

A POPULATION STUDY OF THE BABOON (PAPIO URSINUS
KERR, 1792) IN THE SOUTPANSBERG DISTRICT.

by

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OPSOMMING.

Die doel van die studie was om o.a. 'n populasie-sensusmetode vir die bobbejaan te ontwikkel. Dit het daartoe gelei dat kennis i.v.m. die ekologiese en sosiale gedrag van die bobbejaan ook ingesamel is.

'n Bobbejaantrop is saamgestel uit diere van verskillende ouderdoms-klasse en beide geslagte. Wanneer populasie-digtheidbepalings gedoen word, moet daar vasgestel word hoeveel troppe in 'n gebied voorkom sowel as die getal individue per trop. Faktore wat bydra tot variasie in tropgrootte moet ook bestudeer word.

Ekologiese aspekte wat van belang is vir sover dit die daarstelling van sensusmetodes vir bobbejane aangaan is o.a.

- i) Grootte van die daaglikse loopgebied.
- ii) Afstande wat troppe gedurende die dag aflê.
- iii) Benutting van die loopgebied m.b.t. ruimte en tyd.

Gedurende die dag benut 'n bobbejaantrop 'n gedeelte van hul loopgebied.

Die loopgebiede van aangrensende troppe oorvleuel en elke trop benut spesifieke slaapplekke wat hulle ook met ander troppe moet deel.

Die grootte van loopgebiede en die gebruik van slaapplekke hang nie net af van ekologiese faktore soos die beskikbaarheid van water en voedsel nie maar intraspesifieke verhoudings speel ook 'n rol in die ekologie van die dier. Daarom is dit noodsaaklik dat die sosiale gedrag van die diere in 'n trop, sowel as die verhoudings tussen verskillende troppe, bestudeer word om sekere ekologiese begrippe soos die grootte van die loopgebied, te verstaan.

Bobbejaantroppe kompeteer met mekaar vir die gebruik van sekere slaap-, drink- en vreetplekke. Wanneer 'n trop sy slaapplek verlaat vroeg in

die oggend kan hy nie na willekeur enige rigting inslaan nie. Ook kan hy nie, wanneer hy teen skemer terugkeer van die weiveld, in enige slaapplek gaan slaap nie. Al die stappe word gedoen na gelang van die sosiale wisselwerking tussen aangrensende troppe.

Die vraag ontstaan nou watter individue in 'n trop verantwoordelik is vir die besluite wat geneem word i.v.m. die voortbeweging van die trop, keuse van slaapplekke, suipplekke ens. Dominante mannetjies speel hier 'n belangrike rol deurdat hulle onderling saamwerk en ooreenkomstig die trop aanvoer.

Bepaling van die populasiedigtheid is ook 'n vereiste wanneer 'n dier met ekonomiese implikasies bestudeer word. Dit is 'n alombekende feit dat die bobbejaan 'n vernielsugtige dier is en dat veral die boer gevoelige verliese ly in gebiede waar bobbejane gedurig strooptogte op gesaaides of boorde uitvoer. In die laaste paar jaar egter het die bobbejaan 'n steeds belangriker rol begin speel as proefdier in die mediese navorsing. Navorsing wat op die bobbejaan gedoen is dra ook kennis by tot die wetenskap waarby die mens se ontstaan en voortbestaan ter sprake kom.

SUMMARY.

Data on the ecology and social behaviour of the baboon were collected during a study which was undertaken to develop a census method for the baboon.

A baboon troop consists of several individuals of different age and sex classes. For population density studies the number of troops in the area as well as the number of baboons per troop must be determined. Factors responsible for variations in troop size must also be studied. The following ecological aspects are of importance as far as the development of a census method is concerned:

- i) Size of the home range.
- ii) Distances that troops travel during the day.
- iii) Utilization of the home range in relation to time and space.

A baboon troop utilizes only part of its home range during the day. The home ranges of neighbouring troops overlap and every troop utilizes specific sleeping places which it also shares with other troops.

The size of the home range and the utilization of sleeping places do not depend solely on ecological factors such as availability of food and water but intratroop relations also affect the ecology of the animal. Therefore it is essential to study the social behaviour of the individuals in a troop as well as the relationships between adjacent troops in order to understand some of the ecological concepts such as the size of the home range.

Baboon troops compete for the use of some sleeping and drinking places and feeding grounds. A troop cannot follow any direction when it

leaves the sleeping place in the early morning. Neither can the troop enter any sleeping place of its choice in the evening when it returns from the feeding ground. These choices are subject to the interactions between neighbouring troops.

Certain individuals in the troop must be responsible for the decisions made in connection with troop progression, choice of sleeping and drinking places. Males co-operate in as far as these decisions are concerned.

It is essential to determine the population density of an animal with economic values such as the baboon. It is a well-known fact that baboons are marauding animals and that farmers often suffer severe crop damage from baboon raids in certain areas. However, in recent years baboons have become more and more important as experimental animals in medical research. Knowledge derived from research on baboons contributes to the science of man's origin and survival.

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INTRODUCTION

The chacma baboon, which is the object of this study, can be classified as follows after Dandelot (1968).

Order: Primates
Suborder: Anthropoidea
Family: Cercopithecidae
Subfamily: Cercopithecinae
Genus: Papio Erxleben, 1777.
Subgenus: Papio Erxleben, 1777.
Species: Papio ursinus Kerr, 1792, Chacma baboon
Subspecies: P.u. griseipes Pocock, 1911. Rhodesian Chacma baboon.

According to Dandelot "The subspecific status of the forms of the subgenus Papio is far from satisfactory. Many of the described subspecies are at present impossible to confirm,..." and "Still more uncertain are the limits of their distribution."

Knowledge of the systematics, distribution and anatomy of monkeys and apes accumulated during the last century but little was known about their behaviour in the wild. C.R. Carpenter was the first to undertake long-term scientific field studies on free-ranging primates. With his classic study on howler monkeys in 1934 - (See Carpenter 1964) on Barro Colorado Island he initiated the modern trend of sound scientific studies, the results of which gradually displaced the misconceptions that existed on the sub-human primate's ecology and behaviour.

Until the late 1950's no ecological studies of baboons were undertaken. However, Zuckerman (1932) made a field study on the social behaviour of the baboon in the Eastern Cape. Marais's studies on the social behaviour of baboons in the Waterberg mountains in the Transvaal were published in his book "My friends the baboons" in 1939.

More recent studies on primates were carried out by primate research workers such as Hall (1960, 1961, 1962a+b+c, 1963), DeVore and Washburn (1963), Kummer and Kurt (1963) and Crook (1966) who studied the chacma baboon, the olive and yellow baboons, and the hamadryas baboons, and the gelada baboon respectively. More details of the location of recent field studies of baboons are shown on figure 1. Schaller (1963) made an extensive study on the ecology and behaviour of the mountain gorilla whereas Goodall (1965 and 1962) and Reynolds et al (1965) made studies of the chimpanzee's ecology and behaviour. Carpenter imported rhesus monkeys from India in 1938 and these animals were released on Cayo Santiago island, situated just off the east coast of Puerto Rico. Several research workers studied the monkeys in this colony e.g. Carpenter (1942a+b, see Carpenter 1964), Altmann (1962), Koford (1963). Japanese research workers such as Imanishi (1963) and Itani (1959 - see Itani 1963) studied the indigenous Japanese monkey. Recently they have extended their studies to other primates such as langurs in India (Sugiyama, 1965a+b+c, 1966).

Southwick et al (1965) made intensive ecological surveys of rhesus monkeys in Uttar Pradesh, India.

Judging from the amount of field studies conducted on baboons this primate has recently become an extremely important animal.

Altmann (in press) in Kenya and Kummer (1968) in Ethiopia extensively studied social organization of the olive and hamadryas baboon. Lately the sexual behaviour of the baboon in the Northern Transvaal was investigated by Saayman (in press). Two international symposia were also held on the baboon in 1965 and 1967 respectively.

The value of nonhuman primates in medical and biological science has increased world-wide. The Southwest Foundation for Research and Education of Texas imports a few hundred baboon from Kenya annually. In an introduction to the first symposium (1965) on the use of the

baboon as an experimental animal in medical research, Vagtborg stated the following on the costs involved in transporting baboons from Africa to the United States :

"The cost of capture averages about \$1.00 per pound, with a shipping crate large enough to accommodate a large male or two mature females costing approximately \$25.00. The largest portion of the cost of animals delivered to laboratories in the United States consists of air freight costs. Fifty- to sixty-pound males will cost approximately \$250.00, whereas twenty-five- to thirty-pound females will cost about \$175.00 delivered directly from Africa to most regions of the United States."

The baboon has been used as an experimental animal for many years in South Africa (Gilbert et al 1951 and Gillman et al 1946). The Nutritional Research Branch of the C.S.I.R. also uses baboon, amongst other primates, as experimental animals. Medical officials of the Karl Bremer Hospital in Bellville using baboon as experimental animals, recently pleaded for official protection of the animal. The baboon is no longer just a useless mountain dwelling primate since its importance in research to the welfare of the human being increases daily.

Population data on baboon are of value not only as far as the distribution, ecology and behaviour of the species are concerned, but also in several other fields of applied ecology.

1. The primary importance of population data on the baboon is to evaluate the role of the animal as an agent of agricultural and small livestock destruction. Data on abundance, distribution and feeding patterns are essential for such an evaluation.
2. Population data on baboon can be an indicator of baboon acting as a reservoir for human illness. They are susceptible to a wide range

of diseases similar or identical to those on human beings.

3. Baboon are in great demand at medical schools, hospitals and Medical Research Institutes where experiments, which contribute to the survival of the human, are being carried out on this animal.

A primate population study is a long-term project. The present study of 20 months demonstrates only some of the features of its population dynamics. However, this study will act as a basis for further studies.

II. THE STUDY AREAS.

1. Waterpoort census area.

1.1 Situation and Topography.

The experimental census area (see figure 2) near Waterpoort in the Soutpansberg district in the Northern Transvaal is bordered on the east by the Sand River running through the Soutpansberg mountains. A three mile long dirt road runs alongside the Sand River from the Waterpoort-Vivo road to the farm Robertson. The southern and western boundaries are formed by roads running from the farm Robertson through the farms George, Glasgow, Carnarvon and Portland (all situated alongside in a valley) ending up in a T junction with the Waterpoort-Vivo road which serves as the northern boundary of the census area. This road circuit therefore isolates a part of the Soutpansberg mountains. The mountainous area enclosed is about 400 feet above the road level except for that part of the road running on the mountain alongside the river. (See plate 1).

Steep cliffs on the southern side of the mountainous area provide six known sleeping places.

It is a rural area used mostly for cattle farming with isolated homesteads alongside the Waterpoort-Vivo road.

1.2. Vegetation.

At the time of the investigation all plants were in full foliage. The vegetation cover on the northern mountain slopes was denser than elsewhere. Tall trees alongside the Sand River were ignored as sleeping places in this area. The vegetation was dense in the valley except for the barren abandoned native settlements.

2. Messina census area.

2.1. Situation.

This area is bordered by the foot of the Soutpansberg mountain in the south and the Limpopo River in the north. The border of the Sibasa Native Trust area serves as the eastern boundary while the main road from Louis Trichardt to Messina is the western border of the census area. Messina is the only town in this area of approximately 1050 square miles, with Tshipise, a holiday resort, situated 23 miles south-east of Messina.

Baboons are abundant in areas adjoining the census area except for the Soutpansberg mountains, several miles wide in this area, serving as a barrier to their distribution to the south. Baboons do not occur on the southern slopes of the mountains where the country becomes sparsely vegetated and flattened.

2.2. Topography.

Some of the mountain peaks in the study area rise to 5,000 feet above sea level. The area at the foothills of the Soutpansberg mountains averages about 2,500 feet above sea level with a decline of 1,500 feet to approximately 1,000 feet in the Limpopo River valley.

The geology of the southeastern part of this census area consists mainly of basalt, limbergite and sandstone of the Karroo system. Two

distinct sandstone ridges stretch from southwest to northeast almost parallel to the Soutpansberg mountains, throughout the southeastern part of the census area where all the intensive observations on baboon troops have been carried out. Peaks of these ridges reach a height of up to 500 feet above ground level. On the northern side these ridges gradually slope down to flat country whereas those on the southern side have a steeper decline with stretches of steep cliffs, sometimes 100 feet high. The width of these ridges does not exceed half a mile.

Prevalent flat country exists between these two sandstone ridges and the Soutpansberg mountains. Basalt and limbergite types of soil cohere in this part of the study area to form a friable soil with a reddish-brown sandy loam appearance. The soil of the northern part of the census area forms part of the Archaean complex. Granite outcrops cover big parts of the area and in the lower sections layers of quartz pebbles and rock fragments rest upon the decomposed granite (van der Merwe 1941). Both the Njelele and Nwanedzi Rivers rise from the Soutpansberg mountains. These two rivers as well as the Sand River flow to the Limpopo River. Irrigation reservoirs have been built in both the Nwanedzi and Njelele Rivers; thus, due to irrigation schemes, permanent water is available in these rivers. The Sand and Limpopo Rivers, are only flooded during rainy seasons but water pools can be found in the river beds of these two rivers during the dry season.

2.3. The vegetation.

Pole Evans (1936) in his classification of the vegetational types of South Africa referred to the census area as "parkland" whereas Acocks (1953) classified the area north of the Soutpansberg mountains as "Mopani-veld". The census area is also often referred to as "part of the Lowveld".

Mopane Colophospermum mopane is the dominant vegetation in sandy soil

areas, especially in the southern part of the census area. In some places Mopane trees grow about 20 feet tall but scrub Mopane of five feet in height is more abundant.

In the rest of the census area, especially in the more rocky parts, Commiphora species are the dominant vegetation type. Baobab trees, Adansonia digitata, Acacia and Grewia species occur throughout the census area.

Forest vegetation prevails alongside the rivers where tall growing trees such as Acacia albida (Ana tree), A. xanthophloea (Fever tree) A. galpinii (Apies doring) and the Ficus sycomorus (Syccmore fig) are concentrated. The dense undergrowth consists mainly of the dwarf Cassia Cassia petersiana which makes the terrain almost impenetrable. The more abundant grass species in the area are Panicum maximum, Panicum coloratum, Digitaria species, Bothriochloa insculpta, Schmidtia bulbosa, Enneapogon, Cynodon and Aristida species. In some areas the Devil's thorn, Tribulus terrestris, a pioneer forb, covers large areas of ground surface. The Mopane veld with its arid sandy soil has a sparse undergrowth of grass. In isolated areas on the sandstone ridges and the northern slopes of the Soutpansberg mountains Lebombo Ironwood, Androstachys johnsonii, grows in dense hardly penetrable patches.

2.4. The Human Population.

The census area includes approximately 400 farms of which about 30% are inhabited by natives only. A farm on the irrigation schemes along the rivers may be occupied by several farmers, whereas in the rural areas one farmer may occupy several farms. Thus the river areas are more densely populated.

Factors such as the location of farm houses and areas where human activities take place daily may affect the home range utilization of

certain baboon troops, However, it was found that certain troops developed the habit of regular daily visits to orchards or vegetable lands. In areas where natives were the sole occupants, baboons were even more audacious. Baboons entered a certain native compound daily to steal scraps of mealie-meal porridge from the compound. This happened as soon as the men had left for the fields. Damage done by baboons to crops and livestock on farms is described elsewhere (Stoltz and Saayman, in press).

The availability of roads which gave access to the baboon habitat was dependent on the density of the human population. The strategic positions of roads ensured the success of the road census method.

3. The Tshipise study area (See fig. 3)

3.1. Situation.

The area is situated 23 miles south of Messina and is bordered by the Njelele River in the north and by the Soutpansberg mountains in the south. The area of about 25 square miles includes the Nonnet Nature Reserve as well as six farms. On two of the farms, Alicedale and Hayoma, citrus, monkey nuts and tomatoes are produced, all of which are relished by baboons. The four other farms, Werkplaas, Martin, Septimus and Ter Blanche are cattle ranches.

Tshipise, a holiday resort with a hot mineral spring, is situated on the Honnet Nature Reserve at the foot of an isolated kopje. (See plate 2). The resort is usually crowded by visitors during July and to a lesser degree during the rest of the year. The main canal of the Njelele irrigation scheme runs through the farms Alicedale, Honnet and Hyoma. The water flow is stopped during weekends but water is still available at siphons in the canal at Tshipise. Other drinking sites, apart from the canal and the Njelele River, are six manmade reservoirs

and five natural water pools on the six farms (See figure 4 and plate 3). Only the water supply of reservoir No. VI stopped during the dry months. Reservoir No.V went dry temporarily during February 1968 due to a defective pumping unit. Of the natural water reserves only No. 1 is permanent, while the remaining four sources last for only two to three months during the rainy season.

3.2 Topography.

Knowledge of the topography of the study area is essential to the study of the baboon's ecology to enable the observer to locate sleeping sites. The Tshipise kopje is utilized by a single troop that has two permanent sleeping places in this hill.

A six mile stretch of the sandstone ridges has been included in the Tshipise study area. This ridge provides sleeping sites for all but one of the baboon troops that were studied. Eleven such sleeping places are known to the observer. All of these sleeping places with one exception, face south. This ridge is situated two miles from the Tshipise kopje and three miles from the Soutpansberg mountains. The northern slopes of the Soutpansberg mountains have a gradual increase in altitude with only isolated steep krantzies suitable for sleeping places. One of the experimental troops utilizes a sleeping place in a cleft in the northern slopes of the mountain.

3.3. Vegetation.

Primatologists such as Schaller (1965) and Jay (1965a) stated that the detailed description of the plant ecology of a study area is essential in any primate study. This forms an integral part of the study since the behaviour of the primate is noticeably affected by the physiognomy of the vegetation. Baboons inhabit a variety of habitats such as savannah, open woodland, dense bushveld and thick forest.

Differences in the ecology of the animals that occupy different habitats exist; e.g, the same home range of baboons in forest areas is much smaller than those of baboons living in open country.

The Tshipise study area was divided into different communities (See fig. 4) based on the dominant tree species of the community. Distinct plant communities in the study area were located by means of an investigation:-

- a) on foot
- b) by motor vehicle
- c) from 1:18,000 aerial photographs.

Different types of soil are found in the Tshipise area and vary from a sandy type to outcrops of granite. The sandy flats are sparsely covered with grass and none or very little grass grows where Mopane trees or shrubs are the dominant vegetation type. Homogeneous Mopane veld, mixed Mopane - Commiphera veld and mixed Mopane - Terminalia prunoides veld cover the greater part of the study area. However, patches of Acacia species can be located and Acacia senegal is often found in association with the mixed Mopane - Terminalia prunoides veld.

Marula trees form a separate plant community usually at the foothills of the sandstone ridges. Lebombo Ironwood trees grow in abundance on isolated areas of the sandstone ridges, often in association with Grewia species.

Tall growing trees such as Lonchocarpus capassa, Scotia brachypetalia and Acacia nigrescens are found along the dry tributaries of the Njelele River. Other prominent trees such as the Baobab and Nyala (Pseudocacia zambesiaca) trees are distributed throughout the area.

3.4 Climate.

3.4.1 Temperature.

During the study period a meteorograph (Wilh. Lambrecht K.G. Göttingen, Type 253) was used to obtain continuous daily temperature and humidity recordings.

In the Limpopo River valley, north of the Soutpansberg, high maximum daily temperatures are maintained throughout the year.

The mean daily sun period is approximately 13 hours for the summer months (September to March) and 11 hours for the winter months (April to August). Ground temperatures are very high at noon when the baboons are usually inactive.

3.4.2. Rainfall.

Arid conditions prevail in the study area with its average rainfall of 12 inches per year. The total precipitation for the period 1967-1968 is shown in fig 5.

3.4.3. Wind.

A high proportion of squalls from the east prevailed during the July to November period. These strong winds usually blew for days on end but did not seem to influence the baboons' day range. However, if the temperature dropped considerably during a windy spell, the baboons left their sleeping places very early in the morning to take shelter behind nearby rocks.

III. FIELD APPARATUS AND ITS USE.

A fourwheel drive motor vehicle is essential for the study of a baboon population. Many of the roads that were travelled during the study period were impassable with ordinary motor vehicles. The doors of the Landrover were often removed to ensure more accurate surveys, especially during the spoor census surveys.

The data that were collected on troop composition, social behaviour

and feeding activities were obtained with the aid of binoculars (8 x 35) or a telescope (40 x 60). Data were recorded on a portable Phillips tape recorder. Additional drawings and notes on the troop's movements were made in notebooks.

A portable PYE two way radio transmitter set was also used during census operations and sometimes during continuous observations. The main set was connected to a 12 volt battery and remained in the vehicle while the observers carried the small portable sets with them. Several sizes of capture cages were used to trap baboons from known troops in order to obtain accurate data on the sex and age composition of a troop. Baboons were tranquilised in these cages with a carbon dioxide gas pistol. (A derivative of Palmers Cap-chur gun) and syringe. Sernylan (Phencyclidine hydrochloride one mg./kg. body weight) proved to be ^{the} most reliable anaesthetic for these animals while Flaxedil (V- Phenylyltris (oxyethylene)) - tris (triethylammonium iodide) one mg./kg. body weight) injected intracardially, caused instant death.

IV. METHODS AND RESULTS.

A. Sex and Age classes.

In primate studies, it is essential, to be able to classify the individuals of a group into sex and age classes. Baboons in laboratories are easily divided into sex and age classes but this proved to be difficult during field observations. Anatomical features as well as behavioural aspects of the animal were taken into consideration in order to make correct classifications. Five hundred baboons were aged and sexed during capture programs which contributed to the observer's ability to distinguish between sex and age classes at a distance. Full-grown males and females weigh 60 lb. and 35 lb. respectively in the study area. Thus the full-grown male (often a dominant male) is

noticeable bigger than the full-grown female and subadult male. To distinguish between the full-grown female and subadult male is more difficult. However, all males differ from females in that their ischial callosities are completely fused across the middle line below the anus whereas in the female the callosities are separated in the middle by a wide space to form two distinct sitting pads of horny epidermal thickening. The limbs of the subadult male are usually longer than those of the female. Behavioural differences are also a criterium for sex classification since the subadult male is more playful than the female whose behaviour is strictly sexually-socially orientated. Sexing of juveniles and infants were not undertaken during this study. However, it is possible to sex infants during close range observations since the penis of the male infant is much more conspicuous than during the juvenile stage.

Baboons were classified during the field study into age classes according to colour changes in the pelage, size, weight and behavioural features with the aid of binoculars from within 200 yards of the troop. Satisfactory results were also obtained at a distance of 500 yards with the aid of a telescope.

Captured animals were more accurately age-classed since additional data like dental eruption, weight and measurements of appendages became available. Altmann (1962) estimated the age of captured rhesus monkeys according to their body weight, sitting height and dental eruption. Data on age classes of the baboon are still being collected and will be computed when sufficient samples are available.

However, for the field study the animals were divided into the following classes with reference to DeVore (1963a)

1. The infant.

1.1. The newborn infant (birth to fourth month).

The infant is very conspicuous with its black fur and bright pink face, hands, feet and ischial callosities. The infant is completely dependent on its mother for its nourishment, locomotion and protection. The mother devotes most of her attention to her infant and frequently inspects and grooms him. Although the mother will support her ventral clinging infant for the first few days after birth with her frontpaw, its ability to cling to her body is essential for its survival. Females with newborn infants stay in the close vicinity of dominant males. Although other troop members, especially adult females, display a keen interest in the infant, the mother does not permit them to handle her infant within the first two months after parturition. The infant now attempts to ride on its mother's back and, if it succeeds, lies flat on its stomach, clinging with all fours.

1.2. Transition period (fourth to sixth months)

The infant's coat colour changes gradually from black to yellow-grey and its pink face turns black. The infant now rides on its mother's back, sitting upright (jokey style) and wanders up to twenty feet away from the mother. Whereas the interest of other adult females (and its mother) in the infant wane, the interest of older infants and juveniles increase and they will frequently entice the infant into active play. The infant starts taking solid foods.

1.3. The third stage (seventh to fifteenth months)

The infant spends more and more time with play in a peer group. During this stage the adult males become more responsible for the protection of the infant since adult females will readily threaten or

even attack the infant.

The mother weans her infant when it reaches the age of approximately 11 months and when the swelling of her sexual skin indicates the onset of a new estrus cycle. Since the mother now often refuses to let her infant ride on her back or to take her nipple, it often gives cries of frustration when thus rejected.

2. The juvenile (Female:- 15 months to three years. Male:- 15th months to five years)

The female weighs 10-20 lbs. and the male 10-35 lbs. The juvenile spends the greater part of its time with the playgroup and is seldom seen near its mother. The infant in the weaning stage stays in the vicinity of adult males and relies on them for its protection. This behaviour continues during the young juvenile stage. The older juvenile indulges in very rough play and learns to become wary of adult males and to treat them with respect. Older female juveniles spend more time in the grooming clusters of adult females.

3. The adult baboon.

- 3.1. Subadult male (fifth to seventh year)

These males are not yet full grown and weigh between 35 and 45 lbs. They are subordinate to adult males whom they usually avoid.

- 3.2. Adult male (from eighth year)

A male is classified as adult when he is physically and physiologically full-grown. His secondary sex characteristics, like canines, are fully developed.

- 3.3. Adult female (from third or fourth years)

A female is considered adult with the onset of her menstrual cycle, at

which age she will become sexually receptive. At this stage some females may only weigh 20 lbs.

B. Population and troop census methods.

Data on the abundance and distribution of the baboon are essential in order to evaluate the animal's role as an agent of agricultural and small livestock destruction.

The aim of this population survey was to locate each troop in the census area and accordingly obtain an indication of the day range activities and home range sizes of troops.

1. Reconnaissance of the area.

Topocadastral charts (1:250,000) indicate most of the existing roads while additional roads were detected on 1:50,000 aerial photographs. Topocadastral charts were used to construct a plan for a systematic survey of the area by road. The aerial photographs enabled the observer to use landmarks as position indicators. Possible sleeping cliffs were also noted on these photographs.

A systematic survey of the area was carried out by two observers who drove from one farm to the next to question farmers on the occurrence and activities of baboons on their farms. Questionnaires in this connection were also completed with the farmers' aid. Natives in the employment of farmers were sometimes questioned and asked to point out sleeping sites as well as areas that baboons frequented.

The observers also noted distance by using the milestones along the road or distance meters of the vehicle. The positions of the milestones, farmhouses, sleeping sites, rivers, landmarks and fences were then plotted on a 1:50,000 map, drawn to scale.

2. Various census methods.

Several troop census methods (thus population census methods) were developed during the study. Some of these methods were based on direct observation of the troops while other methods were indirect. The biggest problem during this study was to distinguish between different troops and thus to prevent repetitive counts of the same troop in different parts of its home range. Results of the different techniques will be discussed together.

2.1. Method a.

Contact with troops on their day range.

(Direct census method.)

2.1.1. Procedure.

Two observers, on foot or by car, participate in a search for baboon troops. If a troop is located, the direction of movement is noted. One observer then follows the troop while the other one hides in a strategic position. The aim of this operation is to drive the troop past the hiding place of the second observer to enable proper counting. Radio contact must be kept between the two observers.

This technique was applied in the Waterpoort area. In the Tshipise area, where the observers became familiar with the home range utilization of several troops, it was possible to do a troop census from vantage points in the troop's home range. These methods were applied during any time of the day.

2.1.2. Discussion of the method.

After a few encounters with baboon troops on their day ranges in the Waterpoort area, the following became apparent.

- i) Not more than 50% of the individuals of a troop were seen due to the dense vegetation which rendered correct countings impossible.
- ii) It was impossible to come into close range of a baboon troop and it was very difficult to determine the direction of movement.
- iii) A distinction could not be made between different troops on the basis of different compositions. Thus the same troop could be counted twice though the results indicated two troops.
- iv) More reliable results were obtained when the observer was hidden at a vantage point, usually on a hill from where he could observe the troop as they slowly progressed on their day range.

2.2. Method b. Contact with troops at sleeping sites.

(Direct troop census)

2.2.1. Procedure.

A thorough search for all possible sleeping sites in the area was made. Should it appear that a sleeping place was regularly used, then an attempt was made to census the troop at this sleeping site. Counts were made, either when a troop left its sleeping place in the morning or when it returned to the sleeping place in the evening. Morning counts were made only when it was ascertained that the troop had entered the sleeping site the previous evening. The observer then moved into a previously selected concealed position near the sleeping place, an hour before dawn. For evening counts the observer took position in his hiding place two hours before sunset, where the troop's arrival was then awaited.

2.2.2. Discussion of the method.

Morning counts.

- i) The observer had to be in position before dawn as once the baboons became aware of his presence they fled and made correct counts impossible.
- ii) The observer had to visit the site several times beforehand to ascertain which routes the baboons followed when they left their sleeping place. Only then was he able to select an observation spot.
- iii) No light was used when the observer entered his hiding place which made this method extremely dangerous since hiding places were sometimes situated on steep krantzes.

Evening counts.

- i) The observer had to be at his observation spot one to two hours before sunset since the troop was usually close to its sleeping place at that time. The troop used an alternate sleeping site on occasions when the baboons became aware of the observer's presence.
- ii) It sometimes happened that the troop had decided on an alternate sleeping place and that the observer waited in vain.
- iii) The troop sometimes arrived at the sleeping place at dusk resulting in inaccurate counting.
- iv) Troops usually preferred certain sleeping places. Thus repetitive counting of one troop was largely eliminated.

In the study areas at Tshipise, Neltox and Nwanedzi dams, the presence or absence of different troops at the sleeping places were checked by the following method:-

The observer drove from one sleeping place to the next two hours before dusk to check the presence or absence of each troop. If a sleeping place could not be reached by car then another observer was stationed there. Just before dark a baboon troop usually betrayed itself by barking at strange objects and sounds in the vicinity of

the sleeping site. In this way, six to eight sleeping places were checked during one survey in the late afternoon. This survey was also carried out in the early morning when habitual barks by adult males added to the detection of the troop. In the Tshipise study area, eleven sleeping places were checked every morning and evening for a period of 14 days. Five troops utilized these eleven sleeping sites alternatively. Usually counts of two or three troops were obtained in the evening and the rest the next morning. Results of this alternative use of sleeping places are given in figure 12 and will be discussed in the part dealing with home range utilization.

If the observer was unsure of the exact positions of the sleeping places of adjacent troops, then their position were determined by recording the early morning identification barks of interacting dominant males.

2.3. Method c. Contacts with troops at capture sites.

(Direct troop census method)

2.3.1. Procedure.

It is ascertained beforehand whether the troop subjected to control is indeed responsible for the destruction of crops or lambs. Spot observations are made to obtain information on the troop's home range and home range utilization.

The capture cages are then placed in areas where the troop spends a great deal of time. The cages are prebaited for several days until all animals are accustomed to the cages whereupon the cages are set. Usually 15 animals are caught during the first catch while the rest of the troop lingers among the cages and thus enable the observer to count the troop.

2.3.2. Discussion of the method:

- i) Since troops usually visit the cages at specific times during the day, the observer is able to await these troops.
- ii) If bait is placed at several places in the home range, it is possible to determine the size of the troop's home range by checking these baited spots regularly throughout the day.
- iii) The more familiar the observer is with the troop's home range utilization, the greater will his catches be.
- iv) Observation points must be well hidden to avoid scaring the baboons from the capture cages.
- v) The observer must be absolutely certain which troop is involved in the trapping operation.

2.4. Method d. Spoor counts (indirect census method).

It is possible to count the tracks of individual troop members after a troop has crossed a sandy plain or road. (See plate 4). This method is applied to census individual troops. This census method follows a three-phase procedure.

- a) The road survey.
- b) Investigation of spoor at crossing places.
- c) Studying the results of the road survey.

2.4.1. The road survey.

See fig. 6 which indicates the position of these roads.

- 1) All passable roads in the Messina district census area were drawn on a 1:50,000 scale map.
- 2) A road circuit was selected every day on which the spoor census was then carried out.

3) The road was then travelled at a speed of five to fifteen m.p.h. depending on the road surface. An assistant, who sat on the mudguard of the vehicle, accompanied the observer.

2.4.2. Investigation of spoor at the crossing place. (See plate 4)

4) When spoor was detected, the assistant walked 200 yards back on the vehicle's track to count any spoor that might have been missed.

5) The observer proceeded slowly on foot along the road while the following was noted:-

i) All spoor that crossed from one side of the road to the other were counted. Spoor that crossed the road in the opposite direction were also counted and then subtracted from the total count since it was assumed that a baboon crossed the road, then turned back and recrossed the road in the opposite direction only to cross the road again with the other baboons. Dominant males often behave in this way. They first cross the road, then go back to see that all troop members crossed the road.

ii) The direction of the troop's movement was noted.

iii) It was noted whether the spoor was fresh or older than 12 hours. Dung along the tracks was a good indicator of the time elapsed.

iv) The time when the tracks were found was noted.

v) The distances to the nearest sleeping and drinking places were recorded.

vi) The exact spot where the tracks were found was determined from 1/10th of the mile milestones along the road and was accordingly plotted on a map.

vii) If it proved to be impossible to count the spoor when the road surface did not permit clear tracks or when the troop crossed the road in single file, all the other additional data were nevertheless noted.

viii) The results of the day's survey were plotted on maps in the evening.

2.4.3. Studying the results of the road surveys.

ix) The data collected on location, sizes and compositions of troops are given elsewhere in this part of the study.

2.5. Method e. A population census method in mountainous areas.

(Combining direct and indirect census methods).

This method was applied in the Waterpoort census area where it was possible for two observers to drive around an isolated part of the Soutpansberg mountains (See figure 2).

2.5.1. Procedure.

a) The composition and size of troops in this isolated part of the mountain range were obtained by means of direct census methods a and b. Possible sleeping places and landmarks were noted simultaneously. Such landmarks were used as indicators to localise troops during surveys.

b) At a fixed time the two observers left their camp (situated in the study area) simultaneously in separate vehicles. Observer A followed the route to the north, through the mountain pass to Waterpoort (See figure 2). From Waterpoort, observer A followed the Waterpoort-Vivo road for 12 miles in a westerly direction. Observer B followed the road through the valley to the west, to the farm Portland. Thus the two observers moved parallel to one another on opposite sides of the mountain.

c) On the way, observer A drove at 10 m.p.h. along the mountain pass and noted any baboons or spoor of baboon in the pass. The observer stopped at strategic points in the pass to listen for barks of

baboon. The whole mountain area was then thoroughly scanned by using binoculars. The same procedure was followed on the Waterpoort-Vivo road where the observer stopped every half a mile to trace baboon visually or audibly. A telescope was used at places where the road was more than half a mile from the mountain.

d) Observer B followed the same procedure as observer A. On the farm Portland, at the end of the survey, the observers could see one another and radio contact was made.

e) Two surveys were made daily from 5.30 hours to 9.30 hours and again from 15.30 hours to 18.30 hours.

The results of the five surveys are shown on table 1.

It was never possible to observe all four troops known to be in this area on any of the surveys. However, three troops were observed on two of the five surveys.

Altogether four troops were detected prior to this survey.

2.5.2. Discussion of the method.

a) This method relies on the following assumptions:-

i) Every troop will be observed during the course of the survey.

ii) Each troop utilizes a specific home range and a troop on the average travels three miles, (DeVore et al 1965) to five miles each day (Results of this study).

iii) No other troops will filter into the experimental area.

iv) Baboons will betray themselves by barking at strangers in their home range.

b) Shortcomings of this method.

i) The success and accuracy of the experiment are dependent upon the observer's visual and auditorial abilities.

ii) The method relies upon the behaviour of the animal concerned, that is whether the baboon will reveal his position by barking at the observer.

c. Prerequisites for this method.

i) Knowledge of the situation of drinking and sleeping sites is essential.

ii) The results of such an experiment will be more reliable if the survey is carried out in the late winter when most trees have shed their leaves in this part of the country.

2.5. Method f. Estimation of troop size.

It was sometimes impossible to obtain a reliable count of the troop concerned by any of the previously described methods. In such cases the troop size was estimated but the observer continued his attempts to obtain a more reliable troop count.

The estimated counts form part of the population census and cannot be omitted.

3. RESULTS AND DISCUSSION.

3.1. The baboon track and its environment.

A troop progresses slowly under normal circumstances. The baboon's locomotory actions consist of the following:

The left front paw and right hind paw move forward simultaneously.

The latter is placed to the left or right and a little behind the right front paw. Thus when the right front paw moves forward the left hind paw, which moves simultaneously, is placed to the right or left and a little behind the left front paw. (see plate 4).

Thus the spoor imprints of the left appendages are placed close together and the same applies to the right appendages.

The spoor of the baboon is very typical and cannot be confused with that of any other animal. The vervet monkey leaves a similar track but a much smaller one and the trail left by the vervet's tail is very conspicuous.

It is possible to identify big males, juveniles and infants from the prints they leave behind.

In future studies, the measurements of the spoor, especially of juveniles, infants and big males will be recorded to contribute to our knowledge on age class grouping and ratios. Data from measurements of known-age animals proved to be of great importance in practice. The ground surface is most important in this type of survey. Excellent spoor imprints are made on dirt roads with a hard underlying surface covered with a thin layer or powdered sand. Sandy roads also provide excellent spoor imprints but the edges are less sharply defined thus affecting the estimation of time. Spoor imprints on gravel roads are difficult to see and need careful surveying. If a sandy road is travelled at 25 m.p.h., spoor can easily be detected but under poor conditions a speed of 5 m.p.h. is recommended. The best observation possibilities are obtained when driving against the sun. The shade contrast between the imprinted ground surface and the undisturbed surface is then most obvious.

Some social behaviour characteristics of a troop are reflected in its tracks. A foraging troop proceeds in a spread formation and accordingly crosses roads in the feeding grounds in this formation. A troop of 50 baboons often covers a distance of a quarter to a three quarter mile. If, however, the troop is in a hurry or frightened it will cross a road in overlapping single file rows, thus rendering spoor counting impossible. If the troop has walked along the road, then only an estimation of troop size was possible.

The spoor of young juveniles and older infants is usually found

together accompanied by the tracks of their mothers and one or more dominant males. Young infants, carried by their mothers, are not accounted for in this census method.

3.2. Evaluation of the spoor census method.

3.2.1. Home range and baboon tracks.

All monkeys have distinct home ranges and some parts of the home range are used more often. (DeVore et al 1965, Washburn et al 1963, Jay 1965). On the average a baboon troop walks three miles a day (DeVore et al 1965).

DeVore et al (1965) illustrate the day ranges of baboon troops in the Cape Peninsula and Kenya. General routes are obvious in these figures. This is also illustrated in the writer's figures of the day range routes of two troops in the study area. (See figure 13).

From these figures it is clear that baboons usually follow the same routes to drinking and sleeping sites. Thus a troop crosses the roads in its home range at specific places. Residents of that area can usually indicate such crossing places. Thus if baboon tracks are observed along the same road more than 5 miles apart which is the average distance baboon troops in this area travel per day, it can be assumed that two troops are involved. Troops are also identified by counting these spoor and noting the direction they proceed. When two troops live close together it is possible that they will cross the road within one or two miles of one another. In such cases, apart from accurate countings, the direction, progress and time of crossing are essential to distinguish between the two troops.

The purpose of this population census of baboons was to distinguish between the home ranges of different troops upon which population density was determined. Therefore it was essential to note the time as well as the distance of the troop from its sleeping and drinking places. If, for instance, the troop had crossed the road before 11.00 hours then the troop was still

on the advance feeding progress. During the 11.00-13.00 hour period the troop was at the furthestmost point from its sleeping place (See figure 16).

3.2.2. The frequency of use of crossing places.

A sixty mile road (12% of the total distance of all roads included in the spoor census surveys) stretches from the farm Neltax, northeast of Tshipise via Tshipise to make a T junction with the great north road from Louis Trichardt to Messina (See fig. 6). This road was travelled once or twice by one of the two observers who worked on the project. During the May-June 1967 road survey, 22 baboon troops crossed this road. (See fig. 7). An additional four troops were recorded to cross this road during the course of the study (20 months). Thus at the close of the study period 26 troops were believed to have crossed this road during all the different times of the year. These results gave an indication of the error-percentage of the road survey technique should only one survey be carried out. These crossing places were classified either as constant crossing places or occasional crossing places.

i) Constant crossing places:

Eighteen troops crossed this road regularly of which ten troops used the same crossing places as was observed during the first survey. The other eight troops moved their crossing places within half a mile on either side of the original crossing place.

ii) Occasional crossing places:

Four troops (nos. 8, 40, 53 and 54) that were recorded during the first survey, did not cross the road regularly. Troops 40 and 53 altered their daily routes after a new road had been constructed in the area. The water supply utilized by troop 40 also ceased to exist. Troop 54

disappeared from the road probably due to control operations.

Another four troops (Nos. 11, 13, 15, 55) were recorded to cross this road for the first time a year after the first survey had commenced. During the first survey however, troop 11 was detected on an adjacent road and was accordingly included in the population enumeration of the first survey. Troop 13 was known to exist but as this troop ranged just outside the border of the population study area, it was not included in the original population enumeration. However, this troop altered its home range utilization and moved into the study area where it was recorded for the first time at the end of the study period. Troops 15 and 55 were not detected previously and became known several months after the first survey.

Variation in troop size was also recorded during these road surveys. The troop sizes of troops 35 and 53 increased during the 20 months (See figure 7). The variation of the troop sizes of troops 1 and 2 between the first and final surveys need some explanation. These two troops ranged on the border of the census area. Smaller adjacent troops were perhaps recorded during the first survey, thus causing the discrepancy in numbers.

The only other population survey, apart from the present study, to be carried out on primates over a large area, was a census carried out by Southwick et al (1961a, 1961b, 1964) on the rhesus monkey. The method used is basically the same as the roadstrip survey census methods used for herbivores.

The roadside surveys were carried out as follows:-

The observers drove along the road at a speed of 20 m.p.h. while at least one observer kept a constant lookout for monkeys alongside the road. Thus only groups that were visible from the road were included in the population census. To evaluate the reliability of

their roadside surveys, they selected a section of typical roadside and made repeated surveys on this roadstrip. At the conclusion of the experiment, their lowest troop count was three and the highest eleven groups with an average of seven groups per trip. Thus they concluded that their surveys revealed 50% of the total number of groups that inhabited the area alongside the road.

The spoor census differs from this method in that no additional assumptions are necessary since the method suggests that all troops are included in the census.

From the discussion on fig. 7, it is clear that certain characteristic population properties can be studied through the spoor census technique, e.g. the relation between time and

- i) variation of troop size.
- ii) variation in home range utilization
- iii) influence of human population and home range utilization.

3.2.3. Testing the validity of spoor counts.

The following examples demonstrate the validity of spoor counts.

The spoor of two adjacent baboon troops, 500 yards apart, were counted on the morning and evening of the same day by two observers. The counts for the morning were 64 and 18 respectively against 58 and 24 respectively in the afternoon. It could be that the small troop was in a process of splitting from the bigger troop and that individual baboons were moving to and fro between the two troops. These spoor counts were made under excellent conditions.

A very large troop's spoor was counted on five different occasions and counts of 118, 115, 117, 118 and 120 respectively, were made under favourable conditions.

Spoor counts of a particular troop on different ground surfaces

were compared. The following is an example of such a comparison: The first spoor count of 60 was done on soil excellent for spoor counting, while the second spoor count (48) was made on an unsuitable surface. The third and direct count revealed an actual number of 64 animals in this troop.

3.3. The population density.

The population densities of the Waterpoort and Messina census areas were obtained separately. More baboon troops (See table 2) were studied in the Messina than in the Waterpoort census area.

A method for the determination of population density in the Waterpoort mountainous areas has been described previously (census method e). The sizes of these four troops were determined prior to the application of census method e through direct counts at sleeping sites or in feeding grounds. This census transect (\pm 30 miles, see fig. 2) represented one twentieth of the entire western part of the Soutpansberg mountains which stretched from the Louis Trichardt-Messina highway in the east to Vivo in the west. The population density for the experimental transect was four baboons per square mile. These figures were then applied to estimate the total population density of baboons in the mountain areas and it was calculated that 2,440 baboons inhabited the approximate 600 square miles and not 8,000 baboons as was estimated from figures obtained from 120 questionnaires put to farmers in the entire area.

The experimental census transect represented all the different habitats of the mountain area. From this 30 square mile transect a 10 square mile quadrant was selected (Waterpoort quadrant A) for comparison with the Waterpoort B and other quadrants in the Messina census area. The second sample quadrant, which was cruised by walking the railroad line next to the Sand River, represented the population

Table 3. The location and description of seven 10-mile quadrants in the Messina and Waterpoort census areas.

Name of quadrant	Type of habitat				Human population activities.
	Mountain	River	Broken veld	Open bushveld	
A. Waterpoort	"				Baboons seldom hunted. Native inhabitants.
B. Waterpoort	"	"			Baboon never hunted. Only native inhabitants.
C. Nwanedzi	"	"			Baboon never hunted. Native inhabitants only.
D. Antonvilla.		"			Baboon never hunted. Mining area with native compounds.
E. Honnet			"		Baboon seldom hunted. No inhabitants.
F. Mentz				"	Baboon seldom hunted. No inhabitants.
G. Mopane				"	Baboons occasionally hunted. Farming area.
H. Messina district	"	"	"	"	See text

Table 2. The number of troops encountered within population density determinations.

a) The Waterpoort census area.

Number of troops	Total baboon	Baboons/ mile sq.	Remarks.
4	122	4	Experimental transect—the four troops of census method e in 30 sq. miles.
5	150	15	Quadrant B- troops in Sand River valley in 10 sq. miles.
11	391	-	Troops in area between Waterpoort and Mesekwaspoort.

b) The Messina census area.

155	5276	5	All troops in the census area.
Total:175	6939	-	

density in river vegetation. The population density of this quadrant differed from the first in that it was much higher.

In the Messina census area all census methods previously described have been applied. The bulk of these results however was derived from spoor counts which were carried out during May and June 1967. The average population density for the whole census area was five baboon per square mile. (See table 2). However, this figure was not constant in the different habitats of the census area. Five ten-mile quadrants were selected in the different habitats of the population and the population density of each square was then determined and compared with the population densities (see table 3) in other squares, as well as with the two transects of the Waterpoort census area (see fig. 9).

The baboon population densities in the different sample quadrants are illustrated in figure 8.

3.3.1. Sleeping sites and population density.

The population density was highest at Antonvilla (census quadrant D) in the river vegetation alongside the Limpopo River (see plate 5). In this area baboons moved freely across the river during the dry season when only occasional water pools or streamlets were found in the dry river bed. The adjacent Rhodesian area was sparsely inhabited by human beings but baboons were highly populated there. Many baboon troops in this area slept in tall trees. In the Mentz (F) and Mopane (G) areas baboons also slept in Baobab trees. The population densities in these two areas, however, resembled the average overall population density of the Messina district (that is 5 baboon / mile square). Baboons in the Waterpoort B census quadrant slept in krantzes and seldom in the river vegetation of the Sand River. However, tall growing trees were scarcer in this area than in the Limpopo River.

In the Nwanedzi area (C) baboons slept in both krantzies and trees. Four of the troops slept alternatively in trees and krantzies while two troops slept permanently in krantzies.

3.3.2. Habitat and population density.

The habitat of the Waterpoort B census area resembled that of the Nwanedzi area (C) in many ways. The population densities of these two areas did not vary much. The population density in broken veld country, Honnet (E) census area, exceeded the population densities of all quadrants in mountain areas. One explanation for this higher population density in broken country is the occurrence of many preferred food items such as Marulas, sweet tasting honey dew on Mopane leaves and various legum-carrying Acacias which are not found in the mountains. Baboons are becoming adapted to life in open grasslands (DeVore 1963). In the study area, three distinct baboon habitats were found. Baboons are gradually dispersing from the mountainous areas to the more open bush country. However it has not been proved yet that baboons prefer such open bush country. Concerning DeVore's (1963) above statement, Rowell (1964) who studied forest-living baboons in Uganda, wrote "... I should like to open a re-examination of these assumptions" since DeVore implied that baboons were becoming adapted to a open grassland living at the expense of their ability to live in other environments. The writer is in agreement with Rowell since baboons of the study area inhabited three different types of environment.

3.3.3. Human activities and the population density.

In studying the ecology of an animal species it must be considered that changes, caused by human activities in the habitat of the animal, might have lead to the animal's adaptation of his needs to this new "abnormal" habitat.

A low human population did not seem to have any effect on the density of the baboon population. However, in agricultural areas where humans extensively exploited the baboon's habitat, the population density seemed to decrease. The human population density in the Messina district was very low and the surviving baboons successfully learned to utilize the agricultural products and human produced water resources.

3.3.4. Troop size and population density.

From figure 8 it is clear that the population density in census quadrants B, C, D and E corresponds to the increase in number of troops. In census quadrants A, F and G, however, the population densities were at their lowest and remained practically constant. They resembled H which was the average population density for the whole Messina census area but the number of troops varied. In census quadrant F (Mentz), baboons slept in Baobab trees in open "bushveld" country which, according to the population density, was not a preferred baboon habitat. Census quadrant G (Mopane) was situated in an even more heavily human populated area which could have contributed to the formation of smaller but more numerous troops than in the case of A and F. Thus heavily human populated areas could possibly sustain more troops, but the total population remained unchanged. This characteristic of the population change in number might be due to various reasons. Small troops were secretive and could more easily evade attacks from their sole predator in these areas, the human being. Both A and G quadrants were situated on the border of the baboon's population distribution to the west.

This low baboon population density in heavily human populated areas and in deficient habitat leads to the concept of limiting factors.

3.4. Limiting factors in the distribution of the baboon.

The most important factors in the limitation of the baboon's distribution in the Soutpansberg and Messina districts are:-

- a) Sleeping sites.
- b) Human population density.
- c) Drinking sites.

The situations of A, F and G census quadrants have previously been noticed. According to figure 9 these quadrants are situated on the border of the distribution of the baboon population. Baboons do not occur in areas where no mountains or rocky sleeping places or tall growing trees exist. The population density is at its lowest in open bushveld (quadrants A and G) and thus it is quite acceptable that the lack of adequate sleeping sites limit the baboon's distribution.

In hilly country or where steep rocky walls occur next to dry rivers a few baboon troops survive. This is the case at Coila (see fig. 9). Broken veld country prevails in the areas alongside the Magalakwin and Limpopo rivers which contributes to the higher population density in these areas.

The presence of humans may be responsible for the baboon's restriction to the mountains at Louis Trichardt, Vivo and Waterpoort. The human population is reasonably high at these foothills of the Soutpansberg mountains. These areas, previously inhabited by baboons, were invaded by humans who used the areas for agricultural purposes, breeding of domestic stock and residential areas. In some of these areas, however, baboons survive e.g. the broken veld country northeast of Waterpoort.

On the southern and northeastern sides of the Soutpansberg mountains the country flattens out which, apart from human invasion, contributes to the absence of baboons in these areas.

These restrictions, however, were only temporary in areas that were sparsely populated by humans as in the Messina district. In the long run these restrictions proved to be in the baboon's favour since they learned to utilize the inexhaustible source of food and water. Human activities caused the baboon to disperse to areas where water became available and where baboons could not have survived before. (See distribution of human constructed drinking sites in the Tshipise study area. (Fig. 3) However, mountain and river areas remain the preferred baboon habitats since water is usually available there.

From questionnaires put to 120 farmers in the Soutpansberg and adjacent areas, it appeared that 50 percent of these farmers were of the opinion that the baboon population was increasing while 37 percent reasoned that a constant population was maintained. According to those who believed that there was an increase in population numbers, more and bigger troops occurred. Only 13 percent of the farmers believed that the population density had decreased during the past several years. Some 80 percent of the latter owned farms in mountainous areas. Several farmers around Mopane stated that baboons had penetrated the area recently.

Thus it can be concluded that a gradual dispersion of baboon troops takes place from mountainous areas to the flat open bushveld areas that were hitherto believed to be a barrier to the baboon's distribution. It is impossible to make any statement as to whether the baboon population in the census areas is increasing or decreasing, since troops that previously inhabited mountainous and riverine areas, may now be found in open bushveld country.

3.5. The influence of habitat on troop sizes.

Of all the troops that were censused in the Messina census area, the sizes of only 16 percent of these troops were estimated. Complete

Table 4. Regional differences in the sizes of baboon troops.

Area.	Number of troops	Range	Mean	Babcons/ sq. mile.
Drakensberg, Cape Peninsula, Eastern Cape.	15	15-58	31	-
Waterpoort	20	15-45	34	-
Messina district	155	8-118	38	5
South West Africa	20	8-65	27	-
Southern Rhodesia	18	12-109	46	-
Amboseli, Kenya	15	12-185	80	25
Nairobi Nat. Park, Kenya	9	12-87	41	10
Murchison Falls, Uganda	8	14-48	27	-
Queen Elizabeth Nat. Park, Uganda	2			30-40

analysis of age and sex classes was made in 13 percent of the troops. The rest of the population (71%) was censused either by direct counts (not analysed) or spoor counts. As stated previously, infants carried by their mothers were not included in spoor counts. The number of infants which might have been omitted in the spoor census ranges from 0 to 10 in the different troops. (See table 7). On average, three infants could be added to the troops subjected to spoor counts. This assumption was not considered in the composition of figure 10 because of its unreliability.

Troop sizes in the study area ranged from 8 to 118 with a central tendency between 20 and 55. (See figure 10). Figures on troop sizes given by Hall (1965a), DeVore and Hall (1965) and Rowell (1964) were compared with the figures found in the study area. (Table 4).

The numerical sizes of baboon troops in Southern Africa vary considerably. These variations exist in different as well as in the same areas. In the present study the average troop size seems to be the largest in the Messina area. These figures correspond to that of the Rhodesian areas while the figures of the Waterpoort area correspond to the figures of olive baboons at the Murchison Falls in Uganda.

Sizes of baboon troops in Southern Africa seem to range between 8 and 118. DeVore and Washburn (1963), Rowell (1964) suggested that the baboon population density was related to environmental factors such as food supply and sleeping places, but the sizes of troops depended upon the social behaviour of troops. In the Nairobi National Park, De Vore et al l.c. found no correlation between troop sizes and vegetational zones. For example, the home ranges of two troops of 13 and 165 animals respectively, overlapped extensively. DeVore and Hall (1965) suggested that ecological and environmental conditions could influence the troop size.

The central tendency of group size varied in relation to the relative

Table 5. The number of troops and average troops size of baboons inhabiting river, mountain and broken veld habita in the study areas.

Habitat	Number of troops	Total baboon	Average troop size	Range
Mountain	24	806	34	15-75
River	42	1685	40	8-110
Broken veld	109	4448	41	10-118
TOTAL	175	6939		
Average			38	8-118

abundance of food. The central tendency of troops was lowest in the arid South West African area, highest in Southern Rhodesia and between these two extremes in the Cape Peninsula, Eastern Cape and Drakensberg of South Africa. (DeVore and Hall 1965). Kummer in the discussion of DeVore's (1965) article stated that the size of a hamadryas group was influenced by the ecological environment. Hamadryas baboons slept on vertical rocks that were numerous in western parts of the area and scarce in the eastern areas. The increase in troop size in the east, where food was abundant, forced large numbers of baboons onto the few available rocks. However, if a fight broke out amongst such a big (but unstable) unit, it split into smaller units of 30-50 baboons. These units were constant in size.

When comparing the troop sizes of the different environments in the study area, it was found that troops in broken veld and river habitats were larger than troops in the mountain areas. (See table 5)

3.6. Troop composition and troop regulatory factors.

Troops have been classified in sex and age classes in both the Messina and Waterpoort study areas. In Table 6 these data are compared with that of other workers.

3.6.1. The adult sex ratio.

The data on adult sex ratio (male/female) by Hall (1965b) for baboon groups in the Cape 1:3:3 do not correspond with the present data (1:1.6). The lowest male/female ratio found in an individual troop was 1:5 in the study area while ratios such as 1:10 and 1:9 were found in the Cape and Kenya respectively. The sex ratio for the forest-living baboon in Uganda is 1:1, according to Rowell (1964) a ratio usually reported for arboreal species.

The adult male/female ratio of 330 baboons captured in the study area,

Table 6. The composition of baboon troops in South Africa,
Rhodesia and Kenya.

Troop	Adults		Total Adults	Immature ♂ & ♀	Troop total	Adult male/ female	Female/ immature
	male	female					
Cape C ⁺	8	18	26	54	80	1:2.2	1:3.0
Table Mountain ⁺	3	12	15	13	28	1:4.0	1:1.1
N ⁺	1	10	11	9	20	1:10.0	1:9.9
Total in Cape ⁺	12	40	52	76	128	1:3.3	1:1.9
Kariba main ⁺	13	31	44	59	103	1:2.4	1:1.9
Kenya SV ^x	5	12	17	24	41	1:2.4	1:2.0
" SR ^x	6	7	13	18	31	1:1.2	1:2.6
" AR ^x	1	9	10	18	28	1:9.0	1:2.0
" LT ^x	2	3	5	12	17	1:1.5	1:4.0
" MR ^x	1	6	7	5	12	1:6.0	1:0.8
Total Kenya ^x	15	37	52	77	129	1:2.5	1:2.1
Messina R	4	5	9	8	17	1:1.0	1:1.6
" BC	6	10	16	6	22	1:1.7	1:0.6
" SQ	7	11	18	7	25	1:1.6	1:0.6
" N	5	10	15	10	25	1:2.0	1:1.0
" MA	4	18	22	7	29	1:5.0	1:0.4
" ME	3	8	11	5	16	1:3.0	1:0.8
" GK	12	23	35	11	46	1:2.0	1:0.5
" KMWA	11	11	22	5	27	1:1.0	1:0.5
" RB	18	28	46	11	57	1:1.5	1:0.4
" W	18	31	49	28	77	1:1.7	1:1.0
" KMW	9	21	30	10	40	1:2.0	1:0.5
" KMO	9	18	27	10	37	1:2.0	1:0.5
" K	10	11	21	8	29	1:1.0	1:0.7

Troop	Adults		Total Adults	Immature ♂ & ♀	Troop total	Adult male/female	Female/immature
	male	female					
Messina S	17	17	34	7	41	1:1.0	1:0.4
" D	17	32	49	17	66	1:2.0	1:0.5
" SM	17	22	39	10	49	1:1.3	1:0.5
" T	8	15	23	12	35	1:2.0	1:0.8
" C	9	12	21	15	36	1:1.3	1:1.3
" RS	13	17	30	12	42	1:1.3	1:0.8
Water-poort I	11	16	27	14	41	1:1.5	1:0.9
" II	7	7	14	10	24	1:1.0	1:1.4
Total Water-poort & Messina	215	343	558	223	781	1:1.6	1:0.7
✕	66	97	163	167	330	1:1.5	1:1.7

+ Hall 1961

x DeVore 1959

✕ The adult male- female and female-immature ratios, determined from a sample of the population (330 animals), captured during control operations in the Messina district.

Table 7. The increase or decrease in troop size within one year.

Troop	Date	Male	Female	Juvenile	Infant 6-18 months	New-born 0-4 months	Total
W	21.7.67	17	27	17	3	4	68
	21.1.68	18	31	12	2	9	72
	24.7.68	18	31	15	3	10	77
RB	10.8.67	20	20	10	1	1	52
	17.10.67	18	24	14	1	3	52
	29.2.68	19	24	7	8	2	60
	26.8.68	15	25	8	11	0	59
	13.11.68	18	26	1	10	3	58
KMO	10.10.67	9	18	4	4	2	37
	23.8.68	9	20	3	2	2	36
KMW	17.10.67	9	21	7	1	2	40
	26.3.68	7	23	5	3	2	40
	22.8.68	13	21	2	3	2	41
KMWA	8.8.67	11	11	2	0	0	24
	21.8.68	11	11	2	2	1	27
GK	9.8.67	15	23	5	1	1	45
	20.8.68	12	23	6	4	1	46
D	6.6.67	17	32	8	2	0	59
	19.8.68	17	32	8	8	1	66
T		18	15	11	1	0	35
		8	15	11	4	6	44

supported the ratio calculated for the overall population. Fifteen solitary males were encountered during the course of the study. Once two solitary males were observed together and on another occasion three were seen together. These males were very secretive and wary and difficult to detect. They are, to some extent, responsible for the difference in adult sex ratios within troops as they originally come from and sometimes return to troops.

3.6.2. Female - immature ratio and the population growth form.

The female/immature ratio in the baboon population in the study area is 1:0.7 (see table 6). These results do not correspond with those of Hall or DeVore who gave an overall ratio of 1:2 for the Cape and Kenya baboon populations.

According to the age pyramids (after Odum 1959) in fig 11, the baboon population in the study area is a declining one. Pyramid A represents 32 troops (1,388 baboons) in the study area while pyramid B represents data on 330 captured baboons from the same population.

More juveniles were captured after the first and second round which could be responsible for the discrepancy in the female/immature ratio (Table 6)

From figure 11 it seems that the population increase in the study area is very low. Table 7, on the natality of several troops in the Tshipise study area, supports this idea. In contrast to this, DeVore (1965) found a population increase of 40% over a period of four years in five troops in the Nairobi park.

Many factors (e.g. predation, subtrooping, changing of individuals between troops and count errors) may account for the discrepancy of some troop sizes within one year. A detectable increase in troop number occurred in four troops (W, KMWA, D and T). Troop RB showed an initial increase but some juveniles were missing during the last

count. Troop sizes of troops KMO, KMW and GK remained more or less constant during the observation year. Nine infants were born during the study period in W troop but five infants of this troop were later found dead. Two mothers carried their dead infants around for several days. The mortality figure of the young age classes seemed to be very high. Thirteen infants were collected for laboratory use during the study period of which 54% died within the first three weeks in captivity, in spite of special precautions. Hall (1962b), could find no evidence as to the cause of death among infants in free-ranging baboon troops.

Since births occur throughout the year in a baboon population, it will prove difficult to determine the ecological natality for any troop, especially if females are not marked.

The loss of juveniles from their troops is perhaps due to changing of individuals between troops or else they have fallen prey to leopard, python and perhaps hyena which occur in small numbers in the area.

The writer must, however, agree with Hall who (in the discussion of an article written by Nelson 1965) stated that baboons were only rarely preyed upon by leopards. Hall referred to a study made by Mitchell in Kafue National Park who found that only two baboons were included in a total of 96 leopard kills over three years. A similar low percentage of baboon killed by leopard was recorded for the Kruger National Park (personal communication). Nelson (1965) observed a baboon troop, during daylight, that was pursuing a leopard. Thus leopard predation seems to be negligible.

Isemonger (1962) described two encounters between baboons and pythons. In the one incident, the python held onto his prey in spite of attacks by other troop members. A python was once found in the sleeping site of troop A in the study area. Pythons might have been responsible for the nightly commotions amongst baboon troops in their sleeping places.

These are only some of the population regulatory factors, while others are still being investigated.

4. Conclusion.

Many observers (Bourlière 1961, Hall 1962a, Schultz 1961) experienced difficulties in making accurate sex and age counts of primate groups. Buettner-Janusch (1965) stated that an accurate troop analysis was only possible after all troop members had been captured. In the Messina area all the members of several troops were captured but three to twelve animals of every troop were released according to the control policy.

Different census methods were developed and applied during the population census to obtain an indication of the population density in the census area. The spoor census technique proved to be the most reliable of all the methods tested thus far. The sandy nature of the soil in the study area appeared to be an essential condition for successful spoor counting.

Although there are several sandstone ridges in the study area, most troops leave these ridges during the day to cross some roads on their day range. The spoor census technique is an indirect method of obtaining information on troops' sizes and composition yet it supplies the most reliable results in the shortest period. The spoor census technique is employed under the following circumstances:-

- i) When it is impossible to locate the troop in a favourable position in order to carry out a direct count.
- ii) When the precise location of the sleeping place, where direct counts of the troop can be made, is unknown.
- iii) When the observer is unable to do a complete count of the troop.
- iv) When a troop is caught unaware and flees into the dense vegetation.

The spoor count of a troop can be done within 15 minutes whereas it may take several days to obtain an accurate direct count of the troop. Successful direct troop counts can only be done if the following conditions prevail:

- i) When a troop approaches or leaves its sleeping place.
- ii) When the troop moves as a whole; e.g. when they are crossing a road and the observer is in a favourable position to do a count. Sex determination can only be done if the troop moves very slowly.
- iii) Results of direct troop counts are naturally more reliable than any other indirect census method but are much more difficult to obtain.

Primate population studies were only recently undertaken but in general only small samples were taken as representative of the population density e.g.:-

Along a 27.6 kilometer road from Dharwar (India) to the west, Sugiyama (1967) counted 44 groups of hanuman langurs. The population density of this primate species was accordingly estimated to be 100 langurs square kilometer.

Rahm (1967) obtained the population density of chimpanzees on the western shore of lake Kivu in the Congo through the application of different spot checks. The census was mainly based on visual and acoustic contacts with the animals during 19 continuous observation days.

Data on population densities of the yellow baboon Papio cynocephalus were collected through field studies carried out over several years on a relatively small baboon population in some National Parks of Kenya (DeVore and Washburn 1961, DeVore 1965). DeVore described no census method. He studied one troop after the other thereby obtaining the data on the population density in his study area.

Hall (1960, 1965) presented data on troop sizes of the chacma baboon, Papio ursinus, in the Cape Province but these figures were inadequate

for determination of population density.

From the present study it has become clear that population density depends upon the availability of food, water and sleeping sites. Human activities may lead either to the increase or decrease of the population density in certain areas.

DeVore and Hall (1965) found that the population density of baboon in Kenya varied in different areas. During the discussion in the present study on population density in different habitats, it has been pointed out that population density varied from ± 5 to ± 36 baboons per square mile. Thus it is obvious that the selection of sample areas is an important aspect that must be taken into consideration during population density studies.

Population census results, which incorporate a relatively expansive area, exist only for the rhesus monkey of Southern India (Southwick et al 1961a, 1961b and 1964) and for the gorilla of Central Africa (Emlen and Schaller 1963).

Through the present study, Papio ursinus is therefore the third primate to be investigated over a relatively big area.

C. Home range determination and utilization.

Data on the size and utilization of, as well as overlap in home ranges, were collected during the application of census methods in the Messina census area. Data were furthermore specifically collected during intensive home range studies in the Tshipise study area. (For the description of this area, see "The study area.") Investigations on the size, overlap and utilization of home ranges have also been carried out in the Cape Province, South West Africa, Kenya, Uganda and Ethiopia by various authors. The results of these studies will be compared with the present study at Tshipise.

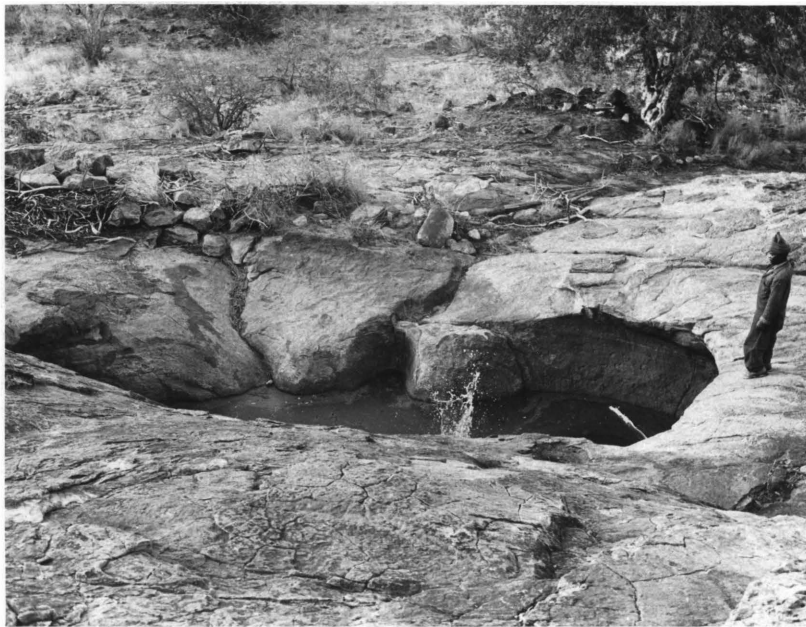


Plate 3. Drinking place No.1, a natural waterhole in the brokenveld area of the Honnet Nature Reserve.

1. Methods.

1.1. Selection and habituation of troops.

1. A troop was used for home range studies only if it was possible to keep in contact with it throughout the day.
2. Two troops were selected for home range studies. The first one was the W troop at Tshipise, that came into daily contact with humans in certain parts of its home range. This (W) troop utilized agricultural products from adjacent farms. It also scavenged on refuse dumps behind the camp terrain. The second troop, RB troop, was a more "natural" troop since it saw humans only occasionally and no agricultural products were cultivated in its home range.
3. At the onset of a throughout the day observation period, it was ascertained which sleeping place the specific troop used the previous night in order to locate the troop early the next morning.
4. The observer moved into a position before daybreak from which he could observe the sleeping place without being detected by the troop.
5. The troop was followed at a distance, as soon as it moved off on the day range, for the rest of the day.

1.2. Procedure when following a troop on its day range.

1. The troop was never induced to move. This was achieved by keeping at such a distance from the troop that it was under observation without being ill at ease. This distance varied for different troops. Most baboon troops in the census area did not allow a human being within 200-300 yards when they were in reasonably open country. Some troops never grew accustomed to the observer and did not tolerate him within 500 yards. None of the troops became familiar enough with vehicles to climb onto the vehicles in search for food, as described by Hall (1961). The tolerance distance of W troop was minimal, and the observer was al-

lowed within a distance of 10 yards from the baboons when they were in their "core area".

2. When the observer lost sight of the baboons in dense vegetation auditory cues, broken plants and fresh spoor were followed.

3. If the troop was approached after contact had been broken, it was done in full view of the animals.

4. Troops often made contact with one another during the course of the day. After such a contact, the troop was counted to ensure that the same troop was followed. A longer observation distance was allowed when two troops were in contact in order not to surprise the newcomers.

5. As the troop grew used to the observer's presence, the observation distance was shortened.

6. During the throughout the day observations on RB troop, an assistant followed the observer by Landrover on defined roads. Radio contact between the observer and the assistant was kept since it was sometimes necessary for the observer to travel quickly from one observation point to another, especially when the observer lost sight of his troop in dense vegetation. Observations were done from the vehicle whenever possible since all baboon troops accepted a vehicle more easily than a human being on foot. It sometimes took weeks before the troop adapted to the observer, long after they had accepted the vehicle.

1.3. Obtaining data on the size of the home range.

1. The route followed by the troop was noted throughout the day.

The day range of the troop was then plotted on a map, drawn from aerial photographs, every evening.

2. Spot observations provided supplementary knowledge on the movements of the troop. Spot observation data were collected either when

Table 8. Number of days and hours of direct observation of baboon troops during the study.

Period of study.	Number of obser- vation days.	Number of obser- vation hours
July-August 1967	24	188
October 1967	13	140
January 1968	16	166
February- March 1968	13	135
July 1968	11	127
August 1968	14	92
Total	91	848

the observer went intentionally in search for a troop or when he unexpectedly met with a troop. Spot observations lasted a few seconds to a few hours. If the observation period exceeded eight hours, then the observation was classified as a throughout the day observation. Apart from 75 throughout the day observations, about 1,300 spot observations were made on the baboon population in the Messina census area.

3. At the end of the study period, observations on the day ranges were combined to delineate the home ranges of the two troops.

1.4. Observation periods.

Six throughout the day observation periods were carried out between July 1967 and August 1968. (See table 8). It was the observer's aim to do the observation on a troop on successive days but on several occasions it proved impossible to follow a troop throughout the day. RB and ST troops sometimes visited drinking place IV simultaneously. Since it was not advisable to venture too close to the drinking place while the baboons were drinking the observer often followed the wrong troop when they left the drinking place. The situation grew worse when, due to dense vegetation, a troop count was out of the question. This happened especially during the August 1967 preliminary study when of the six observation days, only three days were spent with the RB troop.

Apart from these intensive observations done on troops W and RB, observations of one or two days were also carried out on troops whose home ranges overlapped with those of W and RB troops.

Troop KMWA was observed for three days.

Troop S was observed for three days and was often observed for as long as 6 hours per day.

Troop K was observed for one day and for part of the day during another three days.

Troop A was observed for two days and for part of the day during another three days.

Troop KMO was observed for one day and described in 70 spot observations.

2. Results and discussions.

2.1. Home range utilization.

2.1.1. The Sleeping site.

In South West Africa, the Cape and Ethiopia baboons sleep on steep cliff faces whereas in Southern Rhodesia and Kenya they prefer tall-growing trees (DeVore et al 1965). Zuckerman (1932) found that baboons in the Western Cape Province settled in rocky outcrops wherever they found themselves in the evening. Gelada baboons in Semyen, Ethiopia, sleep on small ledges on vertical rock faces (Crook 1966) as do most baboon troops in the Messina census area. However, some troops in the study area sleep in both krantzies and trees where both these sleeping places are available. The trees preferred as sleeping places are tall-growing trees on riverbanks such as Acacia albida, A. xanthoploea, Ficus sycomorus and Croton megalobotrys. Some troops utilize Baobab trees that are scattered over the open country, as sleeping sites.

In the Tshipise study area, all the troops sleep in steep rocky ledges and cliffs in the sandstone ridges and the Tshipise kopje. The locations of sleeping sites in the Tshipise study area are shown in fig. 3. These sleeping places are recognisable by the accumulation of dung and the accompanying peculiar smell. The rocks are typically urine-stained which gives them a dark sticky surface.

W troop used two sleeping places in the kopje at Tshipise. The main sleeping place faced northeast and the alternative sleeping place,

Table 9. The use of sleeping sites by W troop. Arrows indicate the sequence of use.

Date	Number of occasions used in succession.				
	Site 1	Site 2	Site 11	Site 4	Site 12
4.5.67 to 18.5.67	2	2			
	2	2			
	3	2			
	2				
18.7.67 to 6.8.67		2			
	1	2			
	2	1			
	11				
7.1.68 to 24.1.68	6	1			
	10				
14.7.68 to 19.7.68		2			
	1		1		
	2				
21.7.68 to 24.7.68	1			1	1
	1				
5.8.68 to 9.8.68	1	1		1	
	2				
Total	47	15	1	2	1

southwest . It was twice observed that a part of the troop used a third and a fourth sleeping place in the kopje. The third was situated more to the east and 500 yards below the main sleeping place while the fourth was situated about 300 yards southeast of the main sleeping place. These sleeping places were all situated very high in the kopje when compared with the sleeping places used by other troops in the study area. However, this was due to geological differences within the area and was no criterium with which to determine preferred sleeping places. Table 9 demonstrates the frequency with which the main and alternative sleeping sites were used on successive nights between May 1967 and August 1968. W troop preferred to sleep in the main sleeping place on the Tshipise kopje but on occasions, when disturbed by a human's presence, moved to the alternative sleeping place. Sometimes, after they had been barking during the previous night in the main sleeping place, the baboons utilized the alternative sleeping place the following night.

On a few occasions, W troop did not use any of the sleeping sites at Tshipise but instead slept close to A troop's usual sleeping place or in KMW troop's sleeping place.

W troop was not tolerated in these "new" sleeping places by the other troops which lived there since it was not regularly seen by the usual occupiers of the sleeping sites. W troop's presence evoked heavy intertroop aggression. (See intertroop encounters.)

Observations done on W troop during rainy days, revealed no significant concurrence between preference of sleeping sites and rainy conditions. However, the strong southeastly winds prevalent during July and August could be responsible for the more frequent use of the main sleeping site.

In contrast to W troop that used sleeping sites in an isolated kopje, the choice of a sleeping place by troops RB, GK, K, KMO, KMW and KMWA

Table 10. The frequency of use of sleeping sites (six) by
RB troop.

Date	Sleeping sites					
	3	4	5	7	8	10
August 67						
7	x					
8			x			
9			x			
10			x			
11	x					
September 67						
9	x					
10				x		
11			x			
12						x
13			x			
14					x	
15					x	
16			x			
17						x
19			x			
20			x			
21		x				
February 68						
23			x			
24	x					
25						x
26					x	
27			x			
28						x
29						x

Date	Sleeping sites					
	3	4	5	7	8	10
March 68						
1						x
2						x
25						x
26			x			
27						x
August 68						
(See Fig.12)	1		4		3	5
Total	5	1	15	1	5	14

Table 11. The utilization of drinking sites by baboon troops
in the Tshipise study area.

Troop	Canal	I	II	III	IV	V	VI	VII	VIII	Total
RB		X	x		X	X	x			3+
W	X	X	X	X			X	X		6
KMW		X	X	x	x	x				2+
KMO		X	x		x	x	x			1+
KMWA		X	X	x					x	2+
K		X				x		x		1+
GK		X	X	x	x			x		2+
ST					X	X				2+
A			X	X			X		X	4
Total	1	7	5+	2+	2+	2+	2+	1+	1+	

X = Definite drinking site

x = presumed drinking site.



Plate 6. Sleeping site No.4 in the Tshipise study area.

was influenced by the interaction between these six troops that utilized eleven sleeping places situated on a one mile stretch of the sandstone ridges (See fig. 3 and plate 6).

Troop RB was identified in six sleeping places on 41 occasions between August 1967 and August 1968. From table 10 it is evident that RB troop preferred sleeping places 5 and 10. During a 13 day observation period in August 1968, all troops occupying sleeping sites 3 to 10 were identified. Negative data in fig. 12 indicate that troops GK and K used alternative sleeping places elsewhere. On four occasions it was not possible to identify the troops involved. RB troop, the biggest of the six troops, utilized most sleeping places throughout the length of the ridge. KMO troop, on the other hand, tended to use the same sleeping place.

KMO and K troops often evacuated their sleeping places on RB troop's approach. Usually all these six troops carefully scanned a sleeping place from below before they occupied it. This behaviour was not observed for W troop.

2.1.2. The drinking sites.

Several drinking places were utilized by baboons in the Tshipise study area. Table 11 demonstrates the number of troops that utilized individual drinking sites. On these drinking places, No. IV, V, VI, VII, VIII and the canal were man-made reservoirs. Natural reservoirs in the sandstone-ridges, (No. 1, II, III) were usually dry during the months August to December, but constant water was found in drinking place No.1 (See plate 3). The availability of water in the man-made reservoirs varied according to the presence or absence of cattle on the ranch.

Interaction between troops took place at drinking place No.1 during

the two hours before midday until four hours past midday period. W troop, as a rule, drank from the canal on Honnet, about 200 yards from their main sleeping place, or else in the canal beneath the alternative sleeping place. RB troop drank at three different sites during the study period (No. I, IV and V) but they probably also drank elsewhere during times of water scarcity. RB troop visited No.I drinking site only on exceptional occasions and in doing so altered their day range completely. The surface of waterhole No.I was covered with a thick layer of algae which might have been the reason for the limited use of this waterhole.

In Ethiopia, Kummer (1968) found that hamadyas baboons dug drinking holes in the sand of river beds. The water in these holes was cool and free from algae in contrast to the water in permanent pools. Hall (1962a) found no evidence of regular water drinking amongst baboon troops of the Cape Peninsula. However, baboons in the study area drank daily apart from a few exceptional cases.

2.2. The home range and variation in home range utilization.

It is generally known that, "no wild animal roams at random over the country; each has a home region..." (Seton quoted by Mohr et al 1966) and that "all terrestrial mammals spend their lives in a confined area." (Jewell 1966). Dice (quoted by Robinette 1966) defined the home range as that area which an animal covered in its day to day travels. Jewell (1966) questioned the boundary lines of a home range area as occupied by a certain species, drawn on a map, since a home range did not possess a definite boundary. He suggested that the actual boundary could only be defined after intensive behaviour studies on the species had been carried out. Behaviour characteristics, such as nervourness of animals at the edge of their home range, should be taken into account.

Table 12. The size and overlap of home ranges of different Primate species.

Author	Animal	Location	Home range size	Maximum degree of overlap in home range
Petter <u>et al</u> 1967	Aye-Aye	Madagascar	+ 12 acres	-
Jay 1965	Langur	North India	$\frac{1}{2}$ -5 mile ²	Extensive
Sugiyama <u>et al</u> 1965	Hanuman langur	Dharwar, India	5-16 hectar	Considerable
Hall 1967	Patas monkeys	Uganda	20 mile ²	-
Simonds 1965	Bonnet macaque	South India	2 mile ²	20%
Southwick <u>et al</u> 1965	Rhesus macaque	India	-	80% - 90%
Neville 1968	Rhesus macaque	India	0.02-1.2 mile ²	Extensive
Bolwig 1958	Baboon	Kruger Nat. Park	6 mile in diameter	-
DeVore 1963	Baboon	Kenya	-	50%
Washburn <u>et al</u> 1963	Baboon	Kenya Amboseli	3 - 6 mile ²	-
DeVore <u>et al</u> 1965	Baboon	Cape Kenya Nairobi	3.5-13 mile ² 2-15 mile ²	$\frac{1}{4}$ mile (Hall 1961) -
Present study	Baboon	Tshipise	5 - 9+ mile ²	75%
Reynolds <u>et al</u> 1965	Chimpanzee	Budongo	6 - 10 mile ²	-
Schaller 1965	Mountain gorilla	Congo	10 - 15 mile ²	-

Most authors determined the home ranges of animals by indirect methods which gave a reasonable indication of the range. Recent application of telemetry can be classified as a direct method of home range determination. However, results derived from this method cannot be as valuable as the results of an observer who follows an animal throughout its day range since the animal's behaviour cannot be recorded via the transmitter attached to the animal.

In primates the size of the home range differs considerably amongst the different species. There seems to be a correlation between the species' adaptation to a terrestrial living and the size of the home range. The more terrestrial a species, the larger is its home range (DeVore 1963). This statement holds true, according to table 12, even within the same species; e.g. forest-living baboons (Rowell 1966) occupy a smaller home range (1.5 to 2 mile²) than baboons that live in the "open country" Nairobi National Park (2.0 to 15.0 mile²) (DeVore et al 1965).

Although some correlation exists between the size of the animal and the extent of the home range, e.g. the aye-aye (Petter et al 1967) occupy ± 12 acre and the gorilla 10 to 15 mile² (Schaller 1965) this is not a constant correlation since a patas monkey group has a home range of 51.8 kilometers² (or 20 mile²) (Hall 1967).

The day ranges of RB and W troops during six different study periods are shown in fig. 13a-c. The day ranges were combined to indicate the home range sizes. RB troop had a home range of nine square miles while W troop ranged over an area of five square miles. In RB troop the return route usually paralleled the outward route. The same pattern of day range routes was described for hamadryas baboons (Kummer 1968). From figures given by DeVore and Hall (1965) it was evident that although certain paths were regularly used, no parallel routes were demonstrated. In this respect W troop's home range utilization

resemble those demonstrated by DeVore et al l.c. W troop often changed course during its day range while RB troop seldom behaved in this way. Gelada baboons (Crook 1966) did not usually return to the same cliffs on successive nights. He suggested that this might be due to the longer outward journey compared to the shorter afternoon journey of these animals.

The home ranges of RB and W troops bordered on one another and both overlapped with the home ranges of adjacent troops as shown in figure 14. The home range sizes of baboons depend on ecological and social reasons which are not yet clearly understood (DeVore et al 1965). Sugigama (1967) suggested that the home range sizes of hanuman langurs were determined by the troop size, the vegetation type and the presence of adjacent troops. Struhsaker (1967), however, found no correlation between group size and the size of the home range. According to Burt (1964), in a species such as the baboon, which did not possess a breeding or a birth season and where food was easily obtainable, the variability in home ranges was probably dependent upon population density.

The availability of water directed the course of the day range for RB troop and was accordingly partly responsible for the size of the home range. Since W troop had ample water at their disposal, water did not direct the course of the day ranges. W troop was bigger than RB troop, yet it ranged over a smaller area. Environmental conditions, such as the availability of human provided food and water might be the reason for this difference. However, it must be emphasized that on certain days W troop utilized only natural food and water sources. Encounters between W troop and other troops on the border of W troop's home range are described elsewhere in this study. The behaviour of W troop when in contact with other troops, resembled their uneasiness

when entering the sleeping and drinking sites utilized by other troops. On one occasion W troop's retreat from drinking site II was witnessed after it had been awaiting A troop's departure from the drinking site for one hour. W troop marched with quick pace back to a drinking site in its core area. Thus it could be deduced from this incident that the size of W troop's home range was partly determined by the presence of, and encounters with, adjacent troops.

Home range utilization of W troop varied considerably with the different observation periods. During the July 1967 observation period W troop often raided an orange orchard on the farm Hyoma but during the July 1968 observation period (see figure 13 a + c) it never visited this orchard. Instead, the troop ventured for the first time, during the study period, outside its normal home range boundary (see fig.13c). As demonstrated in this figure W troop was seen for the first time during this period at drinking places No. I, No.II and No.III. Drinking place No.III, which was unknown to the observer previously, was then discovered as the observer followed W troop.

It was obvious that W troop was familiar with the new terrain since it directly proceeded to drinking site No.III. They were also acquainted with sleeping sites 3, 4 and 11. The troops that regularly inhabited these sleeping sites, KMW and A troops, were disturbed by the arrival of the intruders and the encounters that took place between them and W troop were often of a very aggressive nature.

The day ranges of RB troop observed during October 1967, differed considerably from its February 1968 day ranges (see figure 13 a + b). The availability of water was the main reason for these alterations in RB troop's day ranges. Not only did the availability of water influence the routes followed during the day ranges but it also determined the choice of a sleeping place.

Table 13. The distance travelled by troops W and RB during 54 full day ranges in relation to temperature and humidity.

Troop	Period	No. of day ranges	Average max. daily temp. (°C)	Average min. daily humidity (%)	Mean distance (miles) ± S.E.	Range of variation
W	i July 1967	9	not available	not available	3.9 ± 0.24	2.0-6.0
	ii January 1968	12	34.3	43.5	3.5 ± 0.09	4.0 ± 0.18 2.0-5.5
	iii July 1968	10	25.9	47.4	4.5 ± 0.31	
RB	iv October 1967	10	27.7	47.0	5.4 ± 0.09	1.5-6.5
	v February-March 1968	8	28.8	42.5	7.5 ± 0.45	6.5 ± 0.21 5.5-9.0
	vi August 1968	5	26.4	35.2	6.7 ± 0.37	
TOTAL		54	29.1	44.2	5.0 ± 0.23	1.5-9.0
W	ii } summer	30	30.2	44.3	5.2 ± 0.36	1.5-9.0
RB	iv& v)					
W	i&iii } winter	24	26.1	41.3	4.7 ± 0.28	2.0-8.0
RB	vi)					

In October 1967 RB troop drank regularly at reservoir IV and slept in sleeping place No5 which was the nearest sleeping place to the water. During February 1968 RB troop was seen more often in sleeping place No.10 which was the nearest sleeping place to drinking site V. In October 1967 RB troop never visited drinking place No.V which was dry at that time but drank daily from drinking place No.IV, as did S troop. During the February 1968 observation period the position was reversed when drinking place IV was dry and both S and RB troops drank daily at drinking place V. Although RB troop then often passed through the feeding grounds at drinking place No.IV, it only spent about a quarter of an hour daily there in comparison to the two to six hours of the previous observation period. During a five day observation period in August 1968 both these drinking places had water. Cattle crowded at drinking place No.IV which was the reason why RB troop, although it visited this drinking place three times, refrained from drinking. On the two remaining days, RB troop drank at drinking place No.V. Since drinking place No.V was situated on the boundary of RB troop's home range it seemed reasonable to conclude that RB troop preferred to drink at drinking place No.IV. Apart from RB troop, two other troops also drank at drinking place No.V.

2.3. The day range and variation in day range activity.

RB troop travelled longer distances than did W troop and the day ranges of RB troop also showed a greater range of variability. (See table 13). No marked distinction between distances travelled during summer and winter periods was found. In arid areas such as South West Africa, baboons tended to cover greater distances daily and here Hall (1962a) once recorded a distance of 12 miles in contrast to forest living baboons that usually travelled one to one and a half

Table 14. Average maximum and minimum daily temperature and humidity recorded during summer and winter periods in the study area.

	SUMMER		WINTER	
	October- November 1967	January- February 1968	March- April 1968	July- August 1968
Average maximum daily temperature (°C)	29.7	32.9	28.8	23.8
Average minimum daily temperature (°C)	21.6	24.9	19.0	12.0
Highest day temperature (°C)	35.0	39.0	30.0	28.0
Lowest day temperature (°C)	18.0	21.0	15.0	6.0
Average minimum daily humidity (%)	44.0	43.0	42.0	43.0
Average maximum daily humidity (%)	65.0	70.0	60.0	69.0

miles per day (Rowell 1966). The average distance covered per day in Southern Africa and Kenya was three miles according to DeVore et al (1965) whereas the average distance recorded for troops in the study area was 5.2 miles per day.

Kummer (1968) found that the length of the day ranges of hamadryas baboons average 13.2 kilometers with a range between 9.8 and 19.2 kilometers.

The extent of day ranges for W and RB troops were plotted against temperature and humidity readings which were recorded during five of the observation periods (See table 14). In determining the relationship between maximum temperature, minimum humidity and distance travelled, the Pearson Product-Moment coefficient of correlation (Freund 1961) was applied. No correlation existed between minimum daily humidity and distance travelled ($r = -0.06$). However, the distance travelled by a troop decreased noticeably with the increase in daily temperature. (See fig. 15). Using the method of least squares, the slope of the line = - 1.5 intercept = 37.0 and the coefficient of correlation was significant ($r = 0.5$, $p < 0.01$).

Figure 16(a-f) demonstrates the relationship between the activities of the troop on its day range and the time of day. Horizontal lines represent troop movement and vertical lines indicate rest periods. However, individual movement has not been accounted for, thus a vertical line does not imply that all troop members are resting. A troop seldom acts as a unit and some individuals may lag behind to feed on a certain food item while the nucleus of the troop is resting. A vertical dotted line indicates that a troop is stationed at a drinking site while a horizontal dotted line represents drinking in the canal while the troop is on the move.

A troop leaves its sleeping place as soon as sufficient light is

available to allow the animal to investigate its immediate environment. At daybreak (04.50 hours in summer and 06.00 hours in winter) mature males and juveniles are the first to leave their sleeping place but they are often the last to move off on the day range. A troop usually leaves its sleeping place to congregate above the sleeping krantz^a where it lingers/while before departing on the day range at sunrise. However, progression time depends upon weather conditions as well as upon the troop's relations with other troops in the vicinity.

During the October 1967 observation period, RB troop always left the sleeping place after sunrise. This might be ascribed to the close proximity of the observer to the sleeping place.

Both W and RB troops started full progression to the feeding grounds later in winter than in summer months. The troop began foraging as soon as progression from the sleeping place commenced and continued to do so throughout the rest of the day. Feeding was less active during midday rest periods as well as when the troop approached the sleeping place.

RB troop's progression pace was much faster than W troop's, especially during the morning period. According to figure 16 RB troop proceeded rapidly without a rest on the first three miles in the morning, while W troop rested frequently during the early morning period. This might be due to W troop's relative isolation from other troops, the abundant water supplies close to its sleeping place or other reasons. RB troop usually arrived at the vicinity of the drinking site at 10.00 hours. All troop members drank water just before they evacuated the drinking site. The return journey was usually covered very quickly. If the troop was not under stress conditions due to the presence of other troops, then some individuals were observed to drink two or three times within 30 minutes.

Drinking place No.1 was situated very close to the sleeping places of RB troop. Should RB troop visit drinking place No.1 at midday, it had to walk a few hundred yards in contrast to the four miles it sometimes walked before reaching drinking sites No.IV or V. As shown in fig. 16 RB troop drank once and sometimes twice a day. On the few occasions when it visited drinking place No.I, one was at midday, twice late in the evening and once in the early morning. This drinking place was mostly visited in addition to a visit to a drinking place elsewhere. Less time was spent at drinking place No.I than at drinking places IV and V.

No definite movement pattern of the troop as a unit took place when W troop drank at midday except for the few occasions on which the troop moved around the southern foot of the kopje to the dam or canal on the western side of the kopje. Normally troop members gathered in small parties when they went to drink in the canal while the rest of the troop was congregated at the porridge rock or the rubbish dump. Thus, midday drinking was of a less social nature in this troop although sometimes during the early morning or late evening, when the troop started off on or returned from their day range, it progressed as a unit to the canal to drink. Such a situation, when members of W troop did not drink simultaneously, was only observed in the core area of the troop. As soon as W troop moved off to drinking places No.I, No.II, No.III or No.VI the troop moved as a unit. Visits to drinking places I, II & III however, were rare since they were situated on the border of W troop's home range.

W troop usually visited the agricultural fields on Hayoma before or during the harvest season; therefore the relation between time and movement of W troop did not correspond with the relation between time and movement of a more natural troop such as RB troop. When W troop

visited the orange orchards on Hayoma, it spent much time in the vicinity of the orchard to scan the area carefully before it entered. Thus home range utilization was considerably influenced by visits to these orchards. No such agricultural areas existed in RB troop's home range and the troop was independent of food sources supplied by humans. W troop was usually in the vicinity of its sleeping place three hours before sundown while RB troop arrived at its sleeping place more or less an hour before sunset. W troop twice arrived at an unfamiliar sleeping site early in the day. On both these occasions W troop arrived at 15.00 hours at the new sleeping place and first "investigated" it. This was never seen when the troop was in its "core area". Only on rare occasions, for example when chased by another troop, was a troop seen in its own sleeping place during the day. On one occasion GK troop was seen in sleeping place 8 at 11.00 hours where it sat for one hour before moving off. (GK troop used sleeping site 8 twice during the study period).

A graphical presentation of the major vegetation types in the Tshipise study area is presented in figure 4. An analysis of time spent in different vegetation areas of the home range of RB troop has been presented graphically in figure 17. This grid-hour system was prepared after Rowell (1966).

The home range of the troop was divided into quarter mile grid squares. The number of daylight hours spent by RB troop in each grid during the three observation periods (see table 13) was then plotted. Most of the troop's time was spent in the vicinity of sleeping and drinking places. This is obvious from the clusters of dots at these sites. Thus, apart from sleeping sites, RB troop spent most of its time in the vicinity of drinking places NoIV and V.

The small number of available drinking sites in the area often brought

troops together which resulted in lengthy troop interactions characterised by vocal battles and aggressive displays that were largely responsible for the amount of time spent at drinking places.

2.4. "Core areas."

Baboons, as do many other animal species, utilize some parts of their home ranges more intensively than others. Kaufmann (1962) as quoted by DeVore (1963) named this part the "core area" of the home range. He defined the core area as the area where the animal had access to food, water and a sleeping place. This definition was accepted and used as such by scientists who studied free-ranging primates (DeVore et al 1965, Jay 1963, Rowell 1966). DeVore (1963) added that if there was more than one such a core area then it was connected with pathways. A troop might concentrate its activity in one core area for weeks before it shifted to the next area. Jay (1965), Simonds (1965) and DeVore (1963) claimed that core areas of langurs, bonnet macaques and baboons seldom, if ever, overlapped.

The observer, however, found that this definition of a core area held true for only a few troops in the study area, for example W troop. For other troops such as RB troop, Carpenter's (1940 as quoted by Jewell 1966) "foci of activity", was a more appropriate denomination. RB troop had several such "activity areas", instead of one specific core area. These activity areas of adjacent troops overlapped extensively and the core area of one troop might well be the core area of the next troop. This statement was supported during observations on troop encounters where one troop actually displaced another from a sleeping or drinking site. However, since the term "core area" is familiar to all primatologists, it has also been applied in this study.

3. Conclusion

It was essential to follow troops throughout the day to obtain accurate data on the size of the home range and the distances travelled during the day ranges. This often proved exceedingly difficult in the broken veld habitat of the Tshipise study area. However, the sandy nature of the soil permitted the observer to follow the spoor of the baboons after he had lost sight of them in the dense Mopane bush. The two intensively studied troops, W and RB, survived under different conditions. Although W troop could be classified as a more "unnatural" troop because of its scavenging habits, it must be added that few troops in the Transvaal still survive where natural conditions prevail. Thus it was essential to do a home range study on W troop in order to obtain data on the distances that "unnatural" troops might travel. This knowledge was necessary in the population census where it was essential to know how far the different troops in the area might walk on their day ranges.

The day ranges of RB troop, a more "natural" troop, were adjusted to enable the troop to be at the drinking site during the midday period whereas W troop often went to the hotel at that time to collect scraps of porridge from members of the hotel staff.

In contrast to the results of other primatologists, it was concluded that from this study water was the most important factor which determined the day range activities of a baboon troop whereas intertroop relations and food proved to be of less importance than water. The presence of organic as well as inorganic matter in the water may well be the reason for the preference of certain drinking sites to others.

D. Intra- and intertroop relationships (and its influence) on day and home range utilization.

The behaviour and relations of individual members within a troop, as well as the behaviour and relations of interacting troops are exceedingly complex. The behaviour pattern that exist within and between troops should be described and analyzed in minute detail. Such thoroughness, however, is seldom possible for the field worker.

The object of this part of the study was to obtain data on the behaviour and social relations of the baboon troop with minimum interference in their normal pattern of activity. Studies were made on the manner in which troops were organized and integrated with special emphasis on such aspects as dominance, leadership and territorial behaviour.

Part of the study is based on data which were collected during six periods averaging ten days of intensive throughout the day observations including a preliminary study period of five days. These periods are the same as given in the part on home range studies. Although several troops were observed, the results of this study is mainly based on data collected on two specific troops.

1. Study method.

The study methods are described in the chapter on home range utilization.

During one of the six observation periods W troop was observed by two observers who always kept radio contact while they followed the troop on its day range.

Quantitative data were collected on the following subjects during the observation periods.

a) Intratroop relations.

i) Dominance

- ii) Initiation of movement.
 - iii) Distribution of individuals in a troop.
 - iv) Troop progression.
 - v) Subtrooping.
- b) Intertroop relations.

2. Results and Discussion.

It is difficult to discuss behavioural patterns under defined headings since information on concepts such as dominance is given throughout this discussion on behaviour.

2.1. Intratroop relations.

Baboons are social animals that live in well organised troops composed of individuals of all ages and sexes. The troop is the basic unit of the species. Sometimes solitary males occur but little is known about their conduct.

Washburn and DeVore (1963) and Lancaster et al (1965), rejected Sahlins' (1960) idea that sex is the main reason why primates live in social troops.

A baboon female is in estrus (sexual skin fully turgent) for a very short period and only then does she live in close consort with a dominant male. She is usually either pregnant or lactating. Yet the troop stays intact because troop life ensures the maximum protection for every member. The attraction that dominant males and new-born infants hold for other troop members acts to keep the group socially united. The new-born langur infant (Jay 1963) is the centre of attraction in the troop because of the interest that other female troop members display in the infant.

Troop life is organised around the dominance hierarchy of the adult

males. The ranking among adult males is usually clearly defined whereas the dominance hierarchy amongst the females seems to be more variable (Hall and DeVore 1965). Although life in a baboon troop can be described as peaceful, aggressive encounters are not uncommon although serious fighting seldom occurs.

2.1.1. Dominance and Leadership.

Dominance is a well known term used in nonhuman primate behaviour studies. Yet it remains a complex concept which is often poorly understood. Most nonhuman primate species live together in groups or troops. A social rank order or dominance hierarchy exists among all species of social monkeys for instance Japanese and Indian macaques (Carpenter 1964 with reference to his 1942 publication), hamadryas baboons, howler and spider monkeys (Chance 1961).

A baboon male can neither be called dominant nor the troop leader by merely judging his fighting potential or physical strength. Priority of access to food as a means of determining leadership or dominance hierarchy in a troop is not applicable to wild baboons since these animals are widely spaced when foraging. (Hall and DeVore 1965). However, Washburn and DeVore (1963) noticed that dominant males always have the resting place and feeding site of their choice. Dominant males usually occupy a position where the most and best food items are to be found in nature as well as on refuse dumps. Other troop members make way whenever a dominant male approaches, or a subordinate animal will occupy a position that is left vacant by a higher ranking animal.

Subordinate bonnet macaques (Simonds 1965) either give way or avoid looking at dominant animals. When a subordinate animal approaches a dominant animal, it lipsmacks and presents its hindquarters to the

dominant animal. Subordinate baboons usually present to the dominant males. Only on rare occasions did a dominant male present to another high ranking male. Since subordinate animals present more often to dominant males, the frequency of presentation is a criterium for dominance status determination. Presentation of the hindquarters has a second function which is sexually motivated. Fully estrus females present more often than do anestrus females and these fully swollen females present more to dominant than to subordinate males.

Dominant baboon males are groomed more frequently than other males (Washburn and DeVore 1963). Grooming is mainly a function of females and according to Bolwig (1959) this behaviour pattern is derived from a physiological background. However, according to Washburn and DeVore (1963) grooming serves to strengthen the social bond within the group. Furthermore, grooming has a biological function in that external parasites are removed from the skin and hair. Apart from the abovementioned features, dominance is further exhibited by certain other behavioural patterns. One or more dominant males may take part in some of these behavioural patterns, depending on the circumstances. Co-operation exists between dominant males when the welfare of the troop is threatened whereas aggressive behaviour patterns which involve the obtaining of leadership, is a battle between dominant males only.

The existence of a dominance hierarchy assures peace and order in the troop (Washburn and Devore 1963). Dominant males do not allow fights in the troop and quarrels are immediately stopped. Thus weaker animals are protected from danger outside as well as inside the troop. Kaufmann (1967) observed 98 fights between members of a rhesus monkey group of which 91 fights were broken up by high ranking males. Leaders of a Japanese monkey oikia (group) (Imanishi 1963) never quarrelled in their feeding grounds but they co-operated to control



Plate 7. Male Y, in the lead of W troop urges male ST, by means of visual communication and body movements, to follow him.

oikia members.

No evidence of clear cut dominance was found in W troop in the study area at Tshipise. Three large males, male Y, male B and male ST, each with his specific functions, co-operated to maintain leadership in the troop, to direct troop movement and to display vigilance behaviour which assured the safety of the troop (see plate 7). The function of each male will become clear during the following discussion.

Male Y: This male weighed about 60 lbs. and was in excellent condition. He was of a more robust physical stature and seemed to be much older than the other two dominant males. The absence of his canine teeth confirmed this belief. Y was always accompanied by mothers and their offspring. Mothers more often groomed him and preferred his company to that of the other two dominant males. The following field observation demonstrates this male's affection for infants.

Field Observations: 15/1/68 - 16.00 hours.

Male Y rests close to a mother who holds her infant. Three transition period infants and one eighteen months old yellow infant play in the close vicinity of male Y. An estrus female joins the party and settles down to groom Y. The yellow infant walks past the estrus female and climbs onto Y. The estrus female makes several attempts to intrude upon Y and the infant's game, by pulling the infant from Y. She succeeds in lifting the infant by his ear and dropping him onto the rocks below. The infant responds by screaming. Y is obviously irritated by the infant's screams. He grabs at the nearest animal who happens to be a mother with her infant. The estrus female chases the yellow infant into a tree from where he continues his screaming. Y runs to the tree where the estrus female is threatening the infant. Y ignores both the threatening female and the screaming infant and chases a

juvenile who happens to be in the close vicinity, into a tree. Y furiously breaks off branches in an attempts to reach the juvenile. Eventually the juvenile falls from the tree whereupon Y ceases his aggressive behaviour and returns to his resting place. The three infants as well as the yellow infant, followed by two mothers, return to Y where the infants resume their play activities.

Although dominant males often attack estrus females with whom they are in consortment it would appear from the above incident that Y could take the part of neither the estrus female nor the yellow infant. Male Y never attacked infants and rather displaced his aggressiveness onto other troop members. Such displaced aggressive behaviour patterns are often difficult to analyse.

On another occasion, at dusk, it was observed that Y went to sleep alone, accompanied only by mothers with infants. Another function of Y was to direct troop movement. This function will be discussed under "initiation of troop movement". Y usually took the lead when his troop suffered under conditions of stress as for instance when a troop entered the core area of another troop. Under such conditions males B and ST tended to occupy positions in the rear of the troop. Should W troop leave such a dangerous area, then B usually occupied a front position. Although Y was usually surrounded by females and their young during intertroop encounters, he betrayed no sign of fear during threatening circumstances as did B. Thus Y once led a second attack on troop A when all the males under leadership of male ST had retreated in the initial attack.

Male B displayed vigilance behaviour more often than any other member of W troop. Upon a warning bark from a troop member this male usually investigated the situation. When the observer approached the troop too closely, he was threatened by B. A threat display consisted of



Plate 8. An infant approaches male B, but it immediately returns to its mother as soon as visual contact was established between them. Apparently this male was not fond of handling infants.

jerky movements of the chest and head together with quick scratches with the hands on the ground or while in a tree he would shake the branches. Threat behaviour towards observers decreased after several observations. Jays whereupon "special vigilance behaviour" (Hall 1960) was taken over by another troop member, usually an old female.

In contrast to other dominant males, B was never observed to handle or carry an infant. On several occasions infants with friendly gestures tried to attract B's attention but they never succeeded since B always ignored them. (See plates 8+9).

Although he usually moved into a position where he had a wide panoramic view, it could not be said that he acted as a sentry as claimed by many authors (Roberts 1951, Steinhardt quoted by Shortridge 1934 and Stevenson Hamilton 1949). Vigilance behaviour as described by Hall (1960) was displayed by this male. During social flare-ups B chased any other animal in the troop but no single animal ever chased him. On rare occasions Y and ST, in a combined effort, chased B. The intolerant nature of this male is demonstrated by the following incident.

Field observation : 23/7/68. 12.20 hours.

12.20 W troop is approaching drinking site II on the border of its home range. All communicative grunts, that are typical amongst troop members in dense vegetation, stop. A female of another troop barks far away. All members of W troop grow very silent while they advance to the drinking site.

12.47 Male B climbs to a vantage point in a tree and orients to the south to where the female barked previously.

13.00 Y goes off to drink while B remains in the same position. The observer approaches B and he starts threatening the observer.

13.30 Four females sit in the vicinity of B. One female presents to

a mother with an infant whereupon the presenter is allowed to play with the infant. Another female, not yet fully swollen, presents to B but he ignores her. A black infant runs from his mother to B with ears flattened and lipsmacking. B looks over his shoulder at the infant without any facial expression. The infant immediately stops his approach and returns to his mother.

13.40 The partly swollen female again presents to B and remains thus standing in front of him. B aggressively grabs at the female who quickly jumps out of his way.

13.45 B follows Y and ST who have moved in the direction where the presence of the other troop has been indicated by the bark of a female. Under certain circumstances B led a part of W troop while Y, accompanied by the rest of the troop, had no visual or auditory contact with B. B, as Y and ST, had his specific functions during intertroop encounters. Herding was usually performed by B when two troops met (see troop interaction).

Male ST was the third dominant male of W troop. He stopped squabbles in the troop more often than did the other two dominant males. This behaviour pattern was different to that of B who very often was responsible for flare-ups in the troop. The control of sub-dominant males also seemed to be one of his functions. (See troop interaction). This male exceeded B in body weight. ST associated more often with Y than with B. Once, when W troop became divided, ST led one party back to the sleeping place.

ST's function during intratroop activities is demonstrated by the following field example.

Field Observation 24/7/68. 16.45 hours.

16.45 The troop rests at the foot of their regular sleeping kopje.

B accompanied by a few troop members, slowly ascends the kopje on his way to the main sleeping site.

17.00 A subdominant male C chases a female to where Y sits with mothers and infants. Y jumps up and tries to prevent C from chasing the female whereupon C chases Y. ST arrives on the scene and he chases C. Y sits down again and mothers and infants return to him.

17.20 Y walks off in the direction of the alternative (No.2) sleeping site. ST barks once, walks to Y and displaces Y, thus preventing Y from continuing his march to the alternative sleeping site.

17.25 ST follows B to the main sleeping site. Several animals join ST, and all follow male B to the sleeping site No.1. Y remains stationed with mothers and infants.

17.50 (Night fall). Y moves off to a sleeping site, accompanied by six mothers and their young well out of sight of B and ST.

This incident reveals how ST attempted to maintain the social bond in the troop. ST seems to keep the troop intact, since he was clearly upset by Y's intention to sleep elsewhere. It is difficult to draw conclusions from this incident on the behaviour of Y.

A further function of ST was revealed by observations on intertroop encounters. Y and B moved to the rear of the troop, accompanied by females and infants, while ST was at the vanquard of the troop. ST led the attack (as well as the retreat) of the troop. B herded the females with their young in the opposite direction of the approaching troop while ST and all male members of W troop, attacked the other troop (see intertroop encounters).

Although mothers with infants accompanied Y more than they did ST, he was often seen to pick up an infant. During aggressive conflicts between dominant males, Y and ST often picked up an infant when directly approached by B. With the infant in his arms, the male

concerned then ran off a few yards and sat down to groom the infant. B then immediately stopped his aggressive intentions directed to either ST or Y. Thus, by picking up an infant, ST and Y submitted themselves to B. Rowell (1967b) found that aggressive encounters between baboon males ended immediately if one of the males concerned should pick up an infant to cuddle it. Kummer (1967) found the same behaviour pattern in hamadryas baboons.

The following experiment was carried out to demonstrate the functions of the dominant males of W troop. An adult male baboon (male X) weighing 57 lbs., was captured from troop No.23 and released into W troop. Troop No.23's sleeping place was situated 12 miles to the west of W troop's main sleeping place.

30/10/68. Male X marked by means of a bright coloured neckband, is placed in a small holding cage near the alternative sleeping place of W troop. Troop W arrives in the late afternoon. A few subdominant males approach and sit down close to the cage, before they proceed to the sleeping place.

31/10/68.

09.08. W troop arrives at the cage. A young male starts barking from a nearby tree while orientating towards X. Several juveniles and subdominant males gather in a semi-circle around the cage.

09.19. The barking of subdominant males subsides upon Y's arrival.

09.22. Male ST walks to male Y. Both males look down at the cage.

B is far from the cage - he ignores the scene.

09.23. Female M, who was previously released from the same cage after she was captured from an adjacent troop, approaches the closest to the cage.

09.31. B barks twice. Y circles the cage halfway at about 30 yards.

B barks again from about 100 yards away.

09.38. B moves closer and stares at the cage.

09.39. B herds a few females away from the cage. Y moves out of sight, over the kopje. Many troop members follow Y. B sits on a vantage point above the cage. ST sits on a rock, 100 yards from the cage. All W troop members scream when a native approaches the cage to release X. X runs to B after his release. X stops as he is encircled by troop members. ST runs in a wide circle around this gathering and disappears from sight. B barks and herds females away from X who is still surrounded by about 20 animals.

09.53. ST and Y approach to sit about 15 yards from the group. ST barks violently. A small juvenile touches X. B barks far away to the right. Y approaches X to within 5 yards and stares at him. ST follows Y closely. X moves into the shelter of an overhanging rock. Y grabs and pushes a juvenile down a rock.

09.57. X moves. ST immediately barks and chases nearby troop members. Y barks. B barks continuously but he keeps out of sight. Other males also join in the barking.

10.05. Y and ST approaches within 5 yards from X. Meanwhile X turns his back to them, facing the overhang of rocks.

10.07. Y and ST displace X who moves into a narrow cleft.

10.09. ST moves out of sight and leaves Y alone with X.

10.11. Y chases other troop members in the vicinity of X, while the former barks violently. He runs past X and in doing so grabs at X. ST arrives on the scene and both ST and Y, accompanied by other males, sit watching X. Y grunts, picks up a yellow infant and holds it for a while.

From 10.32 to 10.59. Y sits alone with X.

10.59. ST joins Y. Both males approach X. ST make threatening gestures with his hand.

11.09. Y leaves while ST sits down on the exact spot near the cleft where Y sat previously.

From 11.20 to 11.39, only ST stays with X, and then he follows the rest of the troop.

12.32. All W troop members are now about 500 yards from X who remains quietly in his cleft. Y still keeps an eye on X from a distance.

14.10. The troop returns from its feeding grounds along the same route. ST passes X closely. B and a few troop members drink at the canal.

14.50. A large subdominant male, C, approaches X, while ST follows closely. The latter peers into the cleft. X immediately leaps out and runs in the opposite direction to the troop.

15.50. ST and C chase X for 200 yards whereupon ST turns round.

X stayed overnight in the home range of W troop and did not leave the next morning until W troop disappeared out of sight into its feeding grounds. X returned to his home range and was recaptured again 13 days later at the original trapping site in his home range.

From this field experiment the functions of the three dominant males became clear, and resemble their behaviour when they encountered other troops on their day ranges. Y and ST were more active in protecting troop members from the foreigner while B usually herded troop members away from the potential danger. The co-operation between males Y and ST was remarkable. Similar co-operative behavioural patterns were also observed between the dominant males of S troop.

Field observation: 9/10/67. 15.30 hours.

15.30. The observer awaits the departure of RB troop from drinking site No.IV. Troop S follows troop RB to within 800 yards.

Male D (a dominant male of S troop) is on his way to the drinking

trough which RB troop has just left. As the observer approaches the drinking site, male D retreats 100 yards. The observer also retreats to his original observation post whereupon D immediately returns to the drinking trough. Male E (the other dominant male of S troop) barks continuously from his observation post in a tree 100 yards from the drinking site, as he watches D's movements. (These are the first barks from dominant males on this observation day).

15.33. D proceeds to the trough and then returns to the peripheral members of his troop. E stops barking. D hesitates for a few seconds before quickly making his way past 20 animals to E. He climbs to an opposite branch of the tree where E sits. Communicative grunts are exchanged between the two males.

15.40. D descends the tree and walks back to the drinking site. A yellow infant follows him. E resumes his barking.

15.48. E follows D to the drinking site.

16.00 hours. The other troop members, in single file, follow the two dominant males to the drinking site.

Although this was the observer's first contact with S troop, it was quite obvious that two dominant males co-operated to control troop movement. E might have been nervous on account of either the observer's presence or the presence of RB troop which had just left the drinking site. Therefore it was concluded that E gave warning barks to D as soon as he left the protection of the dense vegetation to move across the open area to the drinking trough.

This observation corresponded with a field observation made by Kummer (1968) on hamadryas baboons. He described how two leader males exchanged contact grunts and glances before the one male moved off in a certain direction whereupon all members followed (p.125).

It is described elsewhere how two dominant males of T troop chased

their troop members past the capture cages after several of their troop members had been captured. This behaviour corresponded with behaviour patterns that Kawamura (1963) described. In an attempt to trap Japanese monkeys, a predominant male chased and even attacked members to prevent them from entering these cages.

It was attempted to capture members of troops Nos. 31 and 32 during a control operation with a large cage and some smaller cages. The smaller cages were set against the sides of the large cage. The aim was to close all the cage doors simultaneously with a string that was operated from a hide-out near the cages.

When members of the troop ventured into the smaller cages, a dominant male rushed into the large cage, threw himself against the mesh and barked continuously, whereupon his troop members rushed out of the small cages. Thus the dominant male prevented his troop from being captured. It became evident during the course of the study that dominant males fulfilled the following functions:-

- 1) Dominant males co-operate in the protection and maintenance of their troops.
- 2) A period of consortment between a dominant male and female is established during the receptive stage of the female's menstrual cycle. Thus the dominant males are responsible for impregnation which brings about a selective breeding mechanism.
- 3) Aggressive behaviour of dominant males confirms the social bond in a troop. In open country a firm social bond amongst ground-dwelling baboons is necessary for self-defence. Aggression also places all individuals in the troop in relative positions. A flare-up occurred when an individual left its subscribed position to take advantage of the position of another.

These conclusions on the role of the dominant male are in accordance

with the findings of Hall and DeVore (1965)

A social hierarchy is claimed to exist between adult males of sub-human primate groups by various authors (DeVore op cit, Sade 1967, Mason 1961). Altmann(1959) however found no indication of a dominance hierarchy amongst howler monkeys. Forest-living species do not possess such clearcut social structures; e.g. the chimpanzee (Reynolds et al, 1965). These groups are smaller and in some cases the existence of a group is only temporary. This results in reduced contact between individuals and consequently less aggression occurs. Aggression among members of KMWA troop (21 members) was seldom observed in contrast to W troop whose numbers exceeded 60.

The social rank of a macaque in the dominance hierarchy is determined by the social rank of its mother. This rank which is established in his early life persists into adulthood (Kawai 1958 and Kawamura 1958 as quoted by Sade 1967). However, this has not yet been confirmed for baboons.

Dominance ranks amongst common langurs (Jay 1965) remained fairly stable and the dominant male whose rank was uncontested by other group members was less active in dominance interactions than other less dominant males.

The dominance status of a male baboon does not depend solely on its fighting ability. The writer agrees with Hall and DeVore (1965) who maintained that a male's dominance status was also dependent upon his ability to gain the support of another male during aggressive interactions.

No evidence of a stable dominance hierarchy between females in W troop was found. Females in estrus or females in the company of dominant males were dominant over other females. The social status of female baboons was difficult to determine (Hall and DeVore 1965)

since it changed with the females' estrus condition (Washburn et al 1961). Jay (1965) reported the same for the female common langur of North India.

2.1.2. Initiation of troop movement.

Goodall (1965), who studied chimpanzees in the Gombe Stream Nature Reserve in Tanzania, accepted a chimpanzee to be a leader if he initiated group movement. Even if he was not in the lead, such a male regulated the speed and direction of group movement.

Male Y, of Tshipise's W troop, usually initiated and regulated troop movement. On some occasions all troop movement came to an end after Y had stopped, even when Y followed at the rear of the troop while the two other dominant males might be in the lead. Y's control of troop movement is illustrated by the two following incidents.

Field observation: 15/7/68. 15.00 hours.

15.00. A part of W troop is on the move with male B in the lead, and male Y, with mothers and infants, in the rear. Y suddenly stops and sits down. B also stops and continuously looks in Y's direction. Y, however, does not respond to B's facial expressions. Only after Y has resumed the journey, does the rest of the troop move again with B still in the lead.

Field observation: 17/7/68. 15.30 hours.

15.30. Y, surrounded by mothers and infants, rests in the shelter of a tree in the near vicinity of A troop's sleeping place. B approaches Y and displaces some juveniles near Y. After sitting for a few minutes, B walks to Y who jumps up and runs to the rest of the troop. (B thus displaced Y). The mothers with infants follow Y whereupon

troop movement takes place.

Thus B forced Y to initiate troop movement, when it seemed that Y had had no intention of doing so. Such displacement behaviour is a valuable criterium for dominance status determination (the displaced animal submits to the displacer). However, in the above example it is obvious that B was uneasy on account of his troop being in another troop's core area.

Observations on other troops suggested the same troop movement initiation behaviour patterns as illustrated by the following example.

Field observation: 22/8/68. 06.30 hours.

06.30. Troop KMWA is detected near its sleeping place. The observer moves away from the troop, about 20 animals follow him. The observer sits down, the animals venture closer, some bark. An estrus female approaches within ten yards of the observer. Upon seeing this, a dominant male (A) charges and chases all the animals in the vicinity of the observer.

07.35. The observer walks to C (another dominant male) who sits 200 yards from the rest of the troop, accompanied by mothers and infants.

07.40. A proceeds on the day range but C and the females stay behind.

07.42. A starts to bark continuously and chases some troop members in the direction of C. Eventually A chases C around for about five minutes. Females and infants scream every time the chase goes through their party.

07.48. The chase stops and A returns to the 20 animals where he came from. C with mothers and infants follow A.

From the above example it is clear that movement initiation does not

always takes place peacefully. One dominant male may be forced by another to move in a direction by threatening him.

Sometimes males combine to initiate troop movement, e.g. one may start the movement which is soon taken over by another one in the lead, as indicated by the following example.

Field observation. 17/1/68. 11.00 hours.

11.00. W troop is at the back of the hotel at Tshipise where the baboons feed on scraps of porridge left behind by native hotel assistants.

11.02. Y walks in the direction of the canal.

11.03. B follows Y. As B overtakes Y, the latter stops and allows B to pass. Females and infants follow with Y in the rear. As Y passes a mother and infant, the youngster jumps onto his back and rides for a few yards. Y stops and looks over his shoulder whereupon the infant jumps off. The troop progresses to the canal.

Thus Y initiated the movement to the canal which was taken over by B in the lead.

"Herding", a behaviour pattern that has not been previously described in the literature, is a method of forcing a troop to turn in a specific direction. Dominant males, and on rare occasions sub-dominant males, are always responsible for this action. The first impression of this behaviour pattern is one of a disordered social flare-up. The males who do the chasing bark continuously whilst they run to and fro amongst troop members. The object of such behaviour is to prevent troop movement in a certain direction and indicate the preferred new direction. Dominant males of T troop became aware of danger when their numbers were heavily reduced by continuous trapping. These animals chased the remainder of the troop away from their preferred daily route to ensure that the troop did not revisit the capture cages. Constant

barking and herding by dominant males took place before leaving their sleeping place in the morning.

Two adult males of Q troop chased all their troop members away from the capture cages by constant barking and running between the cages for similar reasons.

Troop movement by means of herding is also applied during intertroop encounters.

Females sometimes initiated troop movement. Such behaviour was observed especially when the troop was uncertain of its next move, e.g. when the troop had to pass close to the observer to proceed on its usual day range. A female, usually fully swollen and in consort with a dominant male, would then walk in a certain direction. The female urged the dominant male to follow her by looking back at him while she lip-smacked with ears flattened. If the male responded by following her, the rest of the troop would normally respond. It often happened that the male ignored the female.

2.1.3. Distribution of individuals within the troop in relation to time, activity and social status.

In primate groups every individual occupies a certain space and every one has a relative position in the social hierarchy. (Hediger 1961, Carpenter 1942 and 1952, Calhoun 1962 as quoted by Ripley 1967)

Imanishi (1963), Kaufmann (1967), Washburn and DeVore (1963) and Hall and DeVore (1965) reported that the centre of groups of Japanese monkeys, rhesus macaques and baboons respectively consisted of females with their offsprings and leader males. The peripheral part of the group consisted of subdominant males which kept a watchful eye while the group was on the move. Kaufmann (1967) claimed that a definite correlation between social status and spacing existed in the group.

Dominant males sat alone less often than lower ranking males.

Rowell (1966) did not observe the same organisation in forest living baboon troops in Uganda as that described for baboons in Kenya and South Africa (Hall and DeVore 1965). Rowell suggested that this might be due to the shorter distances the forest baboon travelled in contrast to the long distances travelled by baboons which inhabited relatively open country.

During the current field study it was found that family groups (dominant males with mothers and their infants) occupied a "drifting" position within the troop, and were found in the centre as well as on the periphery of the troop depending on circumstances such as time of day, stress conditions, etc.

The family group might lead the troop and occupy this leading position for several hours.

Field observation: 25/7/67. (T=30°C) 13.00 hours.

13.00. W troop sits under trees close to the canal. Y is asleep.

13.20. Y is still asleep. Two pairs of females are grooming one another. Three infants are asleep, one on his side, the other two on their appendages folded in. Six other animals are sleeping on their sides.

14.00. Y awakens and gets up. He slowly ascends the kopje. General movement among troop members are noticeable.

15.30. The two dominant males, Y and ST, are in company with five mothers and their infants. Three mothers are carrying their infants. They move slowly to the south while foraging.

15.45. The rest of the troop follows the family unit at a distance.

16.35. Y still occupies the leading position of the troop. He is accompanied by four mothers, six infants and two small juveniles.



Plate 10. A section of W troop progresses in single-file along a dirt track road.

17.00. Y returns to the alternative sleeping place along the same route that he has followed from 15.30 hours. He is still accompanied by four mothers (two carrying infants), six infants and two small juveniles. The rest of the troop follows in a widely scattered formation.

17.15. Some troop members forage near the alternative sleeping place while others are grooming one another.

Troop formation in this study area was not as clearly defined as that described by Hall and DeVore (1965). Parties consisting of dominant males and lactating females wandered at random between other members of the progressing troop. Thus far it is not possible to ascertain whether the same females followed the same males every day as was found for hamadryas baboons. (Kummer and Kurt 1965 and Kummer 1968) The distribution of members in a troop depended upon the time of day and the environment the troop inhabited at that time. Males in consort with estrus females probably sleep together, since they enter the sleeping place simultaneously. Copulation calls were often heard during the night. The distance between sleeping animals depended upon the availability of sleeping ledges.

When a troop was not influenced by another troop's presence, it left the sleeping site either in a scattered formation or in single-file rows. When the latter progression type was used, it was usually due to geological obstacles which did not allow scattered formation progression. Distances between animals were reduced to a minimum when walking in single file.

Single-file progression (see plate 10) was often practiced by W troop in its core area when speedy movement occurred. This progression type was usually practiced when the troop moved from the sleeping place to the rocks at the hotel where they waited for scraps of porridge.



Plate 11. While foraging in the Mopane veld members of

W troop spread over a large area.

Thorns (*Tribulus terrestris*) that covered the ground surface around the kopje also forced W troop to move in single file along trodden footpaths. When the animals approached their sleeping place, they followed one another closely in small footpaths which they used exclusively. These footpaths connected the favourite spots within W troop's core area.

This progression type was also observed when RB troop moved across rocky areas at the foot of the Soutpansberg mountains. The troop split into three files of approximately equal length and kept this formation over a distance of about a three-quarter of a mile.

Upon reaching its feeding grounds, the members dispersed to cover a large area.

Field observation: 2/4/ 7. (During the day).

In the morning W troop spreads out to cover a distance of 150 yards when it moves off to the feeding site 500 yards from the sleeping site. Troop members spread to cover a distance of 452 yards after they have reached the feeding grounds.

The distances between foraging troop members also depend upon the availability of food and the vegetation type. While on the move communicative grunts are given by all members. Baboons usually spread over wide areas when feeding or resting (see plate 11). This is in contrast to some other primate species e.g. mountain gorilla groups in the Albert National Park (Schaller and Emlen 1964) are very cohesive and group members seldom drift apart. The diameter of feeding or resting groups is usually 200 feet or less.

The spatial distribution of a langur troop varied from 30 to 50 meters when resting or feeding (Sugiyama 1965). Howler monkey groups also tend to stay close to one another during the day while spider monkeys

scatter widely when on their day range. At night, however, they gather together. (Carpenter 1963, his 1942 publication). The patas monkey Erythrocebus patas of Uganda (Hall 1965 and 1967), also a terrestrial primate, does not sleep in clusters since individuals are dispersed up to 400 yards in trees during the night.

Baboons sleep in clusters and distances between troop members decrease considerably under stress conditions. Subtroops or all troop members keep close together when the troop approaches its sleeping place in the late afternoon. The interaction between troops at sleeping places causes tension and distances between members are reduced accordingly. During day time, however, part of a troop sometimes wanders off on its own with the result that troop members become separated over distances of as much as three quarters of a mile. These subtroops may exist for a few hours up to a few days.

2.1.4. Subtrooping.

The problem of troop genesis in subhuman primates is an interesting research topic. In this respect, personnel of the Japanese monkey centre, observers in India and research workers on Cayo Santiago's rhesus monkey colony did a great deal of work on macaques. To understand the process of troop genesis, behavioural characteristics of subtrooping must be studied in detail.

Splitting of rhesus monkey groups occurs frequently. Southwick et al (1965) claimed that specific individuals of the rhesus groups in North India associated regularly to form subgroups.

Struhsaker (1967) found that vervet monkey groups in the Amboseli Reserve divided into sleeping subgroups before sunset. After sunrise they regrouped again. The distances between these subgroups changed every night. The greatest linear distance over which groups were

spread was estimated to be 750 yards. Subgroups were not formed at random but reflected definite social preferences.

Groups of Cercocebus, Cercopithecus, Papio and Colobus species divided during the night (Lumsden 1951). Hadow (1963) stated that large African redtail monkey (Cercopithecus ascanius schmidti) bands seen before sunset might be aggregations of smaller family parties.

Among hamadryas baboons, each male had his own females with young which accompanied him throughout the day. If a female lagged behind her unit, the male immediately returned to her, bit her in the neck and thereby she was forced to follow. (Kummer et al 1963, Kummer et al 1965 and Kummer 1968).

Zuckerman (1932) stated that chacma baboon packs split into small parties when they reached their sleeping places.

Subtrooping as found in subhuman primates was studied by several field workers. However, most scientists spent only one year on field observations. A study of troop genesis is a prolonged project and conclusions on the subject cannot be reached within one year.

The formation, duration and stability of subtroops within RB and W troops will be demonstrated below.

2.1.4.1. Temporarily strayed animals.

Single animals.

No solitary males lived in the home ranges of the troops in the Tshipise area. However, single marauding males were often recorded in the population study area. These solitary males were permanently separated from their troops, in contrast to the females who had temporarily lost contact with their troops and who actively tried to regain contact with them.

Field observation: 16/1/68. 05.00 hours.

05.00. A female of W troop sits alone with her dead infant on top of the main sleeping place. She grooms the infant intensively.

05.16. The female looks around while she utters continuous communicative calls.

05.18. The female starts moving in the direction in which W troop has disappeared earlier, but does not succeed in regaining contact with the troop.

05.32. The female continues her communication calls although she does not provoke any response from other troop members. She sits down at intervals to groom her dead infant.

05.35. The female finally catches up with her troop.

"Abnormal" subtroops (formed by two or more animals).

Once four juveniles of W troop wandered 500 yards from the rest of the troop to scan the area behind the hotel for left-over porridge. Here they were surprised by the observer who came upon them unexpectedly. They all fled back to W troop.

No communication, visual or auditory, was maintained between them and the troop.

Y and a female were once on the rubbish dump all on their own while the rest of W troop was in the orange orchard at Hayoma, about one mile from the rubbish dump. The two animals showed no signs of uneasiness. On a few occasions Y, accompanied by mothers and infants, slept in the alternative sleeping place, while the rest of W troop occupied the main site.

Excluding subtroops formed at night, these "abnormally" composed subtroops returned to the main body of the troop within a few minutes or hours.

"Normal subtroops".

W troop divided at any time of the day with an almost daily occurrence in the early morning when a group of about twenty animals visited the area behind the hotel where they received the left-over porridge from the hotel staff. However, visual contact was usually kept between these animals and the rest of the troop. W troop twice divided into two subtroops while in their feeding grounds. The one subtroop under the leadership of ST, consisted of 35 individuals. Upon approaching the kopje the behaviour of the subtroop guided by Y and B reflected much more confidence than did the subtroop of ST. No visual or auditory communication existed between the two subtroops.

The following example demonstrates the formation of subtroops in W troop.

Field observation: 22/7/68. 07.18 hours.

07.18. B and ST leave for the feeding grounds with two-thirds of W troop. The rest of the troop, which includes eleven mothers and infants, stays behind with Y.

07.24. Some of the mothers with Y give constant communication calls. However, the two subtroops are now separated by half a mile and geological obstacles prevent further contact.

07.31. Y follows the other subtroop. Two subdominant males walk on either side and a little ahead of Y, while the mothers follow in single file.

07.39. Y sits down. The rest of his subtroop continues. When all subtroop members have passed Y, he hastily follows up right into the leading position.

07.47. Visual contact is re-established between the two subtroops.

Y sits down while members of his subtroop run to join the other subtroop halfway. Excited calls and chatters are uttered while dominance demonstrations, such as mounting, are performed after the re-union of the two parties.

The division in this case may be called "abnormal", since 84% of the mothers in the troop were in one subtroop.

RB troop also divided regularly into subtroops, especially during the first observation period. However, visual or auditory contact was always kept during the hours of separation.

Field observation: 16/10/67. 11.00 hours.

11.00. Eighteen individuals of RB troop, including three infants, stray from the main subtroop to forage high along the mountain above the drinking place. No vocal communication is heard.

15.00. The main subtroop leaves for its sleeping place and although half a mile apart, the small subtroop follows immediately. It was obvious from the behaviour of the small subtroop that visual contact had been kept.

Field observation: 20/10/67. 07.45 hours.

07.45. RB troop divided into two subtroops.

08.30. The main subtroop is foraging in its usual feeding grounds. The small subtroop is foraging three quarters of a mile away from the main subtroop. A male of the main subtroop barks and is immediately answered by barks from the small subtroop.

08.32. The wandering subtroop returns to the main troop.

This example demonstrates auditory contact between subtroops and the fact that troop members identify each other in this way.

Both RB and W troops were observed to divide sometimes at dusk after

the troop had arrived at its sleeping place. W troop usually slept in one sleeping place but subtrooping took place on some nights when either the main and alternative, or main and additional, sleeping places were used.

Night observations on W troop were carried out by two observers who went to the alternative sleeping place with the troop. The troop was very dissatisfied with the observers' presence and most troop members shifted to the main sleeping place.

On two occasions thirty-five members of RB troop slept in sleeping place No.4 while the other eighteen members slept in No.3 and No.5 respectively.

W and RB troops once divided into subtroops during the night. They could only maintain auditory contact, since geographical obstacles prevented visual contact. The two subtroops usually congregated the next morning after auditory contact had been made very early in the morning.

Subtroops that existed for periods longer than one night might have represented a step in the formation of a new troop.

2.1.5. Troop genesis.

One evening eleven individuals (2 males, 2 females, 7 young animals) of RB troop arrived at sleeping place No.8. This sleeping place was already occupied by KMO troop. At this stage the rest of RB troop was in sleeping place No.10. Since only 35 baboons were counted in RB troop the previous morning, this suggested that this small party have been on its own for at least two days. Some months later sixteen baboons were reported to range on their own. However, the incident was not investigated.

Troop O, in the population study area, was recorded to consist of 94

Table 15. Troops subjected to control operations.

Troop No.	Original troop size	Remaining numbers	Sex and age classes of the remaining members			
			♂	♀	Juv.	Inf.
14	37	7	1	2	2	2
15	34	5	1	?	?	?
20	22	3	1	2	-	-
21	25	4	1	1	1	1
22	29	8	2	1	4	1
23	32	4	1	2	-	1
69	21	7	1	2	2	1
TOTAL 7	200	38	8	10	9	6

individuals on various occasions.

Afterwards two troops of 73 and 21 individuals respectively were often recorded. It was not clear whether these two troops were independent troops that fed together during several of the encounters, or whether it was one troop at the stage of dividing into two troops.

Data on troop genesis were collected during experimental control operations on baboons in the Messina district. Of all the troops that were subjected to control, the numbers of seven troops were drastically reduced. Table 15 demonstrates the reduction in troop sizes.

In all these troops at least one dominant or adult male (50 lb +) was released. Some animals were marked with brightly coloured collars.

Troop 69 was followed for four days after its numbers had been reduced from 21 to six. The females of this troop persisted in uttering communication calls throughout the day. The troop operated in only a small area, mainly the "core area" of the original home range and they avoided other troops in the neighbourhood. After four months, they still occupied the same area. They did not join any of the adjacent troops. Troops 22 and 23 occupied the same area and sleeping hill. They were the only two troops to use this particular kopje. After their numbers had been reduced, these troops grew very secretive. They remained individual troops but were seen close together on one occasion.

In troop 21 only two adults, one male and one female, were left. Yet they remained a stable troop that still utilized its original home range four months later.

All these controlled troops will be kept under constant observation for the next two years.

New troops can only originate if a big troop divides into two or more smaller troops.

Large baboon troops (DeVore and Washburn 1964) of 77, 88 and 94

individuals respectively, frequently sub-divided in the Nairobi and Amboseli Parks. In such cases the mothers with infants were found in the same subgroup as the large adult males. These subdivisions lasted only part of the day and the troop re-united before nightfall. Another type of splitting was found in a troop of 103 members where the troop divided into two troops of 66 and 37 members each. Each subtroop had a centre (females + young + dominant males), a periphery and the characteristics of a normal independent troop. DeVore et al i.c. therefore, suggested that this subdividing might have been the first stages in the formation of new troops. Large troops became unstable and divisions occurred within a troop of 70 or more individuals. If these divisions contained normal sex- age class distribution, then a new troop might be formed.

However, during the present study it was often found that a few males accompanied by most of the lactating females formed a subtroop which sometimes slept separate from the rest of the troop. These subtroops which did not contained normal sex- and age classes are believed to be the origin of a new troop.

Farmers who have lived for years in the study area claimed that during troop divisions, one subtroop will contain all the infants while the other subtroop consists only of adult baboons.

Koford (1963) reported that in 1956 to 1958, two bands of rhesus monkeys inhabited Cayo Santiago. One band split continuously until in 1962, six bands existed.

No evidence of the congregation of one subtroop with another troop or subtroop is given in the literature. Carpenter (1964 with reference to his 1934 study, Carpenter 1965, Carpenter 1964 with reference to his 1942 study) stated that howler monkey clans sometimes split into two subgroups, thus forming two new clans, or some individuals of a clan

might become associated with a complementary (a male who lived outside a clan) male, thus also forming a new clan.

The following incident may be an additional indication of how baboon troop ontogeny takes place and is also one explanation of the variation in troop size that was often observed.

Field observation: 28/2/68 - Morning.

The observer follows RB troop from its sleeping place to drinking place No.V. RB as well as S troop remain in the vicinity of the drinking site from 11.30 hours to 14.00 hours. Troop members (excluding dominant males) of the two troops intermingle at the drinking site.

14.00. A troop sets off to the west, the direction that RB troop usually follows. The observer, under the impression that this troop is RB troop, follows.

16.00. A member of the troop that remained at the waterhole, barks. Immediately the troop that has been followed, divides into two sub-troops. One subtroop returns to the drinking place while the other "subtroop" continues its journey.

The observer then realised that he had followed S troop instead of RB troop and that members of RB troop had wandered off for one mile with S troop. However, these strayed members returned when a dominant male of their troop barked. Copulation calls were heard while RB's subtroop was with S troop but the observer could not ascertain whether copulation took place between members of S and RB troops. According to DeVore (1963) gibbons, howler monkeys, langurs, baboons and macaques lived in "closed societies" which did not accept strangers. Rowell (1966) found that baboon males moved freely from one troop to the next in the Uganda study area. In contrast to her data

the writer found that a male baboon, introduced into W troop, was chased away by W troop's males. Females, however, that were introduced into W troop, were adopted by the troop (Saayman 1968)

Troop ontogeny and troop permeability may prove interesting subjects for future studies. However, these subjects will require long term study periods since a new troop for instance, may take several years to establish.

3. Intertroop relationships.

Observations on encounters between baboon troops in the study area proceeded from 03.00 hours, throughout the day, until 19.00 hours. Troop encounters were recorded in the early morning while the troops were in their sleeping places. During the day less contact was made between troops and fewer troops were involved in such encounters. Encounters between baboon troops are very complicated and to analyse all the different behaviour patterns involved, proves to be almost impossible. Either the observer was not close enough to witness all aspects of the behaviour, or he was unable to observe both troops simultaneously. Sometimes the behaviour of only that troop which was followed throughout the day was observed because of the possibility of scaring the other troop, especially if the latter was not accustomed to the presence of the observer.

In dense vegetation where visibility was poor, the observer became aware of another troop's presence when the troop under observation behaved in the following manner: All troop members suddenly grew silent. Individuals ascended trees and all oriented in the same direction. Flare-ups might occur within the troop. The other troop usually betrayed its presence by the occurrence of counter flare-ups and the accompanying noises.

Table 16. The frequency of RB and W troops' encounters with other troops.

Number of encounters at different sites.

<u>Sleeping sites</u>	<u>Drinking sites</u>	<u>Feeding grounds</u>	<u>Total</u>
RB - KMO (28)	-	RB - KMO (2)	30
RB - KMWA (2)	-	RB - KMWA (1)	3
RB - GK (8)	RB - GK (1)	RB - GK (1)	10
RB - KMW (26)	RB - KMW (0)	RB - KMW (1)	27
RB - K (7)	-	-	7
RB - S (1)	RB - S (11)	RB - S (1)	13
RB - 60's (1)	-	-	1
RB - W (5)	-	RB - W (1)	6+
RB - A (2)	-	-	2
RB - ? (1)	RB - ? (5)	RB - ? (3)	9
Total	81	17	108
W - A (2)	W - A (2)	-	4
W - KMW (4)	W - KMW (3)	-	7
W - KMO (1)	-	-	1
W - K (0)	W - K (1)	-	1
W - RB (5)	-	W - RB (1)	6+
W - ? (2)	W - ? (1)	-	3
Total	14	7	22

+ Same data

3.1. The area and frequency of contact between troops.

A total of 180 encounters between nine troops have been witnessed during study periods. Hall (1962) witnessed six encounters when baboon groups came into visual contact with one another, once in the Cape Peninsula and five times in South West Africa. All the encounters were peaceful. Troops RB and W were studied in detail during throughout the day observations. Except in a few cases¹, all the troops that came in contact with troops RB and W at sleeping and drinking sites and in feeding groups, were identified. Troop RB encountered as many as five different troops on its day range while W troop, at most, contacted three different troops daily. Table 16 demonstrates the frequency with which RB and W troops made contact with other troops at sleeping and drinking sites and in their feeding grounds.

When the total number of contacts between different troops were compared it became clear that W troop was relatively isolated from other troops.

3.1.1. Encounters at sleeping sites.

The distribution of sleeping sites is demonstrated in figure 3. Troops frequently made contact at specific sleeping sites that were close together. Auditory contact between these troops was likely due to the linear distribution of the sleeping sites on the southern slopes of the ridges. The sleeping places in the Tshipise kopje were an exception. It was not due to a limited number of sleeping places that troop encounters occurred at these sites since occasionally only a single troop was found in one of five adjacent sleeping places. Of all the encounters between RB troop and other troops, 75% took place at sleeping sites. As many as five troops sometimes interacted at sleeping sites.

Table 17. The frequency of encounters between KMW, KMO, S, GK, A and K troops.

Troop		Number of contacts	Troops	Number of contacts
KMW	K	4		
	A	1		
	GK	3	→ K	
	S	1		
	KMO	25	→	
			GK	4
			A	1
			K	6

3.1.2. Encounters at drinking sites.

Troops usually did not arrive simultaneously at drinking sites, thus limiting the frequency of contact at these sites. Accordingly, troop RB contacted only one troop regularly at its regular drinking site. However, encounters at drinking sites lasted longer than those at sleeping sites. (See figure 17). Troops utilizing adjacent sleeping sites might use different drinking sites since waterholes were distributed over the whole area.

3.1.3. Encounters in the feeding area.

Encounters between troops seldom occurred in their feeding grounds. This might be ascribed to the interactions between troops at their sleeping sites in the early morning acting as a spacing mechanism amongst troops. Troops also had stereotyped patterns of home range utilization which contributed to minimize contact between troops. RB troop made contact with six troops in its feeding area whereas W troop met with only one troop in its feeding grounds.

Apart from encounters that W and RB troops made with other troops, table 17 gives data on encounters between other troops in feeding grounds and at drinking and sleeping sites.

These troops interacted with troops in the study area as well as with troops on the border of the study area. The frequency of these latter contacts is unknown.

3.2. The nature of intertroop encounters.

Encounters between troops varied from early morning non-aggressive identification calls (See figure 18) to heavy aggressive attacks and counter-attacks. Early morning troop identification calls were given by all

Table 18. The frequency of morning and evening calls of four interacting troops.

Date 8/68	RB		KMW		KMO		K	
	am	pm	am	pm	am	pm	am	pm
16		X	X		X		X	
17		X				X		
18	X		X	X	X		X	
19	X		X		X			
20	X	X			X	X		
21	X	X			X	X		
22		X				X		
23	X				X	X		
24	X				X	X	X	X
25	X					X	X	
26	X		X		X	X	X	
Total 11 days	8	5	4	1	8	8	5	1

The ratio of morning to evening calls + 5:3

the troops studied. Although W troop was fairly isolated from other troops, an occasional bark was often given by dominant males at the sleeping place. RB troop, two miles from W troop's sleeping site often answered immediately with a counter call. In some cases these answer calls were only given after several minutes had elapsed.

After an eleven day study period on four interacting troops (RB, KMO, KMW and K), it was determined that evening calls were given less frequently than early morning calls. (See table 18).

Although troops KMW and K did not bark in the morning or evening for several days, they were nevertheless aware of the presence of other troops in their close vicinity. The barks of dominant males were a most important behaviour pattern and could be heard over a distance of three miles, depending on factors such as the time of day and the presence of geological obstacles.

In a random sample taken from five troops (figure 18) on the time when dominant males gave their first barks in the early morning, it was found that these barks were given from 03.10 hours to 07.30 hours. It was presumed that barks given at 03.10 hours were abnormal and were probably evoked by the presence of predators in the sleeping site. Adjacent troops immediately answered these early calls. The mean time when these barks were given, was at 05.40 hours, more or less 50 minutes before sunrise. Troop K, the smallest troop in the study area, only barked after 05.40 hours. Table 18 demonstrates the frequency of morning barks during the eleven-day period.

Apart from barks, sounds made by other troop members were good indicators of the behaviour patterns involved in encounters between troops. During eleven days (22 morning and evening periods - the same as those on table 18), the different sounds made by baboons during encounters in the morning or evening when in, or close to the sleeping sites,

were noted.

Whenever possible, sounds accompanying specific behaviour patterns, were checked by visual evidence.

The different behaviour patterns involved in figure 19a+b consists of the following:

i) Double phase barks by males. (fig. 19. a. i. + 19. b. i.)

Of this behaviour pattern Hall (1960) wrote:

"...the double-barking aggressive behaviour in situations apparently of high intensity threat, are all distinctive of the large males and thus contrast sharply with behaviour of any other class of animal within the group."

Barking by dominant males is seldom heard during the day and is only given under stress conditions as described by Hall loc cit.

ii) Barks by females (fig. 19. a. ii).

These barks can be confused with those of subadult males, but during the course of the study, it was noted that females usually barked just after the dominant male or males had barked. Females utter a one-phase bark instead of the typical double phase bark of the male. A "special vigilance" (Hall 1960) function is being performed by these barking females.

iii) Copulation calls. (Fig. 19. a. iii + 19. b. ii).

While the act of copulation lasts, "...the animals grunt quickly with increasing strength. After parting the female's grunts usually merge into a short intermittent roar." (Bolwig 1959). The female pulls away in quick pace from the male.

These calls are readily distinguishable from other sounds heard in

a troop.

iv. Grunts. (fig. 19. a. iv).

When foraging, the chacma baboon gives "rhythmical grunts" which hold the family together (Andrew 1963). However, it was also found during this study that dominant males often gave these grunts during inter-troop encounters, especially when copulation calls or individual screams were given. These grunts seemed to have a soothing effect on other troop members.

v. Deep chesty roars. (fig. 19. a. v.)

"Deep chesty grunts or roars" by dominant males were recorded under stress conditions. These roars have not been described in the literature and were usually given during or after "social flare-ups" as well as during or after herding events.

vi. "Social flare-up or shambles" (fig. 19. a. vi).

When a dispute arose between two troop members with several other troop members joining in the quarrel with loud vocalizations such as shrieks and barks, such an event was defined as a social flare-up or shambles. Such a flare-up usually ended in a chase between the rivals. Dominant males occasionally joined in these flare-ups and the barks given by them during these events were not included in the construction of figure 19. a. i.

vii. Individual screams. (fig. 19. a. vii. + b. iii).

Individual shrieks or screams were recorded when an animal gave a single series of intense vocalization. According to Andrew (1963) calls of this intensity were evoked by threat from a superior and could be regarded as a fear response.

viii. Herding away, (fig. 19. a. viii).

Herding has been described elsewhere in this report. No description of such a behaviour pattern was found in the literature. Social flare-ups usually preceded this act which was generally performed by one or two dominant males. If herding was performed in a direction away from the adjacent troop it was presumed that the troop thereby indicated its subordination.

ix. Herding to. (fig. 19. a. ix).

If herding was performed in the direction of an adjacent troop then it indicated the troop's dominance over the adjacent troop. Herding in the direction of an adjacent troop often preceded the displacement of the adjacent troop.

The frequency with which these different behaviour patterns occurred during intertroop encounters gave an indication of the degree of stress between interacting troops. (See fig. 19. a. + b.)

According to fig. 19. a. i. the dominant male of troop KMO barked more frequently during the different observation periods than did dominant males of any other troop. The number of bark sessions were also more for troop KMO (fig. 19. b. i.). The number of females in troop RB exceeded that of troop KMO by far, yet males of troop KMO copulated more during troop encounters than did males of troop RB. (fig. 19. a. iii.). In 12 (=55% fig. 19. a. iii) of 22 encounter periods, 30 copulation calls (fig. 19. b. ii.) were heard from troop KMO during the eleven day observation period, whereas 6 copulation calls were heard during six (=22% fig. 19. a. iii) of the 22 encounters from RB troop. Thus only one copulation call per encounter was recorded for troop RB, while as many as eight were recorded for troop KMO. Since RB troop, at that stage, had four fully swollen females and KMO troop only two,

it seemed quite reasonable to conclude that stress conditions caused the increased copulatory activities of KMO troop.

The highest frequency of occurrence of these behaviour patterns, as demonstrated in fig. 19. a. iv. + v. was found in KMO troop and the lowest frequency in RB troop. Since these behaviour patterns were usually found amongst baboons under stress conditions, it was concluded that dominant males of KMO troop were either nervous in the presence of another troop or very aggressive. However, since fig. 19. a. viii. + ix. demonstrated the tendency of KMO troop's dominant male to herd troop members away from other troops, it was concluded that the dominant males of KMO troop were not aggressive but nervous on account of another troop's presence. RB troop's dominant males tended to herd troop members in the direction of the other troop thereby revealing the aggressive nature of these dominant males. Herding was not observed in troop KMW during troop encounters. Tension in KMO troop when in contact with other troops is also illustrated in fig. 19. b. iii. since almost twice as many screams were recorded for this troop when compared with RB troop.

Troops KMW and K participated less in vocal battles with other troops (fig. 19. a. + b.). Vocal displays of dominant males were a most important factor by which their troops were identified, protected and placed in a certain position in the social hierarchy existing between troops. The dominant males of KMW troop only occasionally joined in vocal displays with neighbouring troops since they usually avoided other troops. The smallest troop in the study area, troop K, tended to remain neutral during intertroop encounters even though KMO and RB troops often displaced it thereby influencing its home range utilization.

Koford (1963) who studied rhesus monkeys on Cayo Santiago stated that a social status existed between bands resembling that between individuals in a band. Thus, if a band was at a feeding place and a superior band approached, the subordinate band moved quietly away. However, if the band was hungry and reluctant to leave, the dominant males of the superior band would shake three branches or jump up and down in threat displays. The subordinate band might return these threat displays but such a spectacular "display" seldom came to anything since the subordinate band usually withdrew. Larger bands were usually superior to smaller bands, but a band's status also depended upon the relative status of its leader male. A band did not actually have to see the leader male of a superior band to acknowledge its superiority. Carpenter (1963a) stated that fights occurred in the wild when a gibbon group split into two subgroups and one of the subgroups had to find itself a new territory. The dominance of one group over another was dependent upon the relative dominance of the leader males of the two interacting groups.

Imanishi (1963) reported that conflicts between oikiae (groups) of Japanese macaques were seldom observed since the dominance - subordinate relations between the two oikiae were usually established and the subordinate oikiae kept clear of the dominant oikiae.

The following antagonistic behaviour patterns of baboon troops were used to determine the dominance hierarchy between troops. Three of these criteria were the same as those used by Ripley (1967) for Gray langur intertroop encounters.

i. "Displacement - One troop yields its position to another troop" (Ripley loc cit); for instance, when one troop is forced to leave a site such as sleeping and drinking places.

Table 19. The dominance hierarchy amongst troops.

Subordinate troop	Dominant troop									Total
	A	K	GK	RB	ST	KMO	KMW	KMWA	W	
A									1	1
K			1	5		4				10
GK				2						2
RB			2		3					5
ST				8						8
KMO			1	8			1		1	11
KMW				8		1			1	10
KMWA	1			3						4
W	2			1			1	1		5
Total	3	0	4	35	3	5	2	1	3	56

ii. "Chase - A continuous displacement through space". (Ripley loc cit).

iii. Hesitation - One troop waits or follows slowly at a distance while the other troop is at or approaches a drinking site.

iv. Withdrawal - A troop withdraws from a position of its own accord when it sights another troop.

v. Expulsion - Two troops contact passively at a drinking site but one troop is eventually expelled from the site.

vi. "Fight - An attack that is countered." (Ripley loc cit).

The dominance relationships between baboon troops are demonstrated in table 19. Aggressive encounters amount to 31% of the 180 intertroop encounters. Dominant and subordinate troops were easily distinguished during these encounters.

Because RB troop was studied intensively, more data are available for this troop. Troop RB dominated the other troops in the study area in the following degrees of intensity.

- i) Completely - troops K, KMO, KMW and KMWA.
- ii) Partly - S troop
- iii) Equally - GK troop
- iv) Uncertain - A and W troops.

Troop K, the second smallest troop in the study area, was dominated by all the troops with which it made contact. From the behaviour patterns that occurred in KMO troop (fig. 19. a. + b.) it is concluded that KMW troop is only partly dominant over KMO troop.

Southwick (1962) as quoted by Ripley (1967) stated that two types of

intergroup relations existed between rhesus groups, passive and antagonistic.

Most encounters between gorilla groups (Schaller 1963 and 1965) were peaceful and some members of two different groups intermingled freely. Bolwig (1959) stated that violent fights sometimes occurred between baboon troops. Hall (1962) on the contrary, found no sign of hostility between baboon groups in the Cape Peninsula Nature Reserve and South West Africa. Hall (1965) further stated that a small group would drive off a large one that might trespass on its home range. However, he did not know whether baboons would actually attack one another.

Washburn et al (1961) found that baboon troops in the Amboseli Park drank together at the same waterhole in peace. Rowell (1966) observed two neighbouring baboon troops in Uganda that associated quite often and some animals of the one troop moved freely to and fro between the two troops. Rowell suggested that these troops were in the slow process of subdividing.

Passive as well as antagonistic intertroop encounters were observed in the study area.

3.2.1. Passive troop encounters.

Passive troop encounters took place between troops which were accustomed to one another. In such cases visual contact was made between troops sometimes accompanied by vocalization. The two following field observations are examples of passive encounters.

Field observation. 11/10/67. 09.00 hours.

09.00. RB troop arrives at the feeding place where it usually forages before setting off to drinking place No.IV.

09.30. S troop also arrives at the feeding place but remains 200 yards from RB troop. Apart from visual communication, no other communication takes place.

10.05. RB troop slowly proceeds in a southwesterly direction while S troop remains at the same place.

10.30. RB troop ascends the mountain behind the drinking place while S troop still lingers in the same area.

Field observation. 22/8/68. 17.45 hours.

17.45. KMO troop sits on top of its sleeping rock at sleeping place No.8

17.49. K troop comes to a halt 300 yards from sleeping place No.8 and troop members stare at KMO troop. All social activities in K troop cease and all animals keep silent. The dominant male is in the centre of the troop K with the rest of the troop gathered closely around him.

17.56. The dominant male of K troop suddenly moves off to No.10 sleeping place, next to / ^{No.8} sleeping place. His troop follows him closely and after they have retreated about 200 yards, a male of K troop barks once. In both these encounters the arriving troop remained at a distance from the other troop which occupied a certain position. Usually only visual contact was made during these encounters and no threat displays took place.

3.2.2. Antagonistic encounters.

3.2.2.1. Negative antagonistic encounters.

No clearcut distinction exists between positive and negative antagonistic encounters. For this report intertroop encounters were classified as negatively antagonistic if one troop was forced to move from a certain spot upon the approach of another troop. No chasing or attacking

took place between individuals of the two troops. The following field examples are of the negative antagonistic type.

Field observations. 26/3/68. 16.00 hours.

16.00. GK troop forages at the foot of No.10 sleeping place. RB is on its way to No.10 sleeping place.

16.40. RB troop reaches the open Marula veld at the foot of the sleeping place. Visual contact is made between GK and RB troops. Immediately some members of GK troop hurry off in the opposite direction of RB troop.

16.45. RB troop continues moving to the sleeping place in a rest-proceed-rest manner in spite of the fact that GK troop obstructs the way.

16.49. RB troop is 100 yards from GK troop. The baboons sit down and stare at GK troop.

16.51. Two young males, followed by three adult males and two dominant males of GK troop walk in the direction of RB troop. Members of RB troop, including one estrus female, several adult males and one dominant male move to the approaching members of GK troop.

16.52. One of the young males of GK troop retreats to his troop. He is followed by all the members of the exploring party. The dominant male of RB troop pursues the retreating animals for a few yards. The dominant male is followed by the estrus female and another male.

16.53. A juvenile male of GK troop suddenly rushes past the approaching party of RB troop to a juvenile male of RB troop where he adopts an upright posture with his ears flattened and his eyebrows lifted, lip-smacking to indicate his friendly intentions. The two juveniles embrace for a few seconds while standing on their hindlegs whereupon

the wandering juvenile returns hastily to his troop. Members of both troops observe this incident passively.

16.55. GK troop retreats a few yards until it is about 50 yards from the sleeping place. The dominant male of RB troop also moves closer to the sleeping place.

17.02. A dominant male of GK troop suddenly moves off to the right. Twenty-four individuals follow him. The rest of GK troop moves off to the left.

17.04. A mother of GK troop with an infant runs after the dominant male who is walking to the right but when she jumps from one rock to another she falls and screams. The dominant male barks and starts herding his troop over the ridges to No.8 sleeping place, about 300 yards from No.10 sleeping place where the other subtroop joins them at 18.00 hours.

17.05. The dominant male of RB troop watches this procession attentively and then climbs into the sleeping place.

Thus RB troop gradually displaced GK troop without chasing or displaying threat gestures.

Field observation. 22/8/68. 08.05 hours.

08.05. KMO troop is in No.8 sleeping place. RB troop appears from the bush, 40 yards from KMO troop. Visual contact is established between the two troops and members of KMO troop shift their positions. A female of RB troop barks once.

08.06. Four males of KMO troop, including a dominant male, move in-between their troop and RB troop. Seven members of KMO troop, including a female, move closer to RB troop. The wandering party stares at RB troop. The dominant male of the party herds the rest of the party away from RB troop.

08.09. The rest of KMO troop follows the dominant male. Members of RB troop run a few yards after KMO troop. A juvenile male of KMO troop climbs into a tree to watch RB troop.

08.25. RB troop proceeds on its normal day range.

In both these incidents one troop displaced the other troop from a position that the latter had occupied. However, these troops were familiar with one another and not intolerant of one another. One troop directly influenced the day range of the other troop.

RB troop displaced KMO troop during another negative antagonistic encounter after which the course of KMO troop's day range was completely altered.

3.2.2.2. Positive antagonistic encounters.

All encounters where one or both troops threatened, chased or attacked the other interacting troop were classified as a positive antagonistic encounter. The following example was recorded on the farm Jeanette, Messina district. Control operations by means of capturing cages were being carried out at this stage.

Field observation. 25/8/67. 18.00 hours.

18.00. J troop is at the cages but on the approach of JE troop they run off. A male of J troop who has been consuming bait from a cage, does not succeed in finding the cage door in his panic. Three members of JE troop rush into the cage and grab at the unfortunate male. Although they pull him by the hair, they do not attempt to bite him. The male jumps to and fro in his efforts to reach the cage door. All this takes place with loud vocalization. Eventually the male succeeds in escaping and follows his troop.

It is interesting to note that although the males of JE troop threatened and even pulled the male's hair, they did not actually attack. Interaction of a positive antagonistic type can best be demonstrated by the following field example where W troop left their usual home range to enter A sleeping place.

Field observation. 17/8/68. 14.50 hours (Stoltz and Saayman in preparation).

14.50. W troop arrives at the foot of A sleeping place about three miles from their habitual resting site.

15.35. The troop investigates the sleeping place.

15.57. Male B climbs to a vantage point in the sleeping place. (This is the typical behaviour of a troop at its sleeping site).

16.35. Four or five sub-dominant males climb a Baobab tree and orient in a SSW direction. Baboons in the sleeping place also look in that direction. A bark is heard far out in the veld.

16.47. A sub-dominant male in the Baobab tree displays threat gestures.

16.49. B climbs on top of a cliff and then charges at a few animals. B herds mothers and infants over the top of the hill to the north.

16.51. ST takes position below the sub-dominant males in the Baobab tree. B is still herding the mothers and infants to the rear of the troop. Y joins B and females with infants at the rear of the troop.

16.54. ST with about 15 animals, including many small male juveniles, runs down into the veld.

16.58. The barks and roars of big male baboons together with squeals and screams of other members are heard from the veld and reverberate through the krantzes.

17.04. ST's male group retreats in the direction of the herded females of W troop. A group of 21 males of A troop gallops up the hill,

close on the heels of the retreating males of W troop.

17.10. W troop retreats 200 yards from A sleeping place. Troop A occupies A sleeping place. The two troops watch one another.

17.50. It grows dark. Y moves back to A sleeping place. His troop follows him in single file. Y and S are in the front and B in the rear.

18.03. W troop occupies a part of A sleeping place without any further incidents. Some members of the two troops are only 20 feet apart. It was interesting to note that males Y and B did not partake in the attack in spite of their physical dominance over other males of W troop. Schenkel et al 1967 found that dominant males of Colobus monkeys behaved in the same way. The leader of a rhesus monkey band (Koford 1963) also kept in the background during conflicts with other bands. If the other band was superior then the dominant male was the first to retreat.

3.3. Territoriality.

Carpenter (1964, referring to his 1958 publication) stated that territoriality was as much part of the primate's behaviour as of any other vertebrate. DeVore (1963), stated that primate groups were kept apart, not by fighting or aggression, but by daily routines which each group followed within its own range. Pitelka (1959) as quoted by DeVore loc. cit. stated that the importance of territoriality did not lie in the defence of that area, but to the extent to which that area was exploited.

Bourlière (1965) and Colhoun (1963) referred to the territory of an animal as that part of the home range which the occupant staked out and defended, (Defence was referred to as fights between individuals of the same species). Struhsaker (1967) stated that vervet monkey

groups of the Amboseli Reserve defended a well defined territory against adjacent troops. Rhesus monkey groups (Southwich et al 1965) of North India had well defined home ranges but since they did not defend these ranges consistently against intruders, they could not be designated as territories.

Jay (1965) quoted Pitelka (1959) who stated that territories were not maintained by fighting amongst the higher primates but by the exclusive occupation of the area, or by expression of a certain behaviour pattern, fighting excluded. Jay concluded that only in this sense could the term territory be applied to free-ranging primate groups. According to Carpenter (1964 his 1940 study) gibbons occupied a region which they defended against other groups. Although these territories overlapped, groups abstained from entering another's territory while the owner group occupied it. The gibbon defended his territory either by actual fighting or vocalization which acted as a substitute for fighting.

During his field studies on howler monkeys, Carpenter (1965) found that a group did not defend a specific boundary or territory but rather the specific spot in the home range which they occupied at that given moment.

This is also the case for baboons in the study area but it must be added that such a defended spot would be in a troop's core area rather than on the boundary of the troop's home range.

Ripley (1967) claimed that the gray langur of Ceylon had definite territories since groups actively engaged in aggressive fighting. Baboon troops in the study area displayed very much the same behaviour patterns as described for langurs. However, since the core areas of the baboon troops in the study area overlapped extensively, these areas were not defended as they should be if the definition of a territory

was accepted. W troop was chased on five occasions from areas usually inhabited by A and KMW troops respectively. On the other hand, W troop once chased KMW troop from a sleeping place that the latter usually occupied. All this took place on the boundary of W troop's home range. When in a strange area, a troop left the "strange" sleeping place without much noise immediately after there was sufficient light in the early morning. For example, when W troop slept in the sleeping place of another troop, it left the sleeping place at first light. This was an indication of the tension existing in the troop when sleeping outside its habitual core areas.

Haddow (1963) quoted Gilmore (1943) who found that captured cebus monkeys which were released quite a distance from their territory, returned to it. The greatest distance recorded for such a return was six kilometers. Gilmore thus concluded that cebus monkeys must be territorial. The same result was obtained when a captured male baboon in the study area was released into W troop. The male walked approximately ten miles back to his troop.

In conclusion it can be said that the available literature on the territoriality of primates suggests that there is variation in the territorial behaviour of the different species. If the results of their studies were proof enough for Ripley and Gilmore to describe gray langurs and cebus monkeys respectively as territorial, then the writer must classify the baboon as territorially minded.

3.4. Intertroop relations and their influence on population cohesion.

From the preceding discussions on intertroop encounters, it became clear that intertroop relationships influenced the utilization of the home ranges which ⁱⁿ turn contributed to the organization of the population as a whole. Troops which were several miles apart did not

directly effect one another. However, adjacent troops might have an influence on one another; thus, depending on the population density, a continual chain reaction might be in operation affecting the behaviour of all the neighbouring troops in a certain population.

Interaction between neighbouring baboon troops started at daybreak when males of one troop barked. Males of adjoining troops responded immediately. Thus troops were informed of the position and identity of one another. After some time the observer was also able to distinguish between the barks of dominant males of some of the different troops.

Ripley (1967) stated that spacing between higher primate groups was obtained by intergroup avoidance rather than by defensive fighting. Groups adjusted their daily movement in order to avoid one another by visual or auditory means. Early morning broadcasts were given by gibbons (Carpenter 1964 his study 1940), howler monkeys (Altmann 1959) and langurs (Ripley 1967).

The complex pattern of troop interaction was responsible for the direction of a troop's daily movements. The co-existence of baboon troops in a baboon population was partly regulated by daily interactions between troops. Some baboon troops in the study area did not move off unless another troop within their field of vision moved off first. Dominant troops were entitled to choose a direction for their day range. The course followed by a troop was often changed upon the barks of a dominant troop. For example, RB troop once changed course when the animals heard the bark of a dominant male from GK troop, although it was impossible to make visual contact with it. KMWA troop often directed its course in another direction when a dominant male of RB troop barked.

Interactions between troops at drinking places influenced the troop's home range utilization considerably, since troops were sometimes either forced to leave the drinking place of their choice on account of another troop's presence, or to spend hours in the vicinity of the drinking place while they waited for another troop to evacuate the drinking site. This is clearly shown by the following example.

Field observation. 24/7/68. 11.00 hours.

11.00. W troop is on its way to drinking place No.II at the border of W troop's home range. Three hundred yards from the drinking site W troop becomes aware of A troop's presence at the drinking site. W troop stops.

12.30. A troop is still at the drinking site. W troop suddenly leaves for drinking place No.VI in its home range.

Drinking place No.VI was situated three-quarters of a mile from drinking place No.II. W troop covered the distance in 20 minutes, an unusually short period for the distance covered.

During the June 1967 observation period, RB and S troops spent as many as five hours in the vicinity of drinking place No.IV. (see figure 17). Both troops used the same path to the water but only one troop occupied the drinking site at a time. Food was abundant at this site but the delayed progression to the water was due to the interaction between the troops rather than to the availability of food.

Encounters between troops at sleeping sites forced troops to adopt a habit of slow approach to sleeping sites, which could be compared to the time-consuming approach to a drinking site. A baboon troop displayed a remarkable attitude when it approached a sleeping place.

During the approach males, in particular, kept a watchful eye on the

sleeping place for any troop that might have occupied the sleeping place earlier. This might also explain why troops returned to their sleeping place up to two hours before sundown.

Intertroop encounters led to the organisation of the baboon population in the study area.

Conclusion.

In this chapter the behaviour of the baboon expressed by intra- as well as intertroop relations, has been described and discussed. Baboons live in highly organised troops which include adult males and females, subadults, juveniles and infants. A dominance hierarchy which is well marked amongst males and less pronounced in females, exists in the troop. The troop is led by a dominant male or males that combine to form a dominance hierarchy with special functions such as the protection of troop members and the determination of the troop's daily routine as well as its response to other troops. These dominant males are tolerant of other males in the troop.

Some troops meet peacefully whilst others behave antagonistically.

However, adjoining troops meet one another frequently and may even have originated from the same troop, thus making their acquaintance a longstanding one. Peaceful interactions can thus be expected between these two troops. However, the opposite is true when two less acquainted troops meet suddenly. In contrast to the findings of Hall (1961) and DeVore and Washburn (1963), the writer observed several antagonistic encounters amongst baboon troops.

This study proved that behaviour of baboons is highly adaptable and generalisations based on certain observations made in one area, may lead to inaccurate conclusions.

V. CONCLUSION.

This population study contributes to the knowledge of the behaviour and ecology of the chacma baboon, Papio ursinus. This primate, being a terrestrial animal, occupies a larger home range than primate species adapted to a more arboreal living, for example the vervet monkey, Cercopithecus aethiops. A more pronounced dominance hierarchy prevails among members of a terrestrial group. Males are morphologically more adapted for the defence of their groups than the males of arboreal species, where group members respond to danger merely by taking refuge in trees.

When compared to areas studied thus far in the Transvaal, it seems that baboons are heavily populated in the area behind the Soutpansberg where they are claimed to prey upon livestock and raid cultivated crops. However, the nature of this problem is often overemphasized by local people. The mere destruction of this animal is not to be recommended and may lead to an unbalanced ecosystem. Attention will be given in future studies to the role of the baboon in nature as far as food preferences within the ecosystem are concerned. It proved an easy task to control the baboon during the experimental control project which is partly included in this study. If the baboon is so great an agricultural pest as farmers claim, then they would have succeeded long ago in the complete control of the animal had they chosen to do so. Only a very small number of farmers suffer from baboon raids on their livestock and crops. If farmers combine efforts to control baboons, they can destroy this animal completely in river, broken veld and open bushveld habitats within a very short period. Since the social bonds in a baboon troop are strong due to their terrestrial adaptation, social behaviour patterns within the troop

are exceedingly complicated and this makes the animal an interesting and fascinating subject of research. Many anecdotes are retold by local people, most of which have little or no relation to the facts. However, recent studies on this animal revealed some complex behaviour patterns which will undoubtedly serve as a basis for future studies. The knowledge accumulated in recent studies of monkeys and apes will definitely contribute to the study of the evolution of the human primate.

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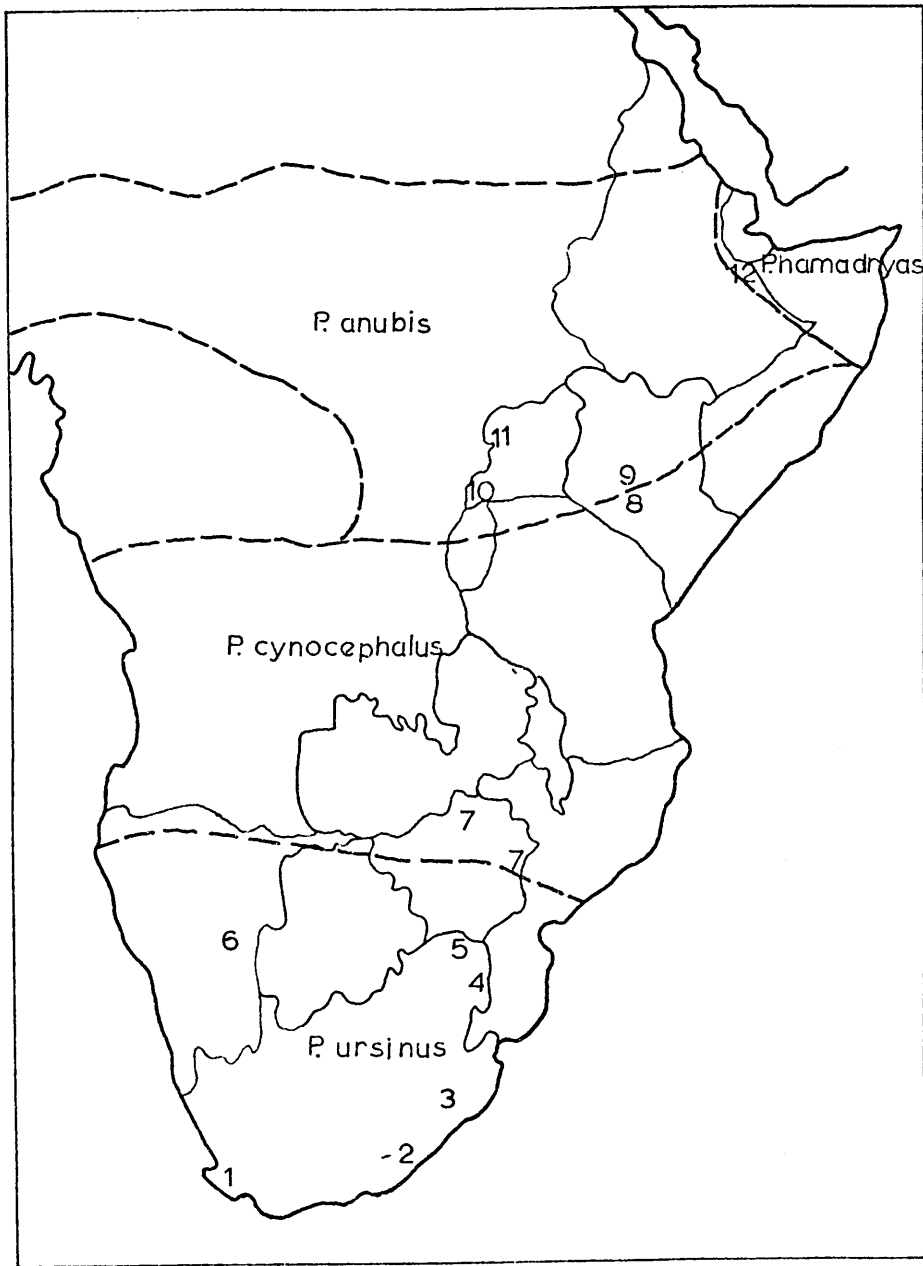
I am thankful to Prof. F.C. Eloff, head of the Zoology dept. of the University of Pretoria, under whose guidance this study was completed. I also wish to thank Dr. G.S. Saayman of the Mammal Research Institute of the University of Pretoria for his support during the preparation of this manuscript. He provided me with some rare photographs and also accompanied me during several observation days during the field study.

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I also wish to thank my wife who accompanied me throughout this study period, for her assistance and encouragement.

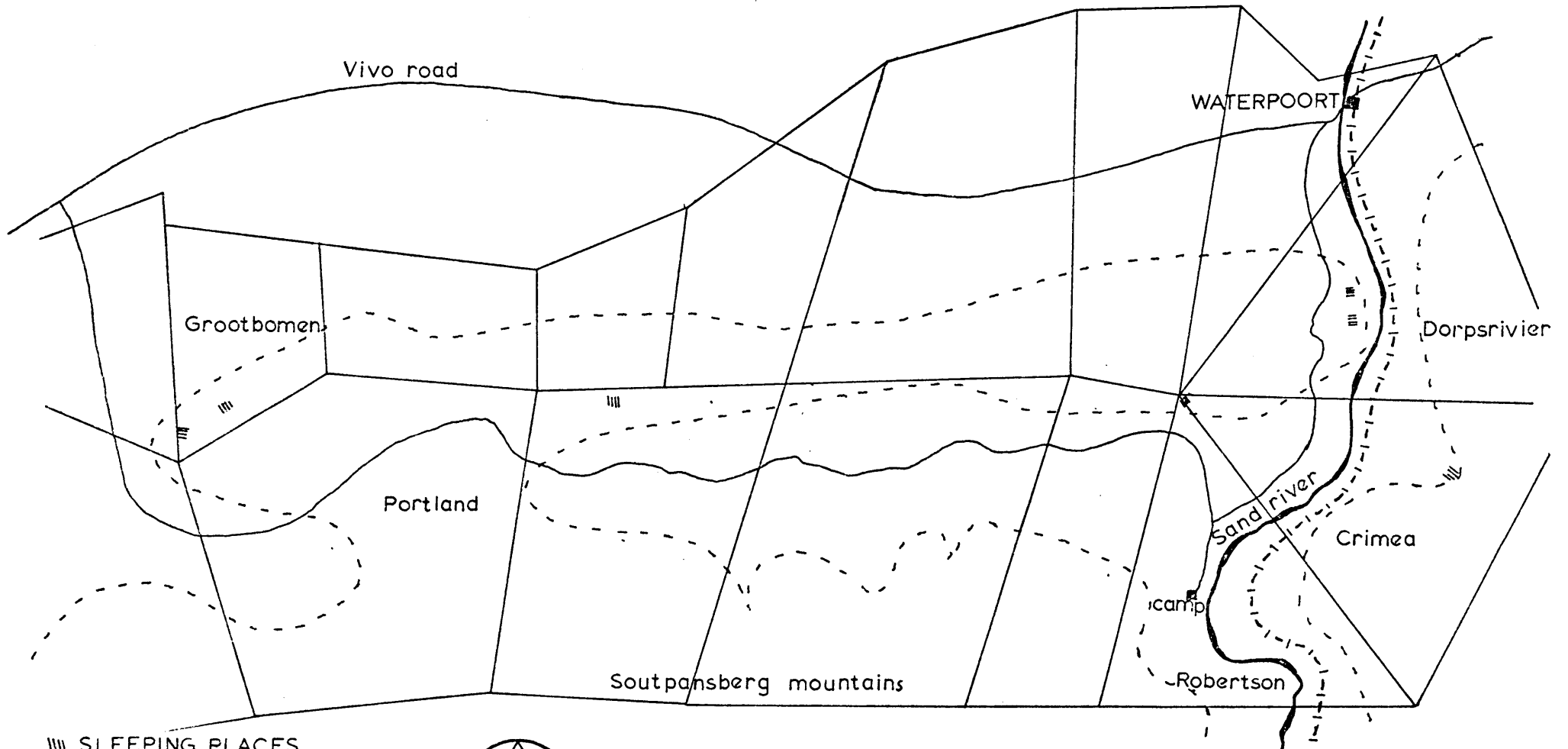
Figure 1. The location of recent baboon field study areas.

Distribution of species after Napier and Napier (1967)



- 1 Cape Peninsula
- 2 Eastern Cape Province
- 3 Drakensberg Mountains
- 4 Kruger National Park
- 5 Northern Transvaal
- 6 South West Africa
- 7 Rhodesia
- 8 Amboseli Reserve, Kenya
- 9 Nairobi Park, Kenya
- 10 Queen Elizabeth N.P., Uganda
- 11 Murchison Falls, Uganda
- 12 Eastern Ethiopia

Figure 2. The Waterpoort experimental census area.



||| SLEEPING PLACES

1 mile SCALE

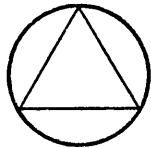
- - - RAILROAD LINE

— ROAD

~ RIVER

- - - MOUNTAIN

— FARM BOUNDARY



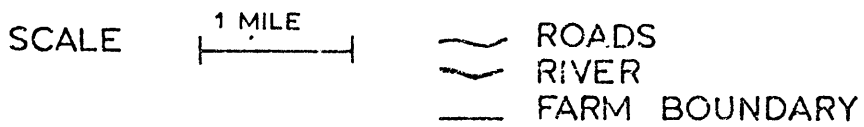
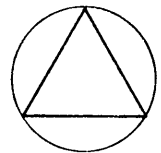
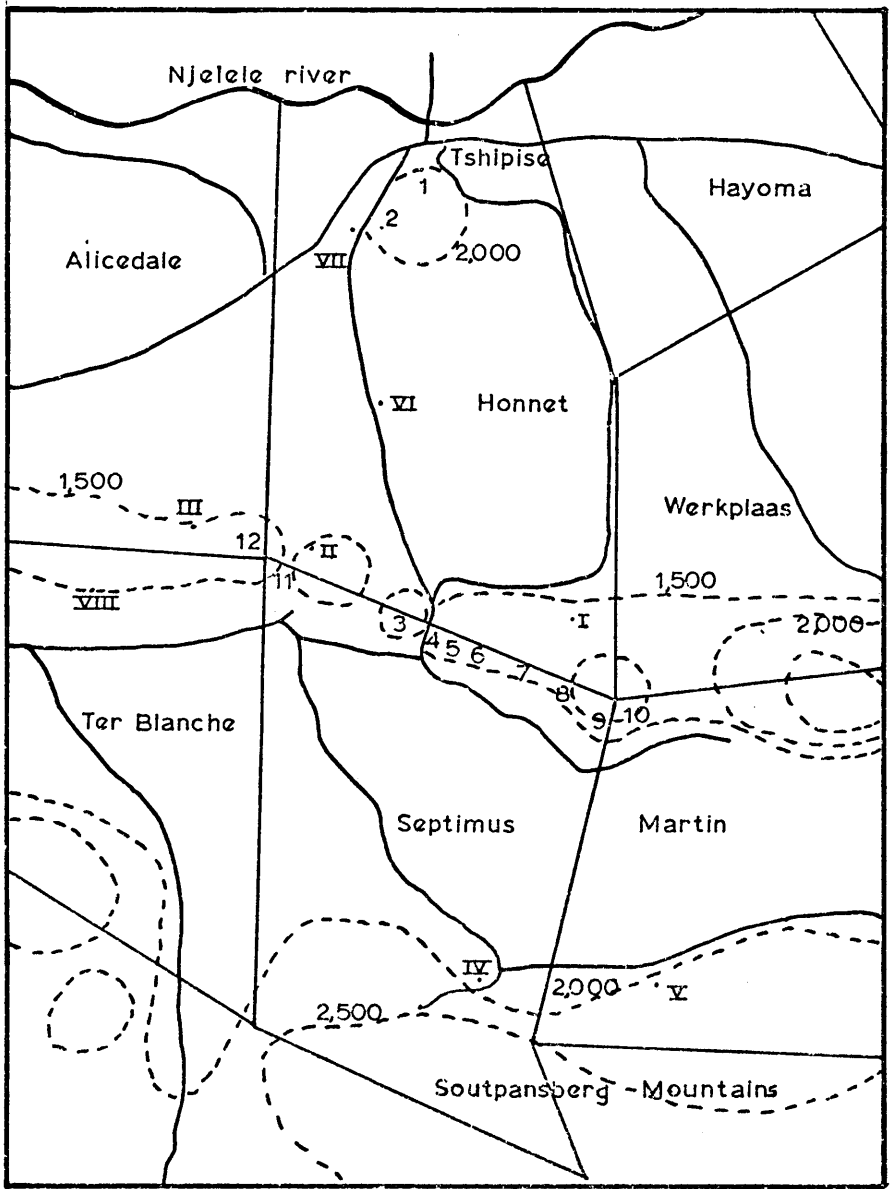
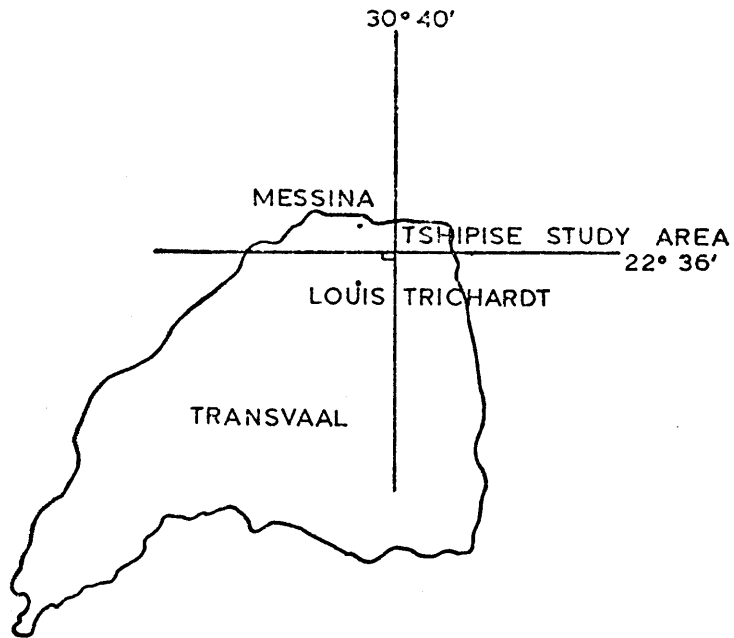


Figure 4. The major vegetation types in the Messina study area. Mopane trees clustered most thickly on the banks of two dry river beds. The routes taken by W troop in July 1968 followed the dense mopane vegetation.

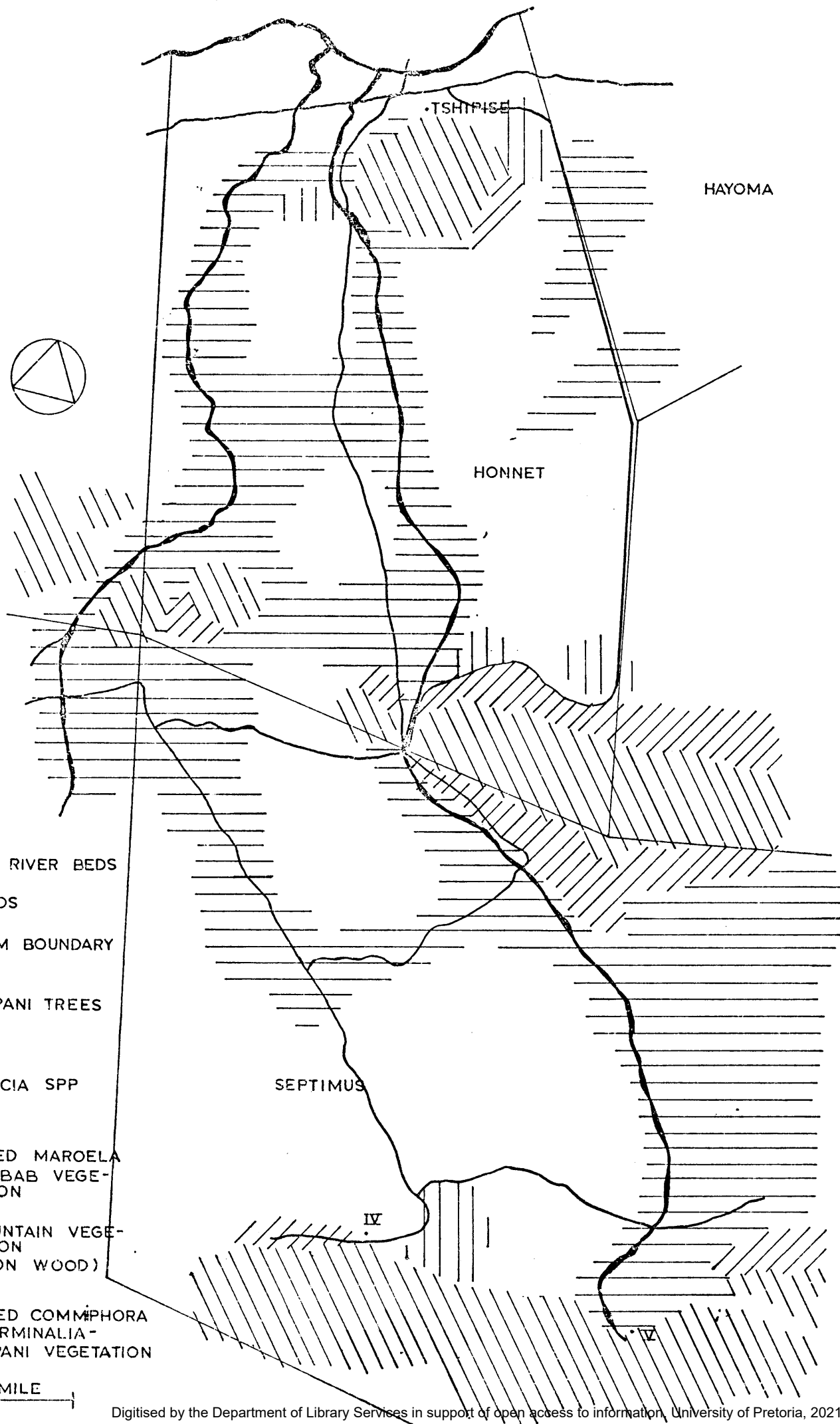


Figure 5. The total rainfall in the study area during the season 1967-1968.

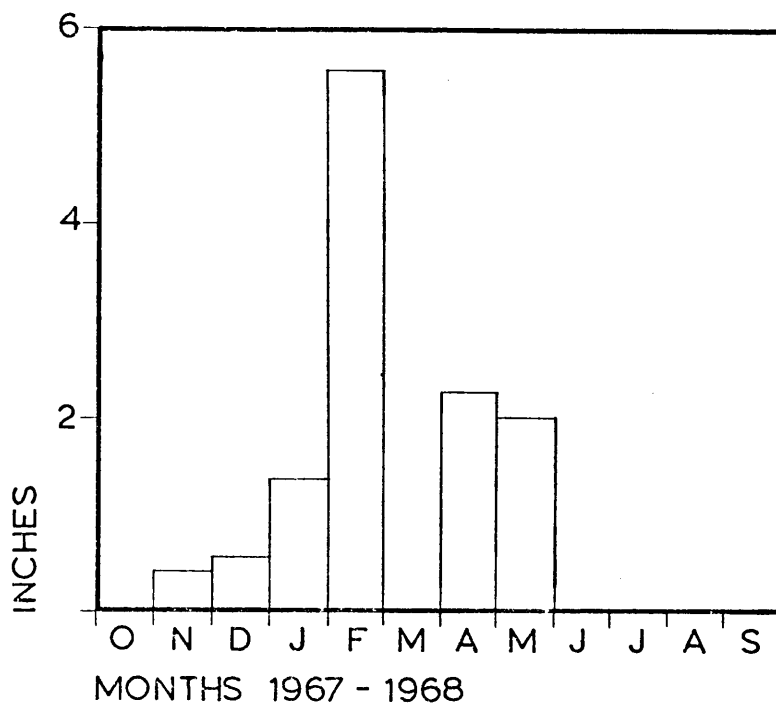


Figure 6. The Messina study area showing all roads travelled during the spoor census survey.

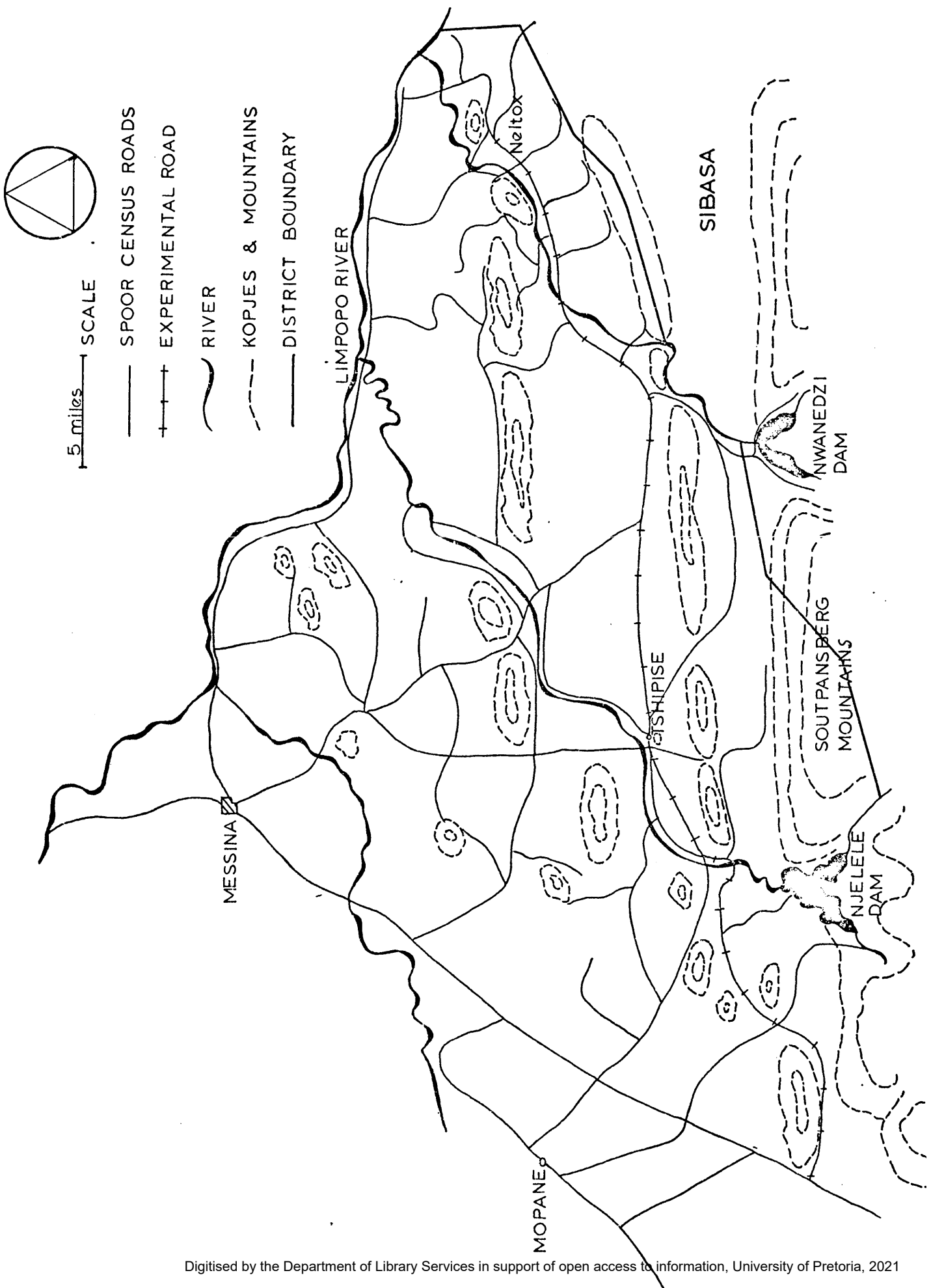


Figure 7. The variation of distances between crossing places as well as the variation in sizes of 26 baboon troops in a 60 mile road strip in the course of one year.

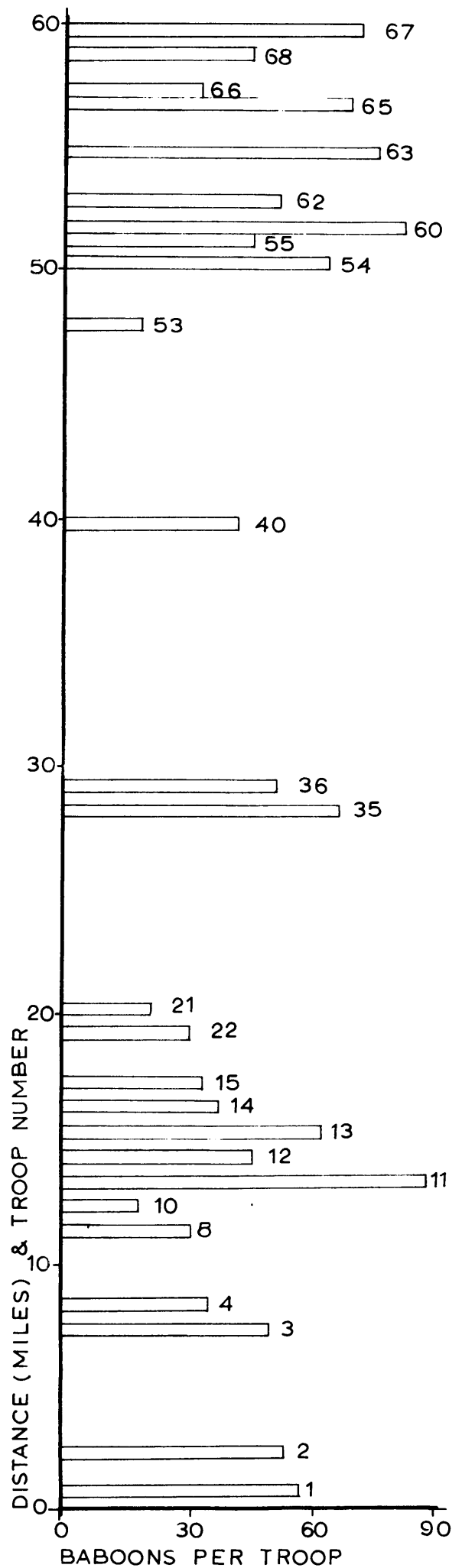
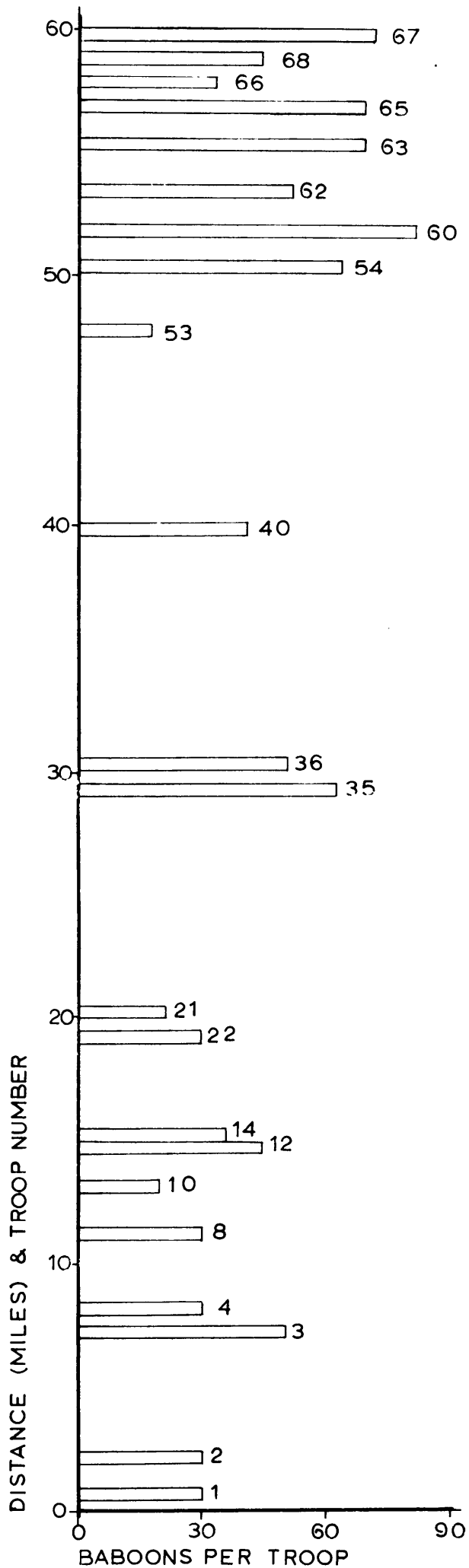


Figure 8. The population density of troops in seven ten-mile quadrants in the census area.

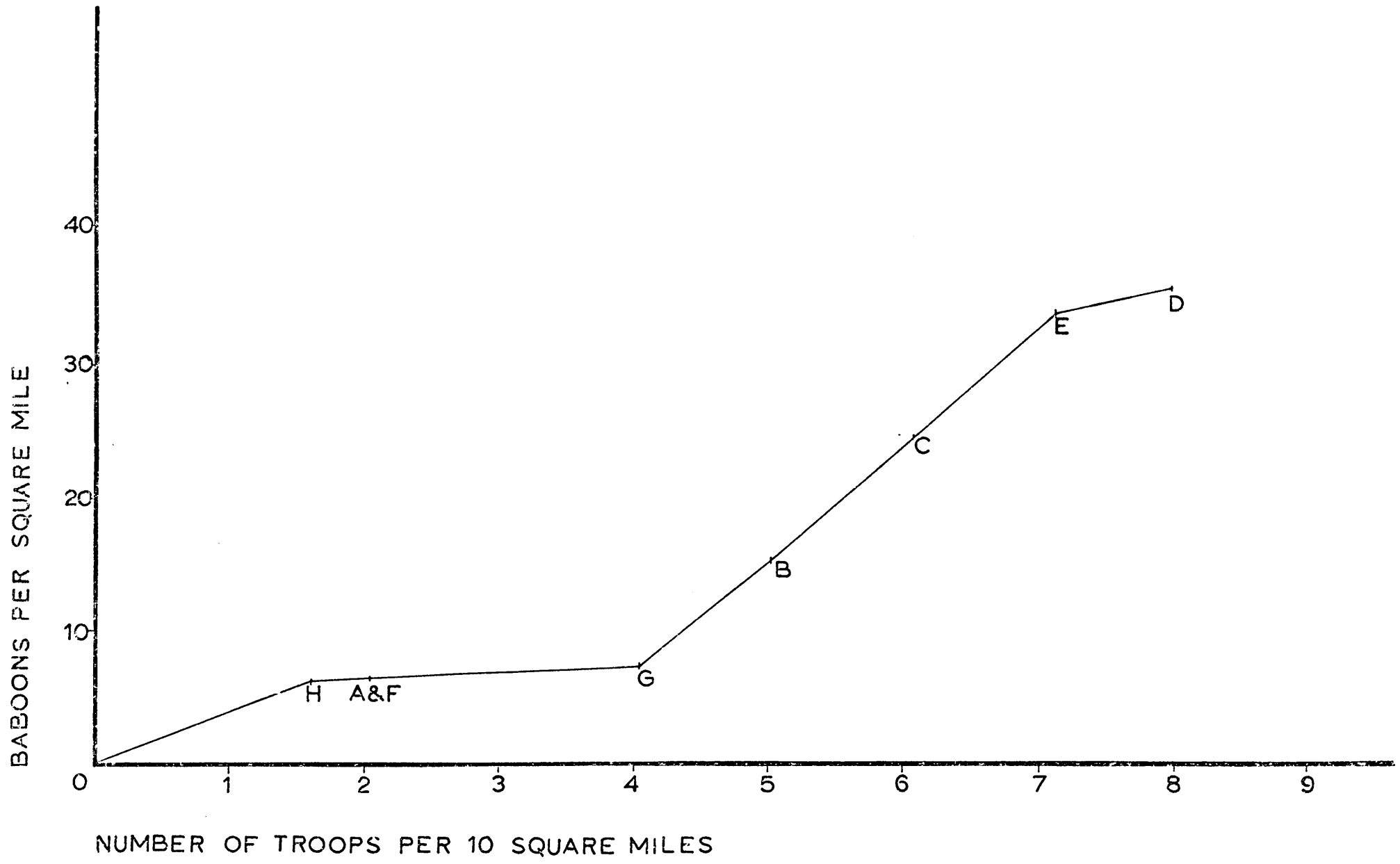
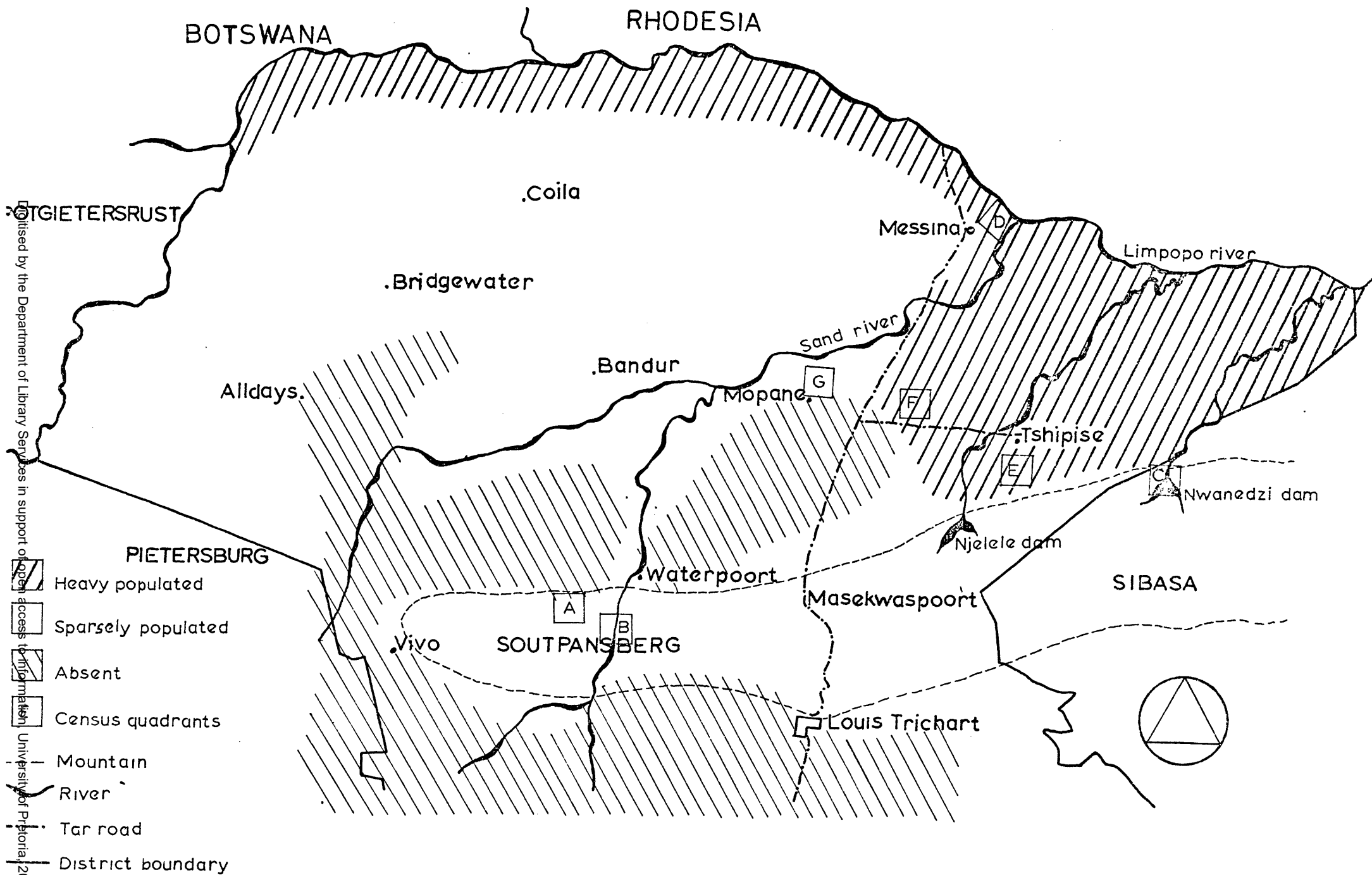


Figure 9. The distribution and population density of baboons in the Soutpansberg district.



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Figure 10. The troop sizes of 175 baboon troops in the census areas.

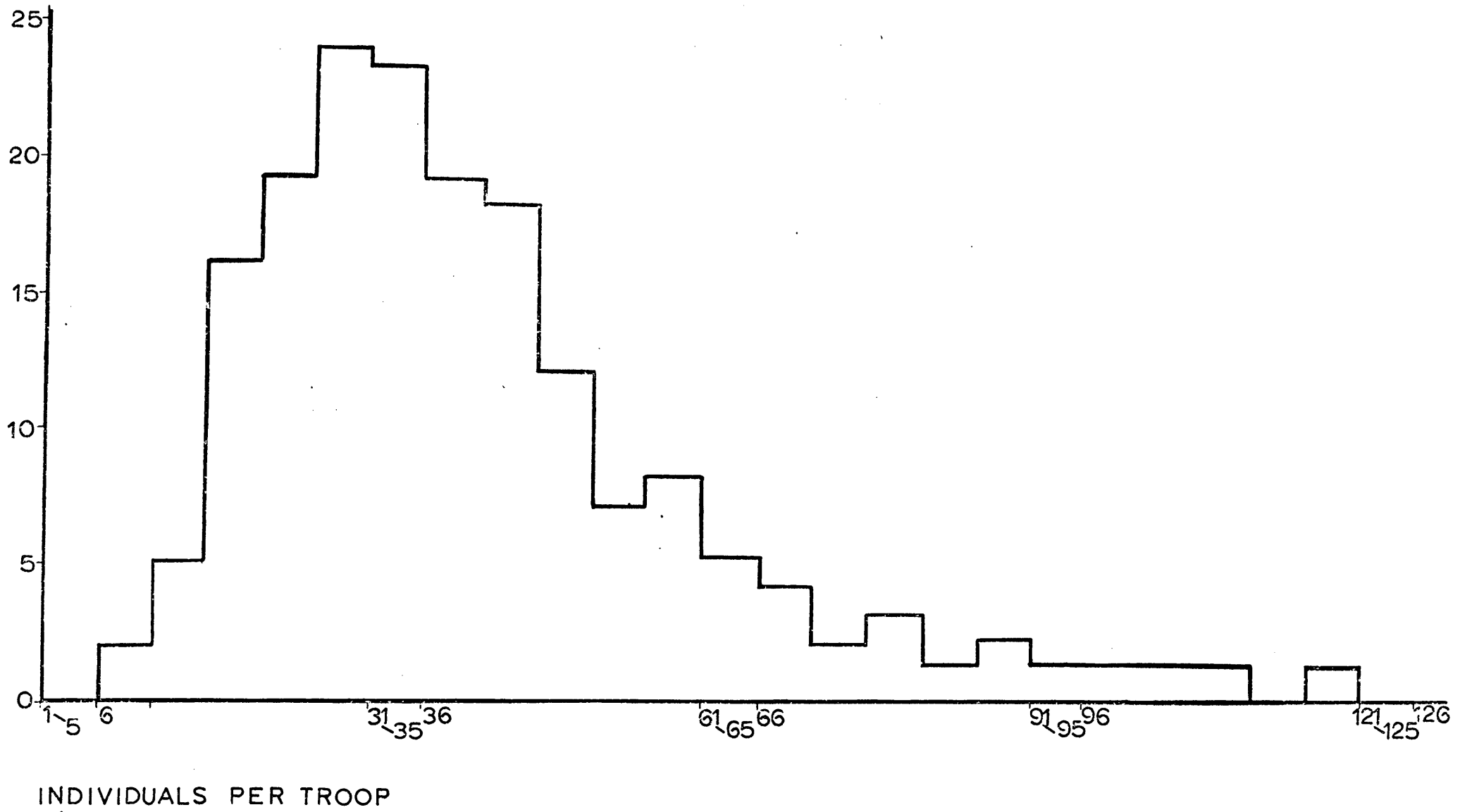
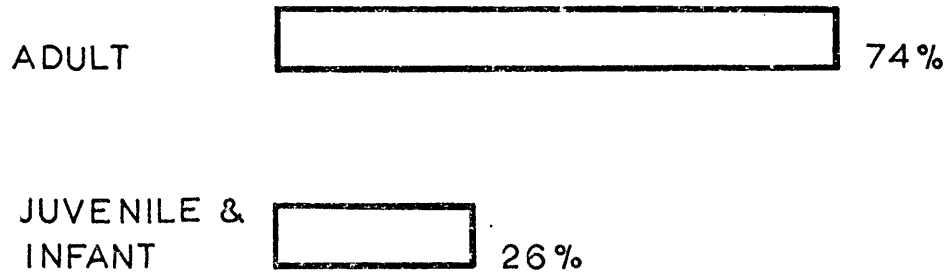


Figure 11. Age class distribution of baboon troops in the
census area.

PYRAMID A



PYRAMID B

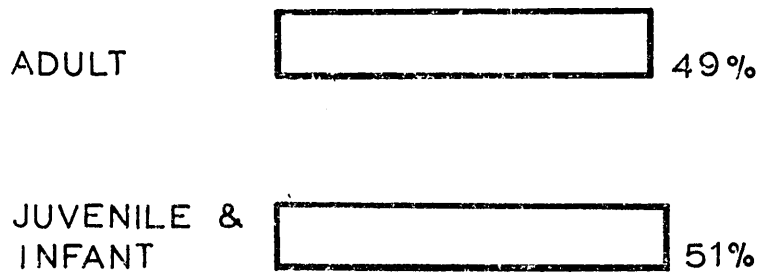


Figure 12. The utilization of eight sleeping sites in the sandstone ridges by five interacting troops in the study area.

Troop RB = □

Troop KMW = ■

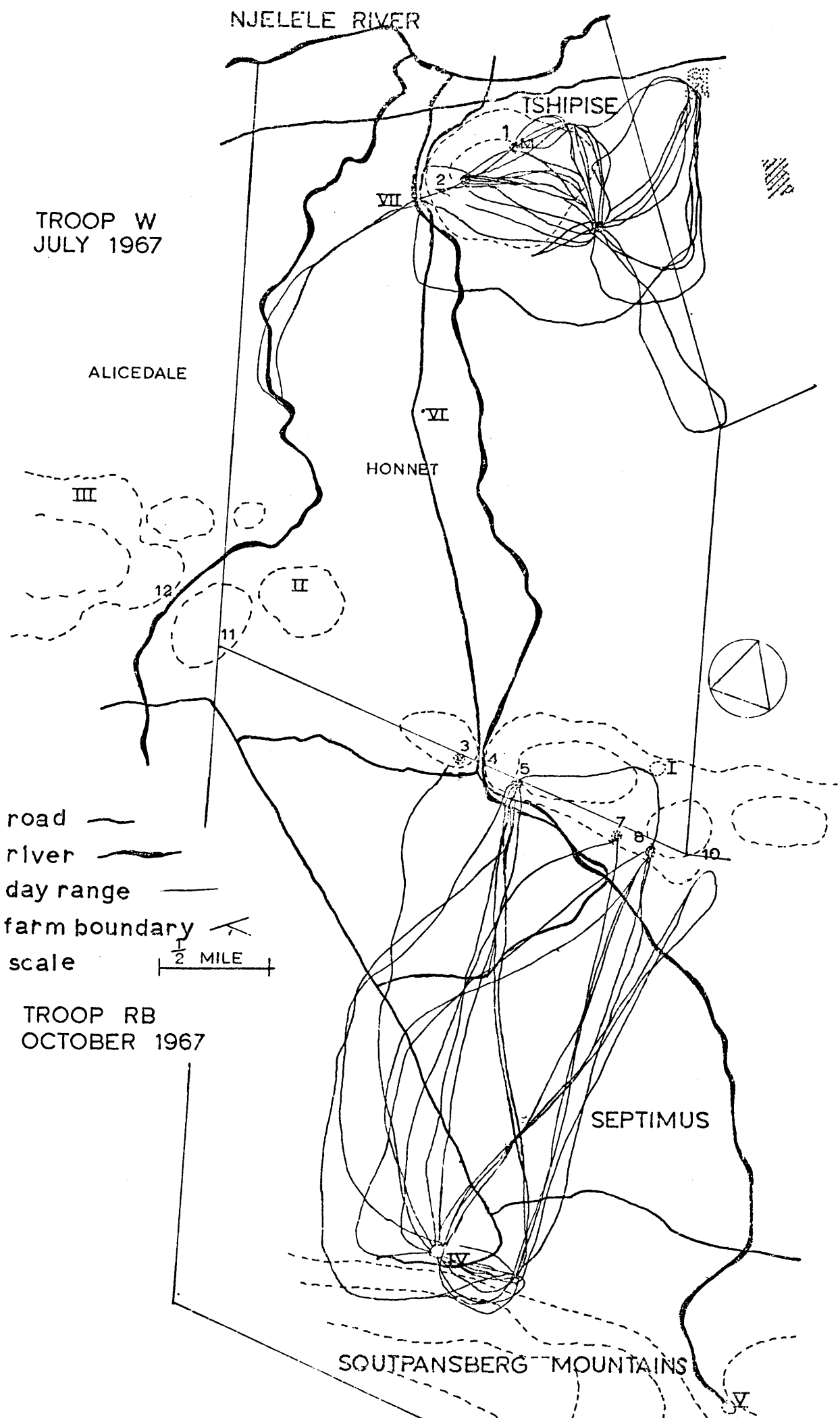
Troop KMO = ○

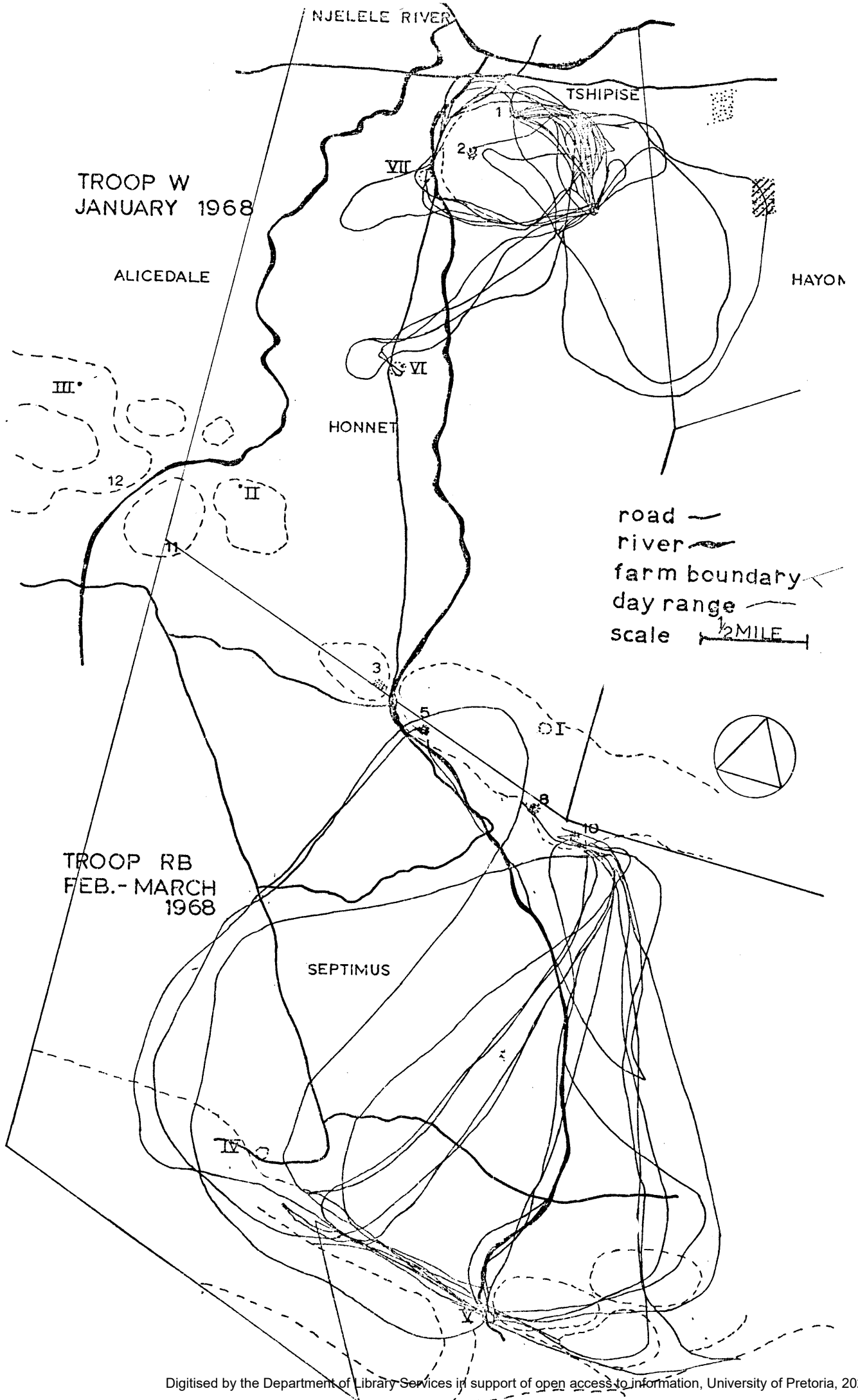
Troop K = ●

Troop GK = ▲

DATE	NO OF SLEEPING SITE							
AUGUST '68	3	4	5	6	7	8	9	10
16	■		□	○	●			
17	□	■		○				●
18	■		□	○	●			
19			■	○		□		●
20			■	○				□
21	■		○	?		□		
22		■	□	○				?
23	■					○		□
24	■			○		□		●
25		■				○	●	□
26			□	○				△
27		■		○				□
28		?	?					□

Figure 13. a - c The day ranges of W and RB troops during six periods of observation between July 1967 and August 1968.





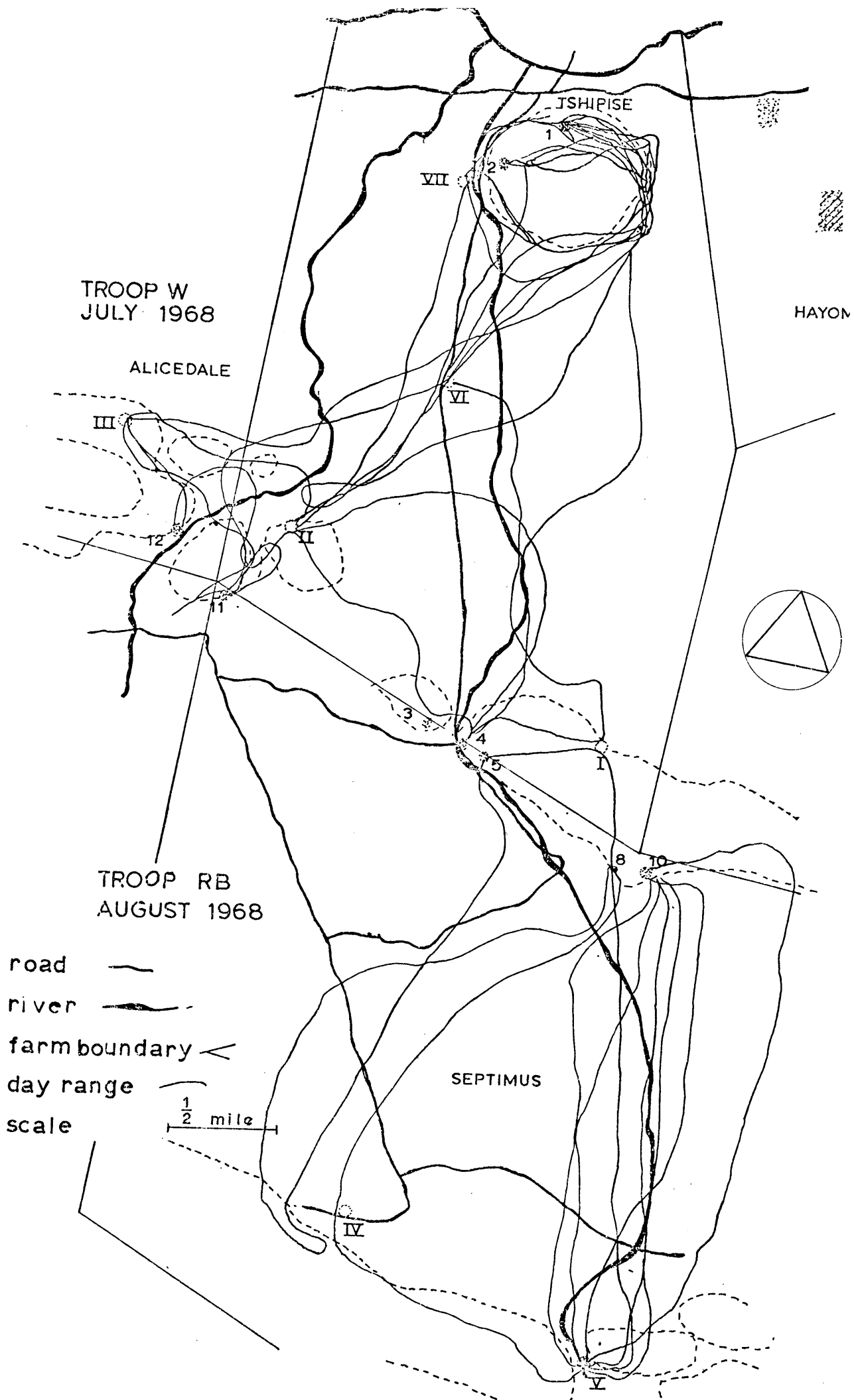
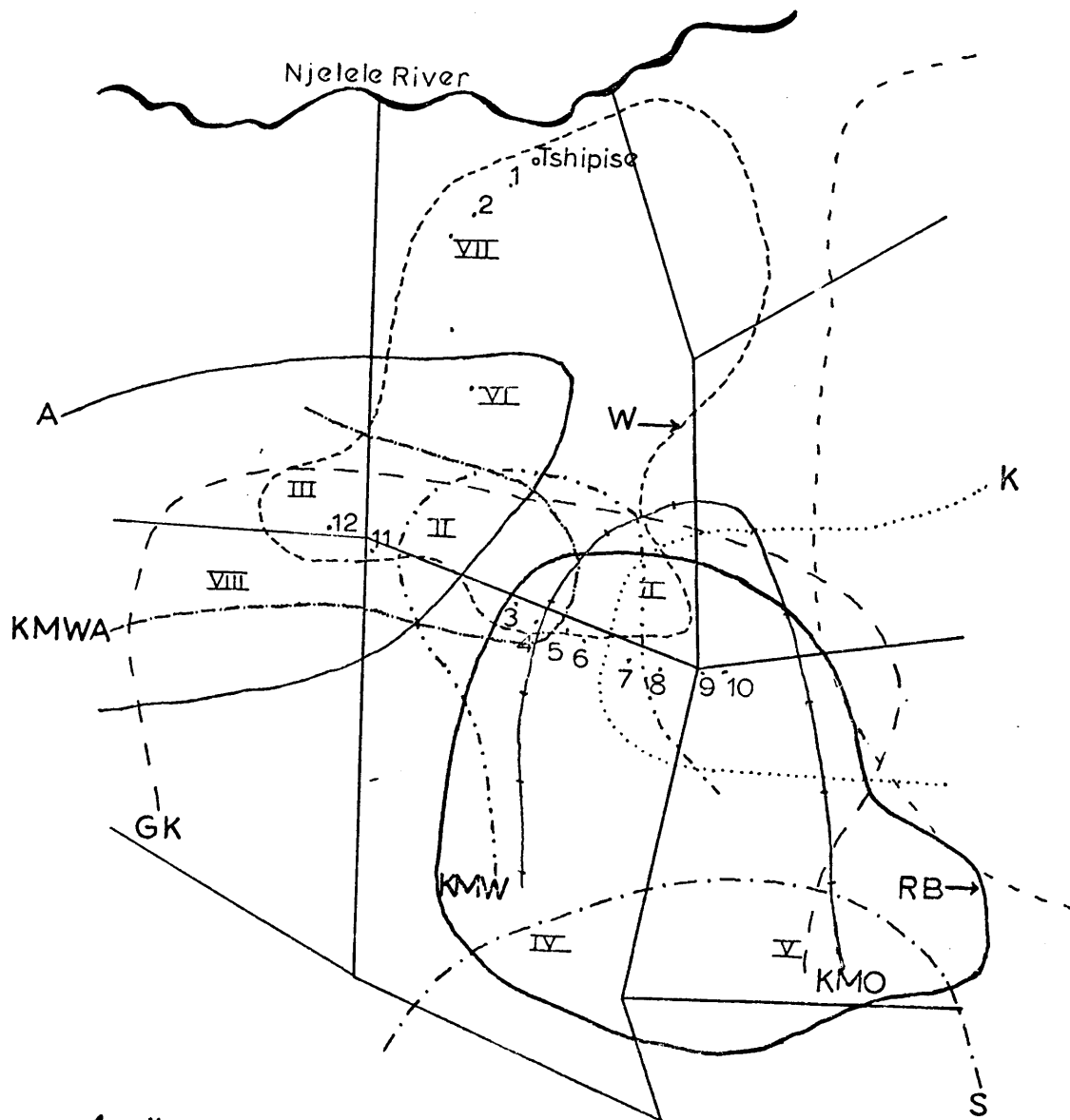


Figure 14. The overlap of home ranges of eight troops in the study area.



SCALE $\overline{1 \text{ mile}}$

— FARM BOUNDARY

1-12 SLEEPING SITES

I-VII DRINKING SITES

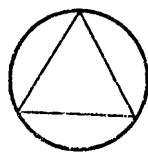


Figure 15. The relationship between daily maximum temperatures and maximum distances travelled by W and RB troops during both summer and winter periods.

TROOP W
 □ JANUARIE 1968
 X JULY 1968

TROOP RB
 △ OCTOBER 1967
 ■ FEBR.-MARCH 1968
 ● AUGUST 1968

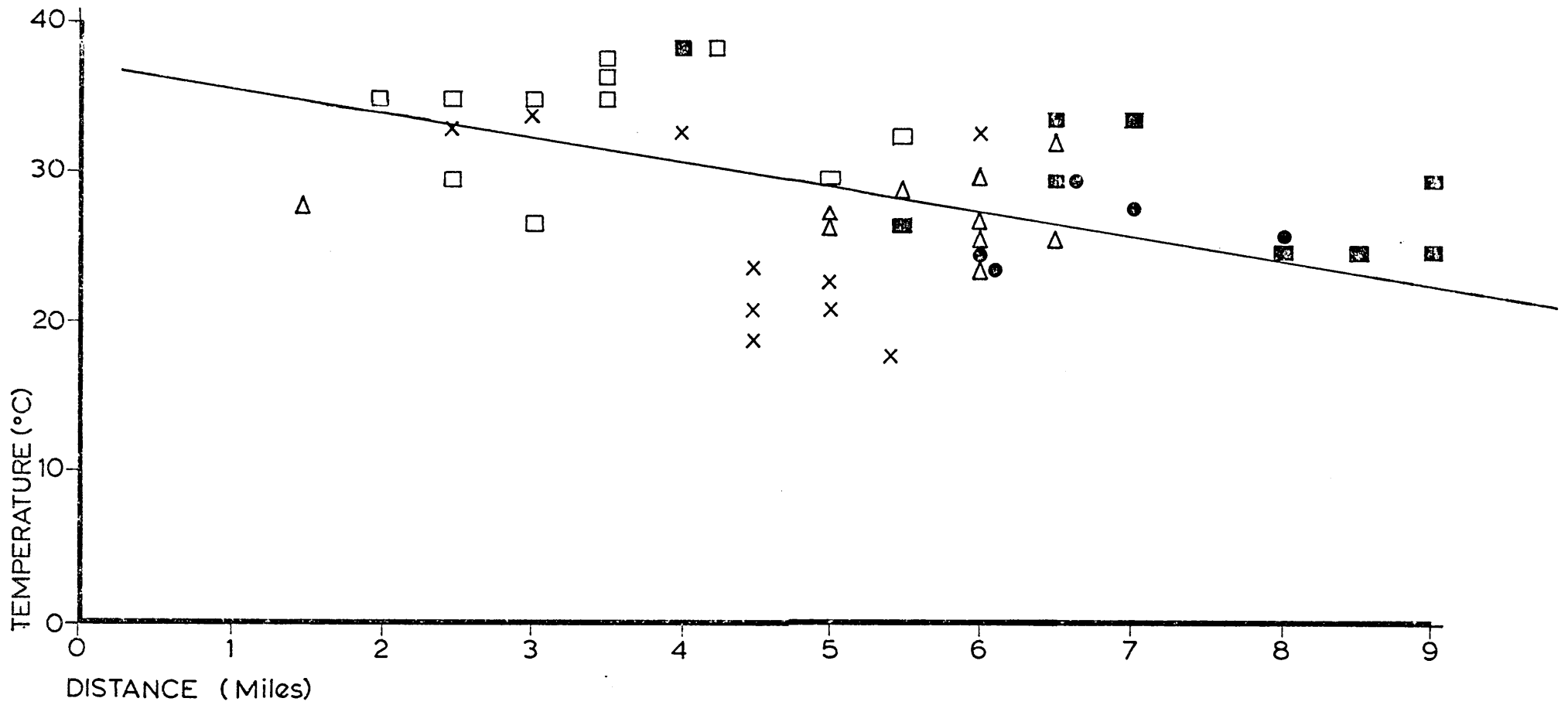


Figure 16. a-f. The relationship between time of day and the day range activities of W and RB troops during six periods of observation. Arrows indicate the times of sunrise and sunset.

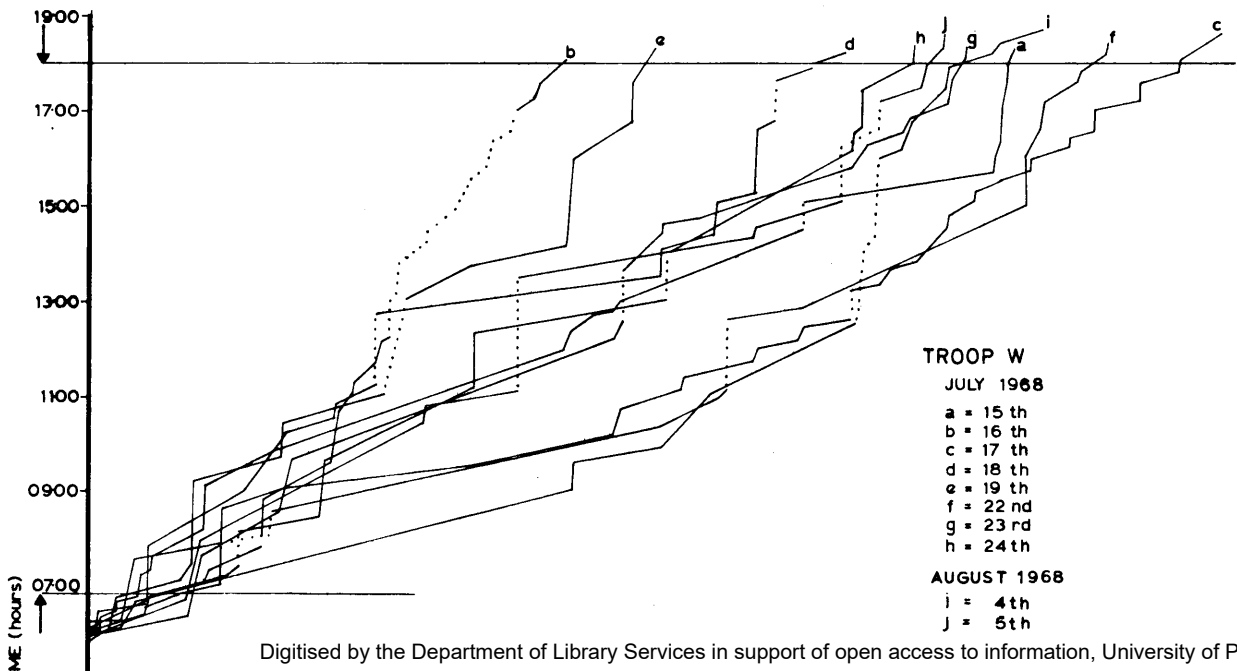
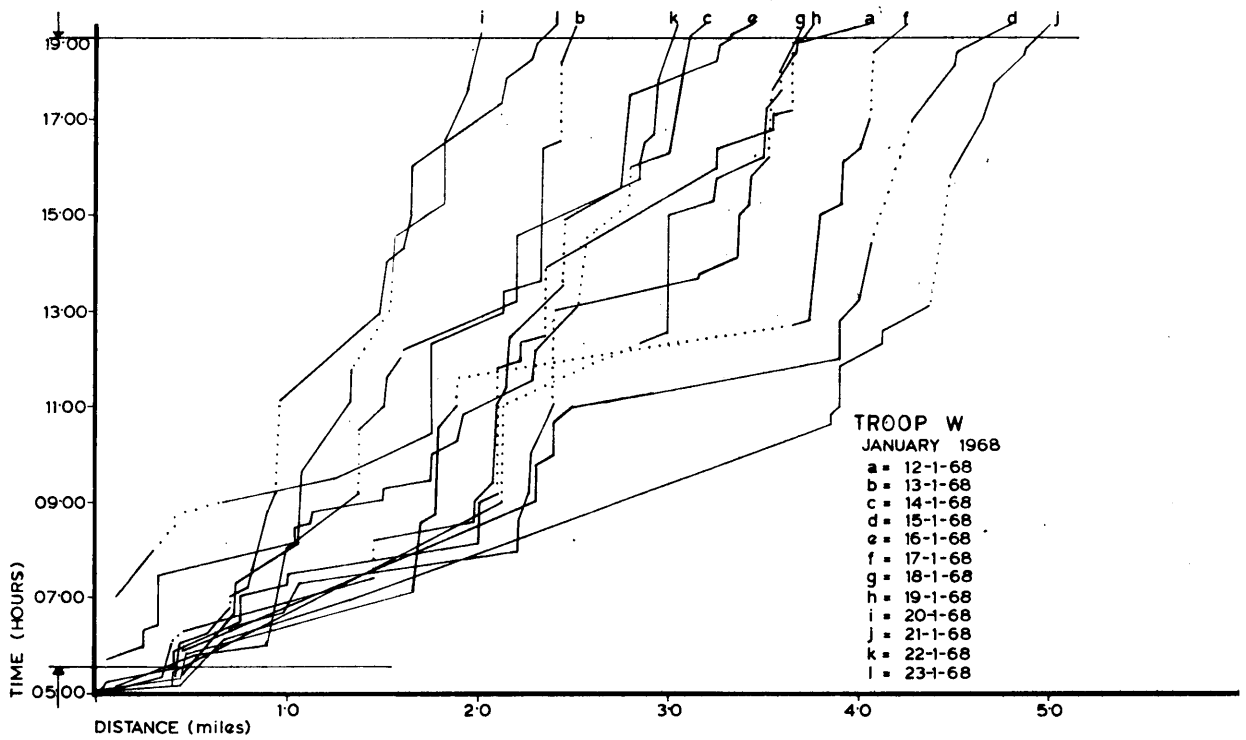
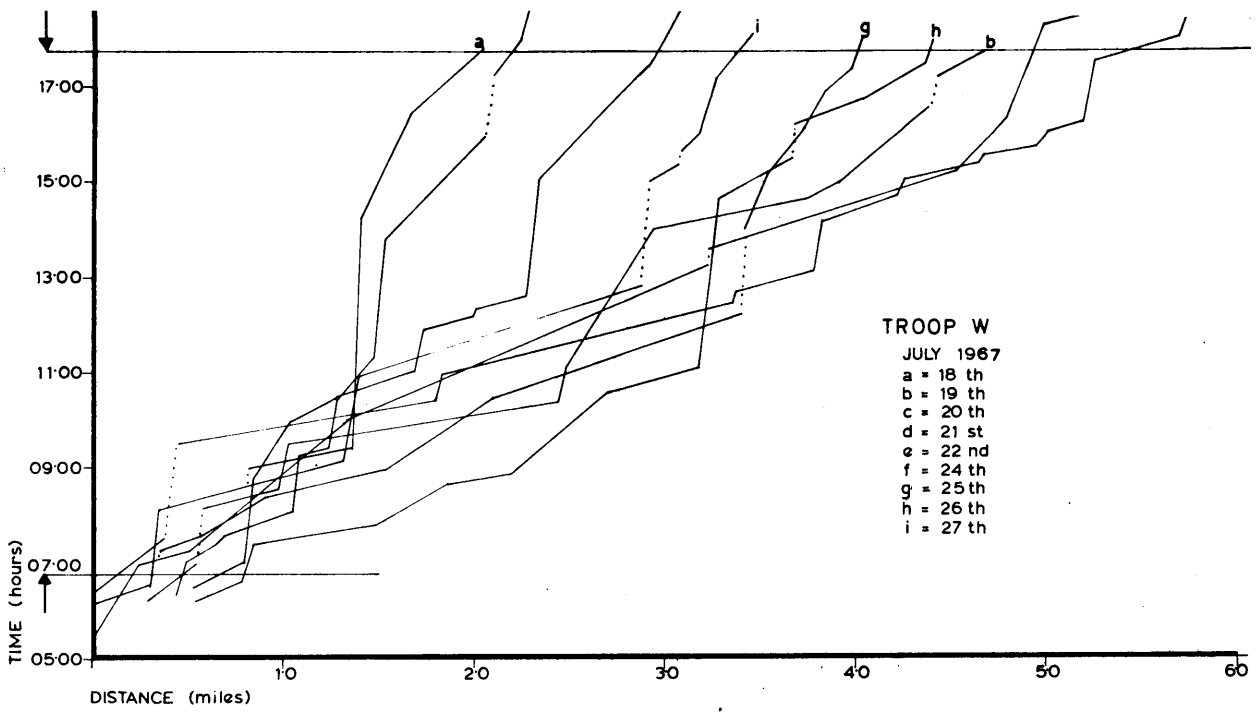
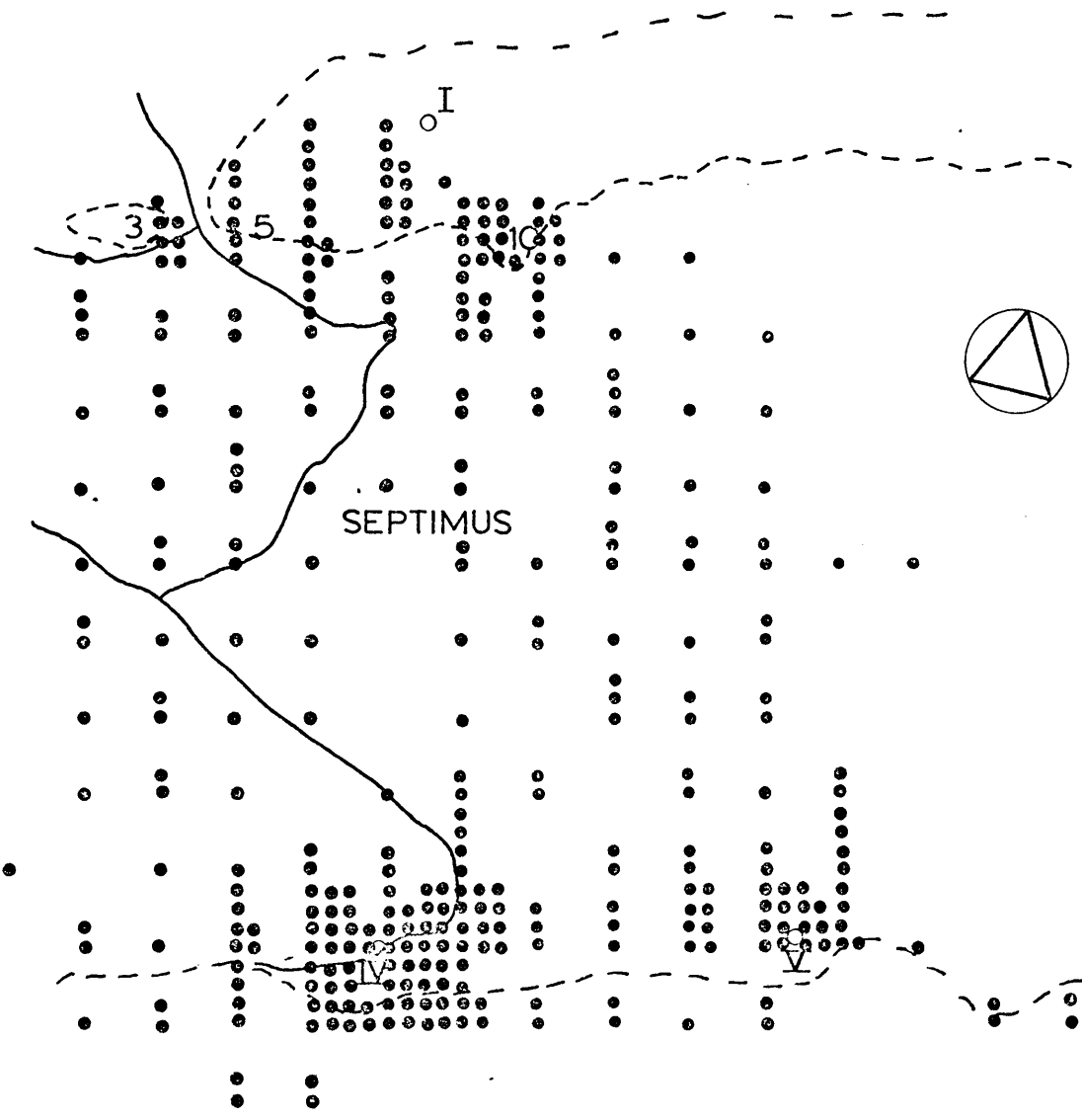


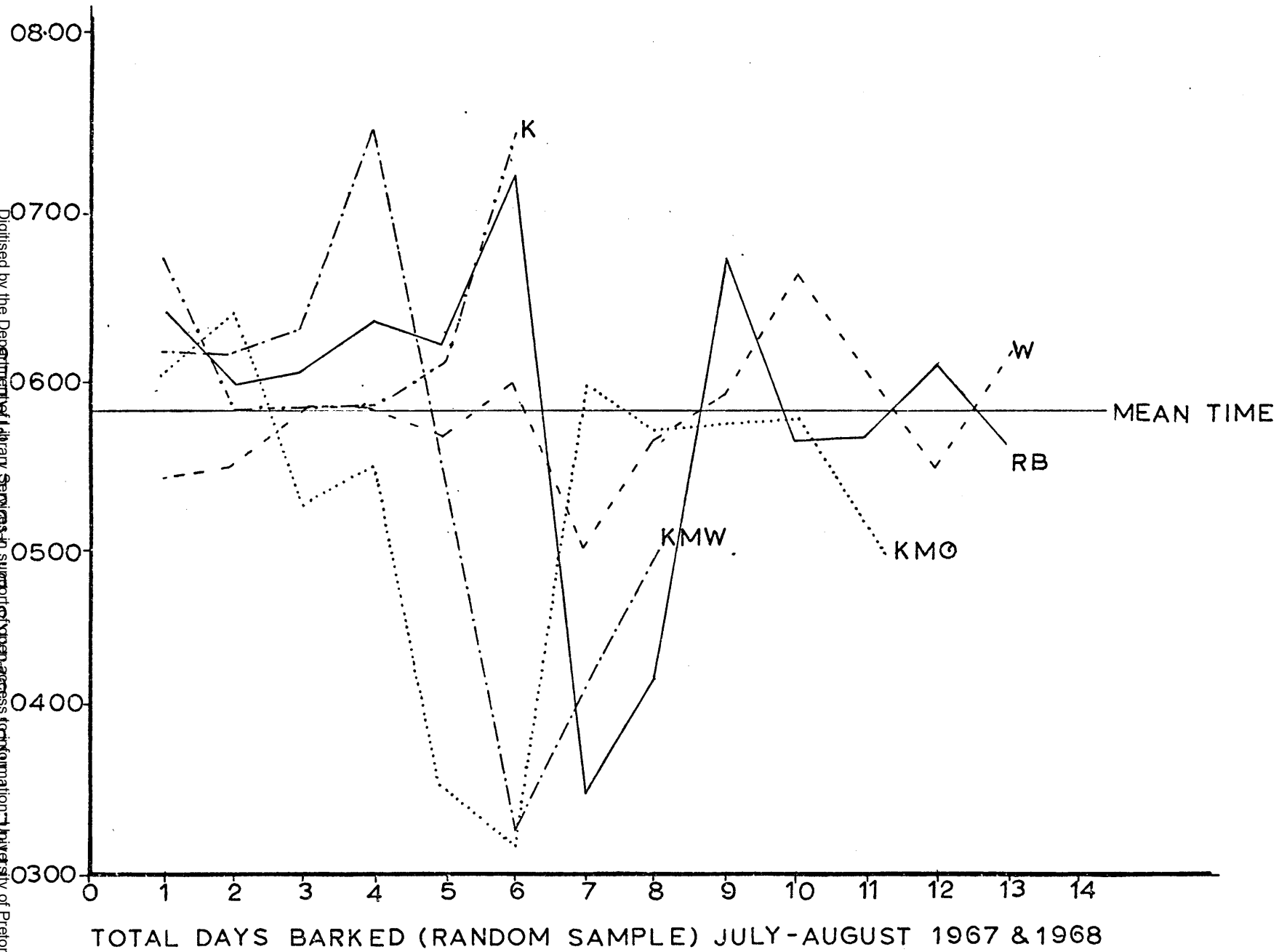
Figure 17. The distribution of daylight hours spent by RB troop in quarter mile grid squares of its home range during 23 full day ranges. Each dot represents one hour; periods in excess of 30 minutes were also recorded as an hour.



SCALE
 1/4 MILE SQUARE

I-IV-V DRINKING SITES
 3-5-10 SLEEPING SITES
 ~~~~~ ROADS

Figure 18. The time when barking encounters commenced between adult males of K, KMW, KMO, RB and W troops in the early morning.



TOTAL DAYS BARKED (RANDOM SAMPLE) JULY-AUGUST 1967 & 1968

Figure 19.a. The frequency (=%) in which different behaviour patterns occur in four troops during 22 troop encounters; Morning and evening encounters were recorded during 11 days; 16.8.68 - 26.8.68.

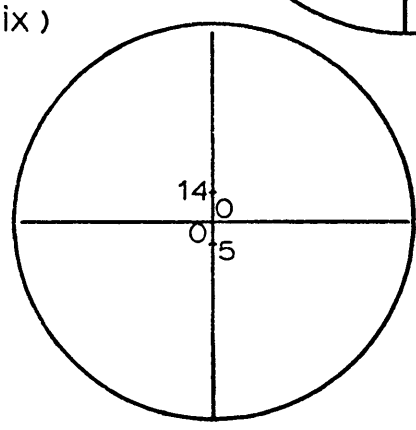
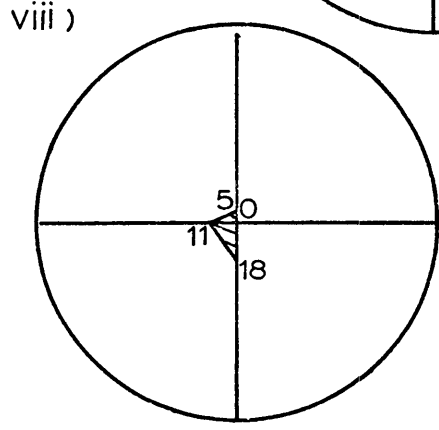
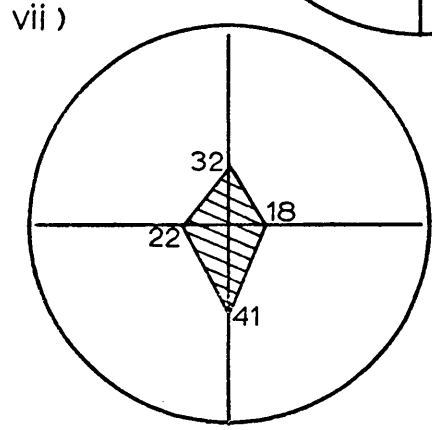
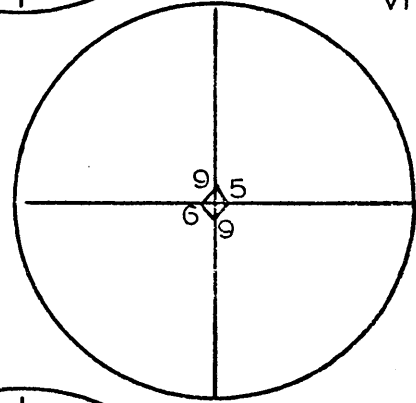
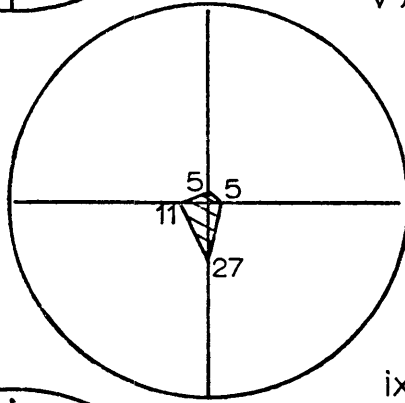
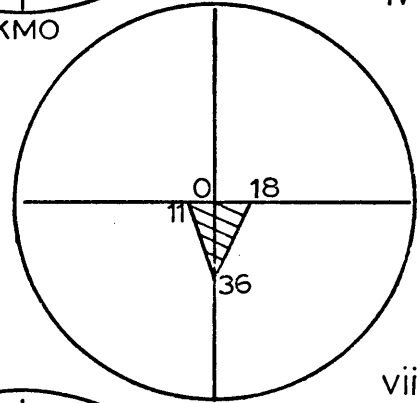
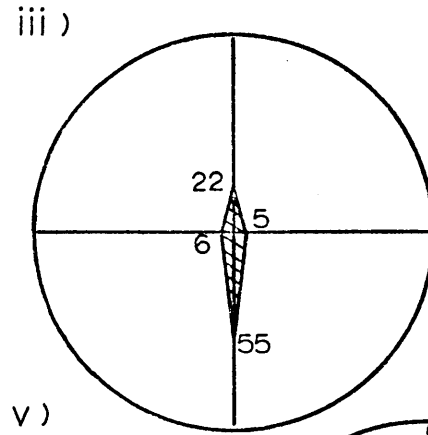
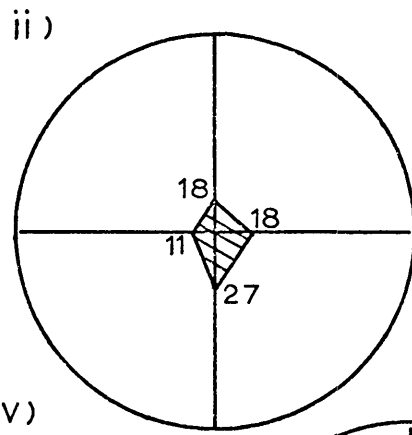
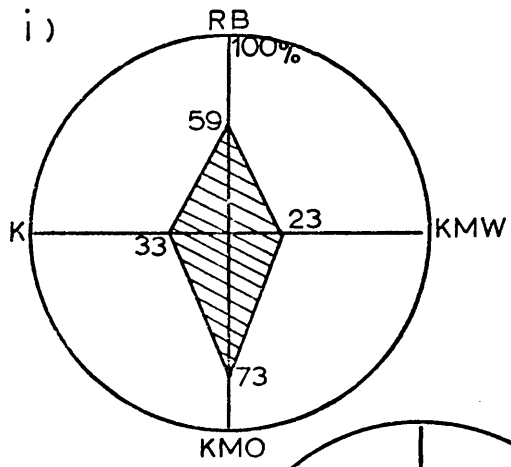


Figure 19.b. The frequency with which individual behaviour patterns were repeated between four interacting troops during a 11-day study period; 16.8.68 - 26.8.68.

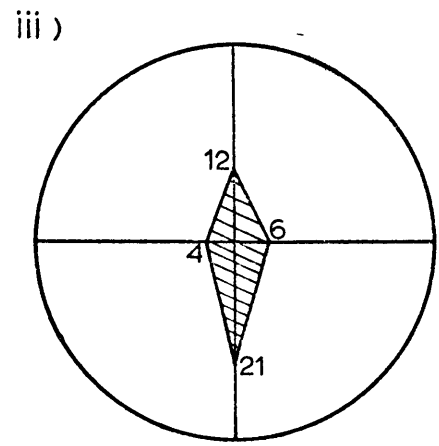
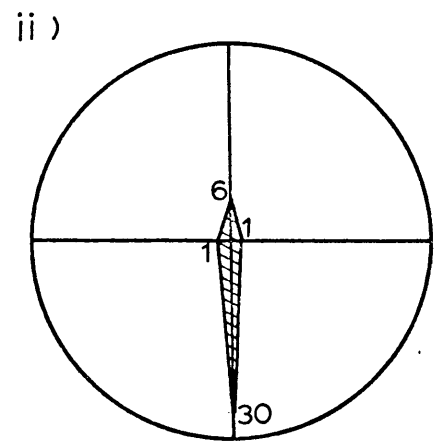
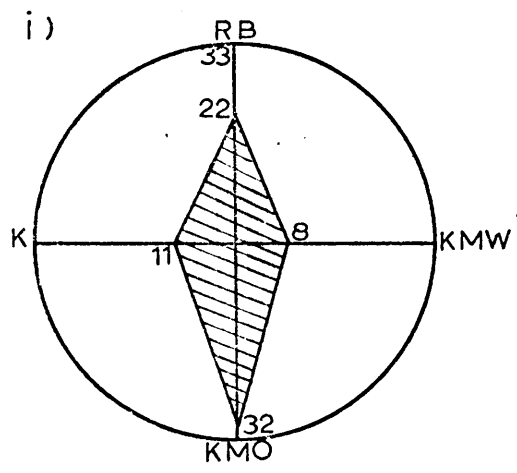






Plate 1. A section of the Waterpoort study area, photographed from the sleeping site of the baboon troop. The railroad is apparent alongside the Sand River.

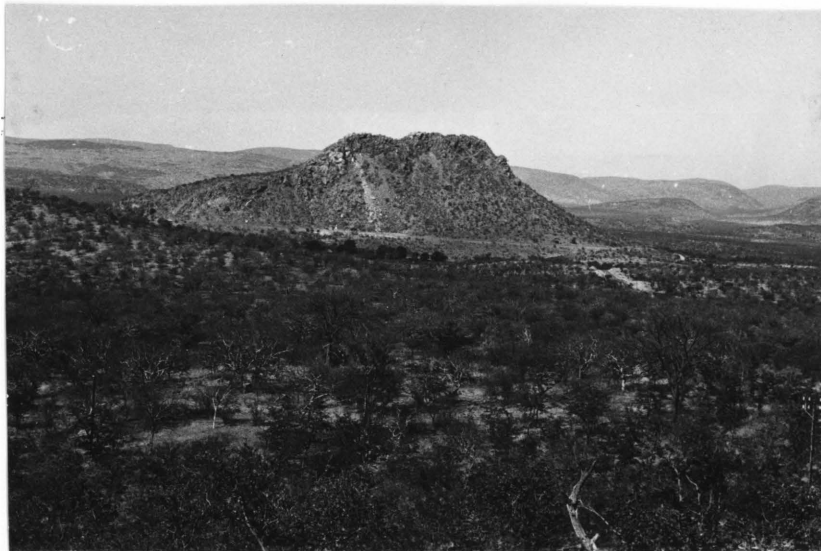


Plate 2. Tshipise kopje viewed from the north. The Soutpansberg mountains are apparent in the background. The canal, a horizontal line at the foot of the kopje, can be seen.

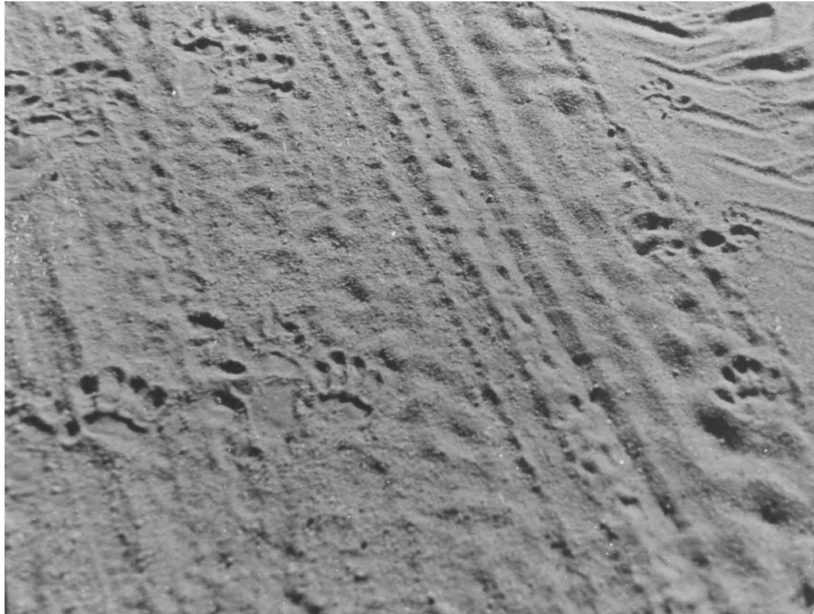


Plate 4. Baboon spoor; clear evidence that a baboon troop had crossed a dirt road.



Plate 5. Tall growing trees on the banks of the Limpopo River  
used by baboons as sleeping sites.



Plate 9. Male Y accompanied by four juveniles, a few of those who usually stay with him during the day.