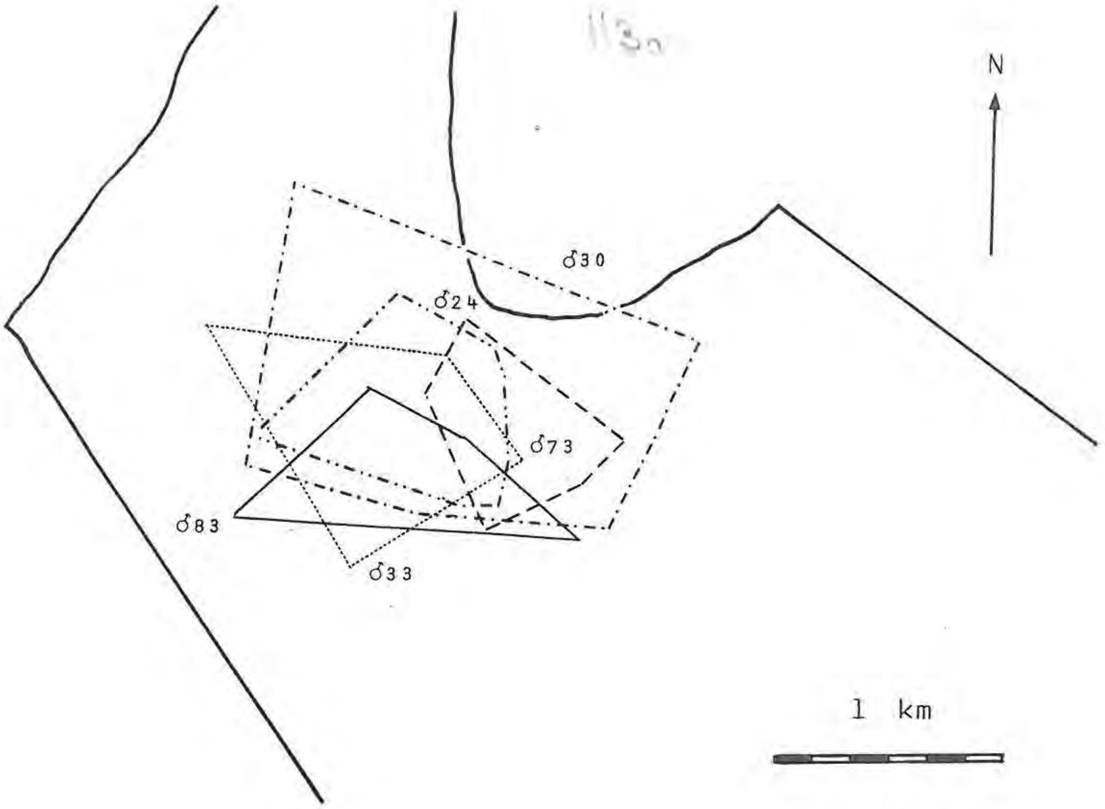

N
♂84
♂32
♂53
♂26
♂28
♂40
♂82
1 km

FIG. 7.9 Home ranges of 3 year old male kudu inhabiting *E. bothae* bush. All animals were seen at least five times.

FIG. 7.10 Home ranges of male kudu, at least 4 years old inhabiting *E. bothae* bush. All animals were seen a minimum of five times.


N
♂30
♂24
♂73
♂83
♂33
1 km

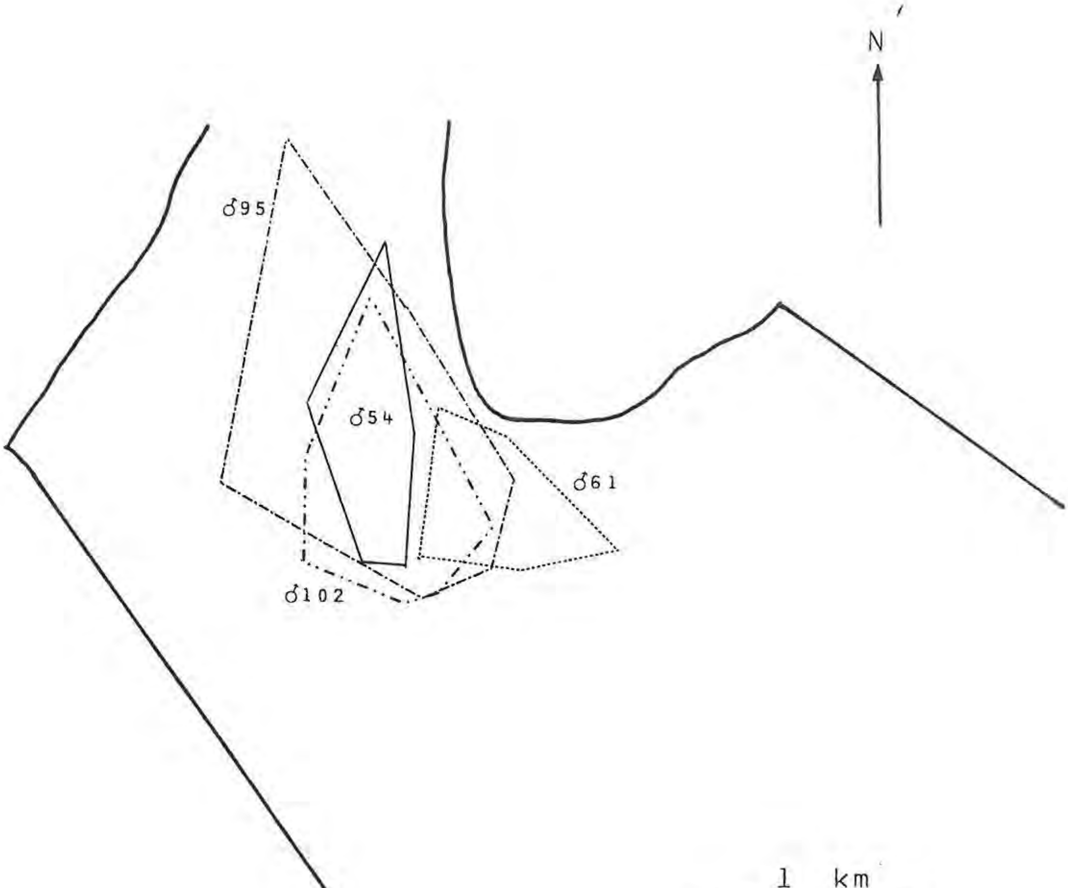

N
♂95
♂54
♂61
♂102
1 km

FIG. 7.11 Home ranges of ten collared female kudu each seen at least five times on the A.V.K.R.

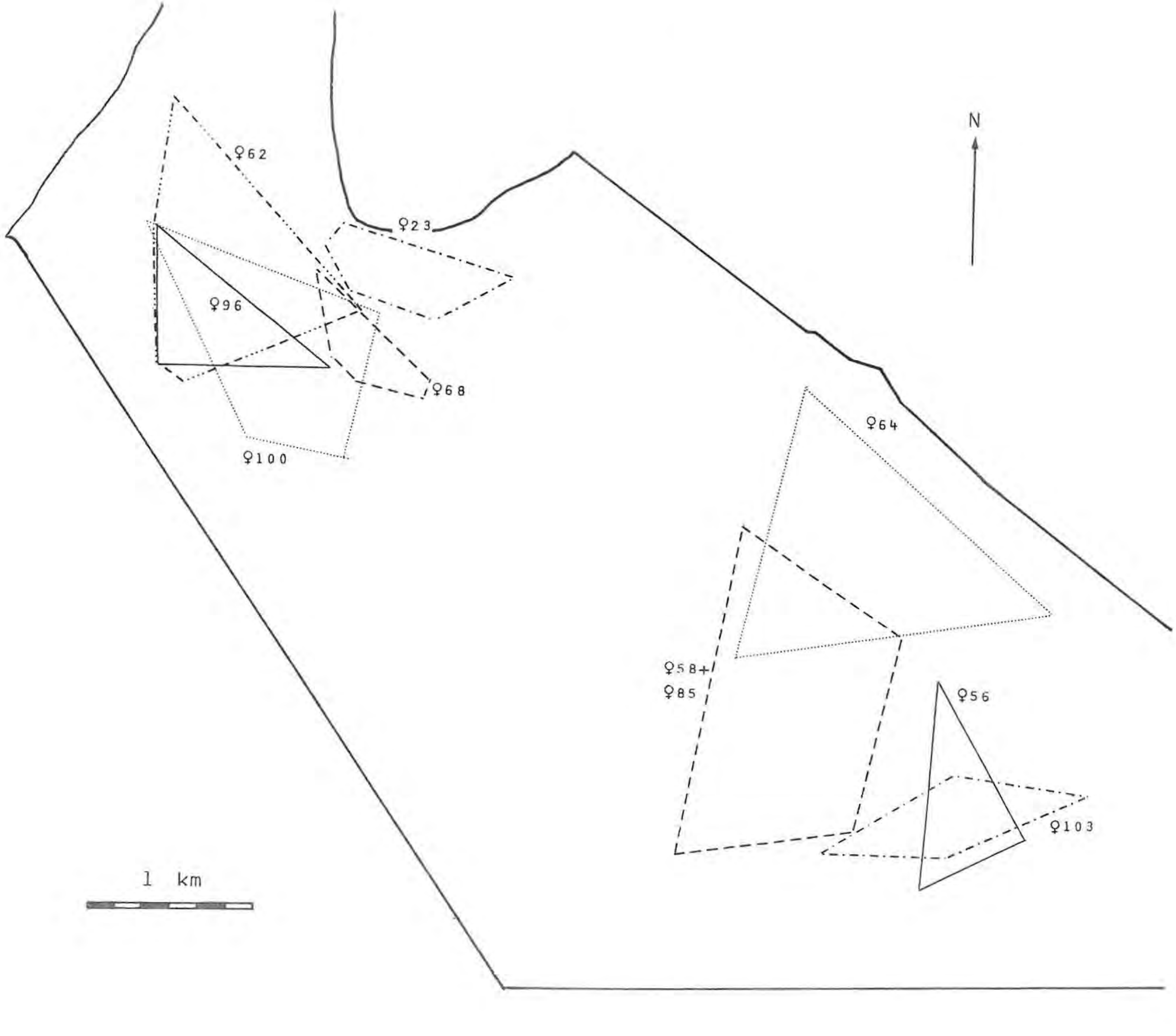

N
♀62
♀23
♀96
♀68
♀100
♀64
♀58+
♀85
♀56
♀103
1 km

FIG. 7.12 Home ranges of eleven collared female kudu each seen at least ten times on the A.V.K.R.

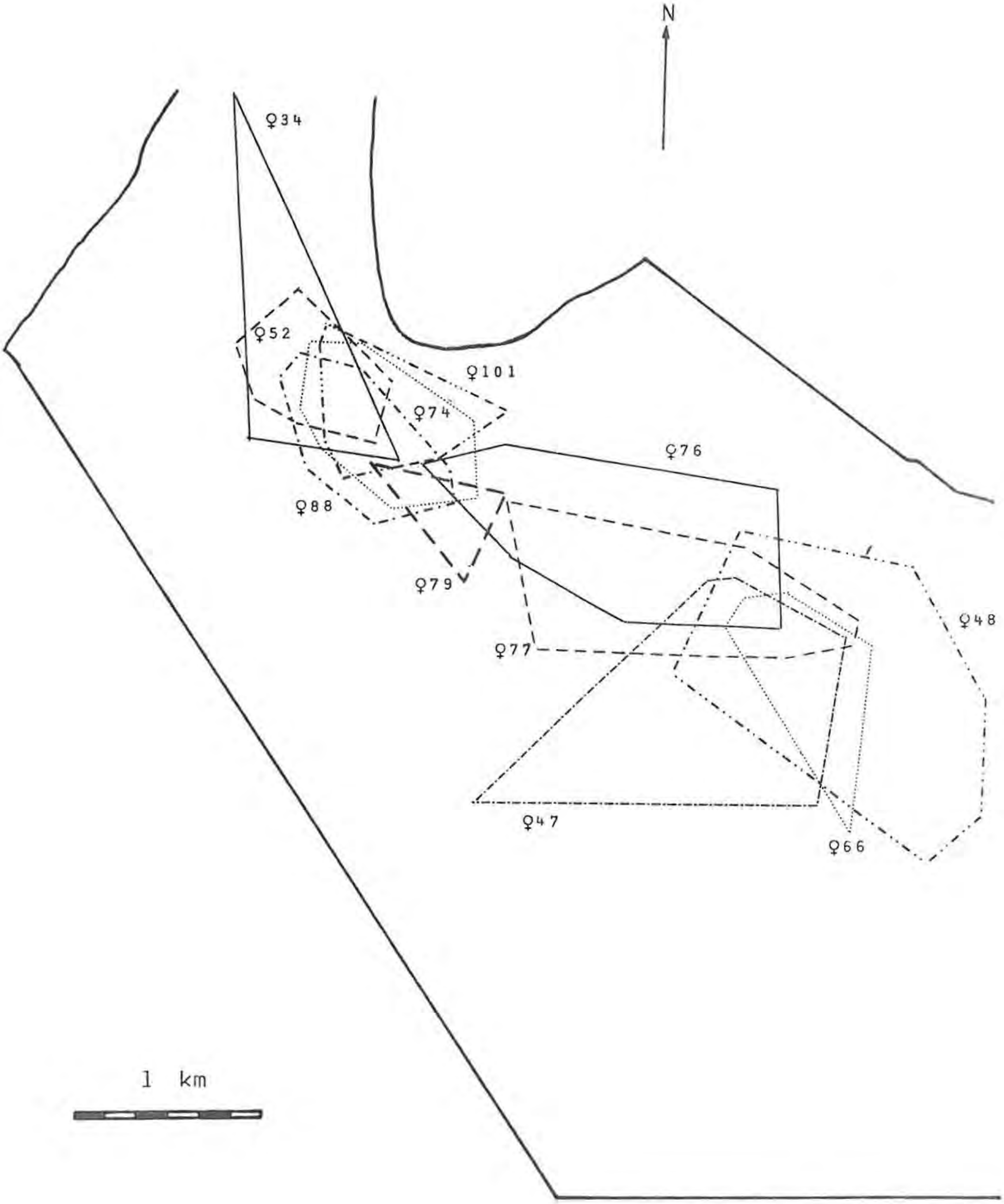
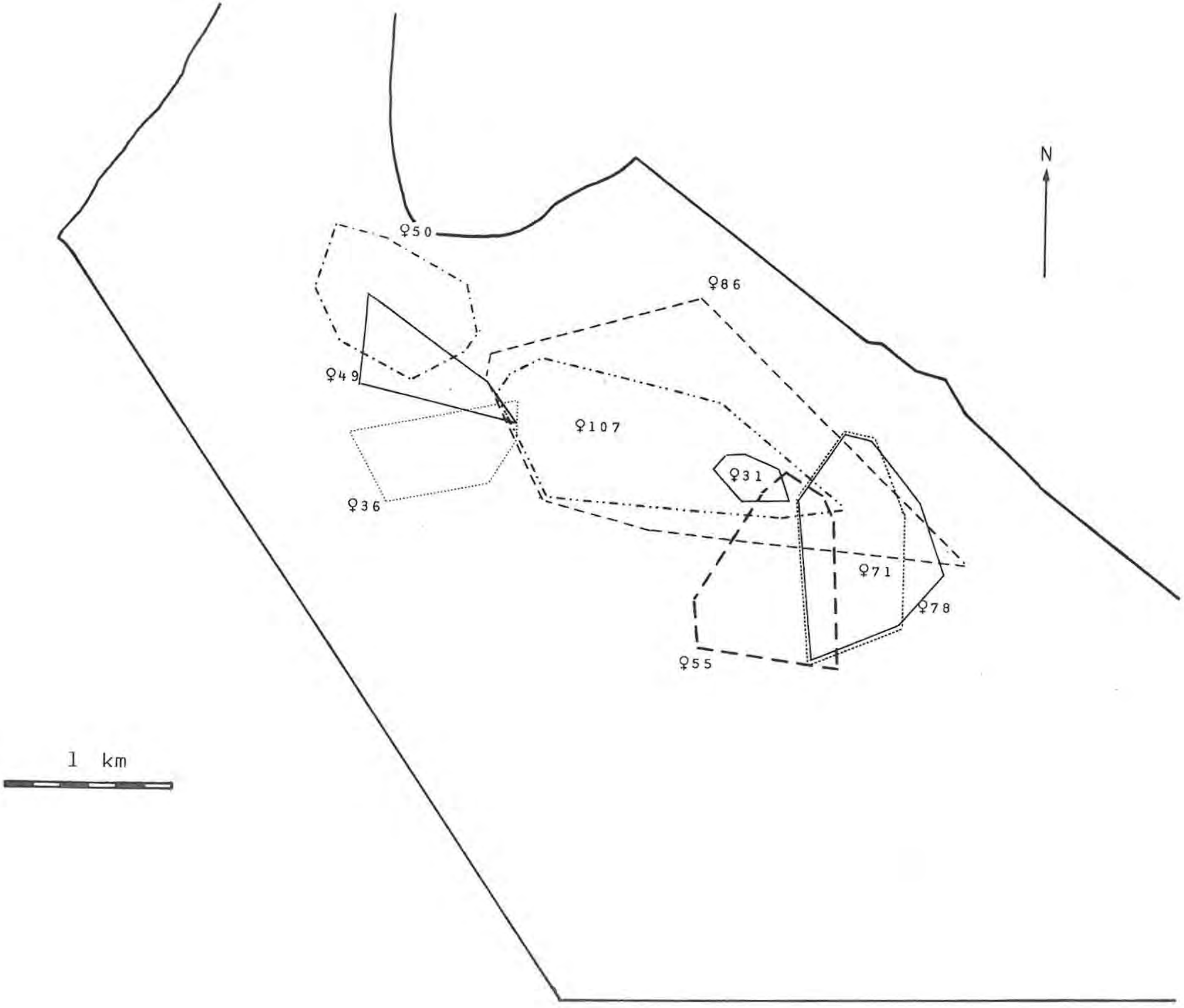

N
♀34
♀52
♀101
♀74
♀76
♀88
♀79
♀77
♀48
♀47
♀66
1 km

FIG. 7.13 Home ranges of nine collared female kudu each seen at least ten times on the A.V.K.R.


N
♀50
♀86
♀49
♀107
♀36
♀31
♀71
♀78
♀55
1 km

Owen-Smith 1977, 1979). Reduced range sizes on the Reserve must be due to either higher productivity (Jewell 1966) and/or less competition (Leuthold 1977). Significant range size differences between kudu inhabiting E. bothae bush and non-succulent bush infer that kudu in E. bothae bush obtain all their energy requirements from a smaller, more productive area. This is corroborated by the home range sizes of kudu inhabiting both vegetation types, which are intermediate between those of kudu confined to non-succulent and E. bothae bush. Contrary to the result of Simpson & Cowie (1967) and Underwood (1978), sex differences in habitat preference were not apparent.

Harestad and Bunnell (1979) have shown that home range size is related empirically to body weight, and that differences in the latter account for a large portion of the differences between male and female (and also subadult and adult) home ranges in many mammals. Leuthold (1977) has also noted such a relationship. Since kudu cows are approximately 66% of the weight of males, this could account for their home ranges being on average, 30% smaller than those of adult bulls in this study.

Subadult males are closely associated with their maternal groups (Chapter 8) and have smaller ranges than adult males. The maternal bond weakens when the subadult male is two years old, and the male's range size subsequently increases (Fig. 7.3 male no. 94). Field observations suggested that home ranges of these males, a) may still incorporate the entire maternal range, b) but increase by up to 50%, and c) then remain relatively constant in size, if not location, (Table 7.4). However, radio-tracking results indicate that young adult males may range over much wider areas and become more sedentary only later in life (Table 7.3, male no. 69). Returned collars from two 3 year old bulls shot on a neighbouring farm some 5 km away confirm this. The same trends are apparent in other male Tragelaphines (Allsopp 1970, 1978; Waser 1975a; Leuthold 1979).

Since field sightings were limited to the Reserve, and were influenced by accessibility and range of visibility, the resultant ranges should be regarded as minimal. Examination of the extent of overlap in individual ranges determined from field sightings and from radio-tracking (the latter is not limited to the same extent) confirm this (Fig. 7.2).

However, results obtained from the three most frequently sighted adult male and female kudu suggest that (with the exception of female 76, see below) an asymptotic relationship may exist between home range size and sighting frequency/length of observation period (Figs. 7.3 and 7.4). The absence of significant correlations between female home range size and sighting frequency/length of observation period in Table 7.5, indicates that the recorded range sizes do reflect the true extent of movement in females. Conversely, significant correlation coefficients from male data suggest that male home range sizes are underestimates (i.e. that a linear rather than an asymptotic relationship exists), largely because a) males have larger ranges than females, b) male ranges were determined from fewer sightings, and c) these sightings were often obtained over shorter periods of observation (Table 7.1).

The atypical increase in home range size of female 76, shown in Fig. 7.4 deserves further comment. Prior to April 1979 this cow was always seen in E. bothae bush, but from April to October 1979 was only sighted in non-succulent bush within the fenced Buffalo Camp. During this latter period her home range size increased from 39 ha to 145 ha. She was lactating in April when recaptured, and was frequently seen with a calf in the Buffalo Camp. On one occasion she was seen to jump the fence and run off into the E. bothae bush, leaving the stranded calf behind. It would therefore appear that the calf was responsible for the shift in range. The cow probably gave birth in the Buffalo Camp, and continued to frequent her range in the E. bothae bush during the lying-out period. As the calf became older (but still unable to clear the 1,4 m high fence), female 76 probably spent most or all of her time with it in this non-succulent bush. Since this vegetation is more open, these kudu would have foraged over a larger area. The cow and calf were still in the Camp in October, but evidently the calf had managed to jump the fence by the end of November, when it was seen with its mother in her former range. The home range shift was therefore probably temporary. No other temporary or permanent range shifts were recorded during this study.

The small home range sizes recorded on the Reserve indicate that kudu in this area do not exhibit extensive seasonal movements. Individual ranges separated according to season (Figs. 7.5 and 7.6) confirm this. While observations suggest that a greater portion of the range is utilized by both males and females during the autumn and winter months, this may simply be due to the greater number of sightings obtained during this period (Table 7.6).

These results are in contrast to those from studies in Rhodesia and Botswana where kudu showed marked seasonal movements (of unstated extent) in response to seasonal fluctuations in temperature and the availability of water, food and cover (Simpson & Cowie 1967; Simpson 1972b; Sheppe & Haas 1976). There is no evidence from this study to suggest that kudu select higher warmer areas during the winter months. Further, surface water availability appears to be of little importance. Kudu were never seen drinking during the day (the preferred time for this activity elsewhere, Weir & Davidson 1965; Jarman 1972) and range sizes were unaffected during the early months of 1979 when most dams and water courses on the Reserve were dry. (Kudu were similarly unaffected by lack of water in other areas, Pienaar 1963; Bigalke 1974; Hirst 1975.) It is therefore extremely probable that kudu inhabiting the Fish River Valley bushveld obtain all or most of their water requirements from the succulent vegetation. Thus, since extensive seasonal movements are not evident from this study, it must be concluded that conditions remain optimal for kudu on the Reserve throughout the year.

Exclusive home ranges do not appear to occur in kudu, because there is substantial overlap within and between all sex and age classes (Figs. 7.7 to 7.13). The question of territoriality in adult males has yet to be confirmed or refuted (Jarman 1974; Owen-Smith 1975; Leuthold 1977) and will be discussed in Chapter 9. However, the considerable extent of home range overlap (up to 100%, Fig. 7.7.) infers that any exclusive use of even a small portion of a home range must involve temporal rather than spatial separation.

Chapter 8

SOCIAL ORGANISATION

8.1 Introduction

Until recently the social organisation of most Tragelaphines was poorly understood, which is still true for the greater kudu. Only one detailed account of this species, concerning grouping patterns and habitat preferences, has been published (Underwood 1978). Other, largely general accounts are based on incidental observations made during culling operations (Wilson 1965, 1970; Simpson 1968). This lack of information (which is probably a consequence of the habitat preferences of the kudu) is further evident in reviews of ungulate social organisation where several tantalizing questions, specifically concerning social relations within the Tragelaphines, have been posed, (Estes 1974; Jarman 1974; Owen-Smith 1975, 1977; Leuthold 1977).

The aim of this study is to provide a sound understanding of the social biology of the greater kudu on the Andries Vosloo Kudu Reserve. Such an understanding is vital to the successful management of any natural population (Geist & Walther 1974; Leuthold 1977). The results are considered in relation to other aspects of the ecology of the kudu, and to other congeneric species.

8.2 Methods

General field procedures have previously been described in Chapters 4 and 6. Since groups could not be followed from a vehicle or on foot (due to the nature of the terrain, the vegetation, and excessive flight distances) they were constantly observed whenever possible for several minutes before the size and composition were recorded. This was necessary because during active periods, individuals would often be partially or entirely hidden in thick vegetation. In spite of these precautions, it is highly probable that some group members were simply not detected, and group size records must therefore be regarded as minimal values. All solitary animals were treated as groups.

Aspects of social and nonsocial behaviour were also recorded from observation of wild and semi-tame kudu, the latter facilitating photographic records.

Temporal and local differences in mean group size and the proportions of animals occurring in different group types were tested for statistical significance by means of d-tests and χ^2 tests (Bailey 1959).

8.3 Results

8.3.1 Presentation of Data

The frequency distribution of group size (Figs. 8.1 to 8.3) illustrate actual grouping patterns but in terms of the population it is more meaningful to determine the proportion of animals occurring in groups of a certain size (Leuthold 1979). Such proportions are therefore shown as dashed histograms in all group size frequency distribution figures.

Highly skewed group size distributions (Figs. 8.1 to 8.3) infer that typical group size (T.G.S.) which expresses the size of group in which the average animal finds itself (Jarman 1974) is more biologically meaningfulthan mean group size (M.G.S.). However, M.G.S. values favour comparisons between different sets of data (Leuthold & Leuthold 1975b); consequently both mean and typical group sizes are presented.

8.3.2 Overall Group Size

A total of 5670 kudu, in 1650 groups, were sighted between December 1977 and November 1979. This includes sightings recorded during two darting operations (209 kudu, 75 groups). As the darting was often highly selective, and the extent of disturbance caused by the helicopter could not be assessed, all data recorded during these exercises have been omitted.

Before data were combined (to increase the sample sizes for further analyses), group size records obtained from

a) different years
b) aerial and ground sightings and
c) different areas on the Reserve were compared to test for any significant differences.

a) Interannual differences in group size.

Group sizes recorded in 1978 did not differ significantly from those obtained in 1979, and consequently data from both years and

FIG. 8.1 Ground sighting frequency distribution of group sizes expressed as a % of all groups (——), and proportions of kudu in groups of different sizes expressed as a % of all kudu seen (----).

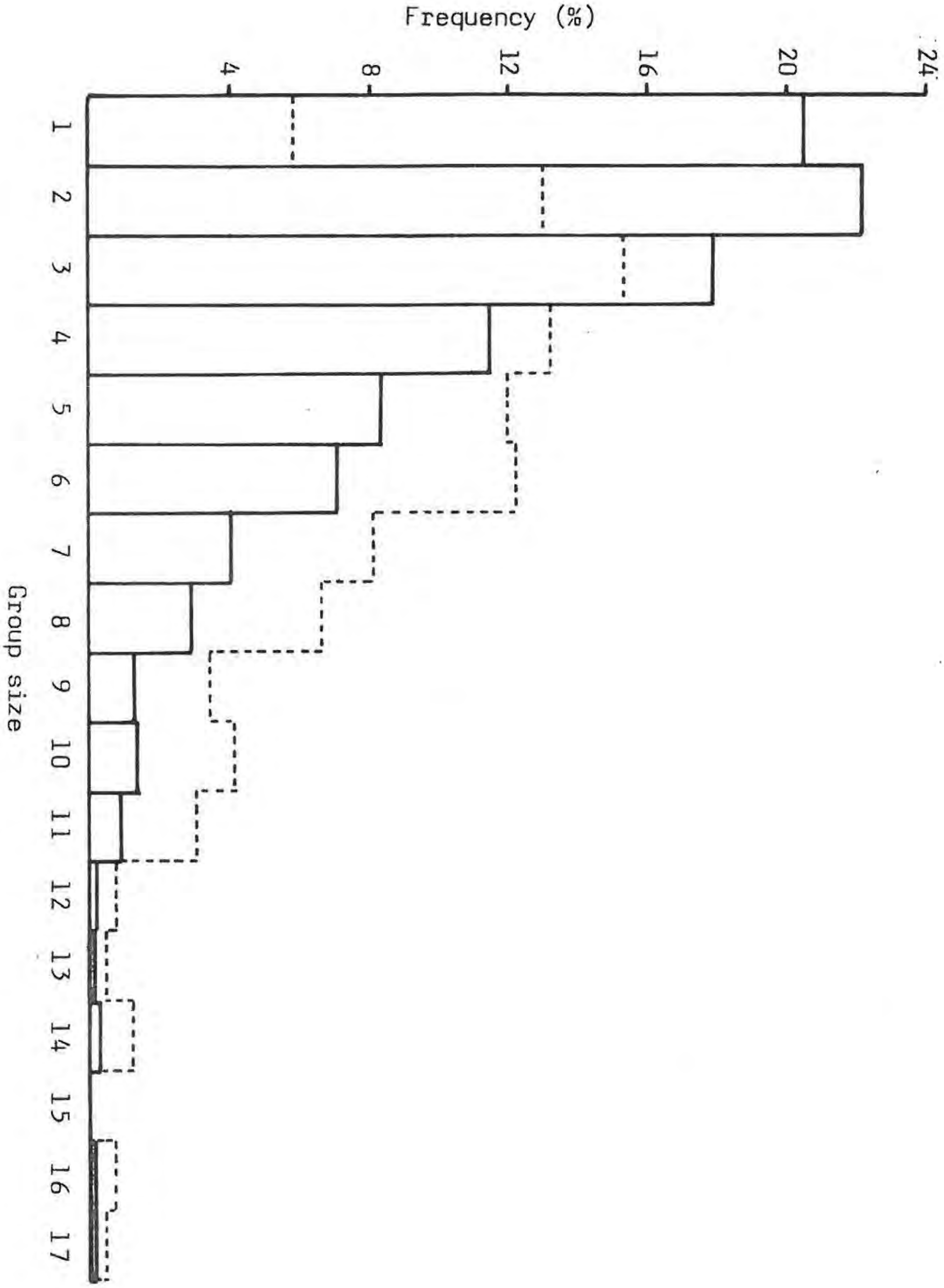

Frequency (%)
4
8
12
16
20
24
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Group size

FIG. 8.2 Aerial sighting frequency distribution of group sizes expressed as a % of all groups (——), and proportions of kudu in groups of different sizes expressed as a % of all kudu seen (----).

123a

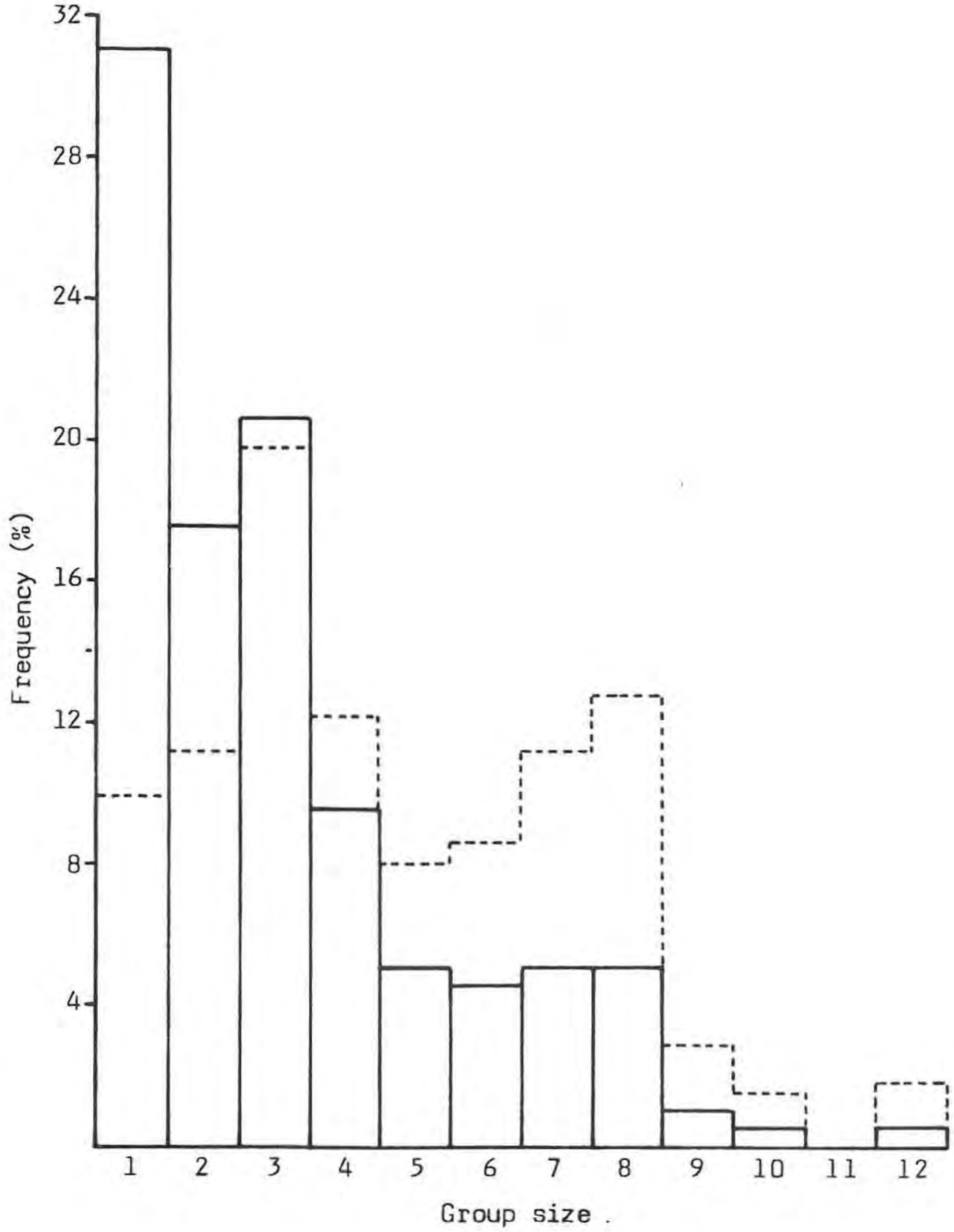
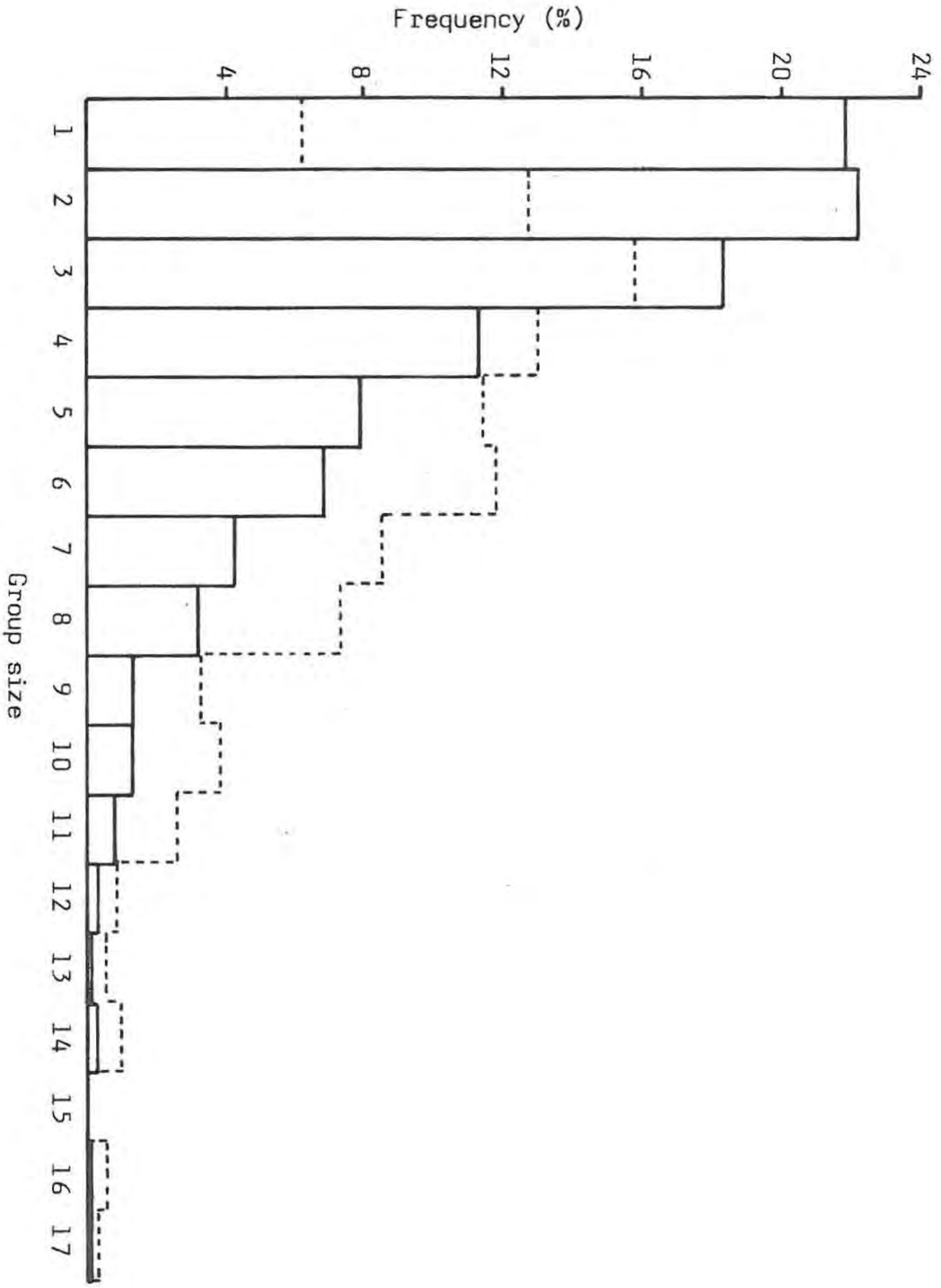


FIG. 8.3 Ground and aerial frequency distribution of group sizes expressed as a % of all groups (——), and proportions of kudu in groups of different sizes expressed as a % of all kudu seen (----).


Frequency (%)
4
8
12
16
20
24
Group size
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

from the same months were combined in all subsequent analyses.

b) Aerial and ground sightings

Group sizes from aerial censuses (Fig. 8.2) differed significantly from those obtained from all ground observations (Fig. 8.1 and Table 8.1, d = 2,25, p<0,02). However, no significant differences were evident when intramonthly comparisons were made between aerial and ground censuses either locally or over the entire study area. As a result, all aerial and ground sighting data have been combined (Fig. 8.3).

c) Local variations in group size

Initial examination of all aerial and ground sightings suggested that group sizes varied in different habitats. Kudu herds were significantly larger in non-succulent bush than in Euphorbia bothae bush (d = 5,37, p<0,001). Such differences, if biologically real, would greatly bias overall group size records on the Reserve, since fluctuations in the frequency of sightings and the time spent observing in different areas were inevitable. However, as indicated above, group sizes in these two habitats did not differ significantly when comparisons were made within the same month. Similar results were obtained when group sizes of kudu inhabiting other vegetation types on the Reserve were compared, and therefore sightings from all areas have been combined.

Since differences in group size were only significant when records obtained over several months were compared, this inferred that grouping patterns varied seasonally. Rainfall is considered to be the most likely environmental factor responsible for such seasonal changes (Jarman & Jarman 1974; Leuthold 1976, 1977, 1979; Rodgers 1977). To examine this, monthly mean group sizes were determined (Table 8.2) and correlation coefficients calculated between M.G.S. vs rainfall:
i) within the same month
ii) in the same and previous months
iii) in the preceding month
iv) in the two preceding months
v) in the three preceding months.

No significant relationships were evident from any of these combinations.

However, when monthly mean group sizes were compared with the

TABLE 8.1 Mean and typical group sizes of kudu seen on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

	No. kudu	No. groups	Mean group size	Typical group size
Ground sightings	4836	1375	3,5±2,5	5,3
Aerial sightings	625	200	3,1±2,3	4,8
Total	5461	1575	3,5±2,4	5,2

TABLE 8.2 Monthly mean and typical group sizes recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Month	No. kudu	No. groups	Mean group size	S.D.	d*	Typical group size
Jan	198	62	3,2	2,1		4,5
Feb	228	86	2,7	1,7	4,22 p<0,001	3,7
Mar	259	86	3,0	2,0	2,06 p<0,05	4,3
Apr	550	163	3,4	2,6		5,0
May	579	165	3,5	2,6		5,4
Jun	601	152	4,0	2,8	2,08 p<0,05	5,9
Jul	495	135	3,7	2,7		5,6
Aug	416	117	3,6	2,3		5,0
Sep	290	77	3,8	2,5		5,5
Oct	614	158	3,9	2,7		5,5
Nov	508	145	3,5	2,3		5,0
Dec	723	229	3,2	2,2	1,99 p<0,05	4,6
Overall	5461	1575	3,5	2,5		5,2

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

annual mean group size value, significantly smaller groups were evident in December ($d = 1,99$, $p<0,05$), February ($d = 4,22$, $p<0,001$) and March ($d = 2,06$, $p<0,05$) and significantly larger groups in June ($d = 2,08$, $p<0,05$). More pronounced differences were evident in the mean sizes of group types described below. Results suggested that changes in the social organisation may be related to the reproductive cycle. Some of these variations could be obscured if monthly data were combined into traditional (climatic) seasons, and for this reason, only data from the same months have been summed.

8.3.3 Group Composition

Using the criteria presented in Chapter 6, it was possible to distinguish the same nine group types described by Anderson (1978) for nyala. These were:-

I Solitary adult females (at least two years old) Plate 8.1a
II Solitary adult males (at least two years old) Plate 8.1b
III Solitary subadult (yearling) males
IV Solitary subadult (yearling) females
V Solitary calves (under one year of age)
VI Bachelor herds (containing two or more males of any age) Plate 8.1d
VII One-female groups (containing one adult female and at least one subadult of either sex and/or a calf) Plate 8.1c
VIII Female groups* (containing two or more adult females or one-female groups Plate 8.1f and g
IX Mixed groups (containing at least one adult female, with or without young, and at least one adult male) Plate 8.1e and h.

Several of these group types may be interpreted as temporary/permanent combinations of others. The stability of these groups should be mentioned briefly before they are discussed in more detail. The basic social unit of the greater kudu is the female group, which is a stable, family or kinship group. The one-female group is probably a fragmented portion of the female group, rather than the latter being

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* As Walther (1972) mentioned, the term "female group" is slightly misleading since subadult males may be present, but the term is preferable to "nursery herds" (Estes 1967, 1974; Underwood 1975) which implies that such groups include unweaned calves.

PLATE 8.1 Aerial photographs of kudu group-types.

a) Solitary adult female (collared) in *E. bothae* scrub.

b) Solitary adult male (collared, almost 4 years old) in non-succulent bush.

c) One-female group consisting of an adult female (collared), a subadult male and a male calf in *E. bothae* scrub.


a


b

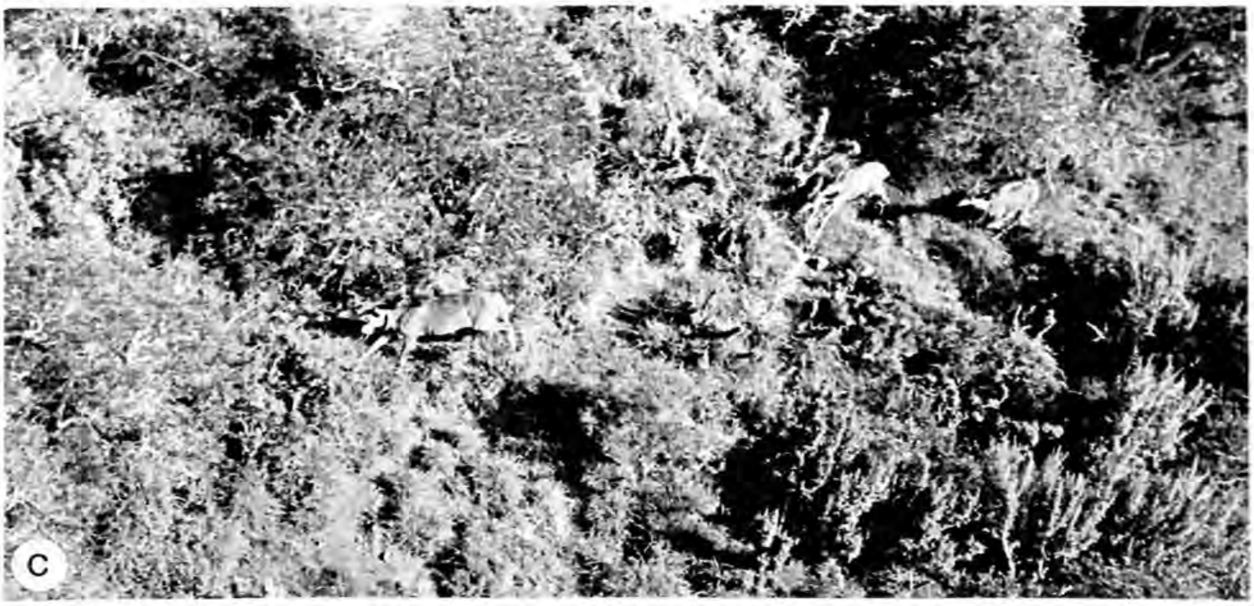

c

PLATE 8.1 continued

d) Bachelor group consisting of two collared 5+ year old males. Note radio collar on leading bull. E. bothae scrub.

e) Part of a mixed group (actually consisting of two adult females and a 5+ year old collared male). Non-succulent bush.

f) Female group consisting of two adult females and a subadult male. E. bothae scrub.

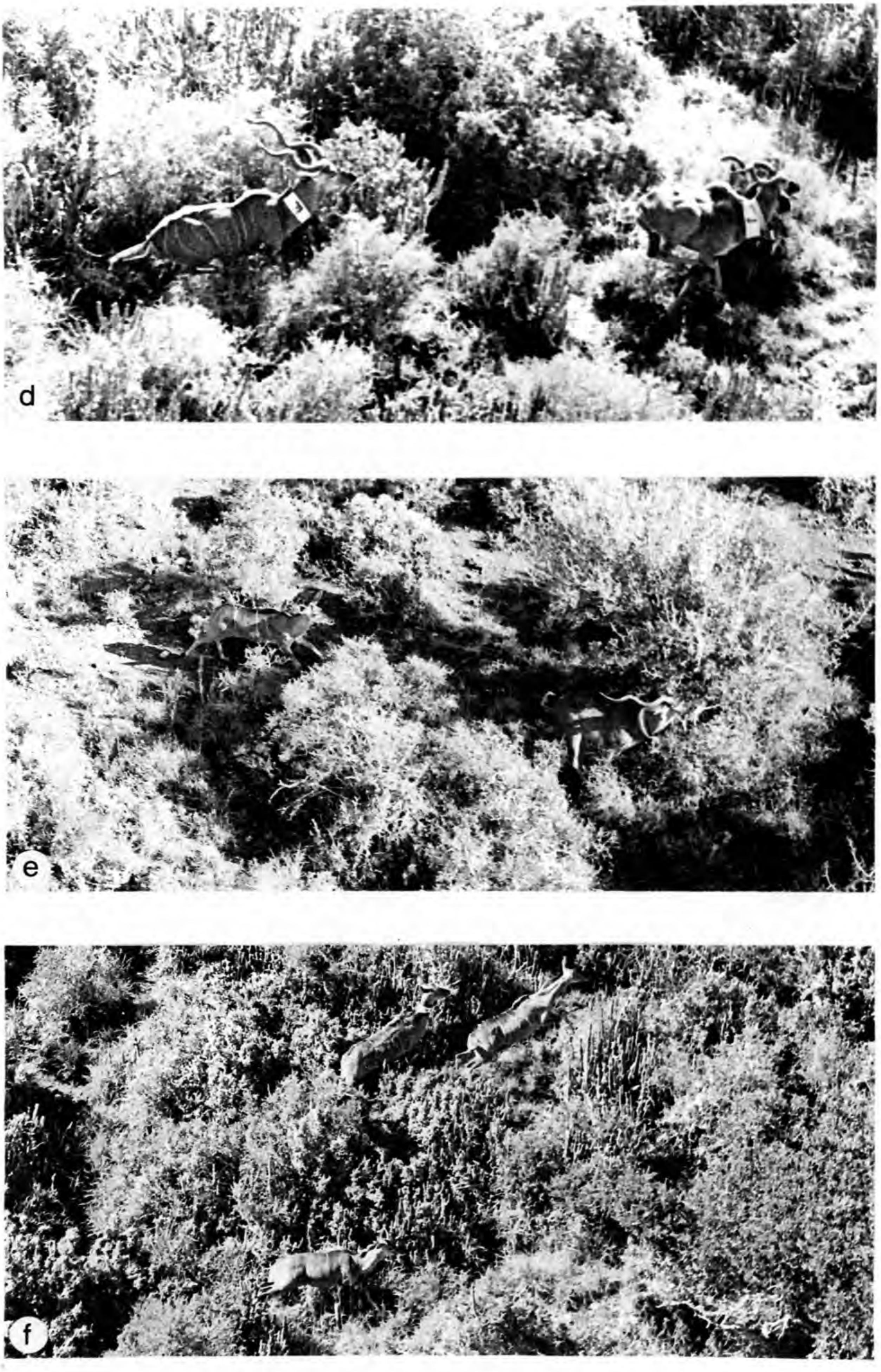
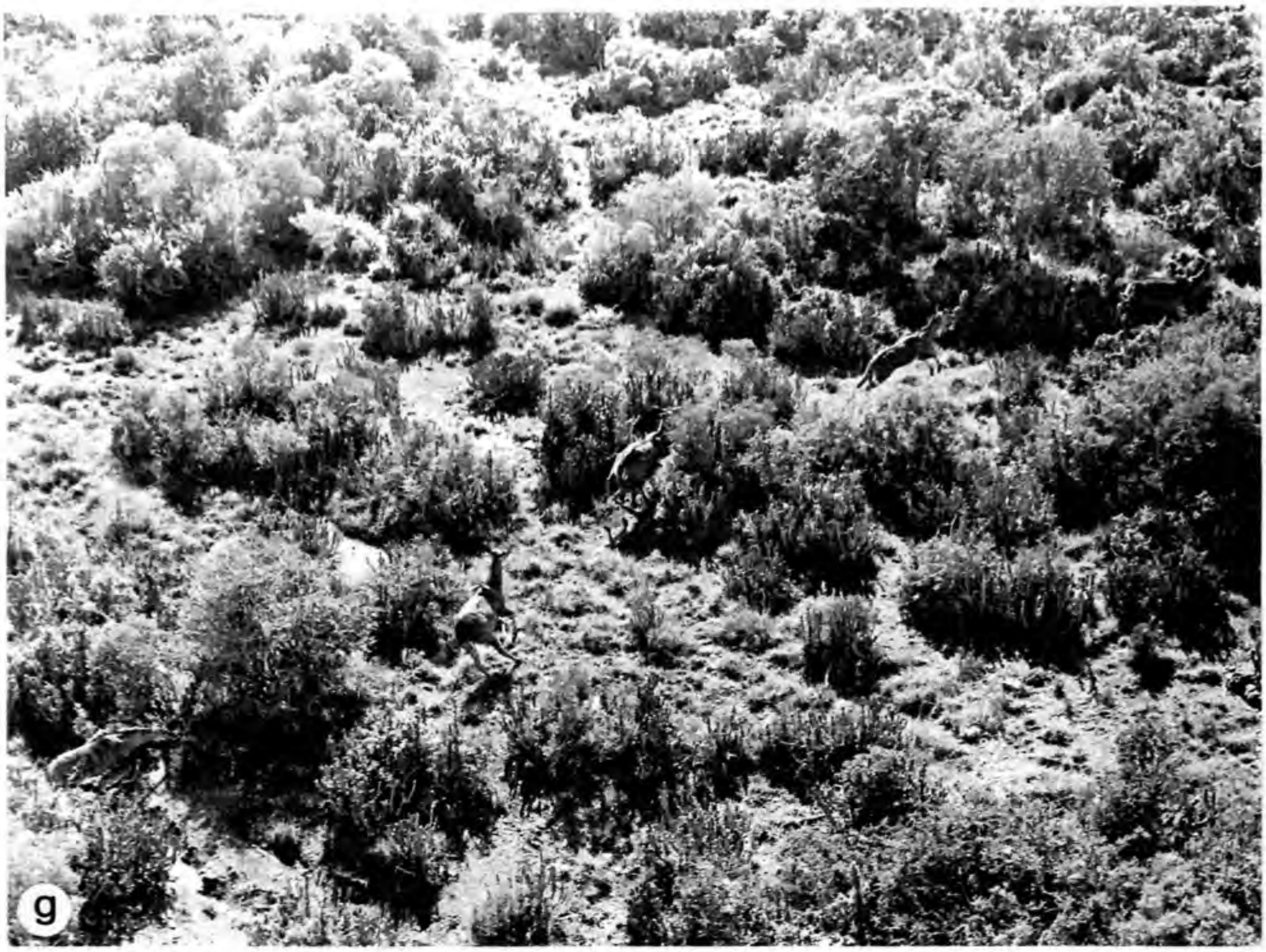

d
e
f

PLATE 8.1 continued.

g) Female group consisting of three adult females, a subadult female (second from right) and a subadult male (following). E. bothae scrub.

h) Mixed group consisting of three adult females and two 4 year old males. E. bothae scrub.


g


h

combinations of one-female groups. In contrast, adult males form loose associations with individuals of either sex.

8.3.4 Sighting frequencies of group-types

As with group size data, group composition records of 1978 and 1979 were compared. Overall, the interannual difference was significant (χ^2 = 16,16, d.f. = 8, p<0,05). However, this was solely due to a significantly lower proportion of solitary subadult males in 1979 (χ^2 = 6,95, d.f. = 1, p<0,01), resulting from the poor calf survival in 1978 (Fig. 6.4). Interannual differences between the proportions of all other group types were not significant, and consequently data from both years have been combined. Sighting frequencies and sizes of these group-types are presented in Table 8.3.

Monthly sighting frequencies of each adult group-type (expressed as a percentage of all groups seen each month) are presented in Figs. 8.4 to 8.6, 8.8, 8.10 and 8.12. Significant variations in these sighting frequencies are detailed below.

8.3.4.1 Solitary kudu

Single animals constituted 21,8% of all sighted groups, but only 6,3% of all observed kudu. Lone adults formed 91,5% of all solitary group sightings. The infrequent observations of solitary subadults and calves precluded further analysis.

The sex ratio of solitary adults was 145 males : 100 females (Table 8.3) which differed significantly from the population sex ratio of 45 males : 100 females (χ^2 = 116,7, d.f. = 1, p<0,001). Even with the inclusion of single adult females with a subadult or calf the ratio 82 males : 100 females still differed significantly from the population ratio (χ^2 = 38,3, d.f. = 1, p<0,001).

The proportion of solitary adult male group sightings (Fig. 8.4) increased significantly in April (χ^2 = 7,57, d.f. = 1, p<0,01), and decreased markedly during October (χ^2 = 4,26, d.f. = 1, p<0.05). Variations in the monthly sighting frequencies of solitary adult female groups (Fig. 8.5) were not significant.

8.3.4.2 Bachelor groups

Bachelor groups constituted 10,6% of all sightings, but were

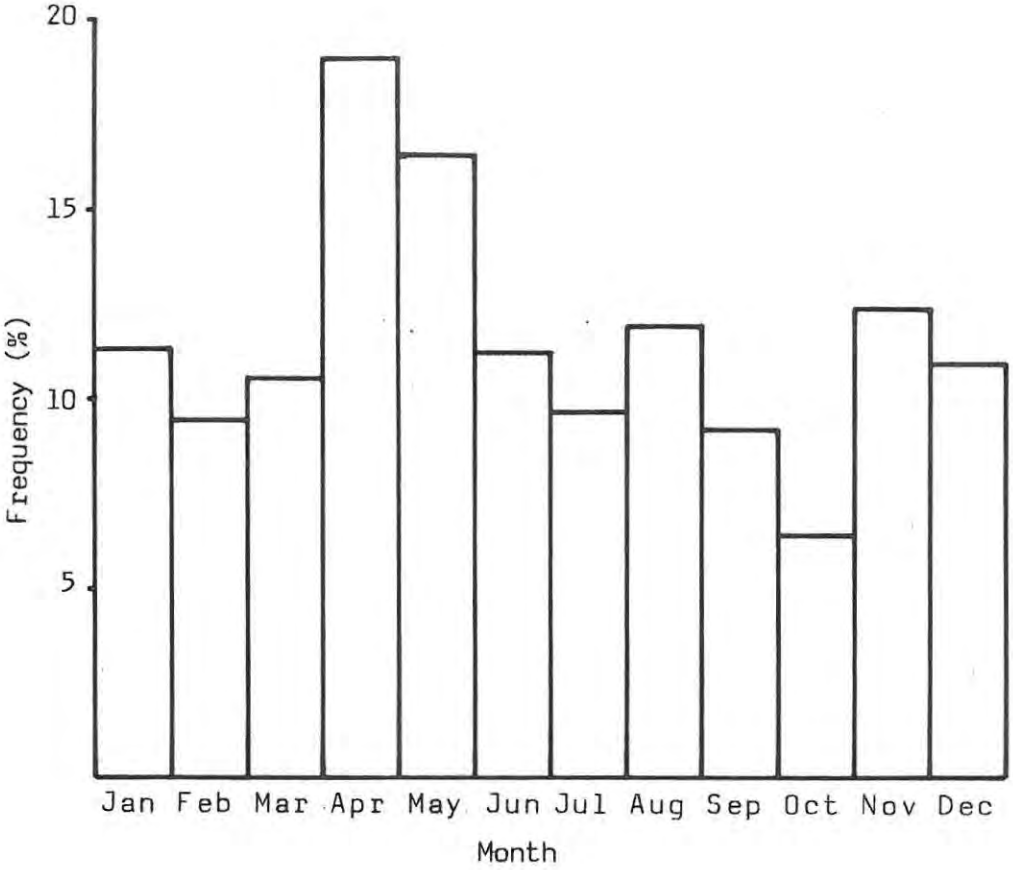
TABLE 8.3 Sighting frequencies and sizes of group-types* seen on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

	Sol Ad ♂	Sol Ad ♀	Sol Sub ♂	Sol Sub ♀	Sol Calf	♂♂ group	1 ♀ group	♀♀ group	Ad ♂ + Ad ♀ groups	Unclassified groups	Total
No. of groups seen	186	128	15	7	7	166	98	577	389	2	1575
% of all groups	11,8%	8,1%	1,0%	0,4%	0,4%	10,6%	6,2%	36,7%	24,7%	0.1%	
No. of animals in group-type	186	128	15	7	7	432	231	2256	2192	7	5461
% of animals in group-type	3,4%	2,3%	0,3%	0,1%	0,1%	7,9%	4,2%	41,3%	40,1%	0.1%	
Mean group size (±S.D.)	1,0	1,0	1,0	1,0	1,0	2,6±0,9	2,4±0,7	3,9±1,8	5,6±2,8		3,5±2,4
Typical group size	1,0	1,0	1,0	1,0	1,0	2,9	2,5	4,7	7,0		5,2

* see text for classification of group-types.

FIG. 8.4 Sighting frequencies of solitary adult males expressed as a % of all groups seen per month.

FIG. 8.5 Sighting frequencies of solitary adult females expressed as a % of all groups seen per month.


20
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Frequency (%)
Jan
Feb
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Apr
May
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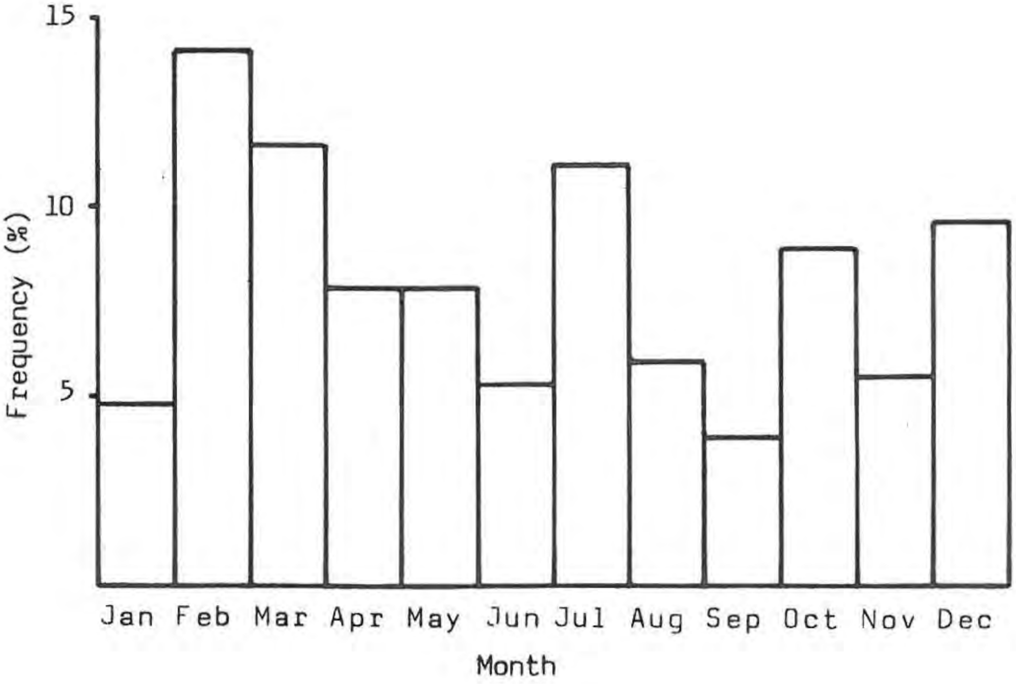
Dec
Month


15
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Frequency (%)
Jan
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Dec
Month

recorded significantly more often during February and October (χ^2 = 4,00, d.f. = 1, p<0,05 and χ^2 = 5,88, d.f. = 1, p<0,05 respectively), and less frequently during April (χ^2 = 7,10, d.f. = 1, p<0,01) and May (χ^2 = 4,76, d.f. = 1, p<0,05). These monthly variations are shown in Fig. 8.6.

Bachelor group size ranged from two to six males (Fig. 8.7) with a mean and typical size of 2,6 (±0,9) and 2,9 respectively. Monthly mean and typical group sizes (Table 8.4) were significantly smaller than the annual mean in January (d = 2,627, p<0,01), April (d = 8,34, p<0,001) and May (d = 3,331, p<0,001).

The composition of these groups is shown in Table 8.5. Seventy-four percent of all bachelor groups were peer groups. Five year old males were seen in 50 bachelor groups (30% of total) and of these 64% consisted of five year old males only. Peer groups formed 48%, 60% and 63% of all groups containing four year, three year and subadult males respectively. However, only 17% of the bachelor groups containing two year olds were peer groups. These males were most commonly seen in the company of older bulls (Table 8.5).

Three year old peer groups were larger than those of five year olds (d = 2,30, p<0,05), four year olds (d = 2,01, p<0,05) and subadult males (d = 4,23, p<0,001) while five year old and four year old peer groups were significantly larger than those of subadults (which never exceed 2 males) (d = 3,04, p<0,01 and d = 3,32, p<0.001 respectively).

8.3.4.3 One-female groups

One-female groups constituted 6,2% of all sighted groups (Table 8.3) but this proportion increased significantly during March (Fig. 8.8, χ^2 = 7,2, d.f. = 1, p<0.01).

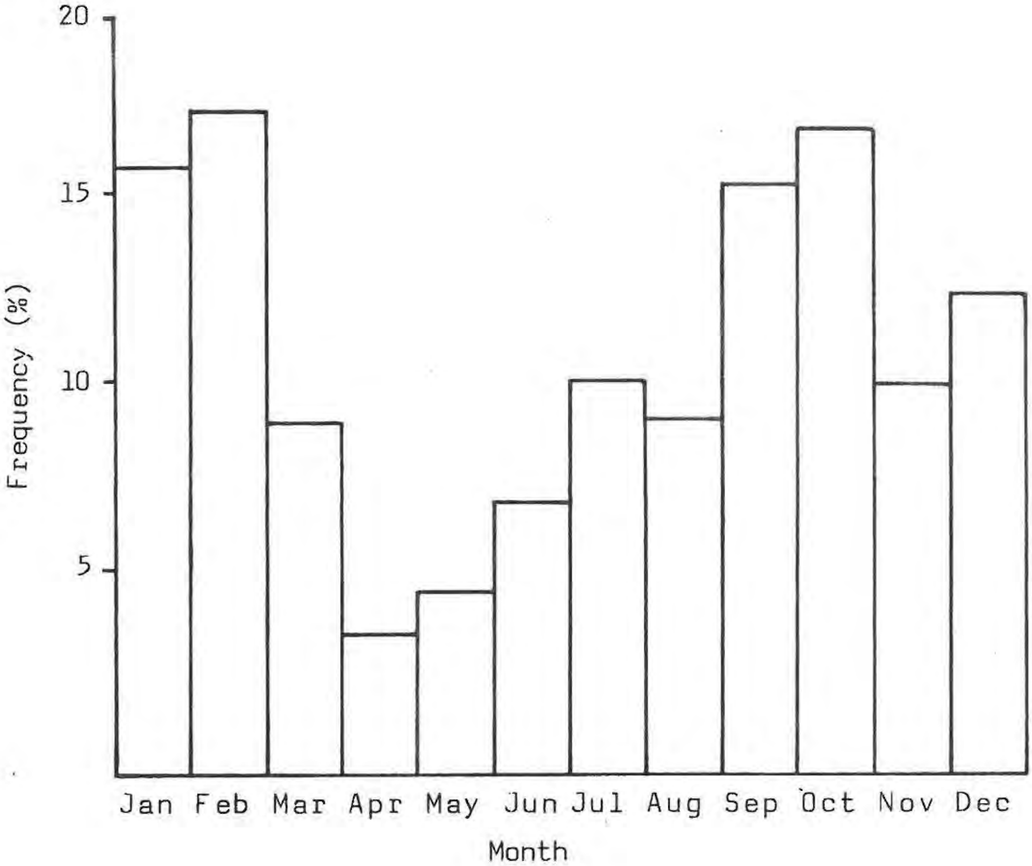
The majority of one-female groups consisted of two animals (i.e. an adult female and one offspring) and group size never exceeded six (Fig. 8.9). Mean and typical group sizes were 2,4 (±0,7) and 2,6 respectively. All groups sighted during January and July contained only two kudu (Table 8.6) and were significantly smaller (d = 5,12, p<0,001 for both months) than the one-female groups seen throughout the rest of the year. One-female groups were significantly smaller than bachelor groups (d = 2,01, p<0,05).

Cows were more commonly observed with subadults (53%) than with either calves (34%) or with subadults and calves (13%). The majority

FIG. 8.6 Sighting frequencies of bachelor groups expressed as a % of all groups seen per month.

FIG. 8.7 Frequency distribution of bachelor groups (——) and the proportion (%) of males within bachelor groups of different sizes (----).

136a


20
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Frequency (%)
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Oct
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Dec
Month

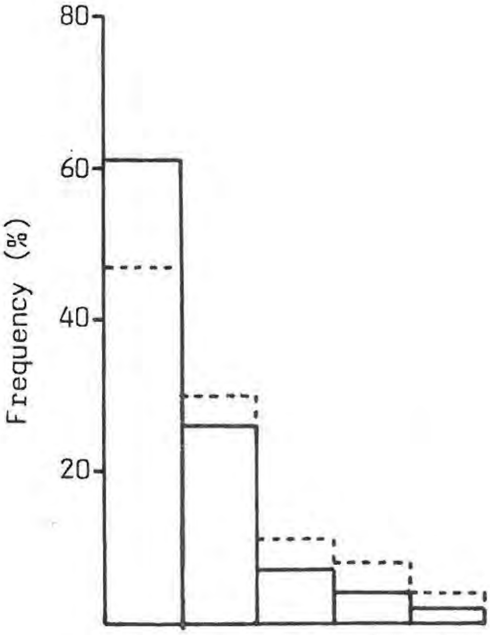

80
60
40
20
Frequency (%)
2
3
4
5
6
Group size

TABLE 8.4 Monthly mean and typical bachelor group sizes recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Month	No. kudu	No. groups	Mean group size	S.D.	d*	Typical group size
Jan	22	10	2,2	0,4	2,63 p<0.01	2,3
Feb	43	15	2,9	0,9		3.1
Mar	20	8	2,5	0,5		2,6
Apr	12	6	2,0	0,0	8,34 p<0,001	2,0
May	17	8	2,1	0.4	3,31 p<0,001	2,2
Jun	26	11	2,4	0,7		2,5
Jul	37	14	2,6	0,9		2,9
Aug	29	11	2,6	1,0		3,0
Sep	28	12	2,3	0,5		2,4
Oct	76	27	2,8	1,1		3,2
Nov	45	15	3,0	1,5		3,7
Dec	77	29	2,7	0,9		2,9
Overall	432	166	2,6	0,9		2,9

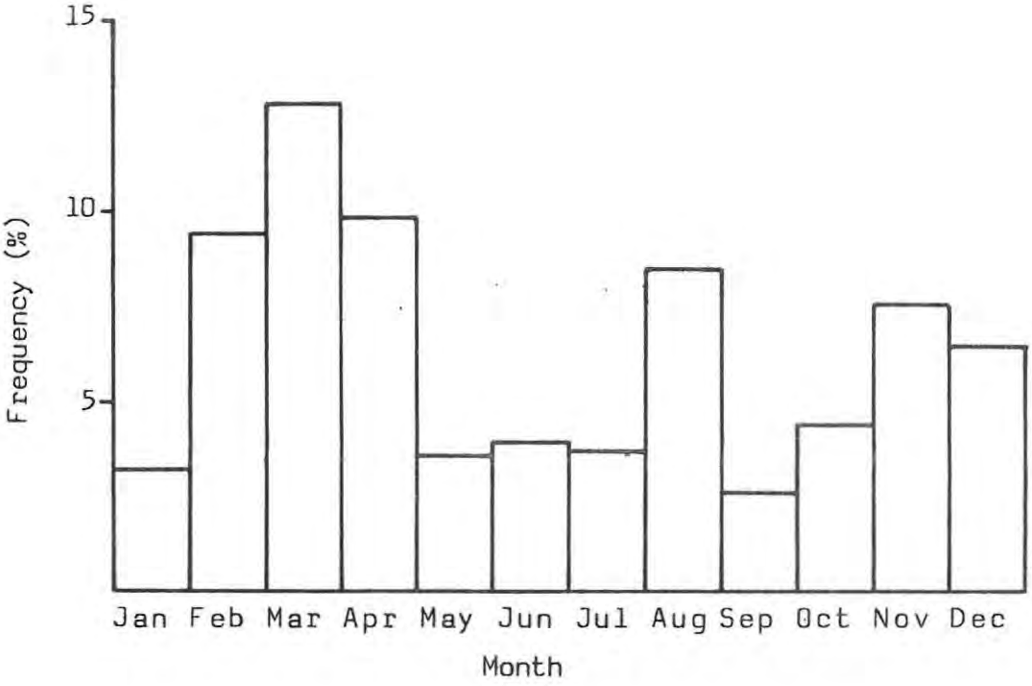
* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

TABLE 8.5 Sizes and composition of bachelor groups recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Group Composition	No. groups	No. males	Mean group size ± S.D.	Range
All 5+yr olds	32(20,4%)	73(17,8%)	2,3 ± 0,5	2-4
All 4yr olds	39(24,8%)	91(22,1%)	2,3 ± 0,6	2-5
All 3yr olds	37(23,6%)	101(24,6%)	2,7 ± 1,1	2-6
All 2yr olds	3(1,9%)	7(1,7%)	2,3	2-3
All 1yr olds	5(3,2%)	19(2,4%)	2,0 ± 0,0	2
5y + 4y	10(6,4%)	27(6,6%)	2,7 ± 0,8	2-4
5y + 4y + 3y	3(1,9%)	12(2,9%)	4,0	3-6
5y + 3y	2(1,3%)	7(1,7%)	3,5	2-5
5y + 3y + 2y	2(1,3%)	10(2,4%)	5,0	4-6
5y + 1y	1(0,6%)	2(0,5%)	2,0	2
4y + 3y	9(5,7%)	29(7,1%)	3,2 ± 1,2	2-5
4y + 3y + 2y	2(1,3%)	7(1,7%)	3,5	3-4
4y + 2y	4(2,5%)	9(2,2%)	2,3 ± 0,5	2-3
3y + 2y	6(3,8%)	22(5,4%)	3,7 ± 0,8	3-5
3y + 1y	1(0,6%)	2(0,5%)	2,0	2
2y + 1y	1(0,6%)	2(0,5%)	2,0	2
Subtotal	157	411	2,6 ± 0,94	2-6
Unaged bachelor groups	9	21	2,33 ± 0,5	2-3
Total	166	432	2,6 ± 0,93	2-6

FIG. 8.8 Sighting frequencies of one-female groups expressed as a % of all groups seen per month.

FIG. 8.9 Frequency distribution of one-female groups (——), and the proportion (%) of kudu within one-female groups of different sizes (----).


15
10
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Frequency (%)
Jan
Feb
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May
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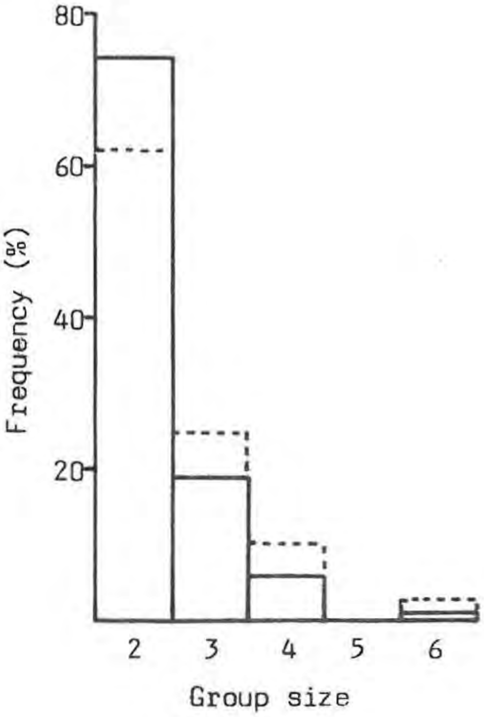
Dec
Month


80
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40
20
Frequency (%)
2
3
4
5
6
Group size

TABLE 8.6 Monthly mean and typical group sizes of one-female groups recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Month	No. kudu	No. groups	Mean group size	S.D.	d*	Typical group size
Jan	4	2	2,0	0,0	5,12 p<0,001	2,0
Feb	16	7	2,3	0,5		2,4
Mar	27	11	2,5	0,7		2,6
Apr	39	16	2,4	0,8		2,7
May	13	6	2,2	0,4		2,2
Jun	15	6	2,5	0,8		2,7
Jul	10	5	2,0	0,0	5,12 p<0,001	2,0
Aug	22	10	2,2	0.4		2,3
Sep	5	2	2,5	0,7		2,6
Oct	18	7	2,6	0,5		2,7
Nov	28	11	2,5	1,2		3,1
Dec	34	15	2,3	0,6		2,4
Overall	231	98	2,4	0,7		2,6

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

of one-female groups (83%) contained only one subadult and/or calf per adult female.

The ratio of subadult males to subadult females in these groups (178 males : 100 females) differed significantly from the population sex ratio $\chi^2 = 37{,}98$, $p<0{,}001$).

8.3.4.4 Female groups

The female group was the most commonly encountered group-type on the Reserve (36,7% of all group sightings) and also contained the highest proportion of kudu (41,3%). Monthly variations in the proportion of female groups sighted (Fig. 8.10) were not significant.

Female groups ranged in size from two to eleven (Fig. 8.11). Mean and typical group sizes were 3,9 (±1,8) and 4,7 respectively, while slight differences in monthly mean female group sizes (Table 8.7) were not significant.

Most female groups (56%) consisted of adult cows only and groups containing subadults (22%) were more commonly recorded than those containing calves (15%) or subadults and calves (7%).

Female groups were significantly larger than one-female groups ($d = 14{,}56$, $p<0{,}001$) and bachelor groups ($d = 12{,}68$, $p<0{,}001$).

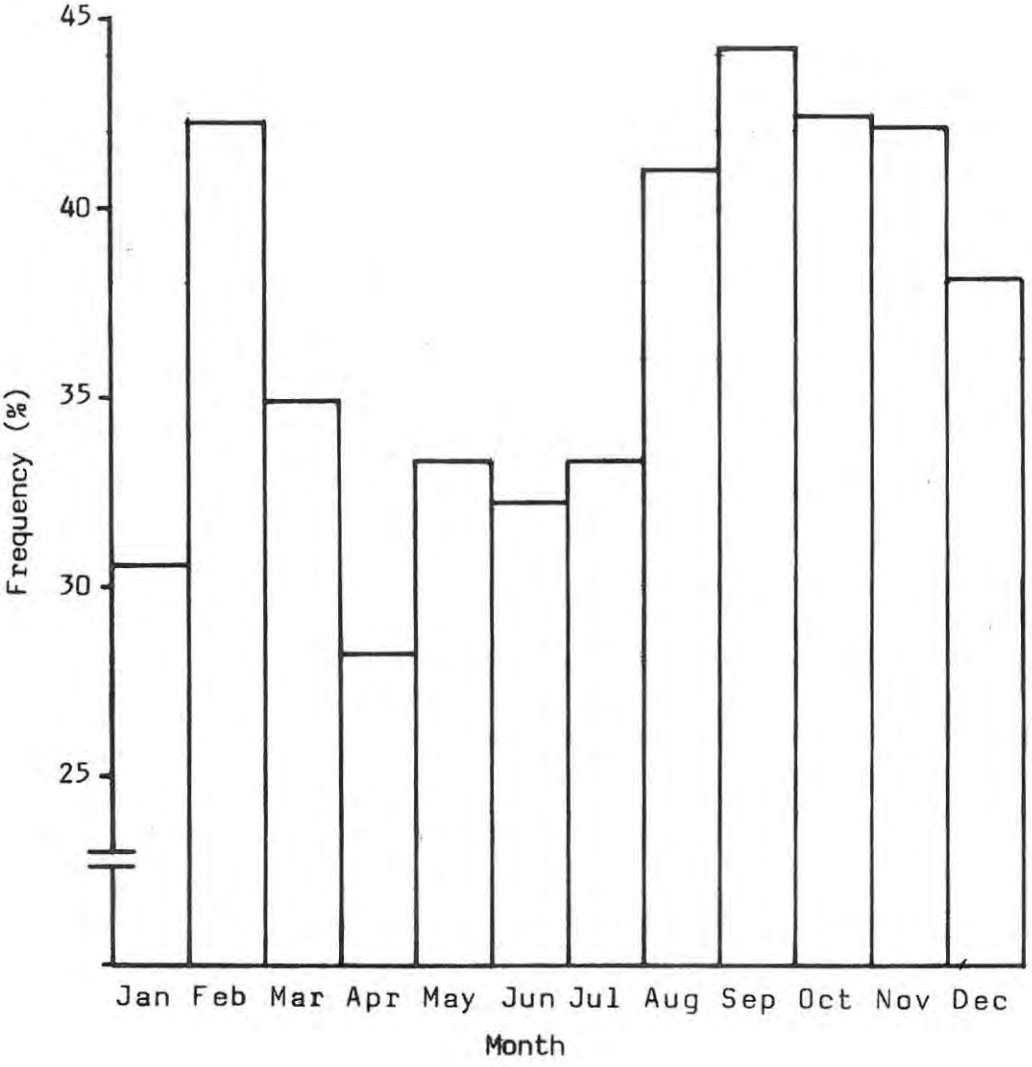
8.3.4.5 Mixed groups

During three months of the year the proportions of mixed groups altered significantly from the overall value of 24,7% (Fig. 8.12). Such sightings were lower in February ($\chi^2 = 10{,}71$, d.f. = 1, $p<0{,}01$) and considerably higher during May and June ($\chi^2 = 5{,}48$, d.f. = 1, $p<0{,}05$ and $\chi^2 = 11{,}61$, d.f. = 1, $p<0{,}001$ respectively).

Mixed groups contained from two to seventeen individuals (Fig. 8.13) and had a mean size of 5,6 (±2,8) and a typical group size of 7,0. Monthly differences in mean group size were relatively small except for February (Table 8.8) when the significantly smaller groups ($d = 5{,}18$, $p<0{,}001$) contained fewer numbers of both adult males ($d = 2{,}27$, $p<0{,}05$) and adult females ($d = 4{,}78$, $p<0{,}001$). For the rest of the year, the mean number of both adult males and adult females did not vary significantly (Tables 8.9 and 8.10 respectively). The mean number of adult bulls in mixed groups (1,5 ± 0,9) was significantly lower ($d = 16{,}87$, $p<0{,}001$) than the mean number of adult females (3,3 ± 1,9). The adult sex ratio (46 males : 100 females) was almost identical to

FIG. 8.10 Sighting frequencies of female groups, expressed as a % of all groups seen per month.

FIG. 8.11 Frequency distribution of female groups (——) and the proportion (%) of kudu within female groups of different sizes (----).



45
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Frequency (%)
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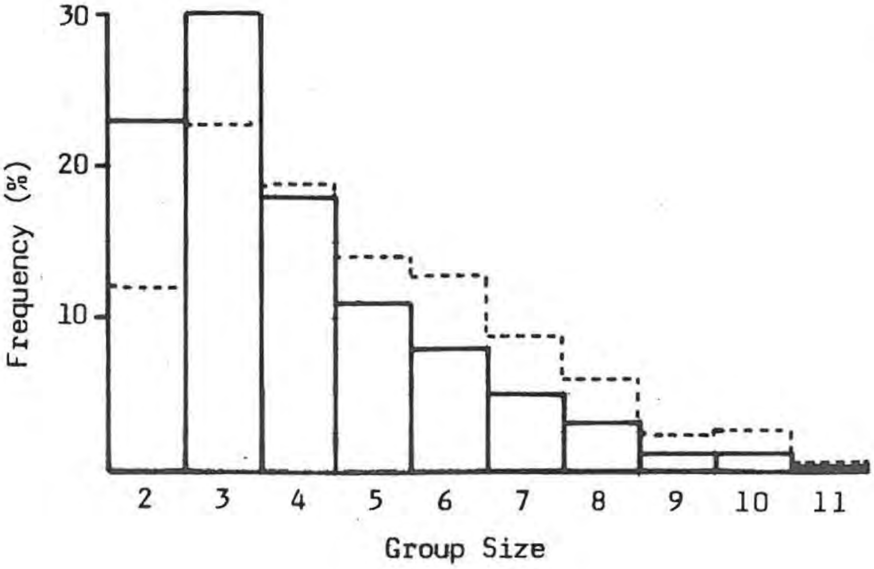

30
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Frequency (%)
2
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9
10
11
Group Size

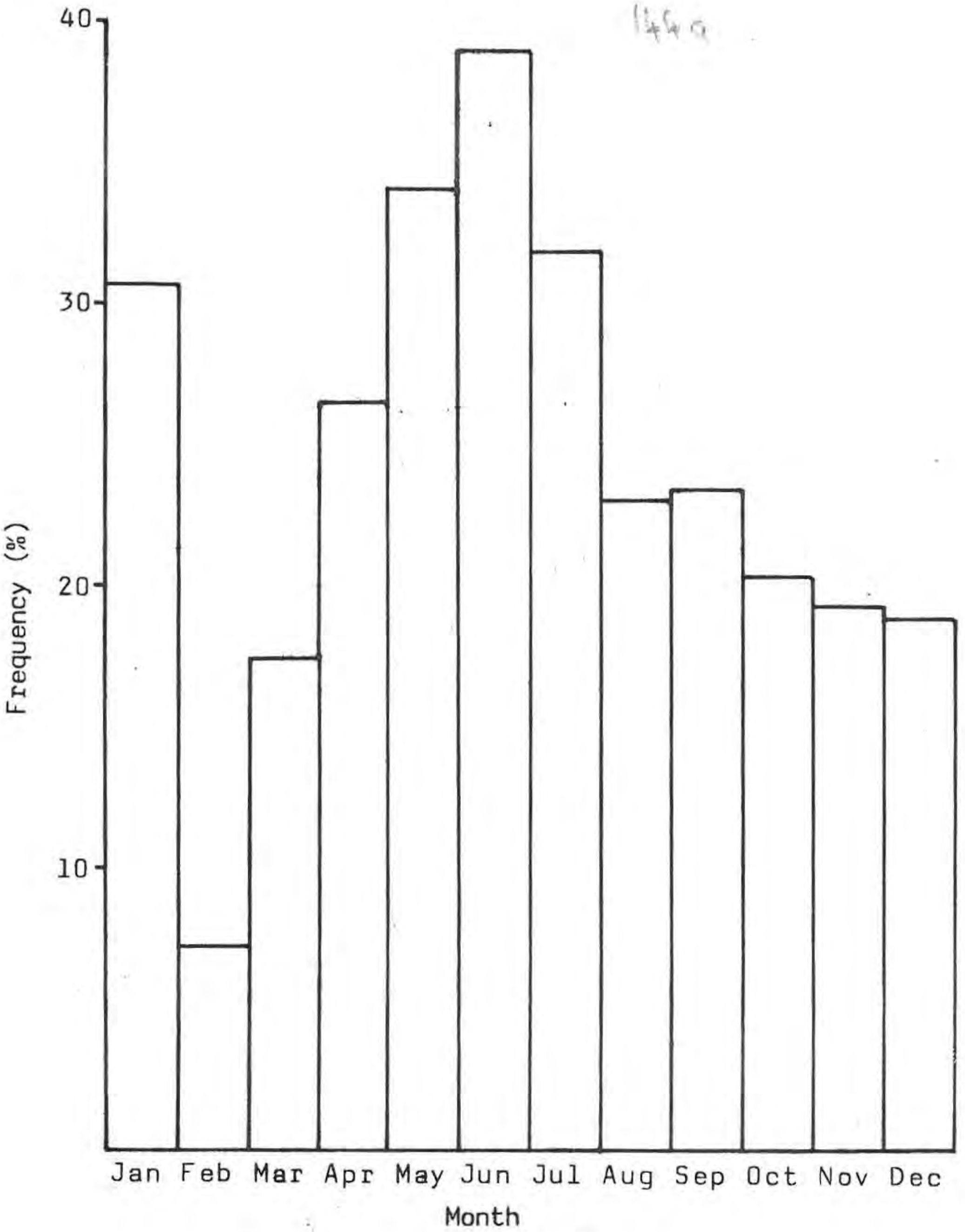
TABLE 8.7 Monthly mean and typical group sizes of female groups recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Month	No. kudu	No. groups	Mean group size	S.D.	d*	Typical group size
Jan	64	19	3,4	1,4		3,9
Feb	127	36	3,5	2,0		4,6
Mar	118	30	3,9	1,5		4,5
Apr	193	46	4,2	2,0		5,1
May	194	55	3,5	1,5		4,1
Jun	174	49	3,6	1,6		4,3
Jul	190	45	4,2	2,0		5,1
Aug	200	48	4,2	1,9		5,0
Sep	135	34	4,0	1,9		4,9
Oct	294	67	4,4	2,0		5,3
Nov	244	61	4,0	2,0		5,0
Dec	323	87	3,7	1,6		4,4
Overall	2258	577	3,9	1,8		4,8

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

FIG. 8.12 Sighting frequencies of mixed groups, expressed as a % of all groups seen per month.

FIG. 8.13 Frequency distribution of mixed groups (——), and the proportions (%) of kudu within mixed groups of different sizes (----).


40
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20
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Frequency (%)
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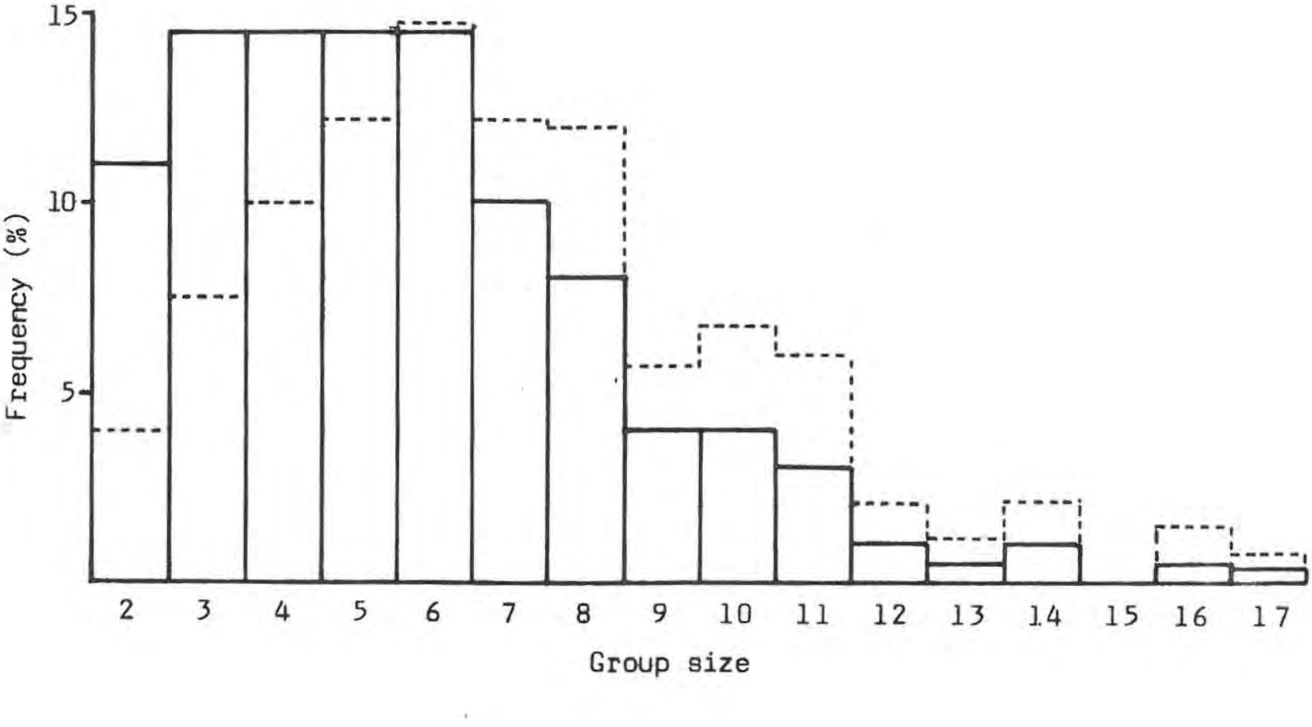
Dec
Month


15
10
5
Frequency (%)
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5
6
7
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11
12
13
14
15
16
17
Group size

TABLE 8.8 Monthly mean and typical sizes of mixed groups recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Month	No. kudu	No. groups	Mean group size	S.D.	d*	Typical group size
Jan	96	19	5,1	2,3		6,0
Feb	20	6	3,3	1,0	5,18 p<0,001	3,6
Mar	72	15	4,8	2,5		6,0
Apr	254	43	5,9	2,7		7,1
May	315	56	5,6	2,8		7,0
Jun	359	59	6,1	2,9		7,4
Jul	230	43	5,4	3,1		5,9
Aug	144	27	5,3	2,6		6,5
Sep	111	18	6,2	3,0		7,5
Oct	201	32	6,3	3,5		8,1
Nov	161	28	5,8	2,4		6,7
Dec	229	43	5,3	2.7		6,7
Overall	2192	389	5,6	2,8		7,0

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

TABLE 8.9 Monthly mean and typical numbers of adult males in mixed groups recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Month	No. kudu	No. groups	Mean group size	S.D.	d*	Typical group size
Jan	37	19	1,9	1,5		3,0
Feb	7	6	1,2	0,4	2,27 p<0,05	1,3
Mar	22	15	1,5	1,0		2,1
Apr	59	43	1,4	0,8		1,8
May	83	56	1,5	0,8		2,0
Jun	92	59	1,6	0,7		1,9
Jul	62	43	1,4	0,9		2,0
Aug	41	27	1,5	0,8		1,9
Sep	34	18	1,9	1,3		2,8
Oct	54	32	1,7	0.9		2,1
Nov	44	28	1,6	0,9		2,1
Dec	63	43	1,5	0,9		2,0
Overall	598	389	1,5	0.9		2,1

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

TABLE 8.10 Monthly mean and typical numbers of adult females in mixed groups recorded on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

Month	No. kudu	No. groups	Mean group size	S.D.	d*	Typical group size
Jan	51	19	2,7	1,6		3,6
Feb	12	6	2,0	0,6	4,78 p<0,001	2,2
Mar	42	15	2,8	1,9		4,1
Apr	144	43	3,4	1,9		4,4
May	184	56	3,3	1,8		4,3
Jun	221	59	3,8	1,9		4,6
Jul	139	43	3,2	2,2		4,7
Aug	81	27	3,0	1,6		3,8
Sep	59	18	3,3	2,0		4,5
Oct	113	32	3,5	2,3		5,0
Nov	103	28	3,7	1,8		4,6
Dec	142	43	3,3	2,2		4,8
Overall	1291	389	3,3	2,0		4,5

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

the population sex ratio.

Mixed groups were significantly larger than female groups (d = 10,59, p<0,001), one-female groups (d = 20,17, p<0.001) and bachelor groups (d = 18,96, p<0,001).

Males were aged in 369 (95%) of the mixed groups. Thirty percent of these contained at least one 5 year old male, in 23% the oldest males were 4 year olds, 3 year olds were the oldest in 19% and 28% contained only 2 year olds. These proportions varied considerably between months (Fig. 8.14).

Most groups (64%) contained only one adult male, and of these 26% included a 5 year old male, 14% a 4 year old, 20% a 3 year old and 40% a 2 year old male. Again, the monthly proportions of different aged males in these "harem" groups varied considerably from month to month (Fig. 8.15).

When two or more adult bulls were present ("multi-male" groups), they were often the same age. This was more marked in 3 year olds (33%) than in 5 year olds (26%), 4 year olds (18%) or 2 year olds (23%). Including the harem groups, 83% of all mixed groups contained males of only one age class.

8.3.5 Sex and age differences

8.3.5.1 Calves (397 animals)

The majority of calves were seen in female groups (46%) and mixed groups (37%). Fifteen percent of all calves were seen in one-female groups, and solitary calves were rarely seen (2%). These proportions varied between months (Fig. 8.16) and significant differences are presented in Table 8.11.

8.3.5.2 Females

i) subadult females (126 animals)

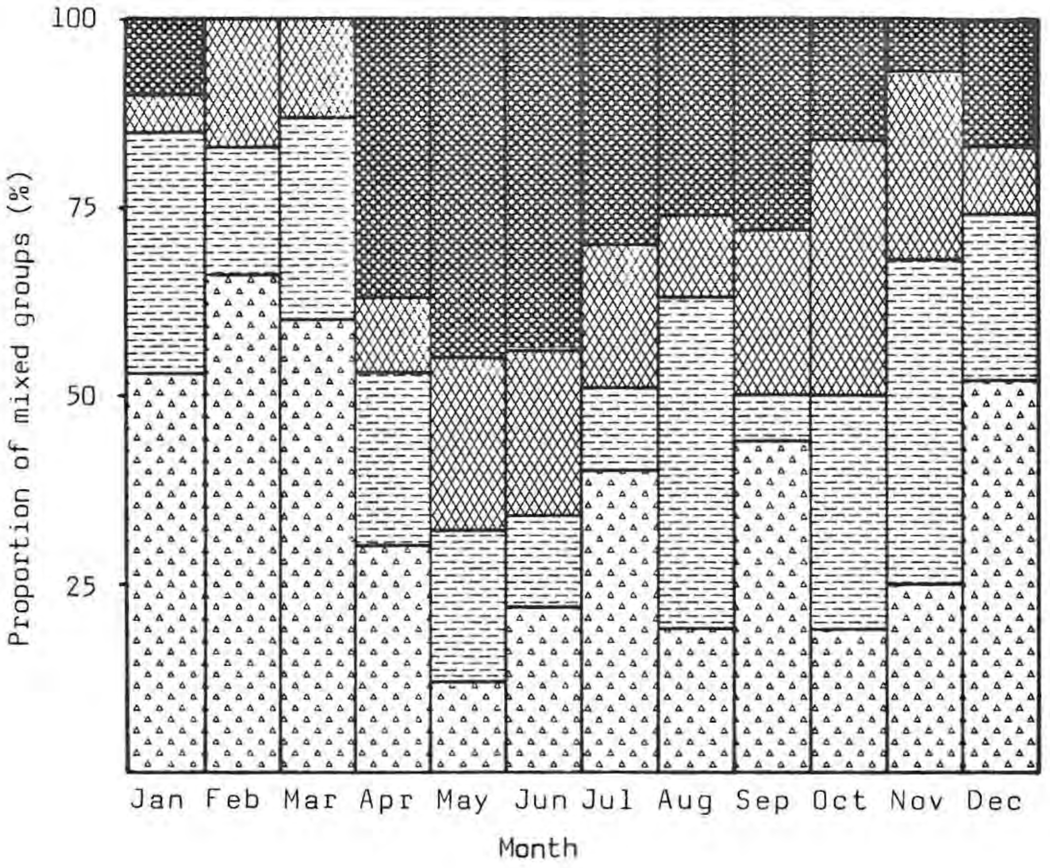
These occurred in four group types through the year with the following proportions: as solitary animals (6%), in one-female groups (19%), in mixed groups (24%) and in female groups (51%). Monthly variations in these proportions are shown in Fig. 8.17. Due to the small sample sizes, differences were not significant except during March when the number of subadult females seen in one-female groups increased considerably (χ^2 = 8,10, d.f. = 1, p<0.01).

FIG. 8.14 Monthly changes in the proportion of mixed groups where the oldest male within the group is a:

▩ 5+ year old
▦ 4 year old
▤ 3 year old
△ 2 year old

FIG. 8.15 Monthly proportions (%) of mixed groups containing a single adult male.

▩ 5+ year old
▦ 4 year old
▤ 3 year old
△ 2 year old


100
75
50
25
Proportion of mixed groups (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

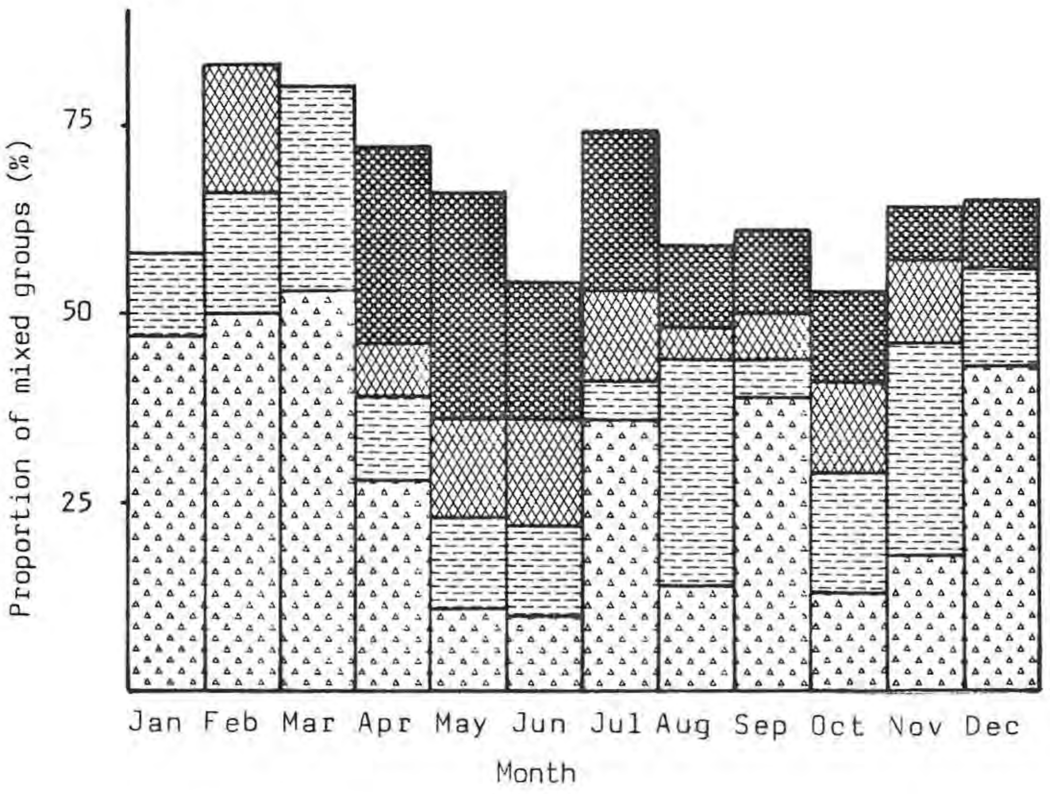

75
50
25
Proportion of mixed groups (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

FIG. 8.16 Monthly and overall proportions of calves occurring in:

⁙ Solitary groups

▦ One-female groups

⊞ Female groups

▥ Mixed groups

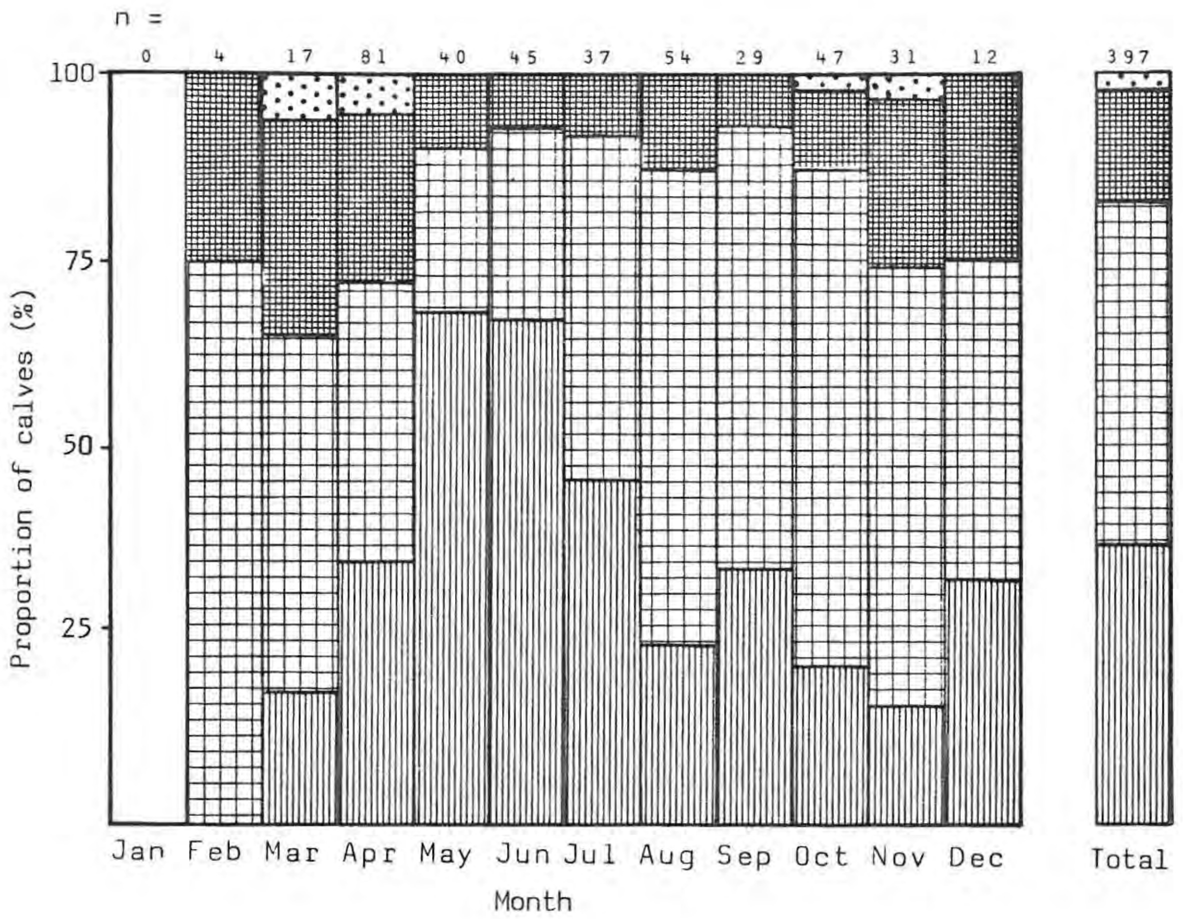
Fig. 8.17 Monthly and overall proportions of subadult females occurring in:

⁙ Solitary groups

▦ One-female groups

⊞ Female groups

▥ Mixed groups


n =
0
4
17
81
40
45
37
54
29
47
31
12
397
100
75
50
25
Proportion of calves (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

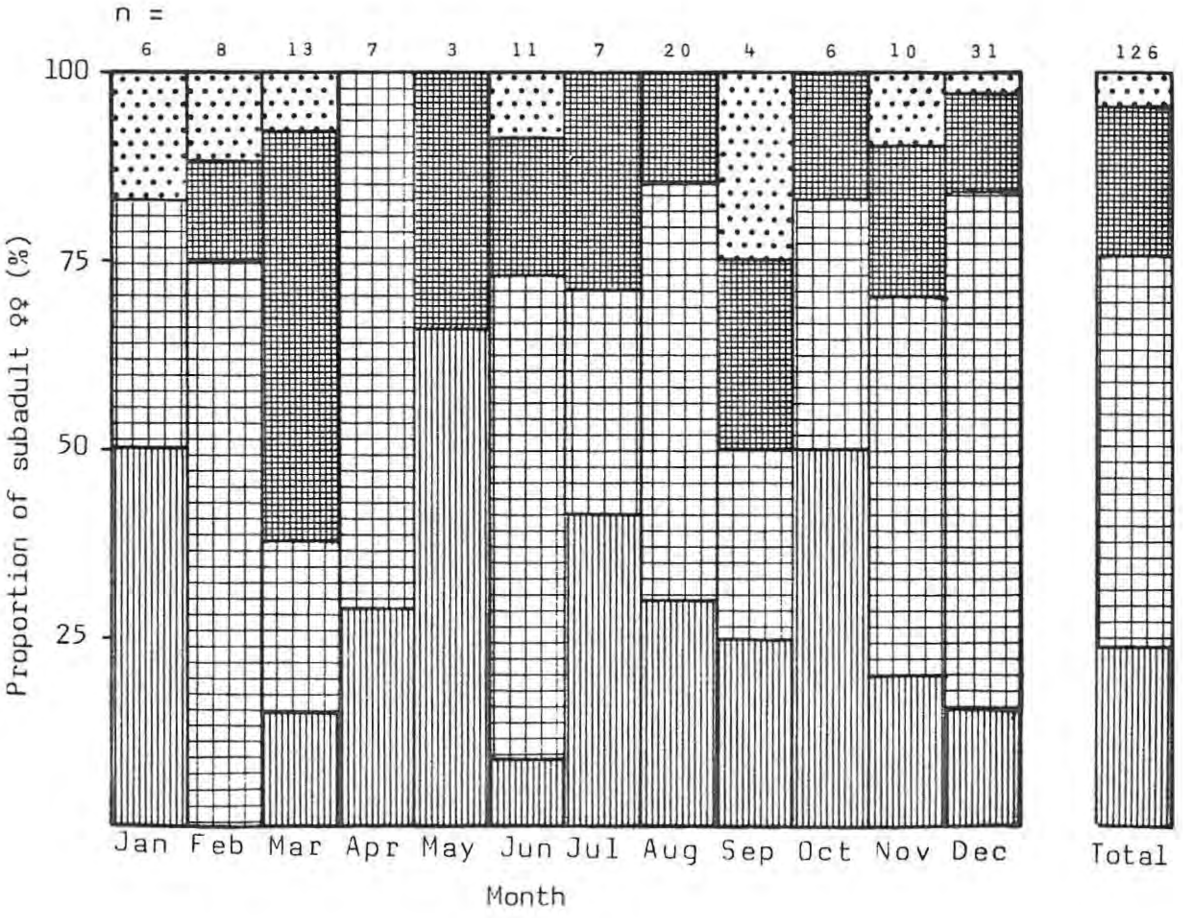

n =
6
8
13
7
3
11
7
20
4
6
10
31
126
100
75
50
25
Proportion of subadult ♀♀ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

TABLE 8.11 Significant variations in the numbers of calves observed in solitary, one-female, female and mixed groups (months with non-significant variations have been omitted).

Month	Proportion of calves in:-			
	solitary groups	one-female groups	female groups	mixed groups
Apr	Increased $\chi^2 = 4,69$ $p<0,05$	Increased $\chi^2 = 4,02$ $p<0,05$	n.s.	n.s.
May	n.s.	n.s.	Decreased $\chi^2 = 4,91$ $p<0,05$	Increased $\chi^2 = 10,03$ $p<0,01$
Jun	n.s.	n.s.	n.s.	Increased $\chi^2 = 10,68$ $p<0,01$
Oct	n.s.	n.s.	Increased $\chi^2 = 3,90$ $p<0,05$	n.s.
Overall	$\chi^2 = 11,52$ n.s.	$\chi^2 = 4,50$ n.s.	$\chi^2 = 19,92$ $p<0,05$	$\chi^2 = 34,17$ $p<0,001$

ii) adult females (3352 animals)

Although the proportions of adult females occurring singly, in one-female groups, female groups and mixed groups differed significantly between years (χ^2 = 10,15, d.f. = 3, p<0,05) this was largely due to the greater porportion of solitary females seen during 1979 (χ^2 = 4,43, d.f. = 1, p<0,05), when more calves were reared (Fig. 6.4). Excluding solitary female groups, yearly proportions of adult cows occurring in other group-types did not differ significantly and all sightings of adult females have been combined.

Most cows were seen in female groups (55%) and in mixed groups (38%). Approximately equal numbers were seen in one-female groups (3%) and as solitary animals (4%). Monthly variations in these proportions, and significant differences are presented in Fig. 8.18 and Table 8.12 respectively.

Groups containing at least one adult female (76% of 1573 groups) had a mean number of 2,8 (±1,7) and a typical number of 3,7 females. Monthly variations are shown in Table 8.13.

8.3.5.3 Males

i) subadult males (347 animals)

The majority of subadult males (92%) were seen in the company of adult cows, while similar numbers were seen in bachelor groups (4%) and as solitary animals (4%). Monthly proportions (Fig. 8.19) varied significantly during April and December (higher number of subadults as solitary animals, χ^2 = 9,00, d.f. = 1, p<0,01 and χ^2 = 4,45, d.f. = 1, p<0,05) and in June when significantly more males were seen in bachelor groups (χ^2 = 4,90, d.f. = 1, p<0,05).

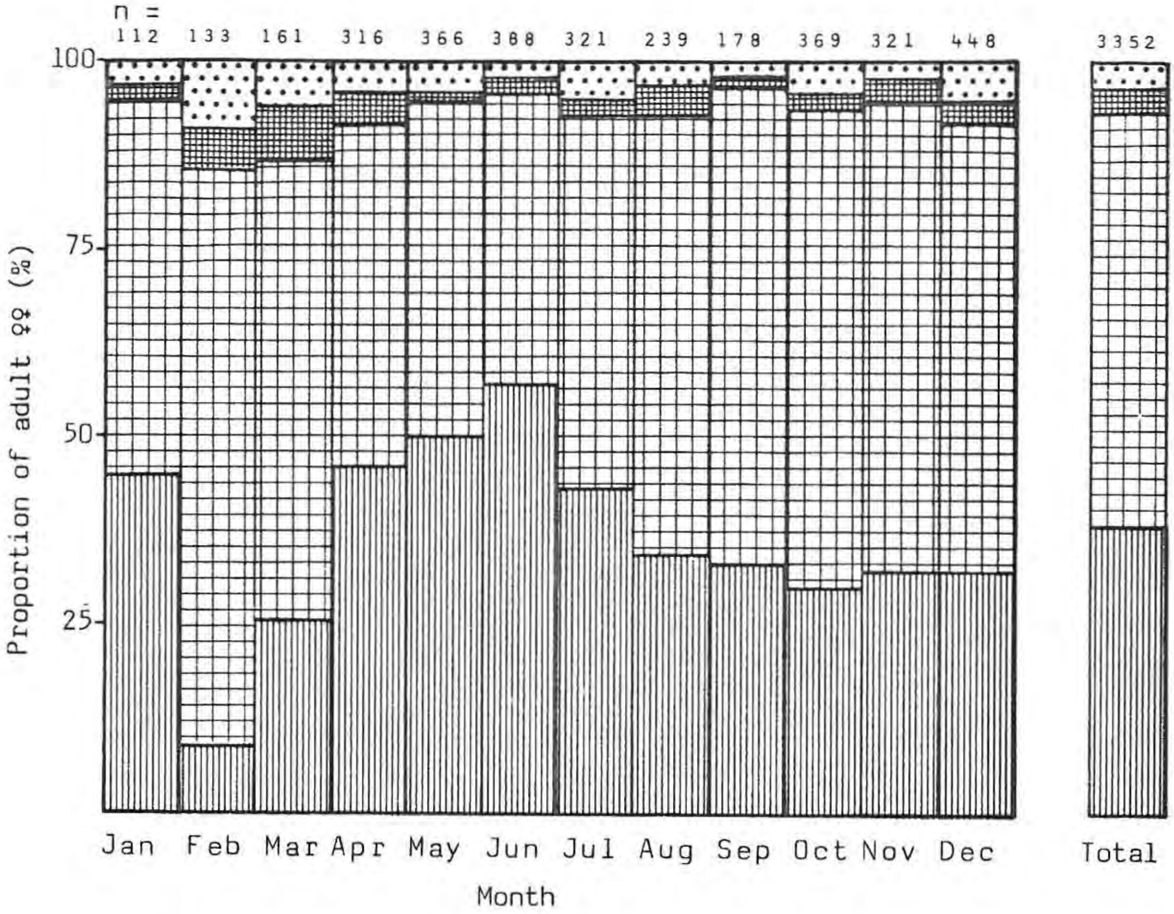
Significantly fewer males were seen in mixed groups during February (χ^2 = 5,82, d.f. = 1, p<0,05). During this time the majority of subadult males were found in female groups (χ^2 = 4,62, d.f. = 1, p<0,05). This trend reversed in June, when significantly fewer subadult males were observed in female groups (χ^2 = 7,75, d.f. = 1, p<0,01) and a greater proportion were present in mixed groups (χ^2 = 5,88, d.f. =1, p<0,05). The number of subadult males in mixed groups was also significantly higher in September (χ^2 = 4,51, d.f. = 1, p<0,05).

FIG. 8.18 Monthly and overall proportions of adult females occurring in:

░ Solitary groups
▦ One-female groups
⊞ Female groups
▥ Mixed groups

FIG. 8.19 Monthly and overall proportions of subadult males occurring in:

░ Solitary groups
▤ Bachelor groups
▥ Mixed groups
⊞ Female groups
▦ One-female groups


n =
112
133
161
316
366
388
321
239
178
369
321
448
3352
100
75
50
25
Proportion of adult ♀♀ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

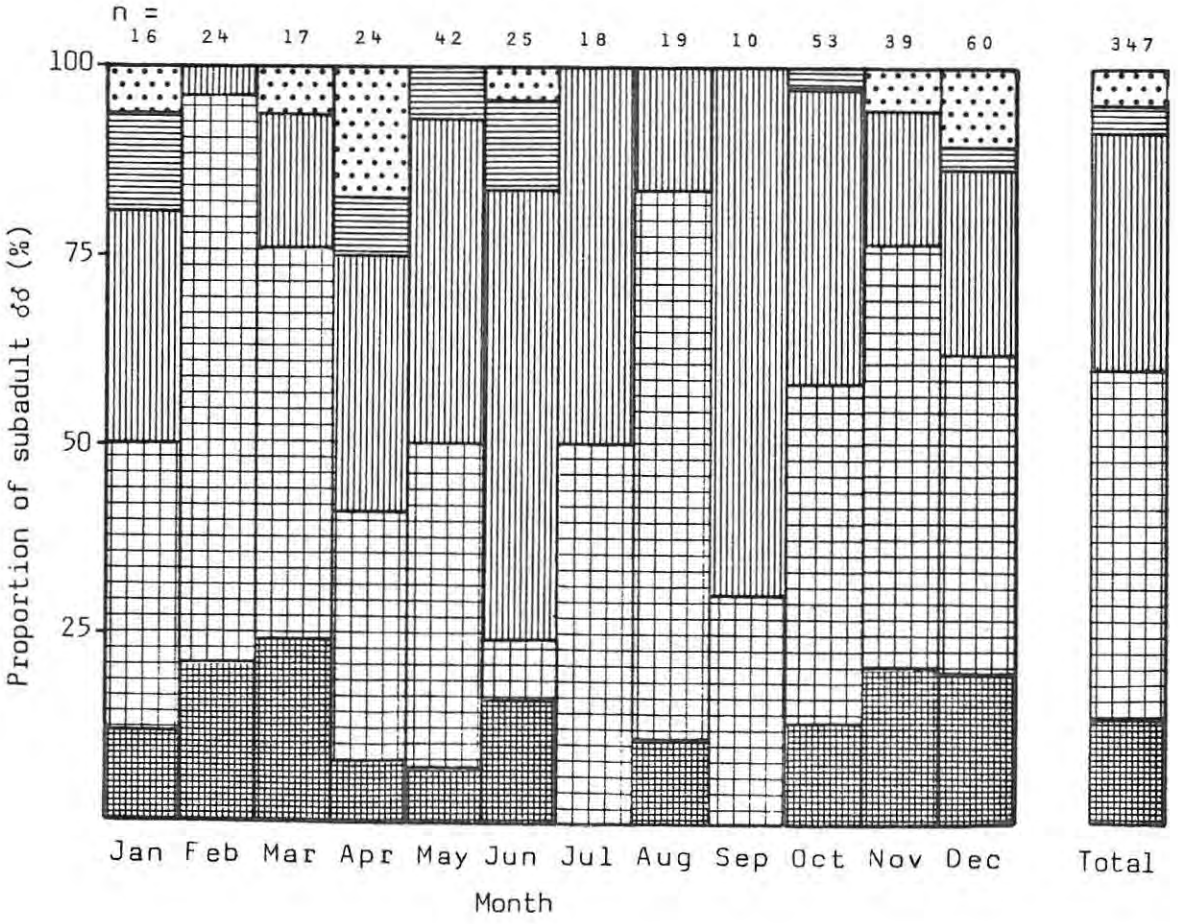

n =
16
24
17
24
42
25
18
19
10
53
39
60
347
100
75
50
25
Proportion of subadult ♂♂ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

TABLE 8.12 Significant variations in the numbers of adult females observed in solitary, one-female, female, and mixed groups. (Months with non-significant variations have been omitted.)

Month	Proportion of adult females in:- solitary groups	one-female groups	female groups	mixed groups
Feb	Increased $\chi^2 = 9,33$ $p<0,01$	n.s.	Increased $\chi^2 = 12,43$ $p<0,001$	Decreased $\chi^2 = 30,00$ $p<0,001$
Mar	n.s.	Increased $\chi^2 = 9,39$ $p<0,01$	n.s.	Decreased $\chi^2 = 6,45$ $p<0,05$
Apr	n.s.	n.s.	Decreased $\chi^2 = 4,62$ $p<0,05$	Increased $\chi^2 = 4,08$ $p<0,05$
May	n.s.	n.s.	Decreased $\chi^2 = 6,74$ $p<0,01$	Increased $\chi^2 = 13,18$ $p<0,001$
Jun	n.s.	n.s.	Decreased $\chi^2 = 16,80$ $p<0,001$	Increased $\chi^2 = 34,31$ $p<0,001$
Oct	n.s.	n.s.	Increased $\chi^2 = 5,25$ $p<0,05$	Decreased $\chi^2 = 5,96$ $p<0,05$
Dec	n.s.	n.s.	n.s.	Decreased $\chi^2 = 5,39$ $p<0,05$
Overall	$\chi^2 = 21,50$ $p<0,05$	$\chi^2 = 26,2$ $p<0,01$	$\chi^2 = 57,16$ $p<0,001$	$\chi^2 = 108,8$ $p<0,001$

TABLE 8.13 Monthly mean and typical numbers of adult females in groups containing adult females.

Month	No. ad ♀♀	No. groups	Mean group size	S.D.	d*	Typical no. ad ♀♀
Jan	112	43	2,6	1,5		3,5
Feb	133	61	2,2	1,5	3,01 p<0.01	3,1
Mar	161	66	2,4	1,5		3,4
Apr	316	118	2,7	1,7		3,7
May	366	130	2,8	1,6		3,5
Jun	388	122	3,2	1,8	2,16 p<0,05	4,2
Jul	321	108	3,0	2,0		4,3
Aug	239	92	2,6	1,4		3,4
Sep	178	57	3,1	1,7		3,9
Oct	369	120	3,1	1,9		4,1
Nov	321	108	3,0	1,8		4,0
Dec	448	167	2,7	1,8		3,8
Overall	3352	1192	2,8	1,7		3,7

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

ii) adult males (1203 animals)

The proportion of adult males in single, bachelor and mixed groups did not differ significantly between years, and consequently data from both years have been combined.

Of the 1203 adult males recorded on the Reserve, 50% were seen in mixed groups, 35% in bachelor groups and 15% as solitary animals. These proportions varied considerably during the year (Fig. 8.20) and significant differences are given in Table 8.14.

Groups containing at least one adult male (47% of 1573 groups) had a mean number of 1,6 (±0,9) and a typical number of 2,2 males. Mean and typical monthly values are shown in Table 8.15.

The numbers and proportions of different aged males seen in solitary, bachelor and mixed groups are given in Table 8.16. Within the adult male population 21,3% of all males were 2 year olds, 30,2% were 3 year olds, 23,5% were 4 year olds and the remaining 24,9% were 5+ year olds. To test whether grouping patterns differed with age, these proportions within the population were used to determine the expected values of different aged males in each group type. These, together with the resulting χ^2 values and levels of significance are shown in Table 8.17. Thus, 2 year old males were under-represented in bachelor groups (and to a lesser, non-significant extent in solitary groups), but extremely common in mixed groups. The number of 3 year and 4 year old males were significantly higher in bachelor groups, while the latter were under-represented in mixed groups. The slightly higher number of 5+ year old males seen in solitary groups was not significant and these males were equally represented in both bachelor and mixed groups.

When monthly variations in the proportion of 2-5 year old males seen alone (Fig. 8.21) were compared with the overall proportions within solitary groups (not within the population), the only significant difference detected was the increased number of 2 year olds during March (χ^2 = 4,83, d.f. = 1, p<0,05). Summed monthly χ^2 values were not significant in any age class.

This same procedure was adopted for the analysis of age class differences in bachelor groups (Fig. 8.22) and mixed groups (Fig. 8.23). Significant monthly variations are presented in Tables 8.18 and 8.19 respectively.

FIG. 8.20 Monthly and overall proportions of adult males occurring in:

⁙ Solitary groups

▦ Bachelor groups

▥ Mixed groups

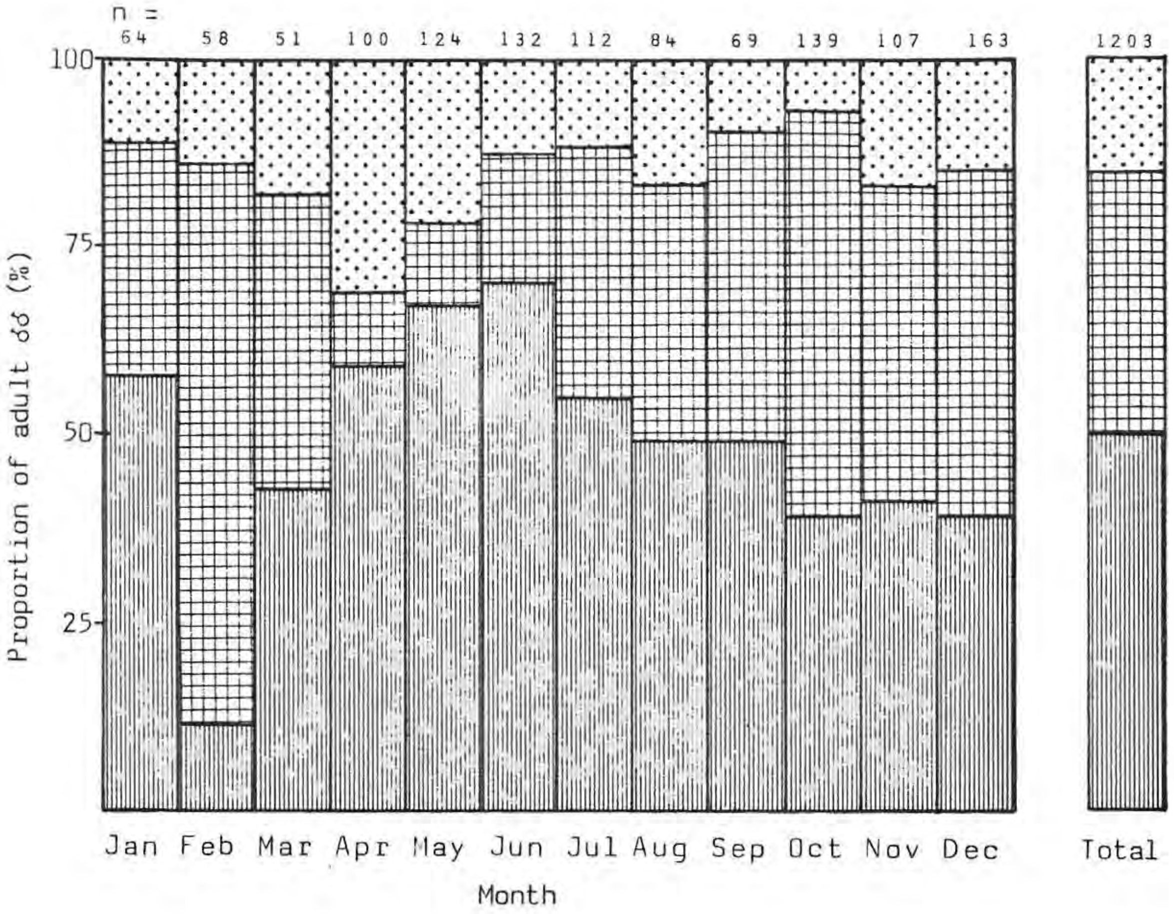
FIG. 8.21 Monthly and overall proportions of different aged adult males occurring in solitary groups.

▓ 5+ year old

▩ 4 year old

▤ 3 year old

△ 2 year old


n =
64
58
51
100
124
132
112
84
69
139
107
163
1203
100
75
50
25
Proportion of adult ♂♂ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

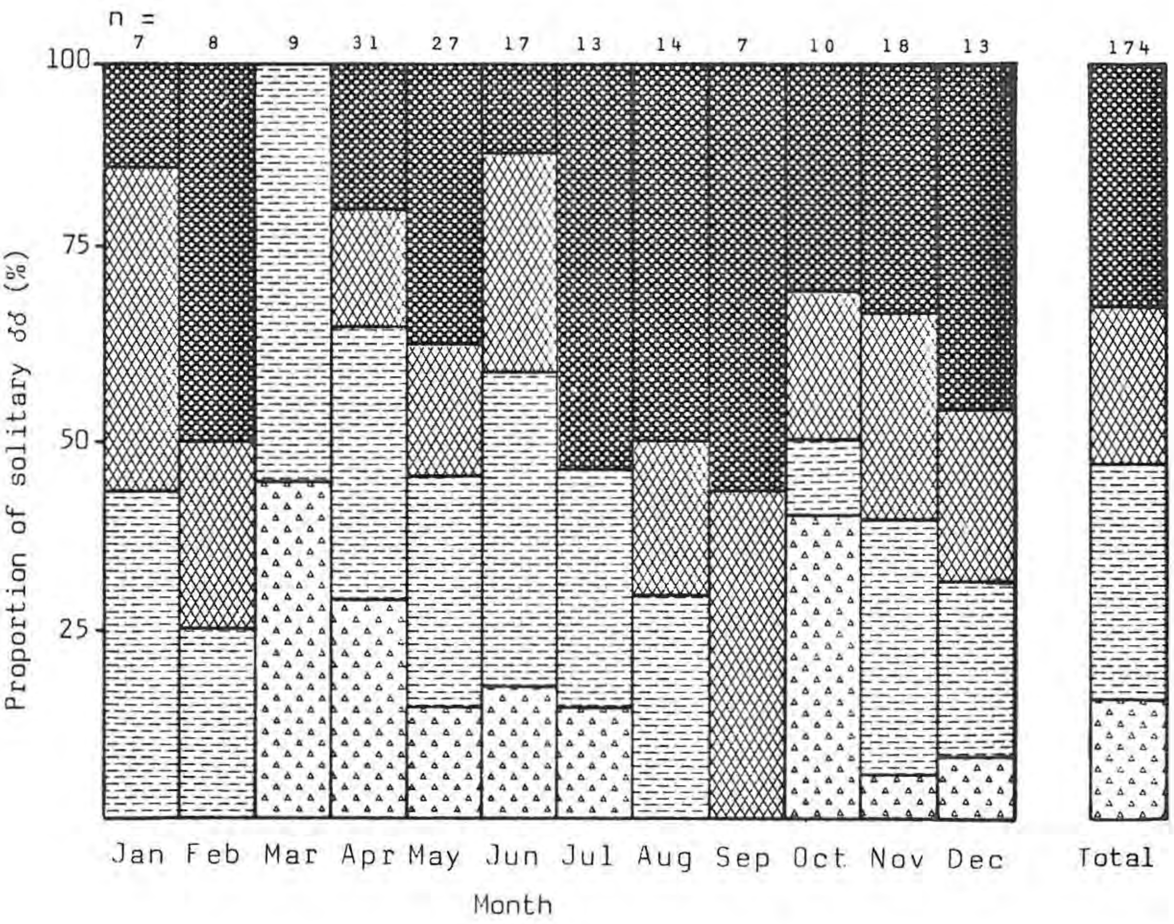

n =
7
8
9
31
27
17
13
14
7
10
18
13
174
100
75
50
25
Proportion of solitary ♂♂ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

TABLE 8.14 Significant variations in the numbers of adult males observed in solitary, bachelor and mixed groups. (Months with non-significant variations have been omitted.)

Month		Proportion of adult males in:-	
	solitary groups	bachelor groups	mixed groups
Feb	n.s.	Increased $\chi^2 = 25,73$ $p<0,001$	Decreased $\chi^2 = 16,50$ $p<0,001$
Apr	Increased $\chi^2 = 15,50$ $p<0,001$	Decreased $\chi^2 = 17,67$ $p<0,001$	n.s.
May	n.s.	Decreased $\chi^2 = 19,73$ $p<0,001$	Increased $\chi^2 = 7,43$ $p<0,01$
Jun	n.s.	Decreased $\chi^2 = 23,00$ $p<0,001$	Increased $\chi^2 = 10,62$ $p<0,01$
Oct	Decreased $\chi^2 = 6,15$ $p<0,05$	Increased $\chi^2 = 14,60$ $p<0,001$	n.s.
Dec	n.s.	Increased $\chi^2 = 5,83$ $p<0.05$	Decreased $\chi^2 = 4,00$ $p<0,05$
Overall	$\chi^2 = 29,01$ $p<0,01$	$\chi^2 = 109,46$ $p<0,001$	$\chi^2 = 47,22$ $p<0,001$

TABLE 8.15 Monthly mean and typical numbers of adult males in groups containing adult males.

Month	No. ad ♂♂	No. groups	Mean group size	S.D.	d*	Typical no. ad ♂♂
Jan	64	35	1,8	1,2		2,6
Feb	58	29	2,0	1,1		2,6
Mar	51	32	1,6	0,9		2,1
Apr	100	79	1,3	0,6	4,79 p<0,001	1,6
May	124	90	1,4	0,7	2,95 p<0,01	1,8
Jun	132	86	1,5	0,7		1,9
Jul	112	70	1,6	0,9		2,2
Aug	84	52	1,6	0,9		2,1
Sep	69	37	1,9	1,1		2,4
Oct	139	69	2,0	1,1	2,73 p<0,01	2,6
Nov	107	61	1,8	1,2		2,6
Dec	163	96	1,7	1,0		2,2
Overall	1203	736	1,6	0.9		2,2

* Only d values (Bailey 1959) indicating significant deviations from the overall mean group size are shown.

TABLE 8.16 Sighting frequencies of adult males on the Andries Vosloo Kudu Reserve between December 1977 and November 1979.

	2 y	3 y	4 y	5+y	Total	Unaged	Total
Solitary	28	54	36	56	174	12	186
% solitary males	16,1%	31,0%	20,7%	32,2%			
% age class	11,5%	15,7%	13,4%	19,7%			
% total sightings					15,3%		15,5%
Bachelors	31	142	128	97	398	21	419
% bachelor males	7,8%	35,7%	32,2%	24,3%			
% age class	12,8%	41,3%	47,8%	34,2%			
% total sightings					34,9%		34,8%
Mixed	184	148	104	131	567	31	598
% mixed males	32,4%	26,1%	18,3%	23,1%			
% age class	75,7%	43,0%	38,8%	46,1%			
% total sightings					49,7%		49,7%
TOTAL	243	344	268	284	1139		
% of all aged males	21,3%	30,2%	23,5%	24,9%			
	243	344	268	284	1139	64	1203
% of all males	20,2%	28,5%	22,3%	23,6%		5,3%	

TABLE 8.17 Proportions of different aged males in the population in various group-types.

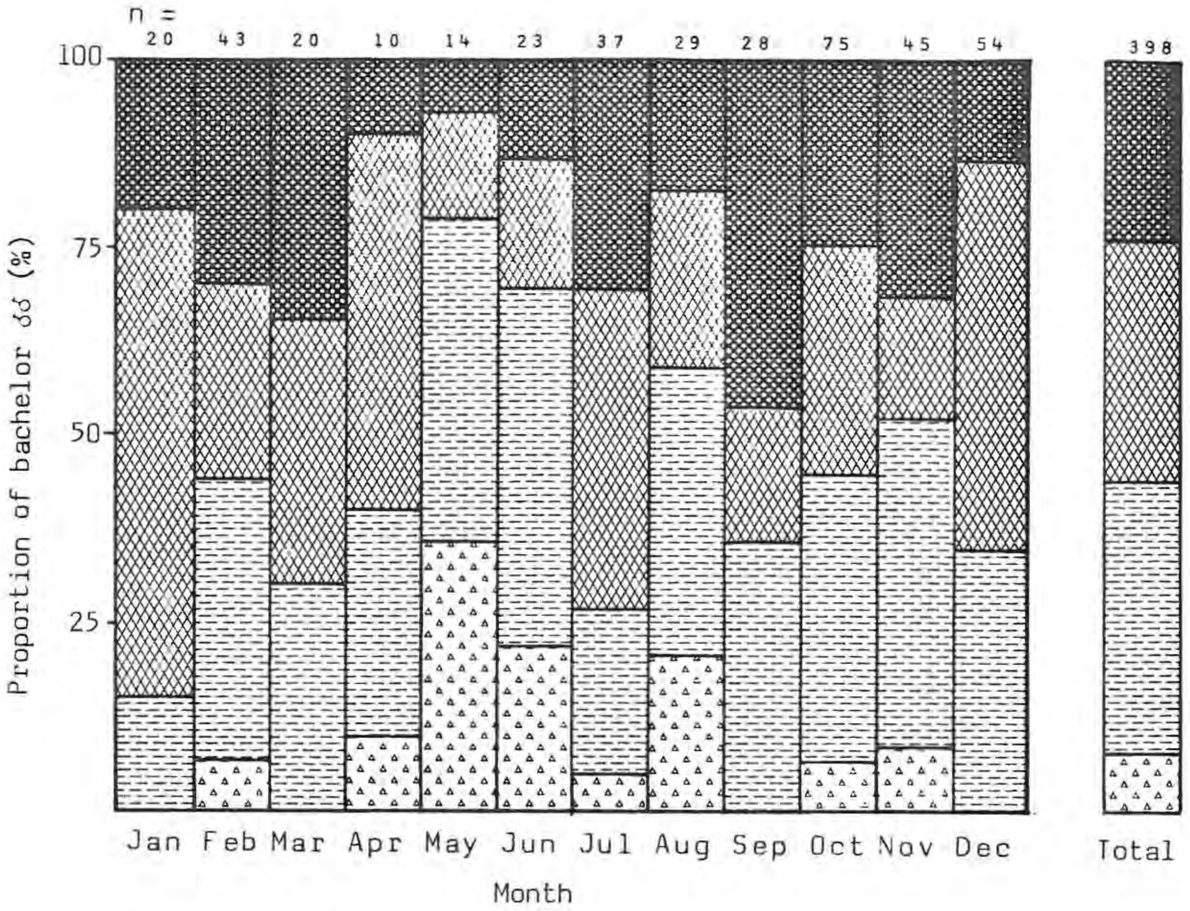
	2 y	3 y	4 y	5+y	Total
Proportion in male population	0,214	0,302	0,235	0,249	1,000
Solitary groups					
Observed number	28	54	36	56	174
Expected number	37,1	52,5	40,9	43,3	173,9
χ^2 value	2,23	0,04	0,59	3,72	
significance	n.s.	n.s.	n.s.	n.s.	
Bachelor groups					
Observed number	31	142	128	97	398
Expected number	84,9	120,2	93,6	99,2	397,9
χ^2 value	34,22	3,95	12,64	0,05	
significance	$p<0,001$	$p<0,005$	$p<0,001$	n.s.	
Mixed groups					
Observed number	184	148	104	131	567
Expected number	120,9	171,2	133,4	141,5	567
χ^2 value	32,93	3,14	6,48	0.78	
significance	$p<0,001$	n.s.	$p<0,05$	n.s.	

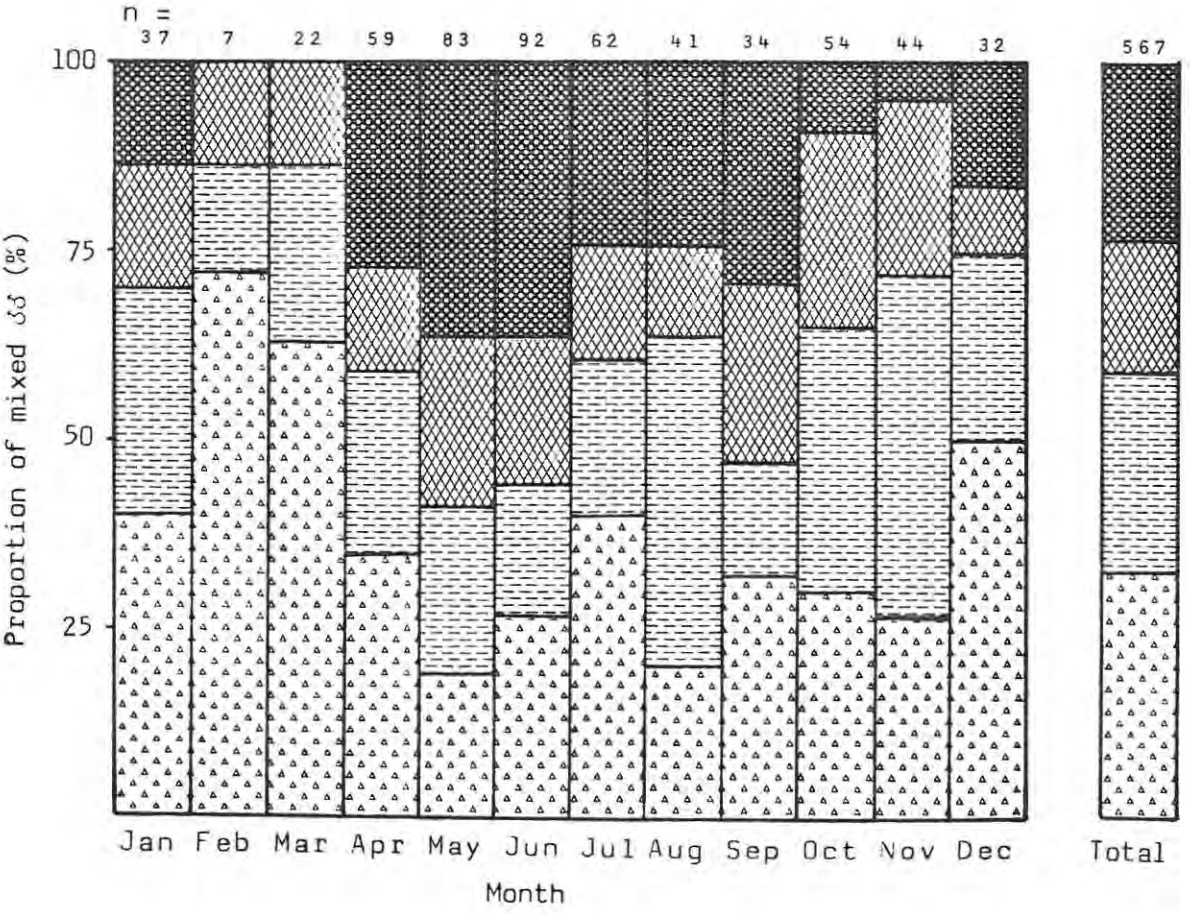
FIG. 8.22 Monthly and overall proportions of different aged adult males occurring in bachelor groups.

▓ 5+ year old
▩ 4 year old
▤ 3 year old
░ 2 year old

FIG. 8.23 Monthly and overall proportions of different aged adult males occurring in mixed groups.

▓ 5+ year old
▩ 4 year old
▤ 3 year old
░ 2 year old


n =
20
43
20
10
14
23
37
29
28
75
45
54
398
100
75
50
25
Proportion of bachelor ♂♂ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month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37
7
22
59
83
92
62
41
34
54
44
32
567
100
75
50
25
Proportion of mixed ♂♂ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

TABLE 8.18 Significant variations in the proportion of different aged males in bachelor herds. (Months with non-significant variations have been omitted.)

Month	2 y	3 y	4 y	5+y
Jan	n.s.	n.s.	Increased $\chi^2 = 6,81$ $p<0,01$	n.s.
May	Increased $\chi^2 = 13,82$ $p<0,001$	n.s.	n.s.	n.s.
Jun	Increased $\chi^2 = 5,68$ $p<0,05$	n.s.	n.s.	n.s.
Aug	Increased $\chi^2 = 5,95$ $p<0,05$	n.s.	n.s.	n.s.
Sep	n.s.	n.s.	n.s.	Increased $\chi^2 = 5,65$ $p<0.05$
Nov	n.s.	n.s.	Decreased $\chi^2 = 3,88$ $p<0,05$	n.s.
Dec	Decreased $\chi^2 = 4,20$ $p<0.05$	n.s.	Increased $\chi^2 = 6,46$ $p<0,05$	n.s.
Overall	$\chi^2 = 36,15$ $p<0,001$	$\chi^2 = 7,10$ n.s.	$\chi^2 = 25,54$ $p<0,01$	$\chi^2 = 15,82$ n.s.

TABLE 8.19 Significant variations in the proportion of different aged males in mixed herds. (Months with non-significant variations have been omitted.)

Month	2 y	3 y	4 y	5+y
Mar	Increased $\chi^2 = 6,71$ $p<0,01$	n.s.	n.s.	Decreased $\chi^2 = 5,10$ $p<0.05$
May	Decreased $\chi^2 = 4,42$ $p<0,05$	n.s.	n.s.	Increased $\chi^2 = 6,08$ $p<0,05$
Jun	n.s.	n.s.	n.s.	Increased $\chi^2 = 6,43$ $p<0,05$
Aug	n.s.	Increased $\chi^2 = 4,98$ $p<0,05$	n.s.	n.s.
Oct	n.s.	n.s.	n.s.	Decreased $\chi^2 = 4,50$ $p<0,05$
Nov	n.s.	Increased $\chi^2 = 6,28$ $p<0,05$	n.s.	Decreased $\chi^2 = 6,49$ $p<0,05$
Overall	$\chi^2 = 22,81$ $p<0,05$	$\chi^2 = 19,37$ n.s.	$\chi^2 = 7,51$ n.s.	$\chi^2 = 33,52$ $p<0,001$

The overall proportions of same-age males occurring in solitary, bachelor and mixed groups are also shown in Table 8.16. Monthly variations within each age class are illustrated in Figs. 8.24 to 8.27 for 2 year - 5+ year males respectively. Significant variations are tabulated for each class (Tables 8.20 to 8.23).

8.3.6 Known individuals

Age-related changes in grouping patterns were also determined from resightings of known individuals and their associations. Selected examples (the most frequently sighted member of each age class) are given in Tables 8.24 and 8.25.

8.3.7 Group stability and inter-individual associations

So far the term "group" has been considered in a purely operational sense. To examine group stability, indices of association between known (collared) individuals were calculated using Leuthold's (1979) formula:-

$$a = 2N/n_1 + n_2$$

where a = index of association, n_1 and n_2 = the numbers of sightings of two individuals during the time in which their periods of observation overlapped and N = the number of times they were seen together. An index of 0,50 or more was considered as indicating a close relationship between the animals concerned.

Indices of association among females inhabiting different areas of the Reserve are presented in Tables 8.26 to 8.28. Relations among males, again separated according to area, are given in Tables 8.29 to 8.30 while those between males and females are shown in Tables 8.31 and 8.32. Frequency distributions of indices of association between collared females, collared males, and between collared males and females are presented in Fig. 8.28a, b and c respectively.

These data must be interpreted with caution for several reasons. Firstly, only marked animals could be recognised and even when seen, individual collars were not identified on every occasion. Therefore, certain indices of association may be minimal values. Secondly, due to limited flying time and possible disruption of groups during the darting programmes, comparatively few animals were darted in the company of marked individuals (these sightings are not considered in

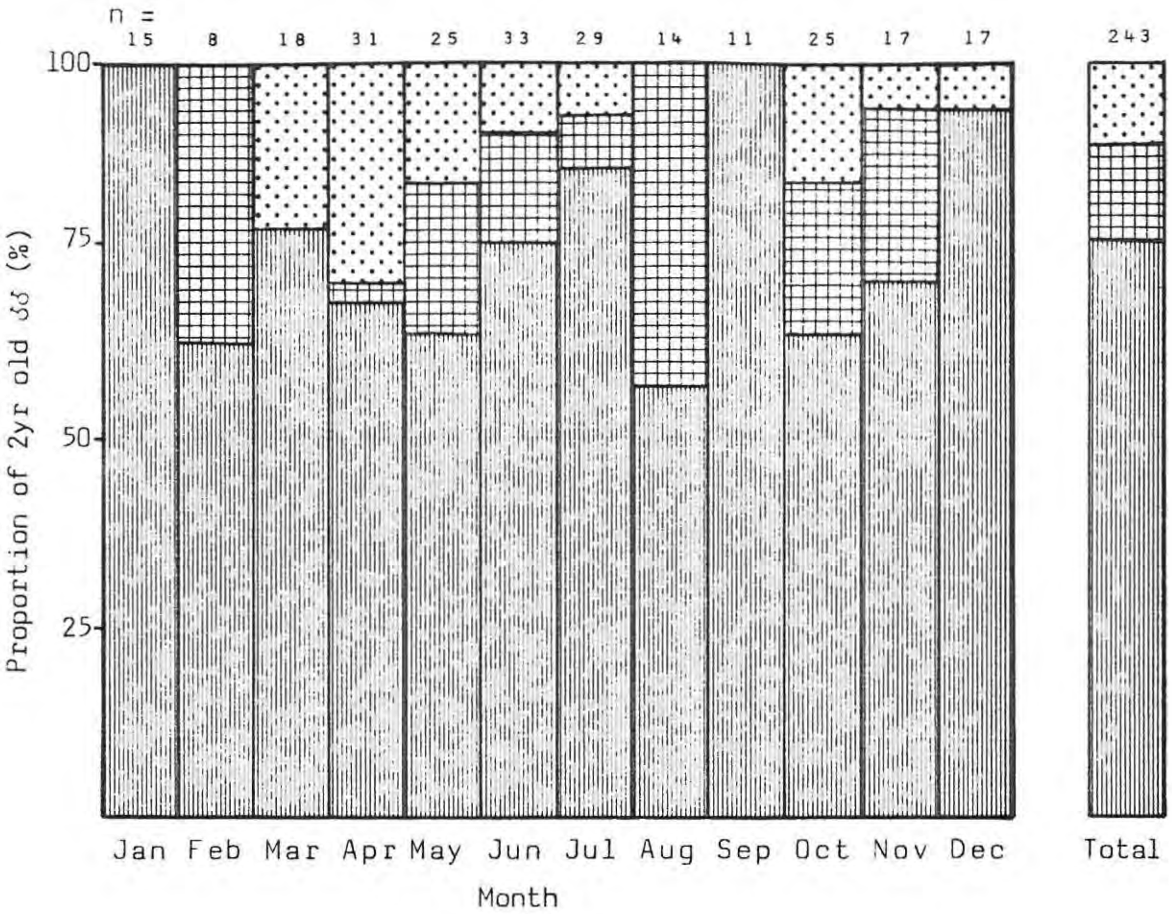
FIG. 8.24 Monthly and overall proportions of 2 year old males occurring in:

░ Solitary groups
▦ Bachelor groups
▥ Mixed groups

FIG. 8.25 Monthly and overall proportions of 3 year old males occurring in:

░ Solitary groups
▦ Bachelor groups
▥ Mixed groups

167a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18
31
25
33
29
14
11
25
17
17
243
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75
50
25
Proportion of 2yr old ♂♂ (%)
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Feb
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Sep
Oct
Nov
Dec
Total
Month

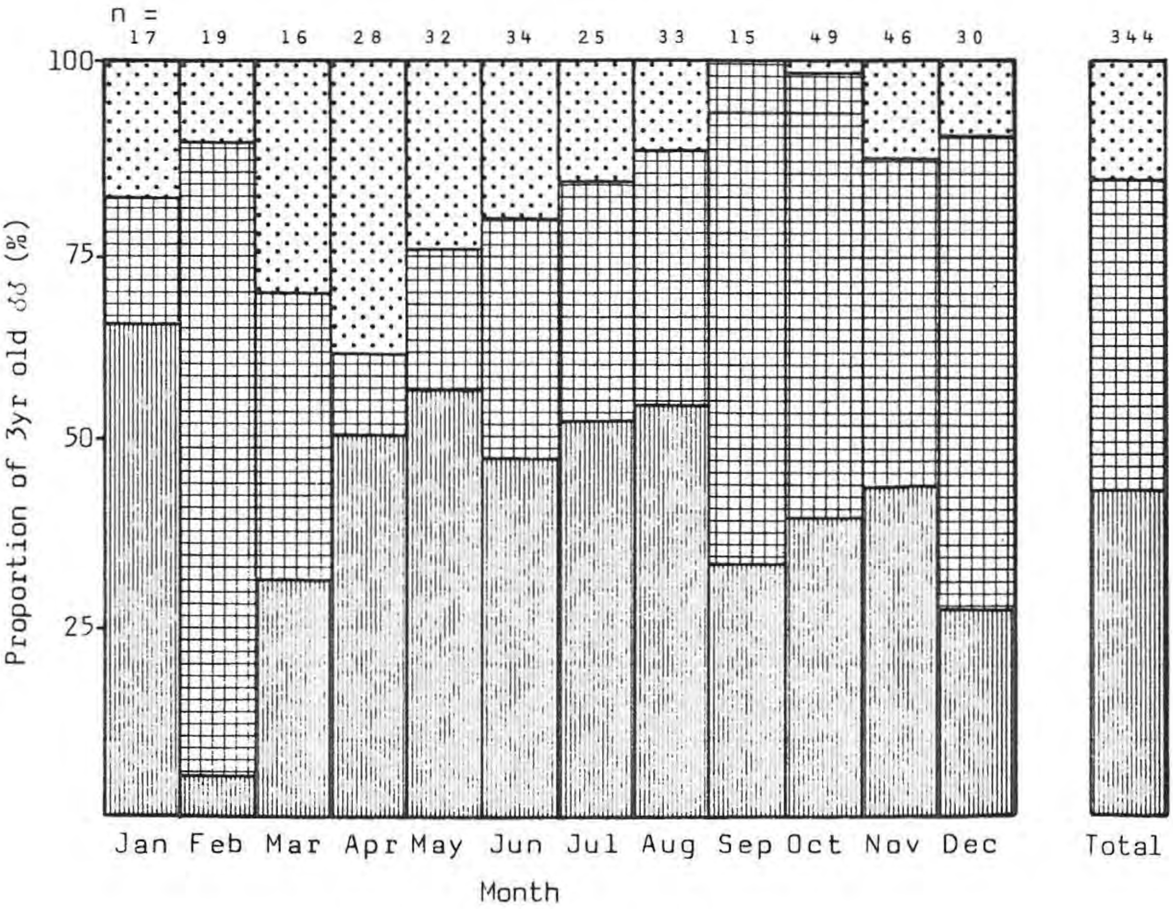

n =
17
19
16
28
32
34
25
33
15
49
46
30
344
100
75
50
25
Proportion of 3yr old ♂♂ (%)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Total
Month

FIG. 8.26 Monthly and overall proportions of 4 year old males occurring in:

░ Solitary groups

▦ Bachelor groups

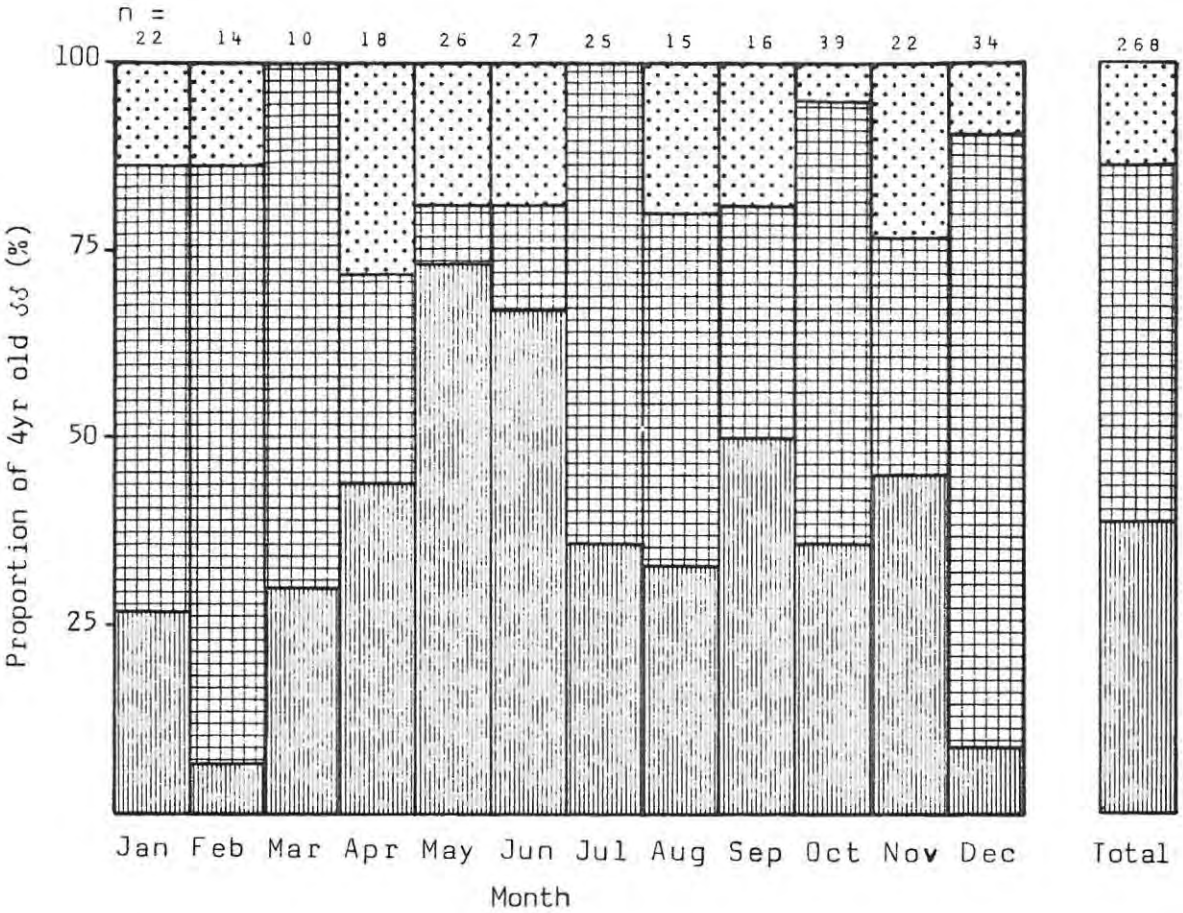
▥ Mixed groups

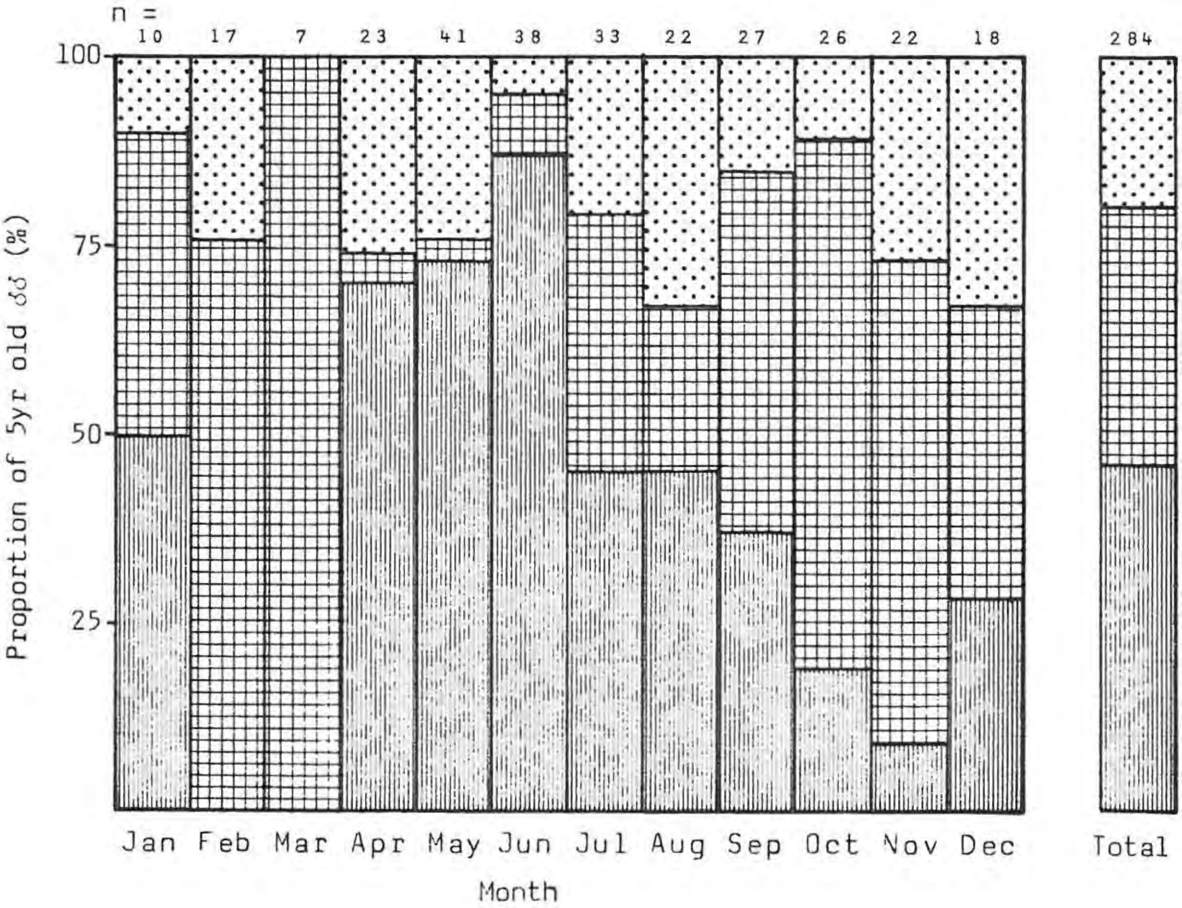
FIG. 8.27 Monthly and overall proportions of 5 year old males occurring in:

░ Solitary groups

▦ Bachelor groups

▥ Mixed groups


n =
22 14 10 18 26 27 25 15 16 39 22 34 268
100
75
50
25
Proportion of 4yr old ♂♂ (%)
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Total
Month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100
75
50
25
Proportion of 5yr old ♂♂ (%)
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Total
Month

TABLE 8.20 Significant variations in the numbers of 2 year old males observed in solitary, bachelor and mixed groups. (Months with non-significant variations have been omitted.)

Month	Solitary	Bachelor	Mixed
Feb	n.s.	Increased $\chi^2 = 4,00$ $p<0,05$	n.s.
Apr	Increased $\chi^2 = 8,10$ $p<0,01$	n.s.	n.s.
Aug	n.s.	Increased $\chi^2 = 9,80$ $p<0,01$	n.s.
Overall	$\chi^2 = 18,11$ n.s.	$\chi^2 = 28,31$ $p<0,01$	$\chi^2 = 5,20$ n.s.

TABLE 8.21 Significant variations in the numbers of 3 year old males observed in solitary, bachelor and mixed groups. (Months with non-significant variations have been omitted.)

Month	Solitary	Bachelor	Mixed
Feb	n.s.	Increased $\chi^2 = 8,62$ $p<0,01$	Decreased $\chi^2 = 6,32$ $p<0,05$
Apr	Increased $\chi^2 = 9,90$ $p<0,01$	Decreased $\chi^2 = 6,37$ $p<0,05$	n.s.
May	n.s.	Decreased $\chi^2 = 3,92$ $p<0,05$	n.s.
Oct	Decreased $\chi^2 = 5,82$ $p<0,05$	n.s.	n.s.
Overall	$\chi^2 = 24,34$ $p<0,05$	$\chi^2 = 32,6$ $p<0,001$	$\chi^2 = 14,29$ n.s.

TABLE 8.22 Significant variations in the numbers of 4 year old males observed in solitary, bachelor and mixed groups. (Months with non-significant variations have been omitted.)

Month	Solitary	Bachelor	Mixed
May	n.s.	Decreased $\chi^2 = 8,72$ $p<0,01$	Increased $\chi^2 = 7,84$ $p<0,01$
Jun	n.s.	Decreased $\chi^2 = 6,14$ $p<0,05$	Increased $\chi^2 = 5,35$ $p<0,05$
Dec	n.s.	Increased $\chi^2 = 33,79$ $p<0,01$	Decreased $\chi^2 = 26,78$ $p<0,01$
Overall	$\chi^2 = 13,60$ n.s.	$\chi^2 =33,79$ $p<0,001$	$\chi^2 = 26,78$ $p<0,01$

TABLE 8.23 Significant variations in the numbers of 5 year old males observed in solitary, bachelor and mixed groups. (Months with non-significant variations have been omitted.)

Month	Solitary	Bachelor	Mixed
Feb	n.s.	Increased $\chi^2 = 8,93$ $p<0,01$	Decreased $\chi^2 = 7,80$ $p<0,01$
Mar	n.s.	Increased $\chi^2 = 8,81$ $p<0,01$	n.s.
Apr	n.s.	Decreased $\chi^2 = 6,02$ $p<0,05$	n.s.
May	n.s.	Decreased $\chi^2 = 12,07$ $p<0,001$	Increased $\chi^2 = 6,52$ $p<0,05$
Jun	Decreased $\chi^2 = 4,03$ $p<0,05$	Decreased $\chi^2 = 7,59$ $p<0,01$	Increased $\chi^2 = 13,72$ $p<0,001$
Oct	n.s.	Increased $\chi^2 = 9,30$ $p<0,01$	Decreased $\chi^2 = 4,08$ $p<0,05$
Nov	n.s.	Increased $\chi^2 = 5,63$ $p<0,05$	Decreased $\chi^2 = 6,59$ $p<0,05$
Overall	$\chi^2 = 12,56$ n.s.	$\chi^2 = 60,98$ $p<0,001$	$\chi^2 = 46,45$ $p<0,001$

TABLE 8.24 Sighting frequencies (in %) with which the most frequently observed males in each age class was recorded in different group types.

No.	Age	solitary group	bachelor group	mixed group	No. of obs.	Mean group size ±S.D.	Vegetation type
40	1yr	-	100%	-	3	2,0±0,0	E. bothae
	2yr	-	33%	67%	6	5,8±4,6	E. bothae
94	2yr	6%	-	94%	18	5,5±3,1	Non-succ.
	3yr	22%	11%	67%	9	3,9±3,4	Non-succ.
78	3yr	35%	47%	18%	17	2,7±1,9	Non-succ.
	4yr	36%	36%	28%	14	2,6±2,1	Non-succ.
90	4yr	33%	33%	33%	3	2,0±1,0	P. afra
	5yr	25%	50%	25%	4	2,3±1,5	P. afra
67	5yr	21%	12%	67%	24	4,6±3,6	Non-succ.
95	5+yr	61%	31%	8%	26	1,6±0,9	E. bothae

TABLE 8.25 Sighting frequencies (in %) with which the most frequently observed females in each age class was recorded in different group types.

No.	Age	solitary group	one-female group	female group	mixed group	No. of obs.	Mean group size ±S.D.	Vegetation type
71	1yr	-	37,5%	25%	37,5%	8	5,3±2,2	Non-succ.
	2yr	-	-	71%	29%	7	5,6±2,2	Non-succ.
88	2yr	-	-	87,5%	12,5%	24	4,5±1,5	*E. bothae*
	3yr	20%	5%	60%	15%	20	4,3±2,8	*E. bothae*
74	3yr	4%	4%	70%	22%	27	4,6±2,0	*E. bothae*
	4yr	10,5%	-	79%	10,5%	19	4,7±2,6	*E. bothae*
107	4yr	-	-	50%	50%	16	6,9±3,0	Non-succ.
	5yr	9%	-	73%	18%	11	4,5±2,3	Non-succ.
52	5yr	-	-	80%	20%	10	4,3±2,7	*E. bothae*
	6yr	-	7%	80%	13%	15	4,1±1,3	*E. bothae*
76	6yr	10%	-	60%	30%	10	7,0±5,4	*E. bothae*/ non-succ.
	6+yr	6%	6%	69%	19%	16	4,6±2,3	*E. bothae*/ non-succ.

TABLE 8.26 Indices of association between individually known females inhabiting Kentucky Kop (values of 0,50 and more are underlined).

♀No.	29	34	38	50	52	62	74	88	96	101
23										0,04
29						0,71				
34			0,08		0,05					
38						0,14			0,15	
50							0,66	0,63		0,02
52										0,13
74								0,76		

TABLE 8.27 Indices of association between individually known females inhabiting the Buffalo Camp (values of 0,05 and more are underlined).

No.	47	48	52	55	66	71	77	86	98	99	107
31	0,46			0,07	0,06						0,15
47			0,04	0,12	0,06					0,09	0,09
48						0,24		0,06	0,21		0,04
55					0,55		0,07			0,12	0,05
66							0,18			0,09	0,09
71									0,71		
77								0,18			0,28
86											0,14

TABLE 8.28 Indices of association between individually known females inhabiting A) the Kentucky Kop-Buffalo Camp ecotone, and B) the Winter Slopes (values of 0,50 and more are underlined).

		A						B	
	♀No.	50	68	74	76	79	86	64	85
	49		0,33		0,06				
	50					0,04			
A)	74				0,02				
	76					0,05	0,04		
	79						0,06		
B)	58							0,13	<u>1,00</u>

TABLE 8.29 Indices of association between individually known males inhabiting Kentucky Kop (values of 0,50 and more are underlined).

♂No. & age*	Θ 28	¶ 30	Θ 32	¶ 33	Θ 53	† 54	∇ 61	¶ 73	Θ 82	¶ 83	Θ 84	∇ 95	∇ 102	Θ 104	Θ 106	∇ 113
¶ 24	0,14	0,07		0,15	0,26						0,10		0,06		0,13	
Θ 28		0,06	0,20	0,13	0,06		0,09			0,09				0,11		
¶ 30					0,12							0,05	0,06		0,11	0,22
Θ 32				0,14		0,11				0,11	0,11			0,13	0,13	
¶ 33								0,08			0,10	0,05	0,06			
Θ 39									0,18							
¶ 83														0,17		
∇ 95													0,26			

* Male age classes:- Δ = 1-2yr, Θ = 2-3yr, ¶ = 3-4yr, † = 4-5yr, ∇ = 5+yr.

TABLE 8.30 Indices of association between individually known males inhabiting the Buffalo Camp (values of 0,50 and more are underlined).

♂No. & age*	∇ 67	¶ 75	¶ 78	Θ 94	† 109
Δ 26	0,05				
∇ 67		0,04	0,03	0,04	
¶ 75				0,08	
¶ 78					0,13

* Male age classes:- Δ = 1-2yr, Θ = 2-3yr, ¶ = 3-4yr, † = 4-5yr, ∇ = 5+yr.

TABLE 8.31 Indices of association between individually known males (adult and subadult) and females inhabiting Kentucky Kop (values of 0,50 and more are underlined).

No.	¶	Θ	¶	¶	Θ	¶	Θ	¶	Θ	∇	∇	Θ	Θ	∇
& age*	24	28	30	33	53	73	82	83	84	95	102	104	106	113
♀No.														
23			0,09											
29	0,09							0,14						
34						0,07								
36			0,06				0,33							
38			0,09						0,13					
50	0,04	0,04		0,08		0,04			0,09					
52					0,05					0,05				0,15
62	,11													
68						0,08								
74	0,03	0,03		0,06					0,03					
88	0,04	0,03		0,10					0,04					
96	0,11								0,14					
100					0,25							0,20		
101			0,04							0,03	0,04		0,05	

* Male age classes:- Δ = 1-2yr, Θ = 2-3yr, ¶ = 3-4yr, † = 4-5yr, ∇ = 5+yr.

TABLE 8.32 Indices of association between individually known males (adult and subadult) and females inhabiting the Buffalo Camp and Winter Slope areas (values of 0,50 and more are underlined).

♂No. & age*	Δ 40	Θ 42	∇ 67	Θ 69	¶ 75	¶ 78	¶ 83	Δ 92	Θ 94	† 97	∇ 108
♀ No.											
31			0,11								
47			0,09								
48				0,08	0,05				0,05		
55			0,05								
56		0,11									
58					0,08						
64				0,27				0,31		0,18	
66			0,09		0,05	0,04					
71				0,09	0,11						
74									0,03		
76									0,04		0,17
77									0,09		
79	0,09						0,09				
85					0,08						
86					0,12				0,66		
98				0,08	0,05						
99			0,07		0,06						
107					0,09				0,08		

* Male age classes:- Δ = 1-2yr, Θ = 2-3yr, ¶ = 3-4yr, † = 4-5yr, ∇ = 5+yr.

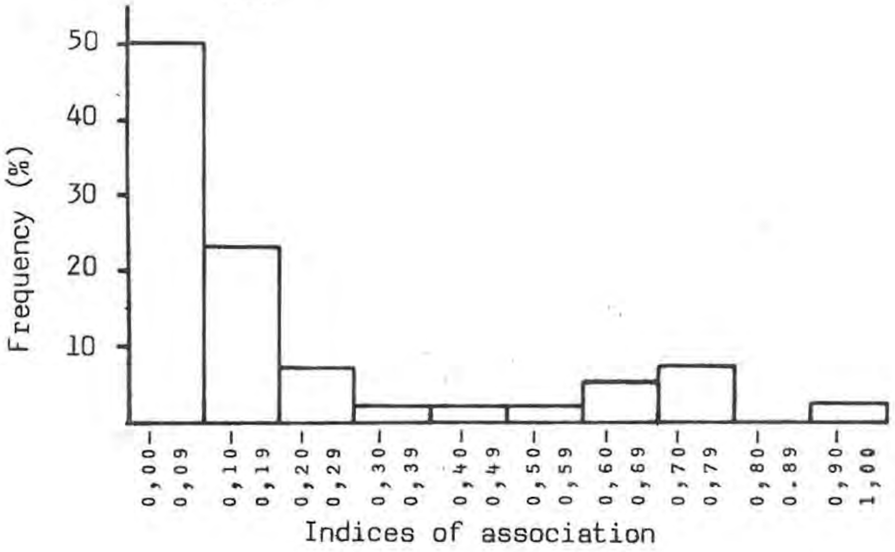
FIG. 8.28 Frequency distribution of indices of association between:

a) individually known females

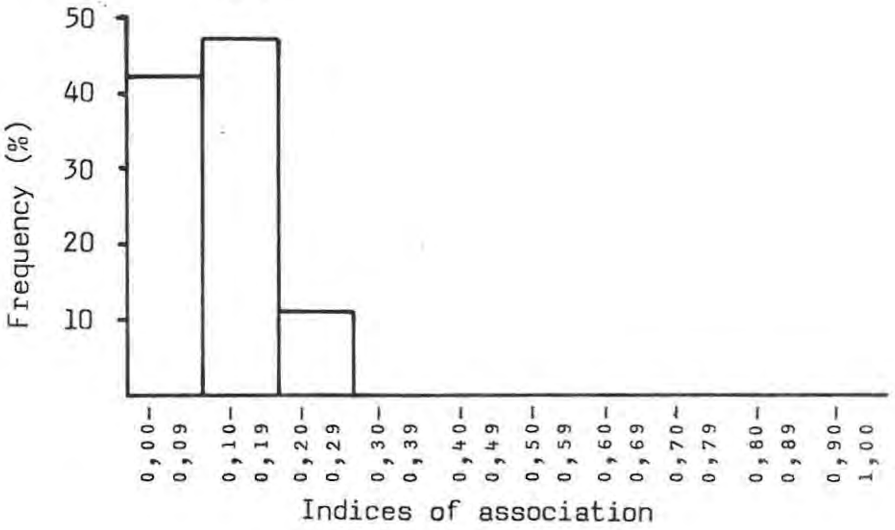
b) individually known males (adults and subadults)

c) individually known males and females

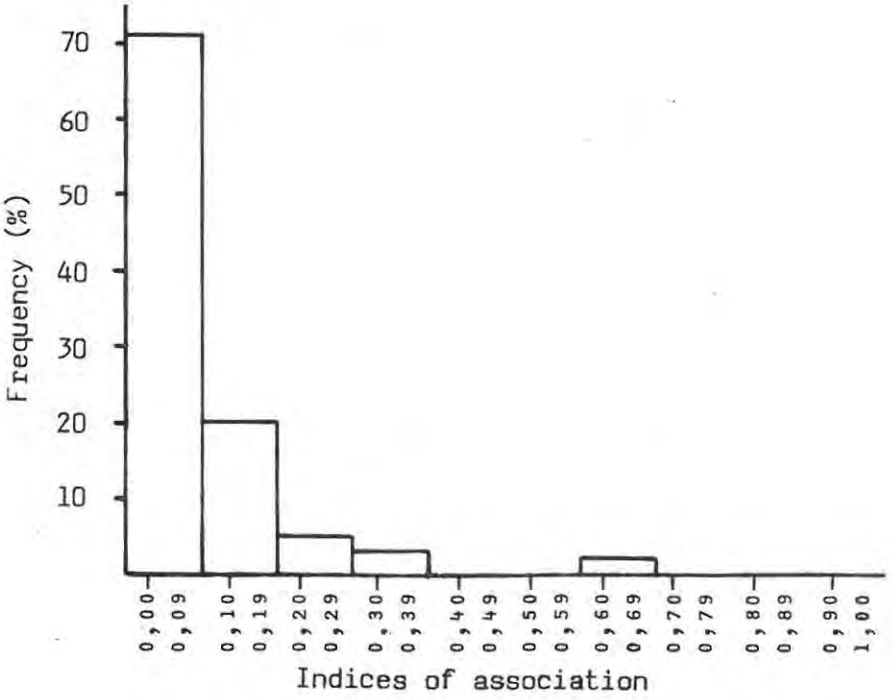
(a)


Frequency (%)
10
20
30
40
50
0,00-
0,09
0,10-
0,19
0,20-
0,29
0,30-
0,39
0,40-
0,49
0,50-
0,59
0,60-
0,69
0,70-
0,79
0,80-
0.89
0,90-
1,00
Indices of association

(b)


Frequency (%)
10
20
30
40
50
0,00-
0,09
0,10-
0,19
0,20-
0,29
0,30-
0,39
0,40-
0,49
0,50-
0,59
0,60-
0,69
0,70-
0,79
0,80-
0,89
0,90-
1,00
Indices of association

(c)


Frequency (%)
10
20
30
40
50
60
70
0,00
0,09
0,10
0,19
0,20
0,29
0,30
0,39
0,40
0,49
0,50
0,59
0,60
0,69
0,70
0,79
0,80
0,89
0,90
1,00
Indices of association

indices of association). Only once was an animal darted in the presence of two marked kudu. The observed associations between these three cows subsequent to their capture are shown in Table 8.33. Finally, sighting frequencies and periods of observation varied considerably between known individuals (Table 8.34).

8.3.8 Social behaviour

Observations on social behaviour were rarely witnessed during the two years of field study, and were largely confined to sexual behaviour (see Chapter 5) and interactions between males. Interpretations of the latter were facilitated by reference to Walther's (1964, 1974) accounts and by observations of a captive male (Plate 8.2 a-e). These interactions are briefly described in Table 8.35.

Aspects of female social behaviour were recorded twice. During September 1978, an adult cow was seen butting the flank of another adult female, while mutual grooming, of the neck and face, was observed once between two adult females.

Consistent "leaders" were not apparent in either sex.

8.4 Discussion

Since visibility was vastly improved during the aerial censuses, the comparable group size data from same-month aerial and ground counts infer that group sizes were recorded reasonably accurately from the ground. The degree of accuracy probably fluctuated with vegetation type however, and as a result, group size records from the more densely structured habitats should be regarded as minimal. These were always smaller than the group sizes recorded in more open areas, but differences were not significant within any one month.

Such differences may reflect a tendency by kudu to form larger groups in more open areas. Such a relationship has been noted in many ungulate species, (Leuthold 1970, 1976; Leuthold & Leuthold 1975b; Junguis 1971; Walther 1972; Hirth 1977; Mitchell, Staines & Welch 1977; Evans 1979) and may be due to several factors (see Chapter 9). The mean group sizes of collared individuals (Tables 8.24 and 8.25) suggest that kudu group size may vary according to habitat on the Reserve, but such variations are slight.

The absence of any correlation between mean group size and rainfall indicates that grouping patterns are unaffected by changes

TABLE 8.33 Observed associations of females No. 50, No. 74 and No. 88.

	female No. 50	female No. 74	female No. 88
With female No. 50 only	-	3	1
With female No. 74 only	3	-	10
With female No. 88 only	1	10	-
With both others	24	24	24
With different kudu	7	5	4
Alone	1	4	5
Total no. observations	36	46	44
% with one or both other females	77,8%	80,4%	79,5%

TABLE 8.34 Numbers of sightings, months of observation and male and female associations of individually known kudu (only individuals with known associates).

♂♂	Total no. of observations	Months under observation	No. of assoc. with known	
			♂♂	♀♀
24	12	13	7	6
26	7	14	1	-
28	16	17	8	3
30	15	17	7	4
32	14	1	7	-
33	15	17	7	3
39	2	11	1	-
40	9	18	-	1
42	11	19	-	1
53	19	13	3	2
54	5	5	1	-
61	7	2	1	-
67	24	19	4	5
69	6	8	-	4
73	15	13	1	3
75	20	17	2	8
78	31	20	2	2
82	9	7	1	1
83	7	9	3	2
84	8	13	3	5
92	4	17	-	1
94	27	20	2	6
95	26	13	3	2
97	2	2	-	1
102	20	14	4	1
104	5	7	3	1
106	4	12	3	1
108	3	2	-	1
109	5	3	1	-
113	4	5	1	1

♀♀	Total no. of observations	Months under observation	No. of assoc. with known	
			♂♂	♀♀
23	9	13	1	1
29	9	14	2	1
31	14	17	1	4
34	15	10	1	2
36	10	18	2	-
38	8	16	2	3
47	21	17	1	6
48	19	22	3	4
49	10	18	-	2
50	36	19	5	4
52	25	21	3	3
55	13	21	1	6
56	8	19	1	-
58	6	15	1	2
62	7	14	1	2
64	9	19	3	1
66	17	17	3	6
68	9	8	1	1
71	15	18	2	2
74	46	18	5	3
76	26	19	2	4
77	16	17	1	4
79	14	19	2	3
85	5	13	1	1
86	17	13	2	5
88	44	20	4	2
96	6	13	2	1
98	19	19	2	2
99	4	15	2	3
100	5	13	2	-
101	35	13	4	3
107	27	18	2	7

PLATE 8.2 Aggressive behaviour of adult male kudu.

*a-c) Horning the vegetation, probably a mild threat display.

*d) Dominance display: broadside display with head-low posture. Note the erection of the mane.

*e) Head-low presentation of horns, a serious threat display indicating a readiness to fight.

f) Two 4 year old males sparring. (Photograph taken in Kruger National Park).

* Aggressive displays of a 4 year old captive male kudu directed at the author.

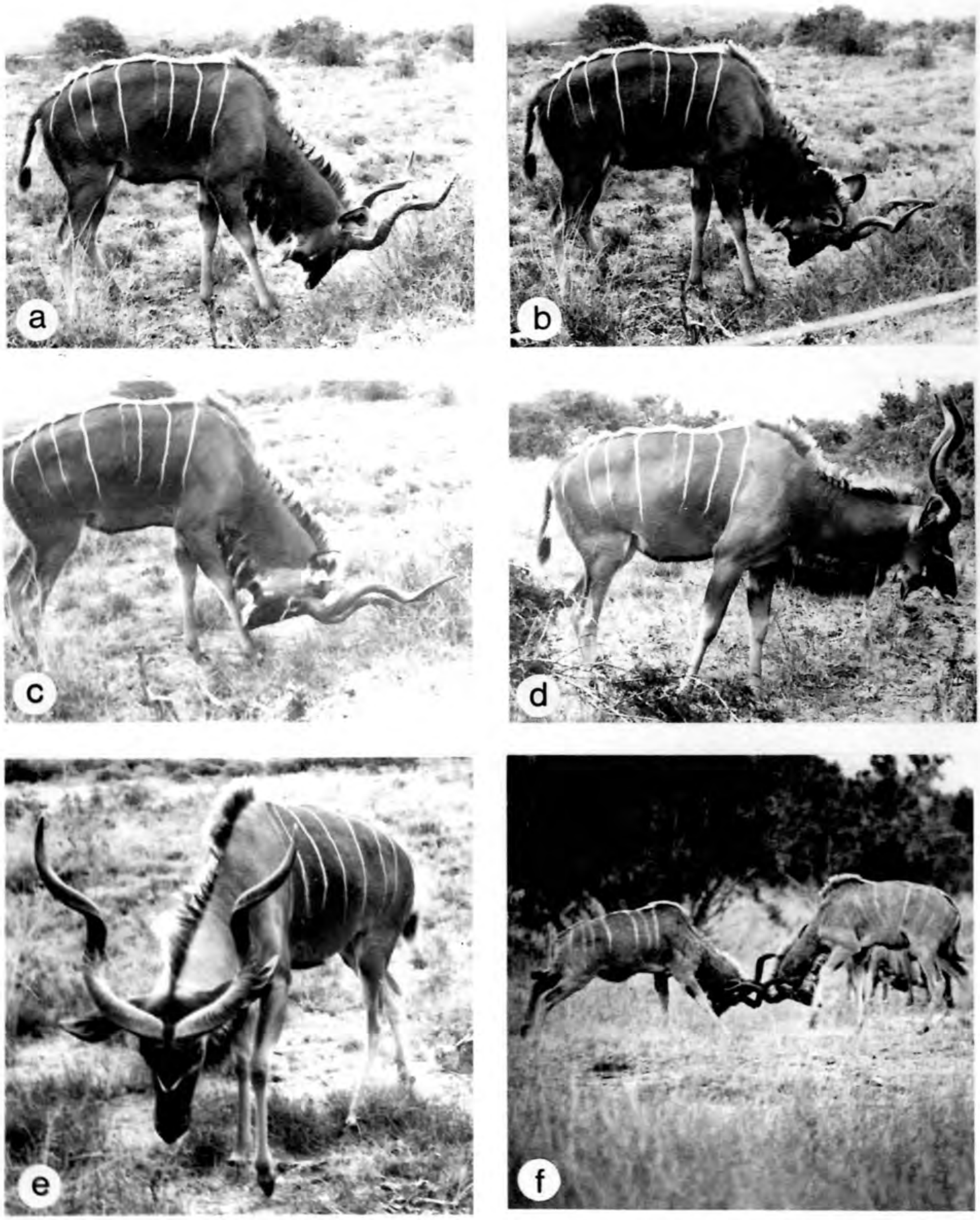

a
b
c
d
e
f

TABLE 8.35 Observed behavioural interactions between males.

Month	Behaviour and remarks
Feb	Sparring between two 3 year old males.
Jun	Sparring between two 2 year old males.
Aug	Sparring between two 3 year old males.
Aug	Sparring between a 3 year old and 4 year old male, and then between the same and another 3 year old male.
Oct	Sparring between two 3 year old males.
Nov	Sparring between two 3 year old males.
Dec	Sparring between two 3 year old males.
Mar	Neck wrestling between two 5 year old males.
Apr	5 year old male pursued a 3 year old male in the company of 3 adult females.
Apr	5 year old male pursued a 3 year old male in the company of 3 adult females.
May	5 year old male pursued a 2 year old male in the company of 3 adult females.
Oct	4 year old male pursued two 3 year old males and then thrashed the bush with horns.
Mar	5 year old male bush thrashing in the company of another 5 year old male and a 3 year old male.
May	Broadside display by 3 year old male directed at a subadult male in the company of 4 females.
Nov	3 year old male displace from shady tree by 5 year old male.
May	Subadult male chased by 3 year old male remained 50 m from moving group.

in primary production, since plant growth is largely determined by rainfall (Coe, Cumming & Phillipson 1976; Leuthold 1977). Similar interannual mean group size records from two years with widely differing amounts and distributions of rainfall confirm this. The relevance of these results will be discussed in the following chapter.

Nevertheless, kudu grouping patterns showed a distinct trend, with significantly fewer animals in groups during the summer months, (except for January, when the sample size was low) and thereafter gradually increasing to the significantly higher numbers observed in June (Table 8.2). The numbers of adult females in groups showed an identical pattern (Table 8.13) and since this was not evident in adult males (Table 8.15) this strongly suggests that intersexual differences in social behaviour are responsible for the changes in mean group size.

The most obvious difference in behaviour between the sexes occurs during the calving period, which is largely restricted to December, January and February (97% of all births, Chapter 5). As in most other gregarious ungulate species (Fraser 1968; Spencer-Booth 1970) female kudu isolate themselves prior to parturition (Junguis 1970; Owen-Smith pers. comm.). The duration of this pre-partum isolation is not known, since sighting frequencies of solitary females (Fig. 8.5) shows no distinct trends. Records from other ungulates range from 3-4 weeks in reedbuck (Junguis 1970) to a few minutes in impala (M. Jarman 1976) but most studies indicate a period of a day or so (e.g. Spinage 1969a; Clutton-Brock & Guinness 1975). After birth, the mother remains with her calf for the post-partum period (Lent 1974) which lasts for approximately 24 hours (Walther 1964). The calf then leaves its mother and selects a hiding place usually against "something vertical" and often under a canopy of vegetation (Walther 1964).

For the next two months or so, maternal-calf associations are rarely seen (Figs. 8.5, 8.8, 8.16, and 8.18) suggesting that calves are actively hiding alone or "lying-out" (Gosling 1969). During this period, mothers may temporarily rejoin their former groups (pers. obs. of collared kudu known to be lactating; Owen-Smith pers. comm.). The amount of time mothers are associated with other females, their own calves, and travelling between the two would depend on the intervals between nursing, the distance separating the maternal group from the calf and the duration of the "lying-out" period.

The frequency with which calves are suckled is probably inversely related to their age (Lent 1974) but records from captive kudu indicate that on average, kudu calves are nursed and groomed three to five times per 24 hours (Walther 1964; Lent 1974). Distances separating mothers and calves could not be determined in the field, but home range data (Chapter 7) demonstrates that these are not as extensive as in several other large ungulates (Spinage 1969a; Leuthold 1971; Leuthold 1978a; Clutton-Brock & Guinness 1975; Wilson & Hirst 1977). Infrequent calf sightings (Fig. 8.16), sighting frequencies of one-female groups (Fig. 8.8) and the proportion of adult cows in solitary and one-female groups (Fig. 8.18) all infer that lying-out continues for approximately two months after parturition. Similar periods have been noted in Kruger National Park (Owen-Smith pers. comm.). The significance of this lying-out behaviour will be discussed in the following chapter.

The proportions of subadult female (Fig. 8.17) and male (Fig. 8.19) kudu seen alone during the calving and lying-out periods suggest that parturient and nursing females are intolerant of their yearling offspring, as are many female ungulates (Leuthold 1977). The formation of subadult male peer groups at this time (Fig. 8.19) is a further indication of the weakening of the mother-young bond (Lent 1974). Such hostilities are probably temporary however, since the proportion of subadult females and males in one-female groups increases during February and March (Figs. 8.17 and 8.19 respectively) resulting in a gradual increase in the mean size of one-female groups (Table 8.6). This infers that previous offspring rejoin their mothers before the latter associate with other adult females (i.e. towards the end of the lying-out period).

Females and their calves return permanently to their former groups once lying-out behaviour has terminated, and are therefore partly responsible for the gradual increase in mean group size which commences in March. Nursery herds comprising aggregations of lactating females and calves, were not witnessed (Table 8.7).

Adult female and calf behaviour during the calving and subsequent lying-out period clearly alters grouping patterns at this time. With such a high conception rate and restricted calving season (Chapter 5), it is perhaps surprising that changes in mean group size and sighting frequencies of certain groups (and proportions of kudu within those groups) are not more pronounced. However, other ungulate studies have shown that intraspecific behaviour may vary considerably during the calving period. Distances separating mothers from hidden calves may increase as calves get older (Junguis 1970; Autenrieth & Fichter 1975) and may vary between individuals (Leuthold 1977). Individual differences in the lying-out period have also been recorded in waterbuck and sable (Hanks, Stanley Price & Wrangham 1969; Sekulic 1978; Estes & Estes 1979). Even the onset of pre-partum isolation and tolerance towards conspecifics may vary between individuals (Gosling 1969; Junguis 1970; Kok 1975; Clutton-Brock & Guinness 1975). It is highly probable that similar individual differences occur in kudu, at this time and that these variations tend to obscure the usual pattern of social organisation.

Similar trends in female kudu grouping patterns during calving were recorded by Underwood (1978). Simpson (1968) suggested that increased mean group size of kudu seen during January and February in Rhodesia may have been social aggregations of females prior to calving. Since his data were not confined to females, his suggestion is highly speculative and the relatively small changes in mean group size may equally well have resulted from a response to the increased rainfall, and hence plant growth, at this time. Jarman (1974) developing Simpson's (1968) suggestion even further, inferred that the supposed aggregations of females during peak calving was an antipredator strategy. Results from this study indicate that such aggregations of cows and calves are extremely unlikely. They are more characteristic of females living in open groups (e.g. Grant's gazelle, Walther 1972; topi and impala, Jewell 1972; Jarman & Jarman 1974; and eland, Underwood 1975) and are not evident in kudu (see below).

Sighting frequencies of bachelor and mixed groups demonstrate that changes in adult male grouping patterns also occur during the summer months. This is most obvious in February when the increased number of female group sightings and the reduced sighting frequency of mixed groups show that fewer adult males associate with female groups. Those that do are most likely to be the only male present and associate with considerably fewer females in the group. Thus most males form bachelor groups (Figs. 8.6 and 8.20).

Such changes are unlikely to result from the influence of female behaviour during the calving and lying-out periods (when groups containing adult cows may be rather transient) because adult intersexual associations, with the exception of some 2 year old males, are loose (see below). It would therefore appear that adult males actively leave the company of females as early as December and most of these associate with other males, usually of a similar age. This is particularly noticeable among 4 year old males while 5 year old males were never seen in the company of females during February and March.

The significance of all-male group formation at this time is not known, but it is tentatively suggested that males within these groups are competing for dominance, which is the prerequisite for access to oestrous females. Dominance hierarchies would therefore be established prior to the rut. Rank is probably age- and size-related (particularly since dominant animals lying down undergo a temporary loss in rank, Walther 1964), so that younger males competing for dominance gain little from being in the presence of more mature males, and form associations with peers. It is within such young peer groups that most aggressive interactions occur (Table 8.35, Plate 8.2f). Fully mature males may be extremely tolerant towards younger males, even during the rut, provided that the latter show submissive behaviour in any competitive situation. Failure to do so would presumably induce dominance and threat displays from the older male (Plate 8.2) which may in extreme cases lead to the eviction of the younger male. Dominance relations and mating strategies will be discussed further in the following chapter.

Sighting frequencies of mixed groups and the proportions of both adult males and adult females within these groups indicate that the rut commences in April and reaches a peak in June (Fig. 8.12, Table 8.14).

The slight increase in mixed group size during the rut (Table 8.8) is due to increases in the number of adult males (Table 8.9) and adult females (Table 8.10). The proportion of juveniles and calves within these groups also increases (Table 8.11). Larger group sizes are also evident in bachelor groups (Table 8.4) but the sizes and sighting frequencies of these two group-types clearly demonstrate that mixed group formation is largely responsible for the overall significant increase in mean group size during June (Table 8.2).

Group sizes gradually decline during the rest of the year (except for October, see below) as do sighting frequencies of mixed groups. Corresponding increases in sighting frequencies of bachelor and female groups confirm that intrasexual associations are more common during the summer months.

However, mean sizes of most group types, and the overall mean group size, show a slight increase in October. In addition, the proportions of adult kudu within these group-types show significant deviations during this month (Tables 8.12 and 8.14). Examination of field records revealed that the ground censuses in October 1978 were conducted under extremely windy conditions. Sightings were largely confined to the leeward slopes of hills, where kudu were found in surprisingly high densities. Clearly the data obtained for this month result from these non-social aggregations of sheltering kudu

8.4.1 Sex- and age-specific differences in social relations

Sighting frequencies of groups containing males and/or females (Figs. 8.4 to 8.12) and the mean number of individuals within these groups (Tables 8.4, 8.6 to 8.10) indicate that females live in stable, cohesive groups but that males form loose associations with members of either sex. Mean group sizes also indicate that females are more gregarious than males, although the size of female groups are biased by the presence of juveniles. Comparisons between the mean number of adult females in groups containing adult females (Table 8.13) and the mean number of adult males in groups containing adult males (Table 8.15) unequivocally show that females are more gregarious. A similar trend is found in many African ungulates (Leuthold 1977).

While adult females could not be aged in the field, adult female grouping patterns suggest that social relations do not alter with age. Group details of the most frequently sighted, marked, cows in each age class (ages were assessed from tooth eruption and wear patterns on capture and recapture) confirm this (Table 8.25).

Subadult females show similar trends, except for the considerably higher proportion seen in one-female groups. This difference may be partially due to divergent sample sizes, particularly since the proportions of both adult and subadult females seen in one-female groups show similar intermonthly variations (Figs. 8.17 and 8.18). However, it is clearly evident from these sample sizes that a large proportion of subadult females were incorrectly classified as adults. This has probably resulted in producing artificial or erroneous similarities in the grouping patterns of subadult and adult females, (and also explains the anomalous subadult sex ratio in one-female and female groups). Sightings of the most frequently observed marked subadult female (No. 71 in Table 8.25) suggest that, as above, young cows spend a considerable amount of time in one-female groups. While such an error may influence conclusions concerning grouping patterns, the fact that 93% of all adult females and 95% of all subadult females were seen in the company of other adult females (Figs. 8.17 and 8.18) suggests that no age-differences in social relations are evident.

The majority (92%) of subadult males were seen in the company of adult females (Fig. 8.19) suggesting that the mother-young bond continues long after weaning.

Sightings of 2 year old males show that associations with adult cows are less common than in subadult males (Fig. 8.24) but much more frequent than in other adult males (Table 8.17). This suggests that the dissolution of the mother-son bond occurs at this time. The actual age at which this happens probably varies, and may explain why 2 year old males associate with older males rather than peers.

Three year old males show an equal tendency to form associations with other males and females (Table 8.17). These groups largely consist of peers and are significantly larger than other peer groups. Male-male relations are even more pronounced in 4 year olds for much of the year and these are the only males to show a significant deviation from their expected level of association with females (Table 8.17 and Fig. 8.26).

The tendency to be solitary is slightly more pronounced in 5 year old bulls than in other males (Tables 8.16 and 8.17, Fig. 8.27), but these bulls most commonly associate with females or with other 5+ year males (Fig. 8.27).

Confirmation that age-related differences in social relations occur in male kudu comes from the grouping patterns recorded from the most frequently sighted marked male in each age class (Table 8.24). Associations of the two 5+ year old males, No. 67 and No. 95, clearly show that social relations may vary considerably between individuals of similar age. (The solitary nature of male No. 95 is particularly noticeable since this animal lived in an area of higher kudu density than male No. 67. In contrast, the latter most frequently associated with females.)

While these results clearly show that male social relationships alter with age, differences between young and older adult males are, seasonally, even more pronounced, and are closely correlated to the highly seasonal reproductive cycle. Associations between subadult males are more marked towards the end of the rut, and to a lesser extent during the calving and lying-out period, when significantly more subadult males are seen alone (Fig. 8.19) probably as a result of female aggression. Two year old males show a stronger tendency to associate with males prior to and after the rut, while during this period they are often seen alone (Table 8.20 and Fig. 8.24). However, like subadult males, their level of association with adult females remains relatively constant throughout the year. In contrast, bulls older than 3 years of age form pronounced associations with females during the rut, and rarely associate purely with other males during this period. This tendency increases with age (Tables 8.21 to 8.23, Figs. 8.25 to 8.27). For the rest of the year and particularly prior to the onset of the rut, associations with other males are more common than a solitary existence.

In summary, changes in social organisation are clearly related to the reproductive cycle, and such changes are most pronounced and complex during the rutting season. Environmental changes within the study area appear to have little influence on kudu social organisation. The relationship between the social organisation and the ecology of this species will be discussed further in the following chapter.

8.4.2 Inter-individual associations and group stability

As Leuthold (1979) points out, determining associations between individuals and the stability of groups requires intensive observations of as many individually recognisable animals as possible. Problems in attempting to meet these conditions have already been described, with the result that indices of association in Tables 8.26 to 8.32 must be regarded as minimal values. Nevertheless, certain trends are apparent from these results.

8.4.2.1 Relations among females

Sixteen percent of all female indices of association were greater than 0,50 (Fig. 8.28a) inferring that close relationships exist between certain cows. Sightings of an individual adult and subadult female over fifteen months yield a perfect association (Table 8.28) demonstrating that the mother-daughter bond continues long after weaning. Circumstantial evidence suggests that such bonds may continue throughout life. For example, three females were each associated with at least one of the other two in over 77% of all sightings (Table 8.33). The ages of these females all differed by at least one year, the youngest being two years old on capture. This suggests that they were possibly directly related. Similar age differences were found in other females with high levels of association. Substantial evidence from Owen-Smith (pers. comm.) confirms that close relationship continue between female kudu and their female progeny.

8.4.2.2 Relations among males

In sharp contrast to those of females, male indices of association never exceed a value of 0,30. This suggests that males only form temporary associations with other males, particularly since marked males were generally resighted less frequently than marked females. Closer examination of the resighting details of males exhibiting indices of 0,20 or more show that individuals were seen together for up to six months, but that during this time both were frequently seen apart. Continuous associations rarely lasted for more than three or four days (pers. obs.).

Although results discussed earlier show that male grouping patterns alter with age, such changes are not evident from the association indices. Nevertheless, while periods of observation vary considerably between individuals, data in Table 8.34 demonstrates that 2-4 year old males associate with more males than do fully mature (5+ year old) bulls. All male associations are therefore temporary, but are more frequent in younger animals.

8.4.2.3 Relations between males and females

The majority of association indices suggest that permanent adult intersexual relationships are not common in kudu (Tables 8.31 and 8.32, Fig. 8.28c). The only index indicating a close association involves an adult female and a 2 year old male. Sightings of both individuals, when only one other adult cow was present, suggest that the collared cow may have been the mother of this male. This association continued until the death of the female thirteen months later.

All indices of 0,20-0,39 involve males between the ages of one and three years. It is quite possible that some of these associations were between males and their mothers, or members of their maternal group. As in relations among males, younger bulls were seen with more marked females than were older males (Table 8.34). The number of marked males seen in the company of marked females (1-5 individuals, Table 8.34) probably reflects the extent of home range overlap and local densities of marked individuals (the same applies to certain female-female and male-male associations) as well as seasonal variations in social organisation, notably during the rut.

8.4.2.4 Group stability

a) Female groups

The high degree of association among certain marked individuals strongly suggests that females form stable, closed groups, with membership confined to related cows and their juvenile offspring. That these groups show no significant variations in size (Table 8.7) or occurrence (Fig. 8.10) throughout the year (thereby demonstrating that nursery herds are not formed) is further confirmation of their stable and closed nature (Rodgers 1977).

Since the frequency distribution of female group size shows no evidence of polymodality (Fig. 8.11), the female group, rather than the one-female group, is clearly the basic social unit. Group stability is most likely to fluctuate during the calving and lying-out periods, but typically these groups contain three to five adult females and their subadult offspring. No collared females were seen consistently on their own or in one-female groups, suggesting that these are probably temporarily fragmented portions of the female group.

Groups containing more than about six individuals are probably temporary aggregations of these social units. With high kudu densities (Chapter 4), and relatively small but widely overlapping home ranges (Chapter 7), such meetings between social units would be common, and would explain the high incidence of low indices of association between females (Fig. 8.28a).

Similar but slightly larger female social units are found in the Kruger National Park (Owen-Smith, pers. comm.). There, larger groups split into two subgroups, but have a common home range and rejoin temporarily on meeting.

b) Bachelor groups

Unlike the cohesive social units of females, males form temporary associations with one another. Fluctuations in the sighting frequencies of male groups (Fig. 8.6) confirm this. Such transient associations are usually formed between two individuals of the same age, except in 2 year old males where associations with older animals are more common (Tables 8.4, 8.5 and Fig. 8.7).

c) Mixed groups

Mixed groups are simply associations between female social units and one or more adult males. (The mean number of adult females in mixed groups suggest that male associations with solitary female or one-female groups are comparatively rare, Table 8.10.) Since the number of males associating with any female group remains relatively constant throughout the year (mean range = 1,2-1,9 adult males, Table 8.9) the size of the mixed group also remains comparatively stable (Table 8.8). However, the number of mixed groups that are formed varies considerably during the year, reaching an obvious peak during the rut (Fig. 8.12). This, together with the variations in the proportions of males of different ages within these groups (Fig. 8.23) indicate the fluid nature of mixed group formation and composition.

Indices of association between adult males and females confirm that such relationships are generally far from stable or permanent, thereby enhancing gene exchange.

The low numbers of adult males within mixed groups suggest that these are not simply aggregations of female and bachelor groups (Tables 8.9 and 8.4), but that most bachelor groups fragment (Fig. 8.6) and individual males join female groups. This is particularly evident in older males during the rutting season (Figs. 8.15, 8.26 and 8.27). For the rest of the year, single 2 year old males are commonly found with female groups (Fig. 8.15). While the association between male No. 94 and female No. 86 suggests that some of these males may still be permanently associated with their natal groups, other indices of association and sightings of marked and unmarked 2 year old males suggest that such relations are atypical at this age. Owen-Smith (pers. comm.) found that most males leave their female groups prior to the rut when they are two years old, but that individuals born late in the season may remain for a further year. Factors causing this dissociation are not yet known. The fact that many leave prior to the rut (Fig. 8.24) suggests that they are not evicted by more dominant males (as occurs in many, particularly territorial ungulates - Estes 1969, 1974; Jarman & Jarman 1973; Gosling 1974; Joubert 1972; Joubert & Bronkhorst 1977; Leuthold 1977; Allsopp 1979; M. Jarman 1979). This view is further supported by the fact that aggressive interactions between males of widely differing ages were rarely witnessed (Table 8.35). Eviction by female (maternal) aggression, as occurs in elephants (Douglas-Hamilton & Douglas-Hamilton 1975; Hanks 1979) and white-tailed deer (Hirth 1977) is also considered unlikely due to the size differences of females and 2 year old male kudu. It is therefore probable that dissolution of the maternal : male-offsping bond occurs gradually and the male leaves to join other males (see next chapter) on his own accord. This tendency is also shown by mountain sheep (Geist 1971), bontebok (David 1973, 1975), buffalo (Sinclair 1977) and to a lesser extent in wildebeest (Estes 1969) and waterbuck (Spinage 1969b). Initially male movements away from their natal group may be temporary, but the low indices of male-female association, together with the high proportion of 2 year old males found with females suggests that frequent but temporary associations with females are characteristic of males at this age. Sightings of subadult males (Fig. 8.19 and male No. 40 in Table 8.24) illustrate that the age at which males leave their maternal groups may vary considerably.

Chapter 9
DISCUSSION

9.1 Factors affecting population dynamics and performance

Kudu density on the Reserve is considerably higher than in many other parts of southern Africa, which largely reflects the high productivity of Fish River Valley bushveld, little interspecific competition, and negligible predation on adults. Small home range sizes and the absence of any seasonal movements infer that kudu on the Reserve occupy an optimal habitat. Reproductive data confirm this. Female kudu reach sexual maturity at an early age, attain the maximum conception rate and conceive at the same time irrespective of their reproductive performance the previous year, (red deer studies have shown that animals in poor condition through inadequate nutrition attain puberty at a later age, may fail to conceive and have retarded oestrous cycles, Sadlier 1969b; Lowe 1969; Verme 1969; Youngson 1970; Guinness, Lincoln & Short 1971, Mitchell 1973; Mitchell & Lincoln 1973; Mitchell, McCowan & Nicholson 1976; Arman, Hamilton & Sharman 1978; Guinness, Albon & Clutton-Brock 1978; Guinness, Gibson & Clutton-Brock 1978).

If it is assumed that there are no differences in fertility between kudu on the Reserve and on neighbouring farms, available data demonstrate that the high density of kudu on the Reserve is unlikely to exceed the carrying capacity. In fact, the standing crop biomass of browsers on the Reserve (approximately 2,600 kg/km^2) is almost half that of the botanically similar Addo Elephant National Park (approximately 4,500 kg/km^2: raw data from Hall-Martin 1978; Mentis 1970; and Coe et al. 1976).

Several studies of both grazing and browsing ungulates in more tropical areas have shown that seasonal changes in grouping patterns are correlated with rainfall and plant production. Group size often decreases during the dry season, presumably to facilitate exploitation of a reduced food supply (Jarman & Jarman 1974; Sinclair 1974, 1977; Leuthold 1976, 1977, 1979; Rodgers 1977; Underwood 1978), but may increase when individuals aggregate in locally favourable areas (Hanks et al. 1969; Geist 1974; Leuthold 1978a, 1978b; Leuthold & Leuthold 1975b; B. Leuthold 1979; B. Leuthold & Leuthold 1978). Results from this study clearly demonstrate that grouping patterns are influenced largely by breeding behaviour rather than environmental conditions. Therefore, it is tentatively suggested that food resources are not limiting at any time of the year in the Fish River Valley area.

Since seasonal fluctuations in protein and water content are probably less severe in browse than grass species (Leuthold & Leuthold 1975a), and growing seasons are longer in dicotyledonous plants (Jarman 1974), seasonal breeding is usually more marked in grazers than in browsers (Leuthold & Leuthold 1975a). The marked seasonality of breeding in kudu (which are almost exclusively browsers; Wilson 1965; Jarman 1971; Hofmann 1973; Hofmann & Stewart 1972; Liversidge pers. comm.; pers. obs.), therefore seems incongruous in such a productive habitat.

The young of many ungulate species are particularly susceptible to predation (Sadlier 1969a; Kruuk 1972; Leuthold 1977), and two strategies have evolved to reduce their vulnerability. In some gregarious species, the young, which may be born in an extremely precocious state, follow their mothers shortly after birth (the "followers", Lent 1974) and therefore immediately become a member of their mothers' groups. Protection from predation comes either from maternal/group defence (as in zebra, buffalo, rhinoceros, and elephant, Leuthold 1977) or from concealment within the group (as in wildebeest, Estes 1974). The success with which young may be concealed is greatly enhanced by the formation of large aggregations and by a highly synchronised calving season, with the result that predators may be glutted on a temporary superabundance of potential prey (Estes 1974, 1976). Calf survival is drastically reduced when these conditions are not met, i.e. in small dispersed herds that show little inter-group synchrony and consequently have low calf densities and less "cover" (Estes 1966, 1974, 1976; Estes & Estes 1979).

The alternative and more common strategy involves active concealment by the calf during the first few weeks of life, thus making detection by predators more difficult ("hiders" Lent 1974). Isolation from conspecifics for most of the time, the prone response and general inactivity of the calf, and the ingestion of the calf's urine and faeces during irregular visits by the mother, further diminish the chances of detection (Gosling 1969; Estes 1974; Leuthold 1977).

While there is a fairly distinct dichotomy in the behaviour of "hiders" and "followers" this may become less pronounced with age. For example, nursery herd formation, which is most pronounced in gregarious hiders such as impala, sable and eland (Underwood 1975; Leuthold 1977), and occurs usually after a comparatively short lying-out period, may be interpreted partly as an anti-predator strategy comparable to that of wildebeest (Jarman 1974; Jarman & Jarman 1974).

Kudu have all the characteristics of a typical "hider" species including cryptic colouration, a distinct lying-out period, the prone response and ingestion of metabolic wastes by the mother (Walther 1964). Compared to data available from other studies (Gosling 1969; Spinage 1969; Jarman & Jarman 1974; Grobler 1974; Kok 1975; Autenrieth & Fichter 1975; Clutton-Brock & Guinness 1975; Wilson & Hirst 1977; Leuthold 1978b; Sekulic 1978), the lying-out period of kudu may be twice the duration of many other "hiding" ungulates, and perhaps more significantly, kudu have a more restricted and synchronised breeding season. Interestingly, those ungulates that have a pronounced breeding season are usually grazers or temperate cervids, both of which experience seasonal fluctuations in food availability and tend to have shorter lying-out periods than kudu (De Vos, Brokx & Geist 1967; Lent 1974; Autenrieth & Fichter 1975; Clutton-Brock & Guinness 1975; Allsopp 1979; Guinness, Hall & Cockerill 1979). Conversely, ungulates that breed throughout the year, as do many browsers (although bimodal peaks may be evident, see Anderson 1979), tend to have longer lying-out periods (e.g. reedbuck, Junguis 1971). Thus the kudu differs from most other ungulates in having a comparatively long lying-out period and a higly restricted calving season.

Anderson (1979) suggests that since kudu are social ungulates, predation on calves has resulted in selection for a single calving peak. Due to lying-out, kudu calves are solitary for the first few months of life, and it is difficult to envisage how a synchronisation of calving, which is not evident in "solitary" species (Anderson 1978, 1979) will enhance the chances of calf survival. Further, although

Gosling (1969) suggests that the efficiency of the lying-out strategy is unlikely to be related to the presence or absence of other calves, and that in terms of predation there is probably no selective advantage for calves born during birth peaks, he also infers that the spatial and temporal separation of calves are prerequisites for effective concealment (Gosling 1969; Estes 1976; Joubert 1970, cited in Sekulic 1978). This is an important point. Since "hiders" usually breed over an extended period, comparatively few calves are hiding in any area at any one time. These conditions are not met by kudu on the Reserve; with a specific birth rate of 100% and a highly seasonal calving period, there must be an abundance of concealed calves from January to March. While it may be argued that synchronisation of births within large gregarious herds can provide a superabundance of potential prey, the lengthy lying-out period, when calves are isolated and presumably vulnerable once detected, may sustain potential predators for at least two months. Therefore, as an anti-predator strategy, lying-out for two months would tend to negate any benefits derived from synchronisation.

It is therefore suggested that the temporary high density of concealed kudu calves facilitates their detection by predators, especially since the nature of the vegetation favours hunting by olfactory rather than visual cues. The largest predator on the Reserve is the black-backed jackal, which is capable of taking calves of both kudu and eland (Pienaar 1969; Roth, Kerr & Posselt 1972). Jackal are particularly abundant on the Reserve (Burdett, pers. comm.; pers. obs.) and it is suggested that their predation on kudu calves is largely responsible for the low calf:cow ratios observed during this study. The conclusion that mortality rates are highest in neonates and young calves (Chapter 6) corroborates this theory. Predation has been found to be the major cause of calf mortality in a number of other altricial hiding ungulates (Sadlier 1969a; Cook, White, Trainer & Glazener 1971; Miller & Broughton 1974; Carroll & Brown 1977; Wolfe 1977). High calf mortality of unknown cause, but where jackal and larger predators are present, has been noted in other kudu populations (Simpson 1968; Hirst 1969; Underwood 1978).

Other factors may also contribute to the high calf mortality on the Reserve, but there is little evidence to suggest that these would be of equal or greater magnitude than predation. Poor condition through inadequate nutrition may be a principal cause of pre- and post-natal mortality in other ungulates, operating directly or in association with other secondary factors such as exposure, disease, maternal neglect, etc., (Robinette, Gashwiler, Low & Jones 1957; Mitchell, McCowan & Parish 1971; Roth, Kerr & Posselt 1972; Wilson, Bartsch, Bigalke & Thomas 1974; Arman 1974; Miller & Broughton 1974; Wegge 1975; Mitchell & Staines 1976; Wilson & Hirst 1977; Guinness, Clutton-Brock & Albon 1978; Staines 1978; Jeffrey 1979), but all the data from this study infer that food is not limiting on the Reserve. Further, while death from exposure during severe winters cannot be ruled out, peak calf sightings in August (Chapter 6) and infrequent discoveries of carcasses (even when considering the more rapid deterioration of young carcasses, Caughley 1976), infer that mortality caused by adverse climatic conditions is low.

Since the coupled effects of seasonal breeding and the lengthy lying-out period probably result in increased mortality from predation, the causation of the timing of calving should be examined. Clearly detailed analyses of the nutritional requirements of kudu, and the nutritional levels of plants available to them throughout the year are required. Until these are available, interpretations of the low calf:cow ratios and the seasonal distribution of births are largely speculative. Nevertheless, data from this study and from births of captive kudu in both hemispheres suggest that the role of photoperiod in influencing the timing of breeding is a primary one and that food availability is of less importance (Sadlier 1969a).

Greater annual range in photoperiod may also account for the more restricted breeding season observed in this area (the southern extreme of the kudu's geographic range). A similar relationship between latitude and reproductive seasonality has been found in several other species (Sadlier 1969a; Spinage 1973; Estes 1976; Sekulic 1978).

Finally, while hiding behaviour is unquestionably an anti-predator strategy, this should not be regarded as its only function. In many ungulate species pre- and post-partum isolation from the group also serves to reinforce the mother-young bond (Leuthold 1977).

Concealment of the calf permits a female kudu to retain social contact with her group (Chapter 8) without affecting the mother-young bond, which develops into mutual individual recognition during nursing and grooming sessions (Leuthold 1977). Interestingly, Walther (1964) found that captive nursing mothers were intolerant towards other adult kudu, particularly during the first few days after parturition, when the neonates' following response may not be confined to the mother. Presumably agonistic interactions resulted from the absence of adequate isolation under captive conditions.

9.2 Group size

Jarman (1974) has suggested that group size is largely influenced by dispersion and availability of the food supply, and anti-predator behaviour. The former imposes an upper limit on the size of a co-ordinated, cohesive group, which will be smaller in selective feeders due to intragroup competition over discretely dispersed food items. Associating with other animals reduces the chances of an individual being attacked by a predator, and also increases the probability of a predator being detected before an attack can be made. Jarman (1974) therefore suggests that groups will tend to be as large as possible without losing cohesion and co-ordination.

While Jarman's (1974) reasoning is essentially sound, it is a little over-simplified. It may be argued that animals living in groups are more easily detected by a predator; however, it is unlikely that the number of attacks on a group is directly proportional to its size. Hamilton (1971) has shown that grouping can be selected for even if the predator's success rate increases proportionately over hunting solitary prey, because the more associates an individual has, the less likely that same individual will be the victim. Bertram (1980) demonstrated that, in feeding ostriches, grouping had little effect in reducing the vulnerability of the group, but considerably reduced the vulnerability of any individual. This "dilution" effect becomes less pronounced with increasing group size, i.e. the first few companions are by far the most important (Bertram 1978, 1980). In the same way, the probability of a predator being detected initially increases rapidly with increasing group size, but quickly levels off (Bertram 1978).

Intragroup competition for food and anti-predator strategies are not the only selective pressures operating on a species; there may be several other costs and benefits from associating with conspecifics (e.g. mate selection, courtship and reproduction, social learning and enhanced feeding rates, Clutton-Brock 1974; Bertram 1978, 1980). Such benefits are unlikely to be of equal value to all members of the group; there may well be inter- and intra-sexual differences in preferred grouping patterns. Finally, optimal group size may be difficult or even impossible to maintain in permanent, closed groups, where all individuals are related. As the group grows through recruitment, it will eventually exceed the optimal size. Division results in sub-optimal grouping which may be less beneficial than remaining at supra-optimal size (Bertram 1978).

Jarman's (1974) suggestion that intragroup competition limits the size of a group is considered invalid in highly productive habitats such as the Reserve. Rather it is suggested that the densely structured vegetation reduces the range of visual communication, thereby preventing the cohesion of large groups of kudu. The larger (but not significantly so) group sizes recorded in non-succulent regions of the Reserve support this interpretation (food is less abundant in this vegetation type, as indicated by larger home range sizes (Chapter 7) and this intra-group competition, if limiting group size should produce smaller rather than larger groups). The formation of larger groups in more open areas has been noted in other ungulate species (Leuthold 1970, 1976, 1977; Leuthold & Leuthold 1975b; Junguis 1971; Walther 1972; Hirth 1977; Mitchell, Staines & Welch 1977; Evans 1979). Several ungulate studies have shown that a positive correlation may exist between group size and population density (Spinage 1969b; Junguis 1971; Laws 1974; Estes 1974; Joubert & Bronkhorst 1977; Leuthold 1977). The latter of course is largely determined by environmental factors, and it is therefore difficult to determine precise influences on grouping patterns.

Nevertheless, the mean group size of kudu on the Reserve is significantly smaller than those obtained from other areas where densities are lower (Table 9.1). This further suggests that the structure of the habitat on the Reserve impedes the formation of large groups by restricting visual communication.

TABLE 9.1 Group sizes of kudu

Mean Group size	Typical Group size	Range	Source
* 9	-	2-15	Owen-Smith (1977)
** 4	-	1-10+	Owen-Smith (pers. comm.)
4,5 (n=42)	-	1-9	Evans (1979)
4,2 (n=185)	5,6	1-11	Wilson (1965)
5,1 (n=35)	8,4	1-15	Wilson (1970)
4,0 (n=246)	5,3	1-17	Underwood (1978)
3,5	5,2	1-17	This study

* female groups

** bachelor groups

Geist (1974) suggested that the anti-predator behaviour of a species is a function of the cover of its habitat. Those living in thick cover may be heard by a predator before they are seen, and to decrease the chances of detection they may reduce auditory signals and have a low number of associatiates.

Further, such species (including kudu and other Tragelaphines, Walther 1964; Jarman 1974; Tello & van Gelder 1975; Leuthold 1977, 1979; Allsopp 1978) rely on crypsis, becoming motionless when disturbed and fleeing only once detected. It is therefore easier to remain inconspicuous (as a group) if there are few associates. Consequently, anti-predator behaviour in this instance may partially restrict the lower and upper limits of group size. Group defence, which is generally limited to larger herds (e.g. eland, Bertram 1978), is absent in kudu (pers. obs.). Waser (1975a, 1975b) suggested that anti-predator behaviour also influenced group size in bushbuck.

Hirst (1969) found that adult male kudu were more susceptible to predation than females. Several studies have revealed the same trend in other species (Wright 1969; Schaller 1972; Jarman & Jarman 1973; Sinclair 1974, 1977; Smuts 1974b, 1976; Leuthold 1977, 1978a). In most instances this differential mortality has been attributed to either males occupying smaller, less co-ordinated groups or the position of the male (usually on the periphery) within larger groups (Hamilton 1971). Since adult male kudu always trail behind females in flight (pers. obs.) and form small bachelor or solitary groups (Chapter 8), both factors would enhance their vulnerability. However, the absence of large predators on the Reserve implies that differential mortality (and hence the widely disparate sex ratio) does not result from selective predation, but rather from some other cause, which is probably socially induced.

9.3 Male dominance and mating strategies

Competition for mate acquisition is usually more pronounced in males, than in females, because in competing a male can increase his reproductive output more than a female can (Trivers 1972). Such competition results in a dominance hierarchy, with the top males often achieving exclusive breeding rights. It also leads to enhanced sexual dimorphism, such as increased body and/or horn size in males (Geist 1974; Clutton-Brock & Harvey 1976; Bertram 1978). Dominance may therefore be assessed by age-related attributes (Geist 1966, 1971; Bubenik 1968; Lincoln, Youngson & Short 1970; Lincoln 1972; Estes 1974; Topinski 1974; Jarman 1974). In such instances, contests between same-aged individuals must be decided by other means including various forms of display and fighting (Geist 1966; Clutton-Brock, Albon, Gibson & Guinness 1979). As well as indicating social rank, the frequencies and/or durations of displays are often related to fighting ability, which may change markedly even over a short period of time (Clutton-Brock & Albon 1979).

Bachelor groups consisting largely of peers are characteristic of kudu (Chapter 8) and many other ungulate species (De Vos & Dowsett 1966; Hanks <u>et al</u>. 1969; Estes 1967, 1969; Leuthold 1970, 1977, 1978a; Jewell 1972; Walther 1972; Gosling 1974; Jarman & Jarman 1974; M.V. Jarman 1979; Hirth 1977; Sinclair 1977).

It is within such groups that the dominance hierarchy develops, often through sparring (Plate 8.4f). If the highest social rank achieved by an individual remains the same irrespective of external circumstances, such dominance is referred to as absolute dominance (Leuthold 1977). However, if the social position is dependent upon some environmental parameter, such as space, then the possessor is said to have relative dominance as in territoriality (Leuthold 1977). Thus, irrespective of whether a species is territorial or not, rank in bachelor males is based on an absolute social hierarchy.

All the data obtained from this study (e.g. overlapping home ranges, the low incidence of aggressive encounters, etc.) indicates that adult kudu maintain an absolute social hierarchy throughout life. Since territorial behaviour is most pronounced in areas of high population density (Estes 1974; Leuthold 1977), its absence in this study is particularly significant. The same conclusion can be drawn from the absence of marking behaviour and specific urination/defaecation sites, since marking would probably be virtually indispensible to territorial species inhabiting highly structured habitats (Leuthold 1974). In addition, the extreme sexual dimorphism (which is most pronounced in the Tragelaphines, Jarman 1974; Estes 1974; Geist 1974) and prolonged growth (male kudu are not physically mature until at least five years old, Estes 1974; Owen-Smith pers. comm.; pers. obs.), corroborates the conclusion that kudu have an absolute dominance hierarchy (Estes 1974; Geist 1974).

Leuthold (1974, 1979) found a very similar level of organisation in the lesser kudu. However, because several adult males were never seen together with a group of females ("the main characteristic of a dominance hierarchy", Leuthold 1974, p 230), he regarded the social organisation as intermediate between a dominance hierarchy and territoriality.

Sightings of more than one fully mature bull in the company of several females were also comparatively rare in this study, but may be partially explained by reference to the population structure. Assuming a population of 1000 kudu on the Reserve, this would consist of 285 males and 637 females (both sexes at least one year old, Table 6.4). The proportion of males in each age class would be: 63 one year olds, 47 two year olds, 67 three year olds, 52 four year olds, and 55 five + year olds, (Table 8.17). Assuming that all matings involve prime (5+ year old) males, then each male has to serve approximately twelve females during the relatively brief rutting season. At this time, the mean number of females in a group is three. Thus, there are four groups of females to every prime male. Not all females will enter oestrus at the same time, and if none within the group are receptive, the male should move on to another group. While competition for mates may be high at the onset and termination of the rut, the low density of mature males infers that, for the majority of the period, such competition between males will be slight. Even when a prime male encounters another attending an oestrous female, a contest need not develop. The possible costs incurred in fighting may be sufficiently great (see Geist 1971; Wilkinson & Shank 1976; Clutton-Brock et al. 1979) that they outweigh the benefits of mating, particularly if the chances of the approachee encountering other unattended females in oestrus are high. However, the benefits are likely to exceed the costs when a prime male approaches a considerably younger male associating with oestrous females. In this situation the smaller animal should avoid possible injury by departing and searching for another group. If he elects to stay, he may be tolerated provided that no interest in mating is shown. Since the ritualised courtship of the kudu is fairly elaborate (Walther 1961) any attempt to mate by the young male would quickly attract the attention of the dominant male, and presumably result in the subordinate's eviction.

Such a strategy assumes that males should avoid all others of the same or higher status. Results from Chapter 8 demonstrate that male-male (usually peer) associations do decrease considerably during the rut, while the proportions of males seen alone and in mixed groups increases substantially.

The same tactic is unlikely to account for the mutual avoidance of lesser kudu males, since breeding is aseasonal (Leuthold 1979) and consequently competition for oestrous females will be considerably higher. Anderson (1978) states that dominance is fiercely contested (but see below) during courtship in the nyala which also breeds throughout the year.

Owen-Smith (1977) has suggested that two forms of mating system may exist in ungulates possessing an absolute hierarchy. The first involves a stable ranking dominance as found in buffalo (Sinclair 1974, 1977) and eland (Underwood 1975), while the second is based on a more temporary roving dominance, which is established in the presence of oestrous females as in mountain and Soay sheep (Geist 1971; Grubb 1974b). Anderson's (1978) reasoning for suggesting that nyala have a roving dominance (e.g. unstable male groups and associations, widely overlapping male home ranges) is equally applicable to the kudu, except that there is no evidence from this study suggesting that dominance is determined in the presence of an oestrous female. However, Anderson's (1978) claim that dominance is fiercely contested during courtship in nyala may be questioned since he rarely witnessed courtship and mating and never observed males fighting.

It is much more probable that kudu, and possibly other Tragelaphines contest for social rank throughout the year, or at least prior to the rut, as do other species with a temporary roving dominance (Geist 1971; Grubb 1974b). Once social positions have been established, methods of assessing the rank of potential competitors in future encounters may be based on individual recognition or on traits that are so subtle that they have so far escaped detection by biologists. Such assessment would explain the mutual avoidance of males that is exhibited by most aseasonally breeding Tragelaphus species (Anderson 1978; Odendaal 1977; Leuthold 1979). Protracted, overt fighting is then only likely during the rut when two equally matched strangers meet. In all other instances the social status of any individual male will largely depend on the ranks of the other males in his company; this will clearly fluctuate as the individual moves from group to group in search of oestrous females. The mating system of kudu and other Tragelaphines may therefore be intermediate between a stable ranking dominance and a temporary roving dominance, especially since these are not mutually exclusive systems (Owen-Smith 1977).

9.4 Comparisons with other Tragelaphus species

The limited comparisons that can be made between the population of kudu on the Reserve and those of more tropical areas suggest that several differences exist in their levels of social orgnaisation. This is most apparent when considering home range size, seasonal movements and group size, and probably reflects the influence of the highly productive vegetation in this area. Detailed comparative studies of impala (Leuthold 1970; Anderson 1972; Jarman & Jarman 1973, 1974), wildebeest (Estes 1966, 1969) and waterbuck (Spinage

1969b; Hanks et al. 1969), have demonstrated the extent to which social organisation may be modified by environmental conditions. Thus, at this stage, only general inter-specific comparisons of the Tragelaphines are considered valid.

The social and spatial organisation of greater kudu on the Reserve closely resembles that of lesser kudu (Leuthold 1974, 1977, 1979), nyala (Tello & van Gelder 1975; Anderson 1978), and bushbuck (Elder & Elder 1970; Allsopp 1970, 1978; Jacobsen 1974; Waser 1975a, 1975b; Odendaal & Bigalke 1979; Okiria 1980). Similarities are also apparent in the mountain nyala (Brown 1969) and sitatunga (Owen 1970) but these latter studies did not examine social organisation in detail and are therefore unsuitable for comparison.

All four species are browsers, and have similar anti-predator strategies, namely concealment, freezing and flight in both young and adults. Group sizes are smaller in bushbuck, which is largely solitary, and increase with increasing body size, being largest in the greater kudu (as predicted by Jarman 1974). In nyala, lesser and greater kudu, female groups are stable, cohesive units, probably comprising of related individuals. Male groups are characteristically loose and open associations and solitary males are common. All species are considered non-territorial in that male ranges show extensive overlap (with the possible exception of bushbuck, although the majority of studies show convincing evidence of overlapping ranges). Absolute dominance has however been questioned in all species examined, since male-male interactions are relatively rare. Home ranges are small and relatively stable, with subadult males usually occupying the largest ranges.

Peak periods of breeding are evident in all species (Simpson 1968; Allsopp 1970, 1971; Davison 1971; Morris 1973; Morris & Hanks 1974; Anderson 1978; Leuthold 1979), but breeding continues throughout the year, except in greater kudu. Seasonal changes in social organisation are therefore more apparent in this species. The three most social species constantly have a significantly disparate sex ratio in favour of females while in the bushbuck the ratio may vary considerably between populations, but is often close to unity. Estes (1974) suggests this equal sex ratio in the predominantly solitary bushbuck results from both sexes being equally vulnerable to predators. However, since predation is not considered to be a likely cause of the disparate sex ratio in the more gregarious Tragelaphus species, reasons for the interspecific differences in the sex ratios of the Tragelaphines remain obscure.

Data resulting from this study clearly illustrate that the social organisation of the greater kudu is very similar to that of other Tragelaphines. Further they do not support Jarman's (1974) placing of the greater kudu into his Class C level of social organisation where species typically exhibit a) the formation of large female groups (6-150 individuals) which are open and not dictated by kinship, b) eviction of young males from the female groups by territorial males, c) visual and vocal displays and pronounced scent marking, and d) frequent mixing between individuals of all ages and both sexes after the breeding season. Rather, this study demonstrates that greater kudu on the Reserve are typical of Class B species, in which Jarman (1974) includes lesser kudu, sitatunga and bushbuck. Species within this class are characterized by having a group size of one to twelve, but usually three to six individuals (with possible slight seasonal variations); common associations between two or more adult females, and a tendency for adult males to become solitary. Anderson (1978) has shown that the social organisation of the nyala is also more typical of Class B than Class C members.

Since his placing of these two species in Class C was not based on results from intensive study, Jarman's (1974) division of the Tragelaphus species into two levels of social organisation is currently considered invalid. Further long-term studies are required in areas where the social organisation of these species may be modified by environmental conditions, before Jarman's (1974) conclusions can be substantiated.

SUMMARY

The spatial and social organisation of the greater kudu, Tragelaphus strepsiceros, was studied in the Andries Vosloo Kudu Reserve, Eastern Cape.

One hundred marked kudu, essential for the accurate monitoring of individual movements and group stability, facilitated additional aspects of the study, including population estimation, reproduction, and age determination.

The high productivity of the vegetation, little interspecific competition and negligible predation on adults were considered the major factors responsible for the estimated population density of 17 kudu/km^2, which is higher than any other published records.

Males reached puberty at about 18 months but probably attained social maturity at about 5 years of age. Spermatogenesis was evident throughout the year and throughout life.

Females reached sexual maturity at 18 months and were capable of producing their first calf at 2 years old. Specific birth rates of 100% were evident indicating that fecundity was not age-specific, calving intervals rarely exceeded one year and kudu were seasonally polyoestrous.

Conception dates were calculated from foetal mass, and birth dates predicted by the addition of a 251 day gestation period. A three month summer calving season was evident and confirmed by field sightings. The foetal sex ratio was close to unity, twinning was not apparent, and calves were usually weaned at 6-8 months.

The disparate adult sex ratio (45 males : 100 females) resulted from differential sexual mortality, especially in older males. Cow: calf ratios showed annual fluctuations and were considerably lower than from other areas. This probably resulted from heavy predation on concealed calves during a highly synchronised lying-out period.

Relatively small, stable and widely overlapping home ranges were evident in this population. Male ranges were slightly larger than those of females and in both sexes range size was inversely porportional to vegetation density. Seasonal movements were not apparent, nor were sex differences in habitat preference.

Grouping patterns were unaffected by environmental conditions, but influenced by reproductive behaviour. Groups were smallest during the calving and subsequent lying-out periods, gradually increasing in size until the peak of the rut.

The kudu social organisation was based on the female unit, a closed matriarchal kinship group consisting of several females and their offspring. Males left their stable maternal groups when 2 years old and formed loose temporary associations with peers. Dominance hierarchies were probably established within these bachelor groups, during this time. Adult males showed a tendency to become more solitary with age, and formed loose associations with females. The low densities of adult males were probably responsible for the low level of competition for mates during the rut. The kudu social system was based on absolute dominance; territoriality was not evident.

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PERSONAL COMMUNICATIONS

BROOKS, Dr P.M. Natal Parks Board, Hluhluwe Game Reserve, PO Box 25 Mtubatuba, 3935.

BURDETT, Mr P.D. Andries Vosloos Kudu Reserve, Private Bag 1006, Grahamstown, 6140.

HEARD, Mr A. Natal Parks Board, Hluhluwe Game Reserve, PO Box 25, Mtubatuba, 3935.

LIVERSIDGE, Dr R. MacGregor Museum, PO Box 316, Kimberley, 8300.

OWEN-SMITH, Dr N. Department of Applied Mathematics, University of the Witwatersrand, 1 Jan Smuts Avenue, Johannesburg, 2001.