THE BIOLOGY OF THE AFRICAN LION

(*Panthera leo*, Linn 1758)

IN THE

KRUGER NATIONAL PARK

BY

BRUCE ROBERT BRYDEN

Submitted in partial fulfilment of the requirements

for the degree of

M.Sc. (Wildlife Management)

in the

Faculty of Science

University of Pretoria

Pretoria

November 1976

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B R BRYDEN

Leader/Promotor: Prof F C Eloff
Dept. of Zoology
University of Pretoria
Pretoria

Co-leader/Co-promotor: Dr U de V Pienaar
Director of Nature Conservation
National Parks Board of Trustees
Skukuza

ABSTRACT

The history of lions in the Kruger National Park is given. Lions were caught and marked to determine the most suitable marking methods as well as fitted with radio transmitting collars to facilitate daily location. Predation in general and the prey population are discussed. Results of biotelemetric tracking are given and discussed. From this is calculated the mass of prey animals killed per year, the daily food intake of a lion and the food requirements of a lion using the "prey unit" as a basis. Factors affecting the success of a hunt, hunting techniques and behaviour at a kill are discussed.

Information on mortality, reproduction, territoriality and movements are presented. Taking into consideration the effect of lion predation, suggestions are made for future research and management of this animal in the Kruger National Park.

ACKNOWLEDGEMENTS

The author gratefully wishes to acknowledge the support received from the following instances or persons:

The Director of National Parks, Dr R Knobel and the National Parks Board of Trustees, who granted financial aid and the necessary facilities to undertake this study.

My supervisor, Professor F C Eloff of the University of Pretoria for his guidance and assistance during the study.

Dr U de V Pienaar, my co-supervisor, Director of Nature Conservation, who drew attention to the need for a better understanding of the effect of lion predation and whose constant interest in the project was greatly appreciated.

The Council for Scientific and Industrial Research (C.S.I.R.) Pretoria for a post-graduate grant of R1 000 received in 1971 and 1972.

Dr G L Smuts, Senior Research Officer in the Kruger National Park, who assisted me and gave valuable advice during the entire course of the study. Thanks are also due for his criticism of the manuscript.

Mr F Bennet, of the C.S.I.R., who constructed the radio apparatus and was always ready to make needed modifications to the equipment.

Mr P van Wyk, Assistant Director Research of National Parks, for his encouragement and advice in determining suitable areas for study.

Dr S C J Joubert, Head of Research in the Kruger National Park, who offered valuable advice and assistance.

Mr G L van Rooyen, Chief Instrument Maker in the Kruger National Park, who always had the necessary equipment in readiness and perfect condition.

District Ranger J H de Kock for his particularly valued assistance and encouragement at all times.

District Ranger M English for his assistance in capturing lions under extremely difficult circumstances.

District Ranger D C Swart for valuable advice and much needed assistance.

Tony and Harold Braack, Technicians, who were always willing to assist in any phase of the study.

Mrs A M M C Prinsloo, Librarian, and Mrs P Y Wood, Assistant Librarian, of the Stevenson-Hamilton library, who were always willing to locate suitable references.

The various Bantu field assistants, who assisted the author at various stages, particularly Philemon Chauke.

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CHAPTER 1. INTRODUCTION

The lion (Panthera leo, Linn 1758), subject of this study, is so well known that a description is not deemed necessary. There is, however, some uncertainty concerning the status of the various subspecies. Roberts (1951) states that the subspecies krugeri occurs only in the Sabie area of the Kruger National Park, and that lions in the northern parts of the study area are probably the result of the mixing of subspecies vernayi and bleyenberghi with krugeri.

In this study the lions of the Kruger National Park will be regarded as belonging to a single population with no difference at the subspecific level.

The range of the lion originally extended the entire length and breadth of the African continent only being absent in the equatorial forests and some desert regions. Its range included the Mediterranean coast as well as parts of Europe and Asia. In Africa it is today only found in the wild state in isolated areas, very few occurring outside game reserves or wilderness areas. In the Republic of South Africa the largest population (± 1 120) occur in the Kruger National Park (Pienaar 1969). Other small populations are found in the reserves of Zululand, Etosha National Park, the northern parts of South-West Africa and the Kalahari Gemsbok National Park. Private game reserves to the west of the Kruger National Park also support lion populations. Here the Sabi Sand Game Reserve, for example, has an estimated population of some 150 lions (Graupner and Graupner 1971).

HISTORY OF LIONS IN THE KRUGER NATIONAL PARK

The first warden of the Park, Lt. Col. James Stevenson-Hamilton, stated that there were nine lions or perhaps a few more in the year 1902 (Stevenson-

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Hamilton 1902-1946). This figure is probably an underestimation but gives an indication of the paucity of lions in the Park at that time.

The year 1905 saw the beginning of a period of predator control. Up to 1923 an average of 26 lions were killed per annum. Considering the size of the Park this number is very small and could hardly have had a significant effect on the numbers of prey animals in the Park.

The fact that so few lions were killed tends to indicate that the number of lions in the Park was indeed low. This view is further emphasised when the means of destruction is taken into account - traps, set guns and hunting. Despite this reduction campaign, lions managed to maintain their numbers at a fairly constant level (Stevenson-Hamilton 1902-1946).

Stevenson-Hamilton (op. cit.) noted that females tended to have larger litters more frequently when they were subjected to intensive hunting.

That lions were still classed as undesirables as recently as 1949 is clearly born out by the following extract from the Wardens Annual Report of 1949 - "Pafuri is fairly free of lions but a small troop of five come in occasionally and I suggest that these be thinned out if they start to frequent Hape." It is not known if these lions were destroyed but only in 1957 were lions again seen in this area.

The afore-mentioned predator control operations were aimed at keeping the Parks' lion population at between 500 and 600 individuals. This was a purely arbitary figure based on subjective observations. Stevenson-Hamilton did his best to stop predator control, but had to give in to public opinion and the press which held that lions were increasing at

such a rate that they were threatening the antelope species (Pienaar 1958).

When predator control was stopped, lion numbers increased rapidly, undoubtedly coupled to the increase in number of the available prey. Pienaar (op. cit.) estimated that there were 880 lions in the Park in 1956. These figures were calculated from the monthly Rangers' reports. In 1969 Pienaar estimated that there were 1 120 lions in the Park (Pienaar 1969).

PURPOSE OF THE INVESTIGATION

This study was suggested by the research staff of the National Parks Board of Trustees, with the aim of gaining an insight into the effects and significance of lion predation in the Kruger National Park. Lions are the major predator in the Kruger National Park and accounted for approximately 66 per cent of the total number of kills recorded in the Park for the period 1933-1966 (Pienaar 1969).

The aims of this study are firstly to determine what effect lion predation has on the major prey species: buffalo, zebra, wildebeest and impala; secondly the effect on the rarer prey species: roan antelope, sable antelope, tsessebe and the eland.

Information on mortality, reproduction, territoriality and movements were also collected with a view to determining the factors limiting growth and spatial distribution of the lion population.

This study was deemed necessary for the efficient management of the major and rarer prey species. No wildlife management programme for an area can be regarded as satisfactory without an intimate knowledge of the predators

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and their prey. It is thus the aim of this study to provide some such knowledge, insofar as predation by lions is concerned.

In addition to the main purpose as described above, it was intended to undertake a general study of predation by the lion.

According to Schaller (1972) many books have been written about the African lion, but most of them by hunters and game wardens who either shot the animals or made casual observations in the course of their duties, e.g. (Selous 1908; Roosevelt and Heller 1922; Stevenson-Hamilton 1954; Cowie 1966). Books were also written by people who raised lions as pets and then returned them to the wild (J. Adamson 1960 and 1961; G. Adamson 1968; Carr 1962). The writer agrees that none of these provide an accurate picture of the lions' social system and its predatory behaviour. Guggisberg (1961) was the first scientist to study lions. Articles particularly on food habits (Wright 1960; Mitchell, Shenton and Uys 1967; Pienaar 1969) and on territorial behaviour (Schenkel 1966), have been published recently. Schallers's work and that of Eloff (1973) are the only intensive direct studies published prior to the present thesis.

THE STUDY AREA

The Kruger National Park, an area which encompasses some 1 901 119 hectares, is bordered in the north by the Limpopo river and in the south by the Crocodile river. The eastern boundary is formed to a large extent by the Lebombo mountain range, while the western boundary is formed by a 500 km long fence. Almost the entire area lies within the semi-arid region of the Eastern Transvaal Lowveld.

The annual rainfall varies from under 200 mm to over 1 400 mm depending

on the year and the area.

Topographically the Park is undulating with scattered koppies of granite or basalt. The highest points in the Park are in the south-west (835 metres above sea level). The country slopes gently towards the Lebombo flats in the east which are 180-240 metres above sea level.

Insofar as the vegetation of the study area is concerned, the most recent and up to date map is given by van Wyk (1972) in his publication on the "Trees of the Kruger National Park".

The drainage is generally west to east by six main rivers. These are the Limpopo, Levubu, Letaba, Olifants, Sabie and Crocodile rivers.

Numerical Status of Prey Animals

The numerical status of the larger herbivorous species in the Kruger National Park, as determined by aerial and ground censuses conducted every August from 1969-1972 is given in Table 1.

For the main purpose of this study all animals except elephant, rhino and hippo will be regarded as potential prey animals. Lions do prey on rhino and hippo and even occasionally on elephant, but so rarely that they will be ignored.

Table 1: Numerical status of the large and medium-sized herbivorous mammals in the Kruger National Park as determined by aerial and ground censuses (August, 1969 - 1972)

Species	1969	1970	1971
Impala	139 550	161 950	147 300
Waterbuck	3 227	3 307	2 490
Zebra	19 465	20 227	16 890
Wildebeest	16 072	13 950	12 557
Giraffe	3 314	3 870	3 647
Kudu	5 530	6 520	4 990
Warthog	4 330	2 917	2 152
Sable Antelope	1 068	1 033	1 030
Roan Antelope	278	266	272
Eland	368	249	305
Tsessebe	584	633	494
Buffalo	19 056	21 142	19 785
TOTAL	221 904	245 730	219 828

CHAPTER 2. MATERIALS AND METHODS

TRACKING, CAPTURE AND PHOTOGRAPHIC EQUIPMENT

Basic equipment consisted of a Land Rover to which was attached a collapsable double Yaggi antenna. A 20 channel receiver for amplifying the radio signal and converting it to an audible signal was also used. Radio transmitters operated in the U.H.F. frequency range. The above were all developed by the Council for Scientific and Industrial Research (C.S.I.R.) for this project.

The capture equipment included:

(a) Van Rooyen crossbow

(b) Van Rooyen modified 20 gauge shotgun

(c) Van Rooyen darts

(d) Palmer Cap-Chur pistol and darts

Details on the above equipment can be found in Pienaar (1973).

Photographic equipment consisted of a 35 mm reflex camera and a 400 mm lens. Other optical aids were a pair of 8 x 35 binoculars and an infrared night scope.

Limitations Because Of The Equipment

The radio tracking equipment on which this project was largely dependant had certain limiting factors. It was these factors that dictated the choice of a pride to be studied. The effective range of the transmitter is limited by the size of the aerial as well as the height of the aerial from the gound, range increasing with height. The signal emitted by the transmitter is incapable of passing through a land mass of any size. For

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these reasons the topography of the study area is critical. Experience showed that flat country with a few high points was ideal. This type of country presented minimal obstruction to the signal and facilitated the relocation of marked lions. The absence of deep gullies and rocky ridges was also desirable as it was essential to travel the terrain in all directions to find marked animals.

The presence of dense bush was also taken into account when selecting study prides, as experience showed that it was impossible to approach lions without disturbing them when the vehicle had to be manouvered through thick bush.

The area for study had to comply with the above as well as having a large prey population and a resident pride of lions.

IMMOBILIZATION

Once a suitable pride had been selected for study the area was baited with a wildebeest, or any other large animal, these being laid out in an area likely to be visited by the pride. The carcase was tied to a tree so as to prevent the lions from dragging it away and in such a way that it could not be eaten too easily by the lions. As the bait was laid out at dusk it was essential to keep the lions at or near the carcase until daybreak, at which time darting was effected and easy relocation of darted individuals was possible.

Where possible, two lions from a pride were immobilized using Sernylan (Phencyclidine hydrochloride) (Parke-Davis) for the one and Ketamine (Ketamine hydrochloride) (Parke-Davis) for the other. The following dosage rates were used:

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Ketamine ± 12 mg per kg of body mass

Sernylan ± 1,75 mg per kg of body mass (Smuts, Bryden, de Vos and Young 1973).

Where large doses of the drug had to be administered the darts were fired from a Land Rover using the Van Rooyen modified shotgun or the crossbow.

For smaller dosages of drug and for shorter distances the Palmer Cap-Chur equipment was used. In the case of lions darted with Ketamine booster doses of the drug could be administered intravenously, depending on the amount of time still required to complete the marking procedure.

Because of the relatively short recovery period of the Ketamine immobilized lion compared to the Sernylan immobilized lion, the former was fitted with a collar first.

Azaperone (R 1929) (Janssen) was used in conjunction with Sernylan as a tranquilizer. It was administered simultaneously by means of the dart syringe. Dosages varied from 50-70 mg per lion depending on its size. The addition of the neuroleptic was not essential in the case of Ketamine immobilized lions but was nevertheless administered by injection once the animal became tractable. Once the marking was effected the animals were injected with a central stimulant: Ritalin (Ciba), 20 mg per animal. The detoxicating agent Guronsan (1 000 mg per animal), was also administered.

It was necessary to stay with the animals until they had completely recovered from the effect of the drug, as other lions, hyaenas and vultures could well take advantage of an immobilized lion and kill or injure it. Ketamine with its short recovery period had a distinct advantage over the

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long acting Sernylan. Recovery time of Sernylan is almost three times that of Ketamine (Smuts et al. 1973).

MARKING

Once the animal was tractable its neck was measured using a flexible steel tape. The basis of the collar was cut to size, two pieces of similar length being utilized.

The collar consisted of three parts:

(a) Collar - Belting

(b) Transmitter Pack

(c) Battery Pack

See Figure 1.

The Collar

This consisted of two layers of 9 x 3 cm "drive belting", a three ply nylon mesh impregnated with rubber. The collar was made of two layers to afford protection to the wires connecting the transmitter to the power source. The two layers were rivetted together to strengthen the collar and to seal the wires between the layers of belting (Fig. 1. Unit (1)).

The Transmitter Pack

The transmitter was enclosed in a brass cylinder measuring 4 x 2,5 cm . The aerial measured 12 x 6 cm . The aerial and transmitter were completely sealed in fibreglass except for a small hole left to give access to the tuning screw. Once the collar was fitted and the transmitter tuned this hole was sealed using a paper plug and Pliobond. The trans-

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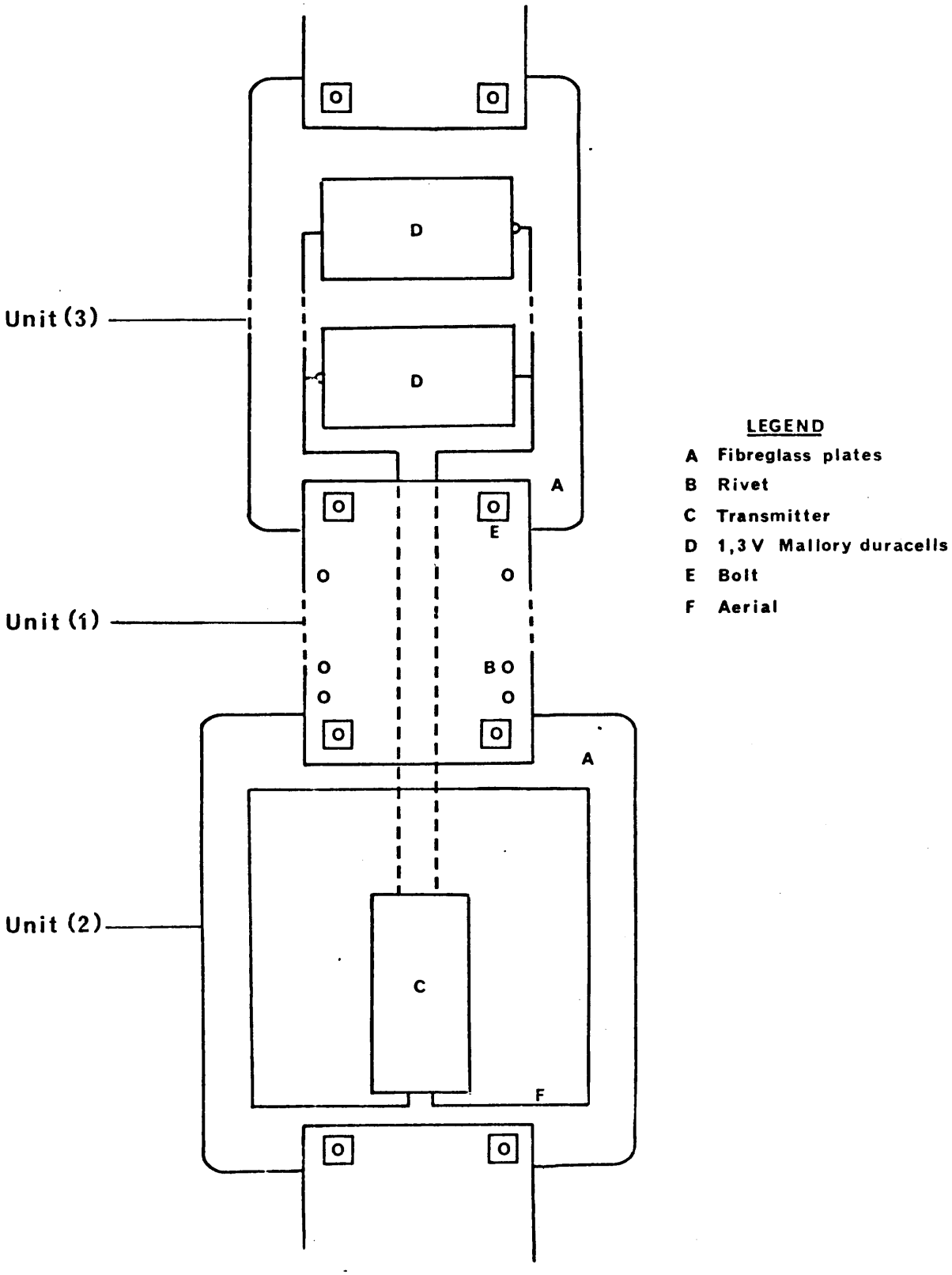

Fig.1. Diagramatic representation of a radio transmitting collar.
(1) Collar: 2 layers of drive belting (9x3 cm)
(2) Transmitter pack
(3) Battery pack

mitter unit was mounted on a fibreglass plate measuring 15 x 8 cm and was moulded to fit the neck of the animal. One five millimetre hole was drilled at each corner for securing the transmitter pack to the belting by means of a 0,5 cm galvanised bolt, the threads of which were destroyed using a pair of pliers. This effectively "locked" the nuts in place. The entire transmitter pack had a mass of 114 grams (Fig. 1. (2)).

The Battery Pack

This consisted of 5 x 1,3 v Mallory Duracells linked in series. The batteries were also enclosed in fibreglass and mounted on a curved fibreglass plate measuring 17 x 5 cm . Mass of the battery pack was 326 grams. The battery pack was also bolted to the belting. The mass of the entire collar was 923 grams. Taking the lion's mass as approximately 180 kg for males and 120 kg for females, the collar was only 0,5 per cent of body mass for males, and 0,7 per cent for females.

The battery pack was made heavier than the transmitter pack since for optimum transmitter efficiency it was essential to have the transmitter on the dorsal surface of the animal's neck. As the collar fitted the neck loosely the uneven distribution of its mass ensured that the transmitter was always on the dorsal surface of the lion's neck.

Fitting Of The Collar

The collar, initially made too large, was trimmed down gradually till it was the correct size, this being when the collar was just too small to be pulled over the animal's head. Once the collar was the correct size, the

loose ends of belting were bolted to the transmitter plate and the nuts "locked" in place. The collar was made as large as possible so as not to hinder feeding. This loose fit also ensured that the transmitter was always in the correct position. Once the collar had been fitted and the transmitter tested the animal was injected with a stimulant to enhance recovery.

Coloured collars were also fitted to certain lions, both male and female, to study movement over a long period. These collars consisted of a single layer of "drive belting" covered with a layer of Sterkolite in various patterns and colours. The Sterkolite was both glued and rivetted to the belting. The collar was completed by bolting the two ends together. Here again the collar was made to fit loosely, so as not to hinder feeding. See Fig. 2.

Tourist reports of marked lions as well as reports from Rangers were used to determine movements over a period of two years.

Suitability Of Various Marking Procedures

Radio Transmitting Collars

Radio transmitting collars were the most important marking technique used in this study.

The life of the battery was the limiting factor in the usefulness of these collars. The estimated life of these batteries was given as nine months, but the effective field life varied from 94-128 days (n = 14). Under field conditions these batteries should therefore be changed approximately every 80 days for safety. This is a distinct disadvantage since capturing the

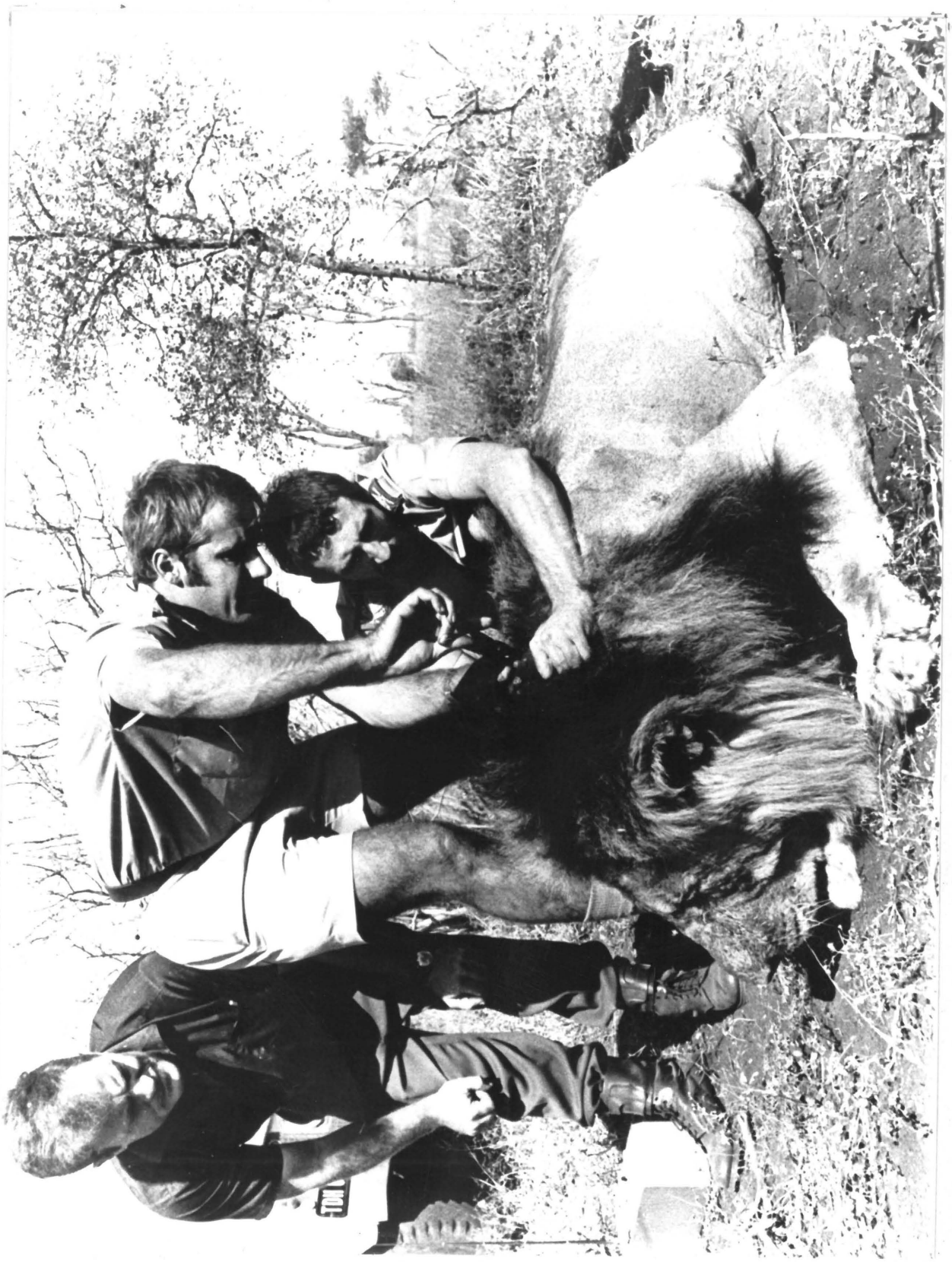

Fig. 2: Fitting of a collar to a lion.

animals caused them to become wild, making observations difficult for approximately one week after recapture. The transmitters had a limited range, approximately one kilometre on flat ground when the animal was lying down. This made location very difficult in those areas where there was no high ground for signal testing. If, however, the animal and the receiver were in line of sight on elevated ground, signals could be heard from up to five kilometres. Considering the small mass of the transmitter relative to the body mass of the lion (0,5 per cent of body mass for males and 0,7 per cent of body mass for females), it would be of little additional inconvenience to the animal if the mass of the collar was doubled to give a longer battery life and/or signal strength.

In conclusion: the radio transmitting collars work well over limited ranges and time periods, but further studies of this nature should employ more powerful transmitters and batteries with a longer life span.

Schaller (1972) found that other lions bit at and scratched the collars; this was, however, not found during the present study.

Coloured Collars

These were used for the long term tracking of marked animals; some of these collars have been on lions for over two and a half years and are still in perfect condition. They are easily seen from a distance even on heavily maned males. Where their use is not prohibited for aesthetic reasons, they were the most effective marking method.

Hot Branding

Schaller (1972) reported that hot branding often caused festering wounds. This, however, was not found during the present study. Animals were branded with a nine inch number on the left hind leg and the brand was still clearly visible after 14 months (Fig. 3.).

Ear Tags

These proved to be too inconspicuous and were easily lost or torn out. Plastic tags were used in all cases. Schaller (1972) had reasonable success with metal tags. The small size of a lion's ear renders tagging and subsequent resighting impractical in areas with a dense bush cover.

Calculation Of The Number Of Lions In The Study Area

Pienaar (1969) estimated that there were 1 120 lions in the Park. This figure is not regarded as being representative of the number of lions in the Park at present and another attempt was made to obtain an estimate of their numbers. The lions' shy nature and relatively small size make it impractical to use direct census methods such as aerial counts to determine their population size and it is therefore necessary to apply indirect methods.

In areas where tourists are absent or unimportant, an extensive marking programme could be carried out. All sightings of marked animals could then be recorded and processed statistically in the required way to give an approximation of population size (Overton and Davis 1969). This method is not practical in the study area with its high tourist volume. Expense in catching lions is also considerable and the procedures extremely time consuming. Ketamine, the drug most suitable, is now obtainable in powder form at R75,00 per 10 grams.

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Fig. 3: Lioness showing hot brand after 14 months.

The method used for calculation of the number of lions in the Park was based on reports sent in by Rangers at the end of each month. These reports give the size of each pride as well as the sexes of the adult animals and the approximate ages of sub-adults. These data were plotted onto a grid map of the Park (Fig. 4), with coloured pins representing prides of different sizes. This was done for each month in 1972. These maps were then superimposed on each other to give a distribution of the lions in the area. These data were correlated to known activity zones of marked animals in each major area of the Park. From this the approximate range and size of each pride was calculated. The instability of the pride as a unit was also taken into account in this calculation.

The figure obtained was used as an estimate of the lion population and employed in calculations on the effect of lion predation.

REGIONAL STUDIES

The study was divided into four sections to cover the important prey populations of the Park, and to investigate seasonal differences in lion predation.

The study was instigated at the beginning of 1971 and the field work was completed in mid-1973.

The Central District - Satara Area - Dry Season

This is a favoured wildebeest and zebra habitat (Fig. 5. Unit (1)).

The Central District - Satara Area - Rainy Season

The second part of the study was also conducted in the Satara area (Fig. 5. Unit (1)).

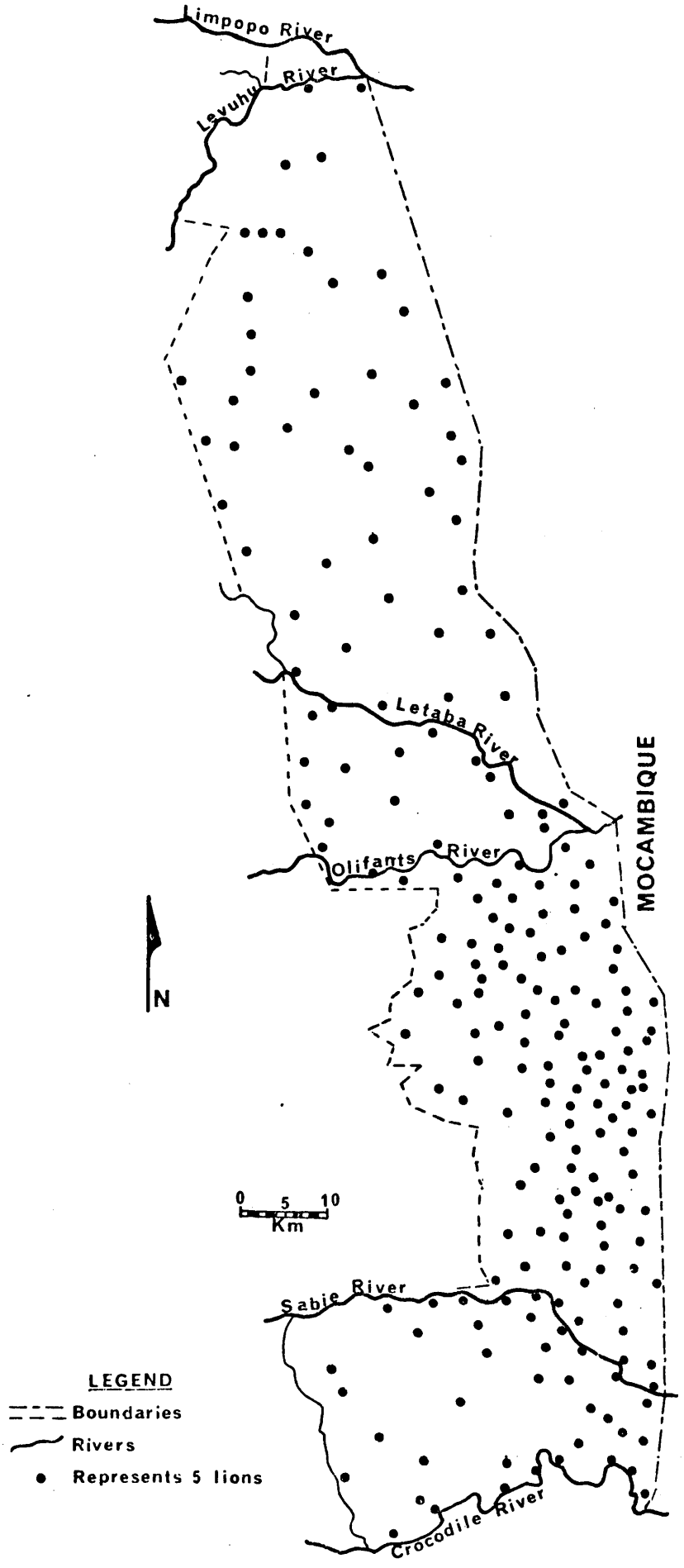

Fig.4. Distribution of lions in the Kruger National Park, South Africa.

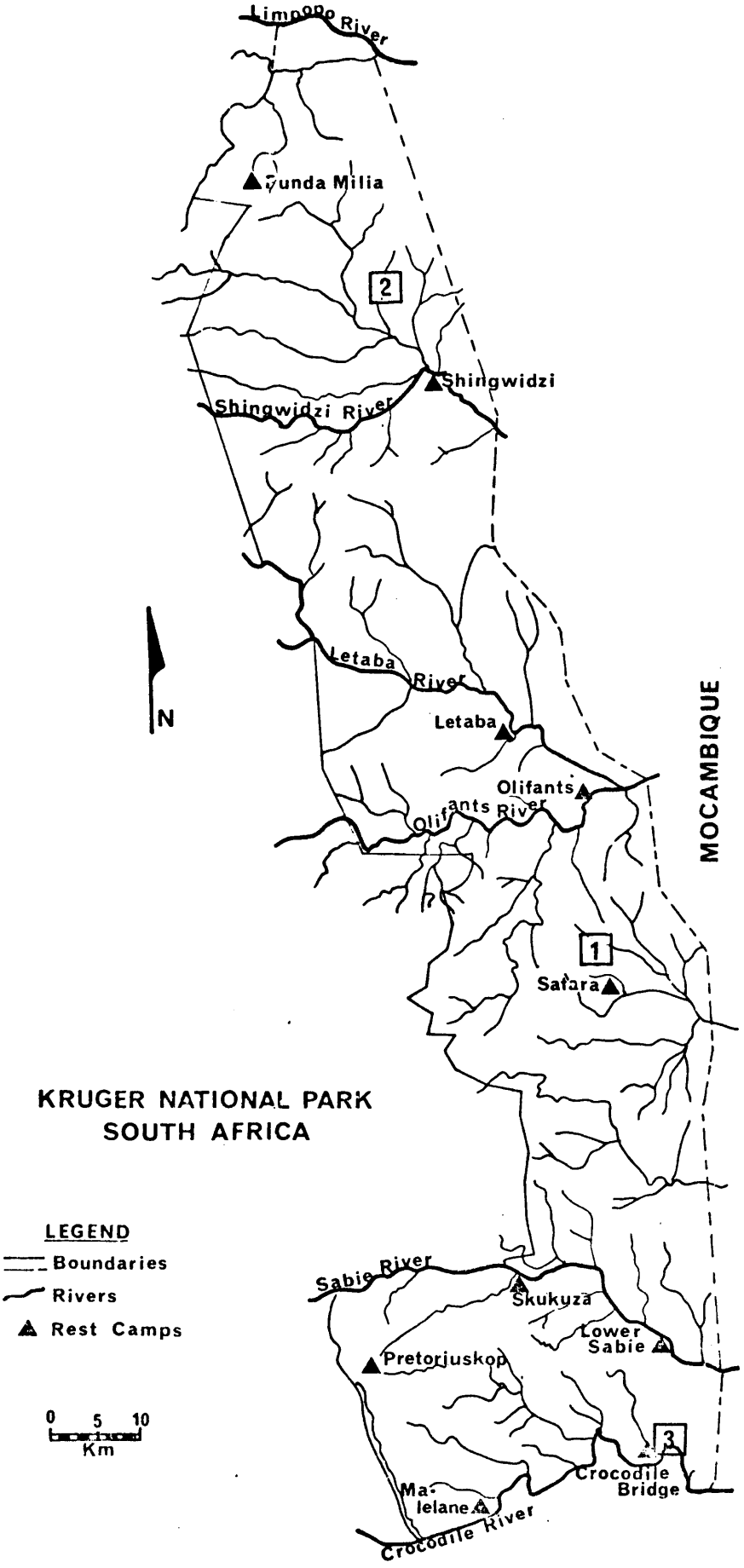

Fig.5. Indication of various study areas.

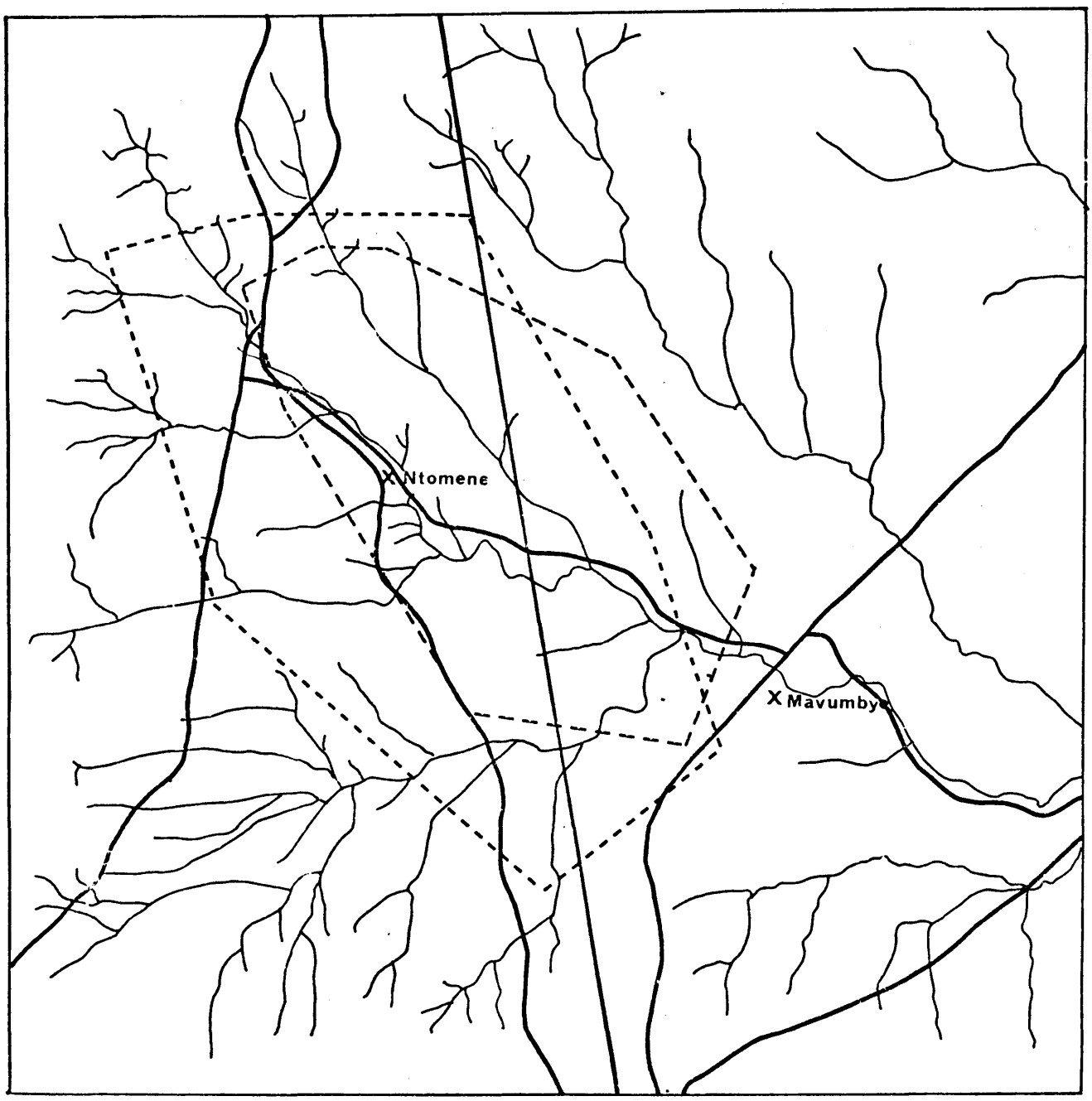

Fig. 5. Unit (1). Activity zones during wet and dry seasons of a pride of lions in the Satara area of the Kruger National Park.

LEGEND

Roads

Streams

X Windmills

Dry season activity zone

Wet season activity zone

0 1 2

Km

N

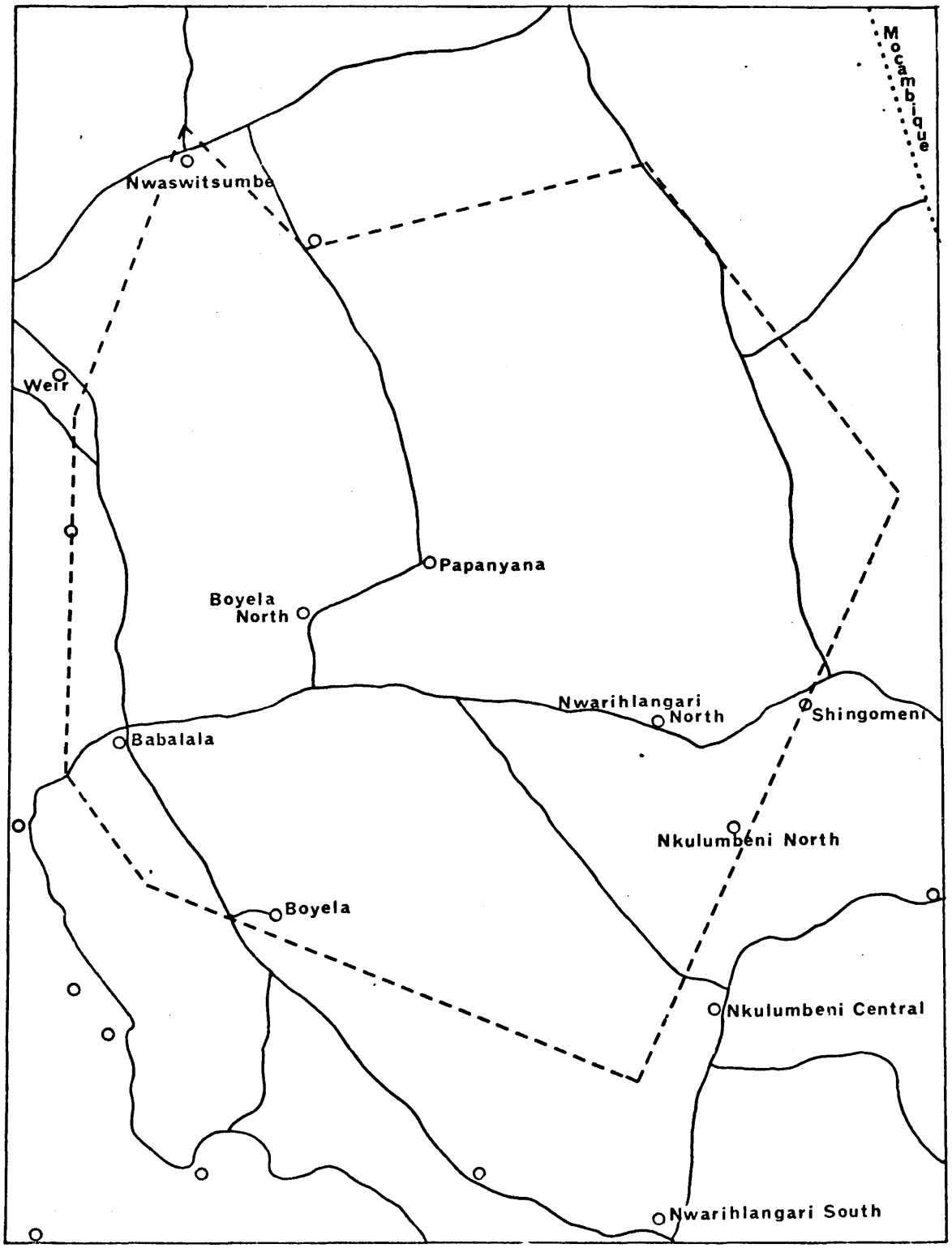

Fig.5. Unit(2). Activity zone of a pride of lions in the Boyela area of the Kruger National Park.

LEGEND

- Permanent water points
- International boundary
- Roads
- Activity zone

N

0 1 2
Km

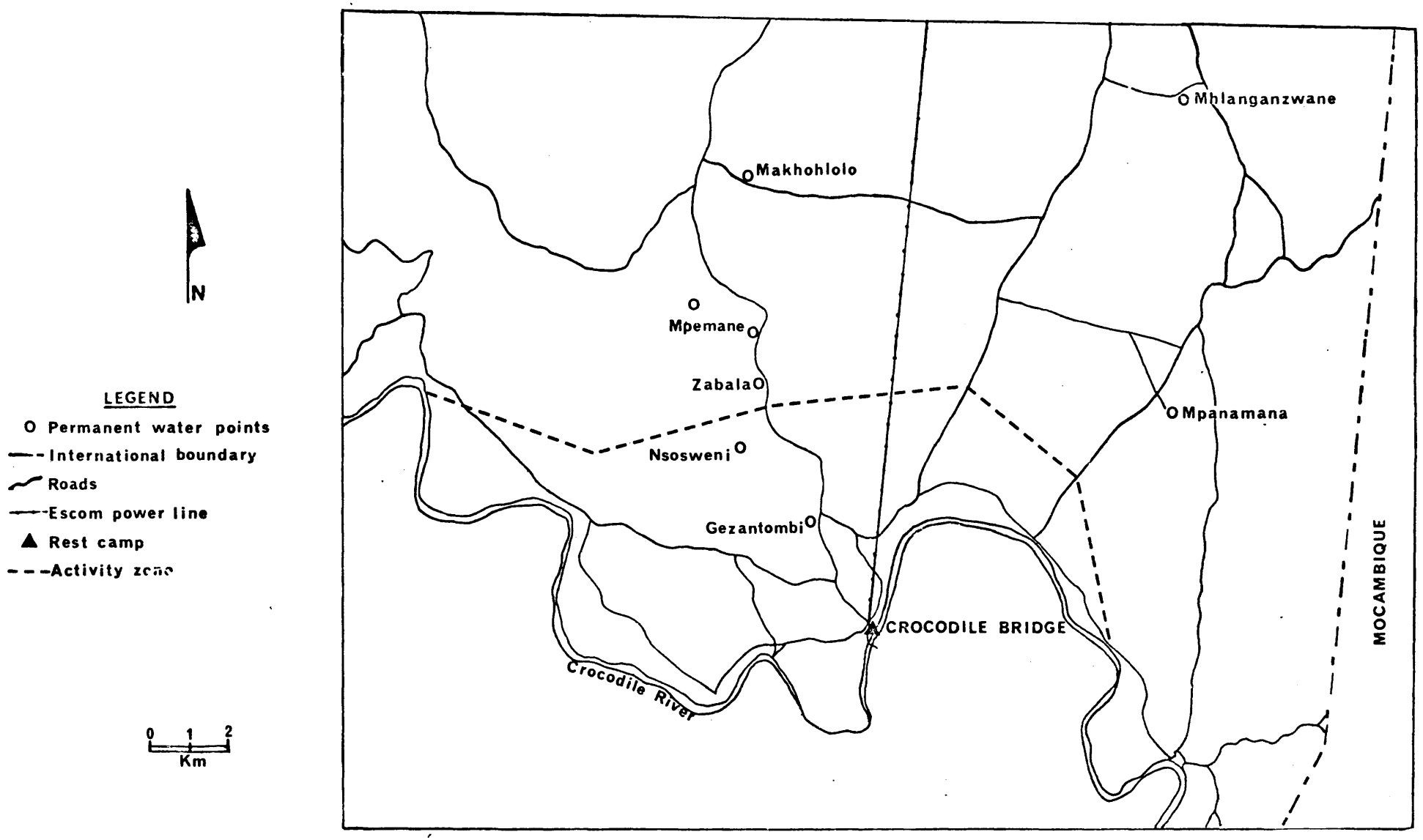

Fig.5. Unit(3). Activity zone of a pride of lions in the Crocodile Bridge area of the Kruger National Park.

The Northern District - Boyela Area

This region includes part of the favoured roan antelope habitat (Fig. 5. Unit (2)).

The Southern District - Crocodile Bridge Area

In this area large herds of buffalo and zebra are found (Fig. 5. Unit (3)).

Daily Location

A Land Rover was driven into the area where the marked lions were expected to be, high ground being selected for the testing point. Since the transmitted signal was in the frequency range U.H.F., it could not pass through land masses and it was therefore essential that the highest point in the area be selected for testing.

The aerial was raised and connected to the receiver. The receiver was switched on, the correct channel selected and the aerial rotated twice slowly through 360°. If no signal was heard the aerial was disconnected and folded into position for transportation. The Land Rover was then driven to the next position where the process was repeated.

If, however, a signal was heard the aerial was rotated slowly until a maximum in the signal was heard. The double Yaggi antenna used in this study has a front and a back, the strongest signal being heard when the front of the antenna is facing the transmitter (Fig. 6). This strong audible signal gives the animals' direction to within 10°.

If the signal was weak, the direction was noted, the aerial folded for travelling, and the Land Rover driven in the appropriate direction. After

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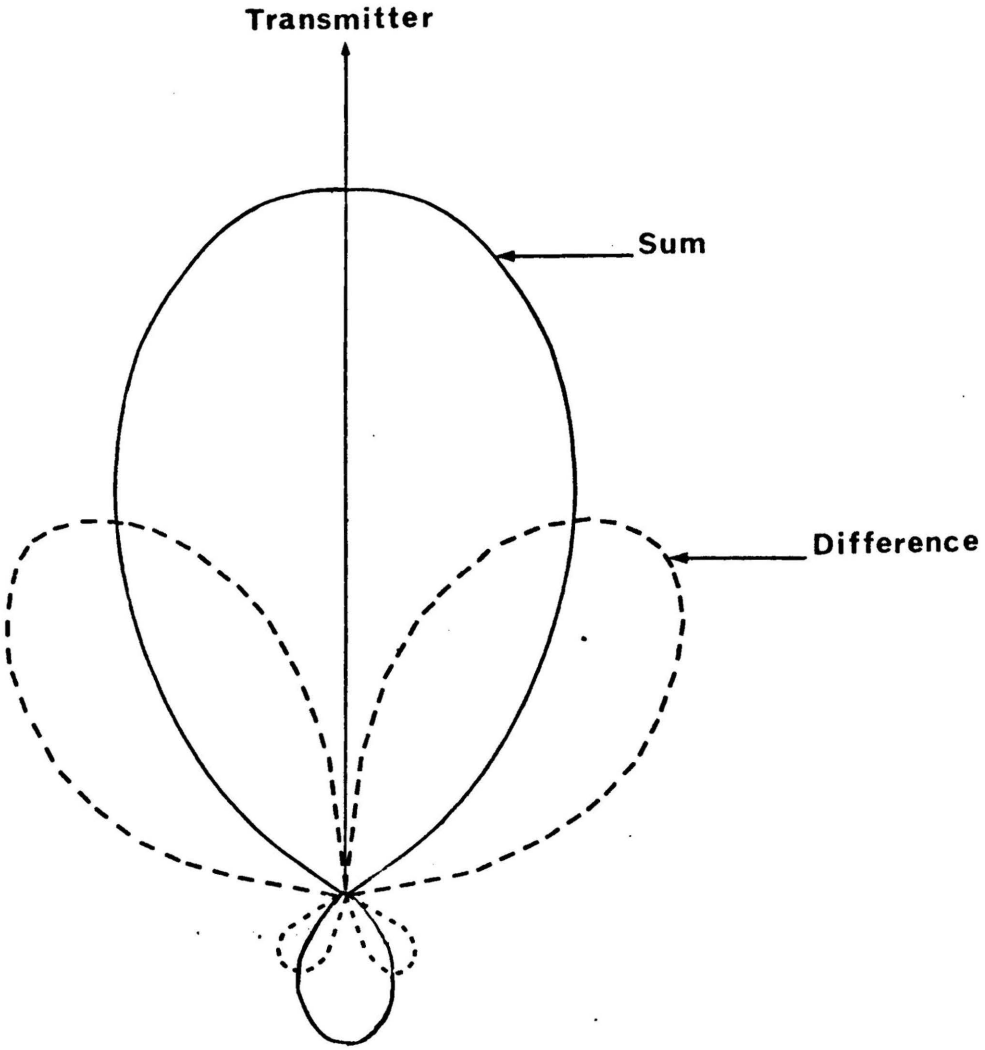

Fig.6. Typical directional pattern of a double Yaggi antenna.

travelling some distance the Land Rover was stopped and a further directional reading taken. When a fairly strong signal was received the two halves of the aerial were separated by a minimum. This null or absence of signal gives the direction of a transmitter to within 1° (Fig.6). The direction was again noted, using a tree as a land mark, and the Land Rover driven in the appropriate direction. This was continued until the lions were sighted. This was usually after the signal became too strong to determine direction accurately. It was found that if the transmitter was less than 200 metres away no direction could be determined since no matter what the position the aerial was in, a very strong signal was heard. At this range visual location was thus essential.

To make spotting easier a field assistant was placed in the back of the vehicle. From this higher vantage point it was easier to locate the lions, which after a while became so conditioned to the vehicle's presence that they scarsely raised their heads when it approached.

If the study area was adequately traversed by roads all the high points on or near the roads were used as testing sites. If no signal was heard at any of these points then the area was travelled in the form of a grid pattern. Again all the high points were stopped at and used as vantage points for signal testing.

As soon as a marked lion was spotted the field assistant crouched in the back of the Land Rover, which was reversed into such a position that the lions could not see him on the back of the vehicle. As soon as this was accomplished the field assistant left the back and climbed into the cab of the Land Rover.

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This was necessary because lions fail to associate people with vehicles and could be approached and observed under as natural conditions as possible. On a number of occasions when it was necessary to have people in the back of the vehicle the lions moved off and/or generally acted nervously. This, however, never happened when there were people in the cab only.

Collection Of Kill Data

Every morning as soon after sunrise as possible, the lions were located by means of the radio. If the lions made a kill during the night or early morning, they were usually still feeding on the carcase or lying nearby - provided the kill was not a small or young mammal.

From the external appearance of the lions' paunch it was easy to see if they had recently fed or not. If it appeared that they had eaten during the night and no kill was found nearby the lions, their spoor was followed, when possible, to their resting place of the previous day. A sharp look-out was kept for vultures, as an aid in finding the carcase remains. Vultures were particularly active in the southern and central Districts of the Park, 150 plus were seen at a kill on occasions. During the study, vultures were seen feeding on dead rabbits and various reptiles. So their importance in indicating small kills is easily seen. Lions are capable of eating entire small animals and young of the larger animals. In these cases not even the vultures find the remains of a kill. This is an error inherent in this type of study which is difficult to eliminate and probably becomes a very significant factor during and immediately after calving and lambing. Generally, however, the lions usually remained on or near most kills until the following evening.

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Only carcases which could be identified beyond doubt as having been killed by the lions were recorded, and credited to them. In one case a lion chased three adult cheetah off a freshly killed kudu and devoured it completely. In this case the lion was not credited with the kill because the cheetah had eaten about three-quarters of the flesh.

The lower jaws of all wildebeest killed were collected and aged according to Talbot and Talbot (1963). Where possible the sex of the animal was determined. In wildebeest this was difficult if the internal and external genitals had been eaten. If there was very little left of the carcase, the horns were used to sex the animals, using the criteria in Talbot (op. cit.) in conjunction with the age.

All zebra skulls were collected, aged and sexed as described by Smuts (1972 and 1974). Impala were aged in months up to 18 months, all impala older than 18 months were regarded as adult. Sexing was easy, due to the absence of horns in the females.

The mass of the remains were determined and the state of the remains and the quantity of flesh left was recorded. At kills where the cubs were present the bones were generally spread over a wide area, making assessment more difficult.

The number of lions at each carcase was recorded, as was the exact position of the kill according to a grid map of the area.

Two animals in each pride were marked for safety, because the reliability of the transmitters was not yet fully proven, nor was the stability of the pride as a unit known. The lions were captured and fitted with collars as

referred to earlier in this chapter.

This method was used throughout the investigation.

Method For Plotting Position Of Kill

Once the kill was located a landmark was selected and the Land Rover driven to it. The distance between the carcase and the landmark was taken from the Land Rover's odometer. The direction of travel was noted using a compass - from these data the position was plotted.

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CHAPTER 3. PREDATION

Predation is an extremely complex interaction of processes, few of which we are able to measure. It is basically the interaction between the behaviour of the predator and prey and includes not only overt behaviour, but also various aspects of physiology, learning and the environment. The effects of these processes are not all immediately apparent, but may later influence the population dynamics of the predator and/or prey.

THE PREY POPULATION

In the period 1966-1972 lions were recorded as having preyed on 37 species (Rangers reports). This included a broad spectrum of animals occurring in the Park from elephants to tortoises. Birds have also been reported as having being caught and killed by lions, notably ostrich, although smaller birds have also been killed.

Authentic records have proved that lions do occasionally attack and kill large prey, such as elephants, rhinoceri and hippopotami (Cowie 1966 and Pienaar 1969). Rhinoceri are not an important prey of lions, possibly because of their scarcity in the Park, but both black and white rhinoceri have been known to be attacked by lions during the course of this study.

Adult hippopotami are rarely attacked by lions, but calves are preyed upon when the opportunity arises. The calves are caught when they leave the water to follow the adult animals to the grazing grounds. In one instance recorded during the study, a calf (approximately 0,75 metres at the shoulder) was caught and killed by lions near the Olifants river.

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The lion is the dominant species in the predator hierarchy and often preys on lesser predators. Cannibalism is a common phenomenon amongst lions and was observed twice during the course of the study.

For the purpose of this study all the associated animals not listed in Table 1. will, however, be ignored in the interpretation of the results, since they form an insignificant part of a lion's diet.

Habitat Separation of Prey Species In The Four Areas Of Study

Broadly speaking the Park may be divided into four main herbivore habitats, according to the numbers of particular species found in these areas:

Riverine Bush And Areas Adjacent To The Main Rivers

These areas provide the major habitat for impala. The south bank of the Sabie river is regarded as typical of this type of habitat. Giraffe and kudu are also found in the area, but by far the most important potential prey species is impala. Other areas of the Park are similar but none show as marked a predominance of impala.

The Lebombo Flats Of The Northern Part Of The Park

This area, mopani shrub savanna, carries 80 per cent of the Park's roan antelope population and has subsequently been set aside as a sanctuary area for this species as well as for sable, tsessebe and eland. Zebra also occur here. This area is bordered to the south, west and north by a favoured buffalo and elephant habitat.

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The Plains Of The Central District

This area contains large herds of migratory and semi-resident wildebeest and zebra, numerous giraffe, buffalo and impala, together combining to form a complex prey community.

The Southern Lebombo Flats

A favoured buffalo and zebra habitat, with impala herds along the rivers.

Prey Behaviour And Susceptibility To Predation

Social organisation has been selectively enforced on animals by various factors among which predation must play a dominant role. This social organisation can roughly be grouped into two classes:

(i) Non-territorial herds, which may include mixed herds, all-male herds and herds of female and sub-adult animals.

(ii) Solitary or territorial animals. Most antelope show some form of territoriality. Lone buffalo bulls are also encountered.

Any study of predation must be coupled with an understanding of a behaviour study of the major prey species. Only through these means can the vulnerability of each age group and sex be established. These data on vulnerability are essential to determine whether predators are in fact selecting a certain section of the population for prey, or merely killing those animals most readily available.

Injured and diseased animals are not normally able to keep up with a herd in the course of its daily movements, and are consequently forced into isolation. By virtue of their isolation these animals are now more suscept-

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able to predation than they would be in the herd. There can be little doubt that lions will seek out and kill such individuals. If, however, an alert, healthy prey animal becomes aware of the lion before the final charge, the chances of its escape are very good. It seems unlikely that the lion in its short rush at a herd of prey animals has time to select a disabled individual. In stalking a herd it appears that the lion stalks the herd as a unit and only selects its prey once the animals have started running off. If, however, the animal fled a short distance and then turned to face the lion it was again vulnerable. In wildebeest and zebra this is often the case,in that the herd flees, stops and turns to look at the lion - often an alarm call is made. The bulls and stallions often leave the herd and approach the lion. These animals are now vulnerable to lion predation by virtue of their isolation from the rest of the herd. Not only this, but these animals fixate on the one or more visible lions. This often leaves their flank open to attack by other unseen lions.

Prey animals when approaching a waterhole often do so with apparent caution. Occasionally, however, entire herds of animals, particularly wildebeest, were seen to break into a run up to one kilometre from the water and continue running right to the water's edge. In this headlong rush they apparently take no precautionary measures. On one occasion a herd of wildebeest ran past a resting pride of lions. One of the lions caught an adult female, which virtually ran into the lion.

Territorial wildebeest bulls are very vulnerable to predation. These animals can be seen day after day in the same spot often not moving more than a few hundred metres except to drink. They are solitary for varying times during the year (Talbot and Talbot 1963). Personal observations have shown

that these lone bulls are readily available as lion kills. Three hunts were observed on lone wildebeest bulls, all of which resulted in a kill being made.

When a member of a family group of zebra is killed, the group stallion or other members of the group often approach the lions and call. Again these animals are fixated on a particular lion or group of lions, leaving them vulnerable to the rest of the pride.

Buffalo when grazing are usually lead by cows and younger animals with the rear being brought up by the bulls. Solitary bulls are often encountered as are small herds of bulls. Mitchell (1965) suggests that this is the cause of the high percentage of bulls in the lion kill list.

Roan antelope show very little or no response to the presence of predators. No apparent caution is taken when approaching waterholes. These animals were seen on numerous occasions to walk straight to a watering point even when other animals, notably zebra, were cautious to approach the water. This behaviour was noted on one occasion when lions were lying up near the waterhole. A herd of 17 zebra was present but would not approach the water. Three roan appeared and walked through the herd of zebra to the water. After they had drunk they left in the direction from which they had comefrom. The lions, five in this case, were invisible to me and presumably to the animals as well. Their presence was revealed by radio collars on two of them. This type of behaviour at danger points could markedly influence the mortality rate of roan.

Small groups of animals are probably more easily approached than are herd animals, this making them more susceptible to predation than animals which

congregate in large herds. The fact that roan in the Park are seldom found in groups exceeding twelve individuals could also play a large part in their susceptibility to predation.

Waterbuck have a marked preference for areas adjacent to permanent water points, showing reluctance to disperse over a wider range even during the rainy season (Pienaar 1969). Lions too show an apparent reluctance to move any great distance from water. Sixty-six per cent of the lion sightings in Section 1 of the study were within a two kilometre radius of permanent water. The waterbuck are thus by their choice of habitat placing themselves in close proximity to lions, and making themselves susceptible to predation by this proximity.

No interaction between kudu and lion were seen during the course of this study and no information could be obtained about any type of behaviour of this species which may make them susceptible to predation.

Collection Of Kill Data

Table 2 gives the kills recorded for lions and other predators, namely: leopard, cheetah, hyaena, black-backed jackal, silver jackal, caracal and serval separately, as well as the total number of kills during the period 1966-1972, plus the grand total of kills during that period.

All kills found in the Park, as given in Table 2., are recorded by Rangers and where possible the predator concerned is also noted. With practice it becomes easy to determine what predator was responsible for the kill, even if the predator had already left the kill. These results were analysed for the numbers of kills in each species and from these figures and yearly census totals, kill percentages and prey preferences were worked out.

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Table 2: Kills recorded for lions and other predators for each year separately, as well as the total number of kills during the period 1966 - 1972, plus the grand total

Species	1966		1967		1968		1969		1970		1971		1972		Totals for 1966 - 1972	
	L	O	L	O	L	O	L	O	L	O	L	O	L	O	L	O
Impala	173	860	221	832	165	736	257	788	245	688	254	766	166	472	1 496	5 142
Waterbuck	72	27	75	22	90	22	105	34	77	33	90	47	51	4	544	189
Zebra	230	2	233	11	172	7	201	15	146	15	153	37	118	9	1 253	96
Wildebeest	352	7	268	5	174	4	254	7	135	1	126	4	119	0	1 428	28
Kudu	90	19	76	32	89	17	105	25	138	47	62	28	34	9	594	177
Giraffe	53	0	55	0	64	0	65	2	65	2	41	2	36	2	371	6
Warthog	10	6	16	7	12	8	20	10	22	6	6	4	9	1	95	48
Sable Antelope	6	0	9	1	18	2	12	0	9	2	6	1	2	0	62	6
Roan Antelope	2	0	6	0	0	0	2	0	3	0	1	0	1	0	15	7
Eland	4	2	10	0	7	0	5	0	6	2	2	0	0	0	34	4
Buffalo	160	1	135	2	146	0	126	4	147	2	87	2	115	0	916	11
Tsessebe	4	1	6	1	2	1	3	1	4	0	2	0	3	0	24	4
Other	18	85	35	111	22	123	29	117	18	143	15	100	10	23	147	702
														TOTALS	6 979	6 413

L : Lion
O : Other predators

6 979 + 6 413 = 13 392

Possible criticism for these data:

(i) There is a bias towards the finding of larger kills because they are not eaten so quickly or so completely.

(ii) The patrol routes of both European and Bantu Rangers tend to follow the water courses and paths to permanent water resulting in a bias towards animals such as waterbuck which frequent the vicinity of waterholes.

(iii) The observers, the Bantu Rangers, who bring in the most data are inconsistent and may be influenced by the European in charge, who may stress the importance of boundary patrols as opposed to patrols which may lead to the discovery of kills made by predators.

In spite of this criticism it is felt that the data are sufficiently accurate to serve as an indication of the actual position, for the following reasons:

(i) Lions, and predators in general, tend to kill animals of their own size and larger (Bourlière 1963).

(ii) Prey animals are to a large extent dependant on water. In the Satara area, 51,5 per cent of all lion sightings are in a 1,5 kilometre radius from water and 66,2 per cent within a two kilometre radius.

(iii) These data on lions are the only quantitative data we have. The mere fact that these data were collected over long periods, negates the inconsistency of the observers.

Of all carcases of larger mammals found, killed by predators during 1966-1972, lions accounted for 52,1 per cent of the total 13 392.

Calculations Of Prey Preference

If the number of kills of a species were represented as a percentage of

the total number of kills recorded (Table 2.), it would give a biased impression of the actual situation. To give a representation of prey preference, the percentage of kills for a species must be expressed as a percentage of the relative abundance of that species (Pienaar 1969) i.e.,

$$\text{Preference rating} = \frac{\text{Percentage of kills}}{\text{Relative abundance of prey}}$$

If waterbuck and impala are used for comparative purposes using the data from Table 3, these two species represent 7,8 per cent and 21,5 per cent respectively of recorded lion kills. The prey preference rating, however, for these two is 7,7 for waterbuck and 0,3 per cent for impala.

Predation Relative To Density Of A Prey Species

Table 4. gives the relative abundance and percentage lion kills recorded (1966-172) for the major prey species.

It is generally believed that predation is to a large extent density dependant (Tinbergen 1946 and Errington 1946). This, however, does not appear to be so in the case of lion predation (Table 4.). There are, however, exceptions, the area immediately south of the Sabie river being the most notable, particularly between Skukuza and Lower Sabie. Impala are the only prey animals that occur in appreciable numbers in this area. Buffalo, giraffe and kudu are sometimes encountered, but so infrequently as to be disregarded as potential lion prey. It is therefore essential that lions prey on impala in this area. Schaller (1972) noted that zebra were selected in preference to gazelles which had a higher population density than zebra, in certain areas and certain times of the year.

Bourlière(1963) states that carnivores tend to prey on animals of similar

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Table 3: Prey preference rating for the main prey species as calculated from data given in Table 4

Species	Preference rating
Waterbuck	7,72
Giraffe	4,27
Kudu	3,62
Eland	3,50
Wildebeest	3,43
Zebra	2,30
Sable Antelope	1,85
Roan Antelope	1,75
Tsessebe	1,48
Buffalo	1,40
Impala	0,30

Table 4: Relative abundance and percentage lion kills recorded (1966 - 1972) for the major prey species

Species	Relative abundance	No. of kills	Percentage of kills
Impala	69,47	1 496	21,49
Buffalo	9,33	916	13,09
Zebra	7,97	1 253	17,95
Wildebeest	5,92	1 428	20,42
Kudu	2,34	594	8,49
Giraffe	1,24	371	5,30
Waterbuck	0,11	544	7,78
Warthog	1,01	95	1,36
Sable Antelope	0,48	62	0,89
Tsessebe	0,23	24	0,34
Eland	0,14	34	0,49
Roan Antelope	0,12	15	0,21

mass to their own. This is corroborated by the findings of the present study.

The figures for percentage kills and prey preference show a definite trend towards the catching and killing of large animals in preference to the smaller animals.

Scavenging

Lions will often chase lesser predators from their kill and consume it. Cheetah are particularly prone to this. Lions have been recorded as having climbed trees to take down leopard kills left in them. The Lower Sabie road, an area carrying a large lion and leopard population is the scene of many such encounters. For example, a lion was seen to chase a leopard up a tree and then proceeded to eat an impala, which the leopard had killed, near the base of the tree.

Lions are attracted by vultures and seem to follow their flight to detect carrion. On the Lindanda flats, while the author was observing a pride of four lions, one of the lions was seen to look up, apparently at a group of vultures flying past overhead. These vultures were landing in trees about one kilometre away. Two of the lions immediately started trotting towards this spot. On following the lions to the spot where the vultures were landing, a dead zebra, the cause of death of which could not be determined, was found. Within an hour there were seven lions at the carcase.

An elephant which had to be destroyed and fell into the Sabie river was partly eaten by lions. One lion waded into the water ignoring the crocodiles eating the carcase and proceeded to gorge itself. The other lions ate from the bank.

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CHAPTER 4. RESULTS OF BIOTELEMETRIC TRACKING

Results were obtained from a four part investigation, which covered the major prey habitats of both the rarer and more plentiful species. As it was believed that there was a seasonal difference in predation, a comparative study in the Satara area was done to cover the rainy and the dry season.

The four parts were:

(i) The Central District - Satara Area During The Dry Season (Fig. 5. Unit (1))

(ii) The Central District - Satara Area During The Rainy Season (Fig. 5. Unit (1))

(iii) The Northern District - Boyela Area (Fig. 5. Unit (2))

(iv) The Southern District - Crocodile Bridge Area (Fig 5. Unit (3))

RESULTS OF KILL FREQUENCY IN THE SATARA AREA DURING THE DRY SEASON

The results of the kill frequency for the Satara area during the dry season are given in Table 5.. These represent the results for a particular pride, consisting of three adult males, two adult females and seven cubs. For the first six days of the study a third male was present at all the kills, after which he was not sighted again. Another male joined the pride on day 41 and stayed with the pride throughout the study. The ageing criteria of cubs is described in Chapter 7. This first section of the study lasted five months, but unfortunately had to be interrupted for short intervals due to problems with the tracking apparatus. This gave a total number of 88 days of observation stretched over a period of five months.

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Table 5: Kills made by a single pride of lion, found in 88 randomly distributed days of dry season observation in the Satara area

Day No	Species	Sex	Age	Lions present		
				F	M	C
1	Wildebeest	M	33-37 months	3	3	7
3	Wildebeest	F	12-14 months		3	
6	Zebra	-	-	2	3	7
13	Zebra	M	3-5 years	1	2	
16	Wildebeest	F	8-12 years	2	2	7
16	Wildebeest	-	3 months			
29	Wildebeest	M	8-12 years	2	2	7
32	Wildebeest	M	8-12 years	2	2	7
36	Wildebeest	-	-	2	2	7
39	Impala	M	Adult	2	1	7
46	Wildebeest	M	8-12 years	2	2	7
46	Zebra	F	11-12 years		2	
51	Wildebeest	-	8-12 years		3	
53	Wildebeest	-	15-20 months	2	3	7
58	Wildebeest	M	8-12 years		4	
61	Wildebeest	-	8 months		3	
64	Wildebeest	M	8-12 years	2	4	
66	Wildebeest	F	5-7 years		3	
74	Wildebeest	F	Old	2	3	7
74	Wildebeest	M	5-7 years	2	3	7
76	Kudu	M	Adult	2	3	7
84	Wildebeest	M	5-7 years		2	

M : Male
F : Female
C : Cubs
100 mm rain between 84 - 88, end of first section
A strange male joined the pride on days 46, 58 & 64

Table 5a: The date, corresponding day number and block number on which observations were made during the dry season by a single pride of lions in the Satara area.

	Date	Day no.	Block no.		Date	Day no.	Block no.		Date	Day no.	Block no.
x	71/06/13	1	L10		71/07/19	30	K11		71/09/27	59	M12
	/14	2	S17		/26	31	N09		/28	60	K12
x	/15	3	N11	x	/27	32	L9	x	/29	61	L9
	/16	4	T12		/28	33	L11		/30	62	K12
	/17	5	J11		71/08/03	34	O12		71/10/06	63	K13
x	/18	6	O21		/04	35	M9	x	/07	64	M9
	/19	7	M3	x	/05	36	O9		/08	65	P13
	/20	8	N10		/05	37	K11	x	/10	66	M10
	/21	9	L10		/09	38	M12		/11	67	K13
	/22	10	M12	x	/10	39	O11		/12	68	L10
	/23	11	K8		/11	40	P10		/13	69	L10
	/24	12	I9		/12	41	L9		/14	70	L10
x	/25	13	M11		/13	42	M10		/15	71	N12
	/26	14	T18		/16	43	O12		/16	72	J10
	/27	15	M12		/17	44	G11		/17	73	M11
x	/28	16	N11		/18	45	K9	x	/18	74	P13
	/29	17	L13	x	/19	46	M12		/19	75	P13
	/30	18	K10		/20	47	K9	x	/20	76	K9
	71/07/01	19	P3		/23	48	K10		/21	77	J9
	/02	20	M6		/24	49	J7		/22	78	P12
	/03	21	O11		/25	50	J12		/23	79	V9
	/04	22	L10	x	/26	51	P10		/24	80	P10
	/05	23	O11		/27	52	K10		/25	81	J12
	/06	24	J8	x	71/09/13	53	P10		/26	82	K11
	/07	25	P11		/14	54	K10		/27	83	N18
	/08	26	O12		/15	55	P3	x	/28	84	P11
	/09	27	S13		/16	56	K10		/29	85	T18
	/10	28	O11		/17	57	P11		/30	86	P11
x	/11	29	M12	x	/18	58	L9		71/11/01	87	S17
									/02	88	T15

x Days on which kills were made

These days of observation were not continuous but were taken as being so, since they were randomly distributed over the five month period.

Discussion Of Tabulated Results (Table 5.).

The pride as a unit killed on an average once every four days. This, however, creates a false impression of the true situation. The males who carried the radio collars were found at all carcasses (with two exceptions). On one of these occasions, one of the radio marked animals was found in company of another male on a zebra carcase (see day 46 of Table 5.).

On day 74 two adult wildebeest were killed and completely eaten. After having gorged themselves the lions were reluctant to walk in their engorged state. They walked with some apparent difficulty, caused by their grossly distended bellies. On the 75th day they still appeared to have full paunches, yet on the night of the 75th day they killed and ate an adult kudu bull. The killing of this kudu must be regarded as being opportunistic, as hunger can almost be ruled out as a motivation factor for killing the kudu. It would be impossible to account for the amount that the young animals eat in a predation study over a long period, so for convenience in this first part of the study the young animals, seven in number and $\pm$ 4$\frac{1}{2}$ months old at the start of the study and $\pm$ 10 months old at the end of the study will be taken as representing two adult animals. Schaller (1972) also equated four cubs with one adult lion. In this instance, however, Schaller does not give the ages of the cubs, which, according to his criteria could be any age up to 24 months. Using the equivalents as stated above for representing the young lions as adults, the seven lions killed

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two wildebeest and a kudu having a carcase mass of 607 kg . The 607 kg represents the approximate total mass of the three animals, minus stomach content mass. The mass of the remains of lion kills was determined where possible. From these data it was calculated that approximately 25 per cent of the carcase mass of the animal was not eaten. Presuming that one quarter of each animal was not eaten and that each lion ate an equal amount regardless of sex, then each lion ate approximately 65 kg over a three day period. The amount of wastage could have been greater than estimated, but this still indicates the enormous quantities of meat a lion can consume under favourable circumstances.

The mean of one kill every four days does not give an accurate approximation to the kill frequency as the interval between kills varied from 0 (day 74) to 13 days (day 16-29) (this was an uninterrupted observation period). The standard deviation for these data was 9,4 days.

For interpretation of the results the fact that the females were absent at 35 per cent of the kills, will be ignored. Lionesses did, however, apparently kill independently of the males and two kills were found in the course of tracking the males. These two kills are not recorded in the table, as it could not be said that the lionesses actually made these kills. Both these were impala under two years of age. The only other impala killed was an adult male. On this occasion there was only one marked male present (day 39). The fact that the lionesses apparently killed two impala in an area where impala are scarce compared to wildebeest and zebra, seems to indicate that the females of this pride were reluctant to tackle the larger prey species, whereas the males caught only the large prey.

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From day 41 the pride was joined by a very distinctive male. This male had a very well developed mane, almost orange in colour and therefore very easily recognised even from a distance. Because of his presence for the last 47 days of this phase, the study should be divided into two parts:

(i) Where the pride consisted of:

2 Adult males,

2 Adult females,

2 "Adults" (7 cubs)

(ii) Where the pride consisted of:

3 Adult males,

2 Adult females.

2 "Adults" (7 cubs).

In the first 41 days of observation there were 10 kills. Therefore the pride of six animals killed every 4,1 days.

In the second 47 days of observation there were 12 kills, or one kill every 3,9 days.

A t-test was applied to both parts and no significant difference was found at the five per cent level (t=0,3438).

One can therefore accept that there is no significant difference between the kill frequencies of the two sections. To simplify later calculations they will be regarded as one unit - relating to the pride consisting of:

3 Adult males,

2 Adult females,

2 "Adults" (7 cubs)

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The mean kill frequency for the pride is one kill every four days, i.e. seven lions kill one animal every four days. Each individual in the pride kills one animal every 28 days, or 13 kills per year, if the dry season conditions held throughout the year.

This study area was well supplied with land marks so it was possible to determine the position of the kill quite accurately. The grid used for this study gave 500 metre square blocks.

It was seldom necessary to travel more than one or two kilometres to a fixed point, so that estimation of distance was made less complicated. The size of the grid used also allowed for errors in distance estimation.

Of the 22 kills recorded 14 or 63,6 per cent were within a 1,5 km radius of the only permanent waterhole (Fig. 7.).

Carcase Mass Of Kills Made By The Pride

In the 88 day observation period the pride made 19 kills representing a carcase mass of 3 956 kg (Table 6.).

Activity Zone

The daily position of the pride was plotted onto the map of the area, using the same method used to determine the coordinates of the kills found.

Of the 68 positions recorded 35, that is 51,5 per cent were in a 1,5 km radius of the windmill and 45, that is 66,2 per cent, in a two kilometre radius. The remaining 23 positions, 33,8 per cent, were randomly distributed over the entire area with a maximum of 7,5 km from the windmill.

During daylight hours the pride was usually found sleeping under trees or bushes. They were nearly always found resting in or near fairly dense vegetation and very seldom found lying up under a tree in a short grass or over grazed area. The only times that the lions were found lying up in

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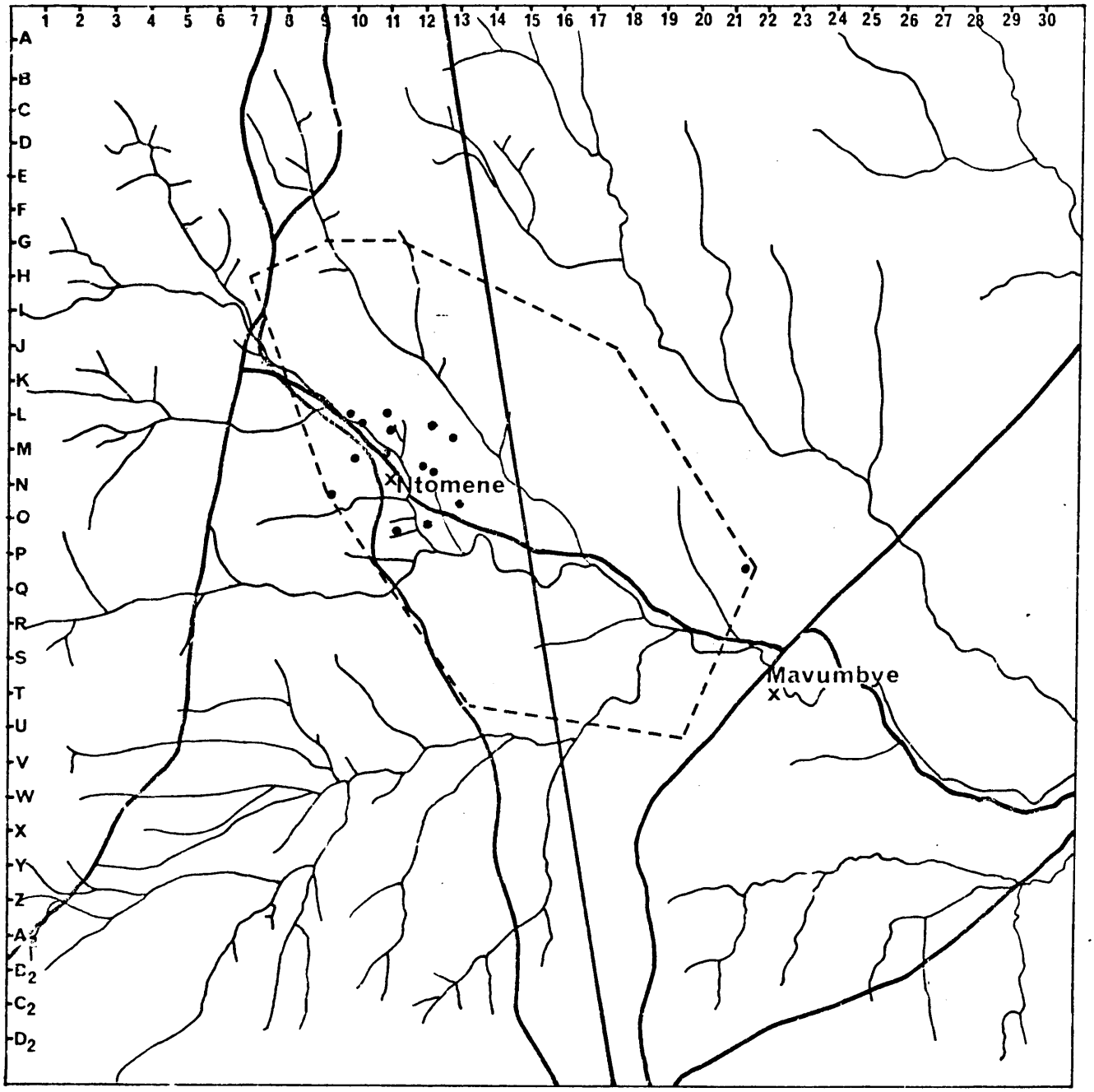

Fig.7. Activity zone and proximity of kills to water of a pride of lions during the dry season in the Satara area of the Kruger National Park.

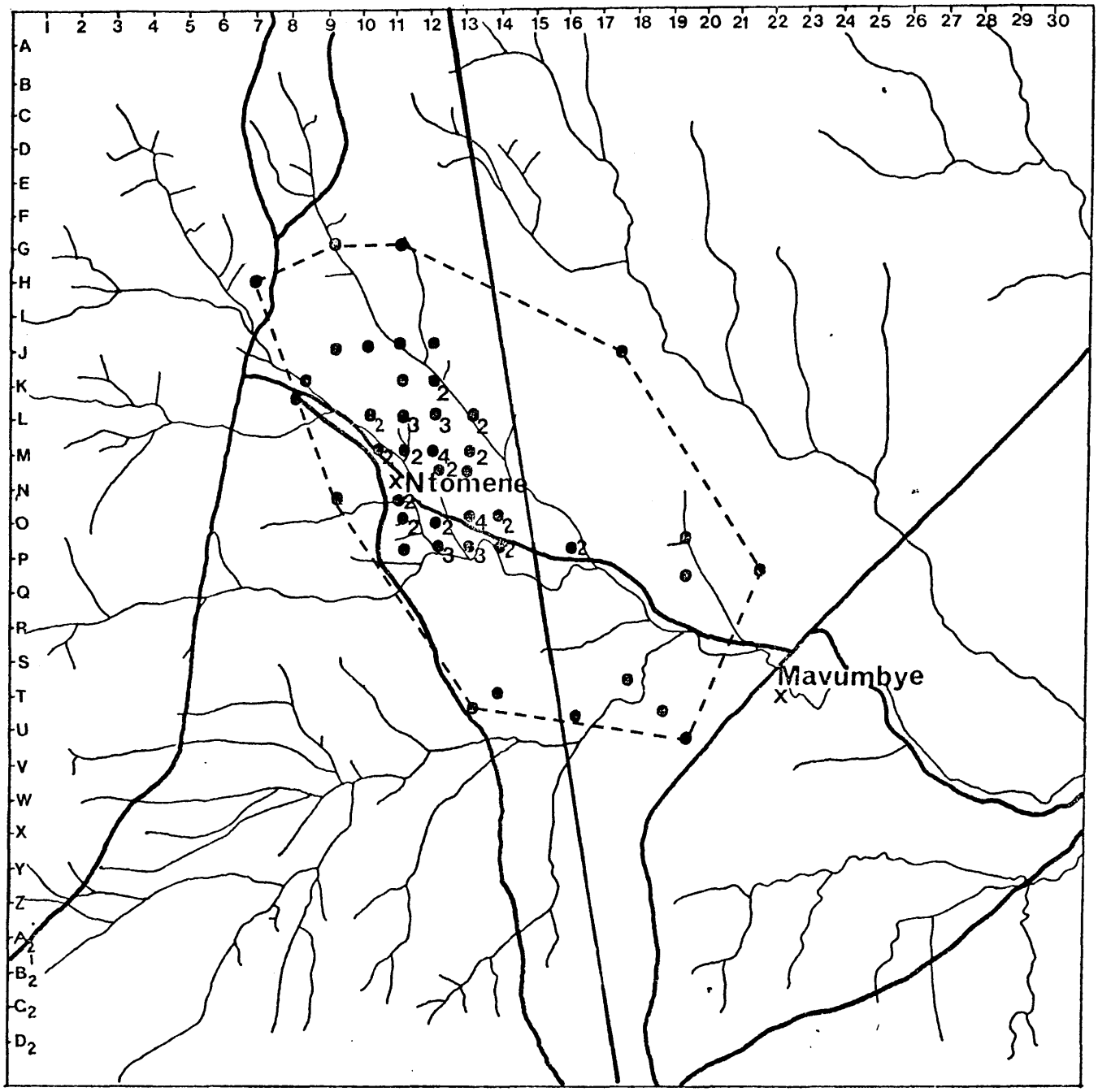

Fig.7a Daily positions with number of recorded sightings per grid of a pride of lions as recorded during the dry season in the Satara area of the Kruger National Park.

LEGEND

- Sightings
- Activity zone
- Roads
- Rivers
- X Windmills

0 1 2
Km

N

Table 6: Carcase mass of 22 lion kills, by a single pride, in the Satara area during the dry season

Species	Age	Sex	Carcase mass in kg
Wildebeest	3 months	-	23
	8 months	-	91
	12-14 months	F	106
	15-20 months	-	142
	33-37 months	M	179
	5-7 years	M	203
	5-7 years	M	203
	5-7 years	-	196
	5-7 years	-	196
	8-12 years	M	212
	8-12 years	M	212
	8-12 years	M	212
	8-12 years	M	212
	8-12 years	M	212
	8-12 years	F	178
	13+ years	F	173
	-	-	173
Zebra	3-5 years	M	264
	11-12 years	F	264
	-	-	227
Kudu	Adult	M	231
Impala	Adult	M	44
			TOTAL : 3 956

M : Male
F : Female

such an area was when they were found on a kill. This is linked to the habitat preferences of the two major prey species, wildebeest and zebra, in this area, which are very seldom found in long grass of heavily wooded areas.

The area within the two kilometre radius of the windmill provided suitable habitats for both lions and their prey species.

The area to the north-east of the new road to the Olifants river is a mosaic of long and short grass areas, while the area to the south-west is virtually all short grass and a preferred wildebeest and zebra habitat. Only five sightings were made in this last mentioned area, i.e. only 13,1 per cent of the total sightings made within the two kilometre radius of the windmill.

Three of these sightings were made while the lions were on kills. The other two sightings were made in isolated long grass areas, with numerous Acacia nigrescens shrubs.

From this it would appear that the preferred diurnal activity zones of this pride of lions was the area to the north-east of the new road which had an admixture of long and short grass areas crossed by various spruits.

The sightings made in the rest of the area occupied by this pride of lions were all made in well wooded long grass areas with one or two exceptions.

The total area covered by this pride was 61 sq km . The method used to obtain this is as follows: Peripheral sightings were joined by straight lines and the enclosed area calculated. Here the mid-point of the block was used to give the extreme position of the animal or pride (Fig. 7.).

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RESULTS OF KILL FREQUENCY IN THE SATARA AREA DURING THE WET SEASON

This section of the study was conducted in the same area as the first section, but observations were made during the rainy season. At intervals it had to be interrupted when it became impossible to travel in the area.

Table 7. gives the kill frequency of 75 days of randomly distributed observations in this area.

Discussion Of Tabulated Results (Table 7.).

In a period of 75 days the pride as a unit killed 17 times, giving an average of one kill every 4,4 days. This is merely an approximation to the actual interval between kills which in actual fact varied from one day (day 21-22), to a maximum of nine days (day 22-31). The maximum period between kills could have been greater, as it was not possible to locate the pride previous to the resumption of tracking on day one, after which they made their first kill on day nine.

When this part of the study started the pride as a whole was in very poor physical condition, so it can reasonably be assumed that they had not eaten for about a week prior to the start of this part of the study. For this part of the study the pride is regarded as consisting of:

2 Adult males,

2 Adult females,

3 "Adults" (7 large cubs).

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Table 7: Kills made by a single pride of lion over 75 randomly distributed days of wet season observation in the Satara area

Day No	Species	Sex	Age	Lions present		
				F	M	C
9	Zebra	F	Very old	2	3	7
x 15	Kudu	M	Adult		3	
21	Wildebeest	M	8-12 years		1	
22	Wildebeest	F	5-7 years	2	2	7
31	Wildebeest	M	8-12 years		1	
31	Wildebeest	F	± 54 months	2	2	7
*35	Wildebeest	F	5-7 years		3	
38	Wildebeest	M	13+ years	2	2	7
43	Wildebeest	M	5-7 years	2	2	7
47	Wildebeest	-	2 months		2	
50	Zebra	F	-	2	2	7
51	Wildebeest	-	14 months	2	2	7
55	Wildebeest	F	36 months	2	2	7
@56	Wildebeest	-	8-12 years	2	2	7
59	Wildebeest	F	54 months	2	2	7
61	Kudu	M	Adult	2	2	7
64	Wildebeest	M	8-12 years	2	2	7
68	Wildebeest	F	-	2	2	7
73	Zebra	F	Very old	2	2	7

M : Male
F : Female
C : Cubs
@ : 13 day break in observations
x : One of the males left the area
* : A strange male joined the pride on day 35

Table 7a: The date, corresponding day number and block number on which observations were made during the wet season by a single pride of lions in the Satara area.

	Date	Day no.	Block no.		Date	Day no.	Block no.		Date	Day no.	Block no.
	71/11/08	1	L9		72/01/02	26	K11		x72/02/10	51	O7
	/09	2	F2		/03	27	P12		/11	52	P10
	/10	3	G3		/04	28	U18		/12	53	H9
	/19	4	O66		/05	29	X12		/13	54	K11
	/20	5	J8		/06	30	K9	x	/14	55	K11
	/21	6	I11	x	/07	31	P8	x	/27	56	Q15
	/22	7	M14		/08	32	P8		/28	57	K11
	/23	8	I9		/09	33	M5		/29	58	K12
x	/24	9	J6		/10	34	L11		x72/03/01	59	T14
	/25	10	P6	x	/11	35	K9		/02	60	T15
	/26	11	U11		/12	36	KL	x	/03	61	M15
	/28	12	K10		/13	37	M15		/04	62	P11
	/29	13	I9	x	/14	38	T17		/05	63	J9
	/30	14	I7		/17	39	O10	x	/06	64	L9
	x71/12/01	15	I9		/18	40	J8		/07	65	Q14
	/02	16	K11		/19	41	H8		/08	66	P12
	/03	17	M3		/20	42	I9		/09	67	P12
	/04	18	M10		x72/02/02	43	E7	x	/10	68	L5
	/05	19	I9		/03	44	H6		/11	69	L5
	/06	20	I9		/04	45	K10		/12	70	J10
x	/07	21	L8		/05	46	P5		/13	71	N13
x	/08	22	L9	x	/06	47	P8		/14	72	I7
	/09	23	L9		/07	48	L12	x	/15	73	E12
	/10	24	K6		/08	49	T15		/16	74	K10
	/11	25	P11	x	/09	50	M14		/17	75	P8

X Days on which kills were made

Table 7b: Rainfall for the Satara area recorded during the dry season (71/06/13 - 71/11/02) and wet season (71/11/08 - 72/03-17) study periods.

Year	Month	Day	Rain recorded (mm)
1971	June		0
	July		0
	August		0
	September		0
	October	28th	12,0
	"	29th	17,3
	"	30th	43,7
	November	1st	27,0
	"	3rd	50,1
	"	12th	2,5
	"	15th	5,0
	"	16th	28,5
	"	17th	15,0
	"	27th	12,5
	December	-	-
1972	January	3rd	8,4
	"	6th	1,5
	"	12th	5,5
	"	13th	7,0
	"	14th	86,4
	"	18th	3,5
	"	21st	3,9
	"	22nd	12,8
	"	23rd	30,5
	"	24th	16,0
	"	25th	7,0
	"	26th	3,0
	February	2nd	2,0
	"	3rd	11,6
	"	5th	2,0
	"	15th	64,0
	"	16th	3,5
	"	22nd	60,0
	"	23rd	9,6
	"	24th	13,5
	"	29th	5,5

March	1st	4,0
"	3rd	1,5
"	5th	4,6
"	9th	7,5
"	12th	4,5
"	13th	1,2
"	14th	6,4
"	16th	10,5

* Records not available.

The cubs are now regarded as representing three adult lions because of their increased age and meat consumption.

One of the males was seldom seen with the pride from day 15 onwards.

The mean kill frequency for the pride is one animal every 4,4 days. Each individual kills one animal every 30,8 days, or 11,5 animals per year, if the wet season conditions held throughout the year.

Carcase Mass Of Kills Made By The Pride

In the 75 day observation period the pride made 19 kills representing a carcase mass of 3 578 kg (Table 8.).

The Activity Zone

The wet season activity zone of the pride was plotted in a similar way to that for the dry season. This is given in Fig. 8.

The area covered by the pride in this period was 143 sq km , compared to the 63 sq km area in the dry season.

Proximity Of Kills To Permanent Water

As can be seen from the map (Fig. 8.), the kills showed no relationship to the presence of the permanent watering point. This is because the prey animals had no need to come to this point as there were numerous veld pools in the area.

Comparison Between The Kill Frequency Results Of The Same Pride During Dry And Rainy Seasons

In the dry season the pride as a unit killed once every four days, or each

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Table 8: Carcase mass of the 19 lion kills, by a single pride, recorded during the wet season in the Satara area

Species	Age	Sex	Carcase mass in kg
Wildebeest	2 months	-	17
	12-14 months	-	105
	33-37 months	F	178
	54 months	F	178
	54 months	F	178
	5-7 years	F	188
	5-7 years	F	188
	5-7 years	M	203
	5-7 years	M	203
	8-12 years	M	212
	8-12 years	M	212
	8-12 years	-	194
	13+ years	M	172
	Adult	-	203
Zebra	Very old	F	226
	Very old	F	226
	-	F	226
Kudu	Adult	M	231
	Adult	M	231
		TOTAL :	3 578

M : Male
F : Female

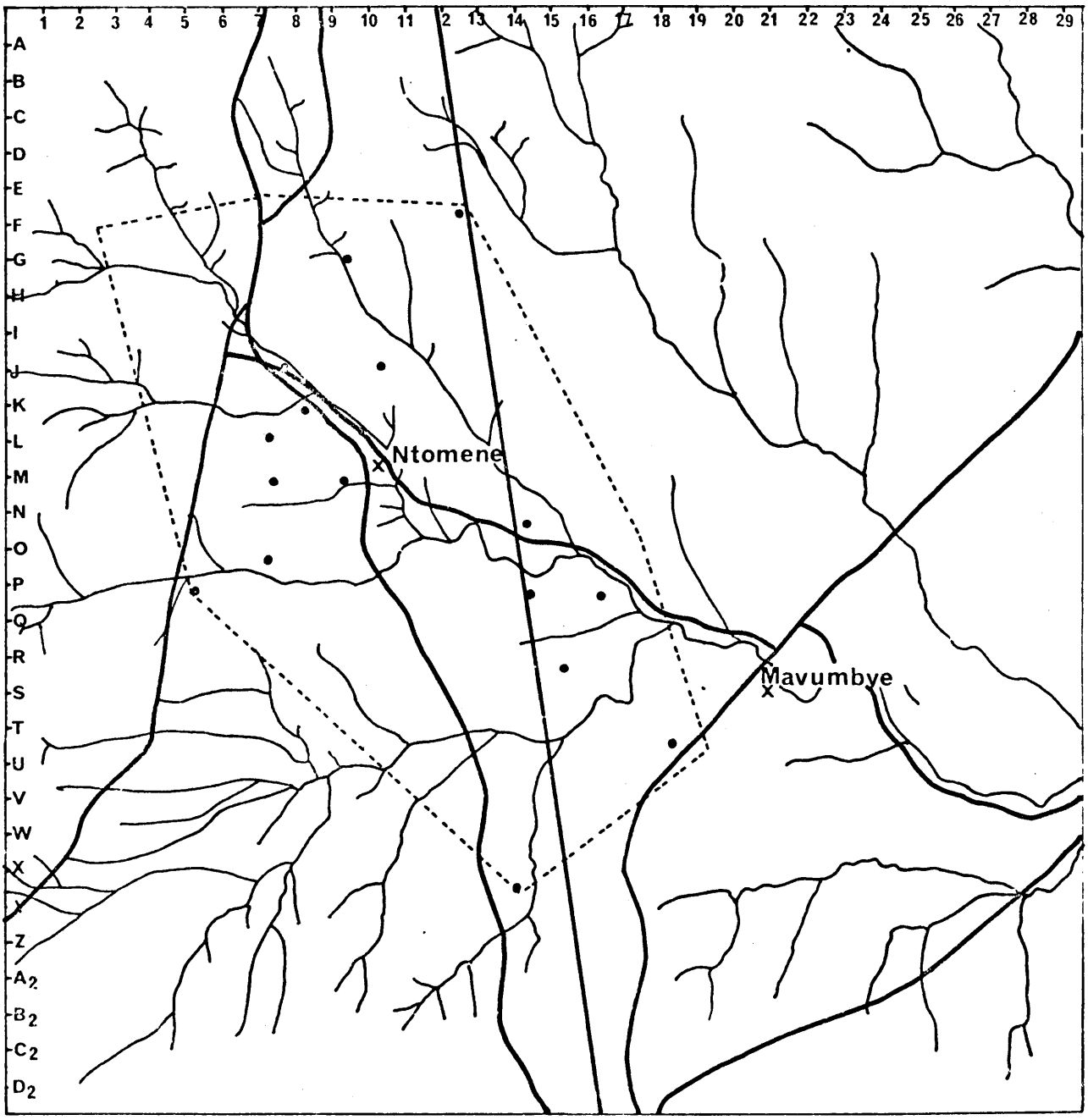

Fig.8. Activity zone and proximity of kills to water of a pride of lions during the rainy season in the Satara area of the Kruger National Park.

LEGEND

- Kills
- Activity zone
- Roads
- Streams
- X Windmills

0 1 2 Km

N

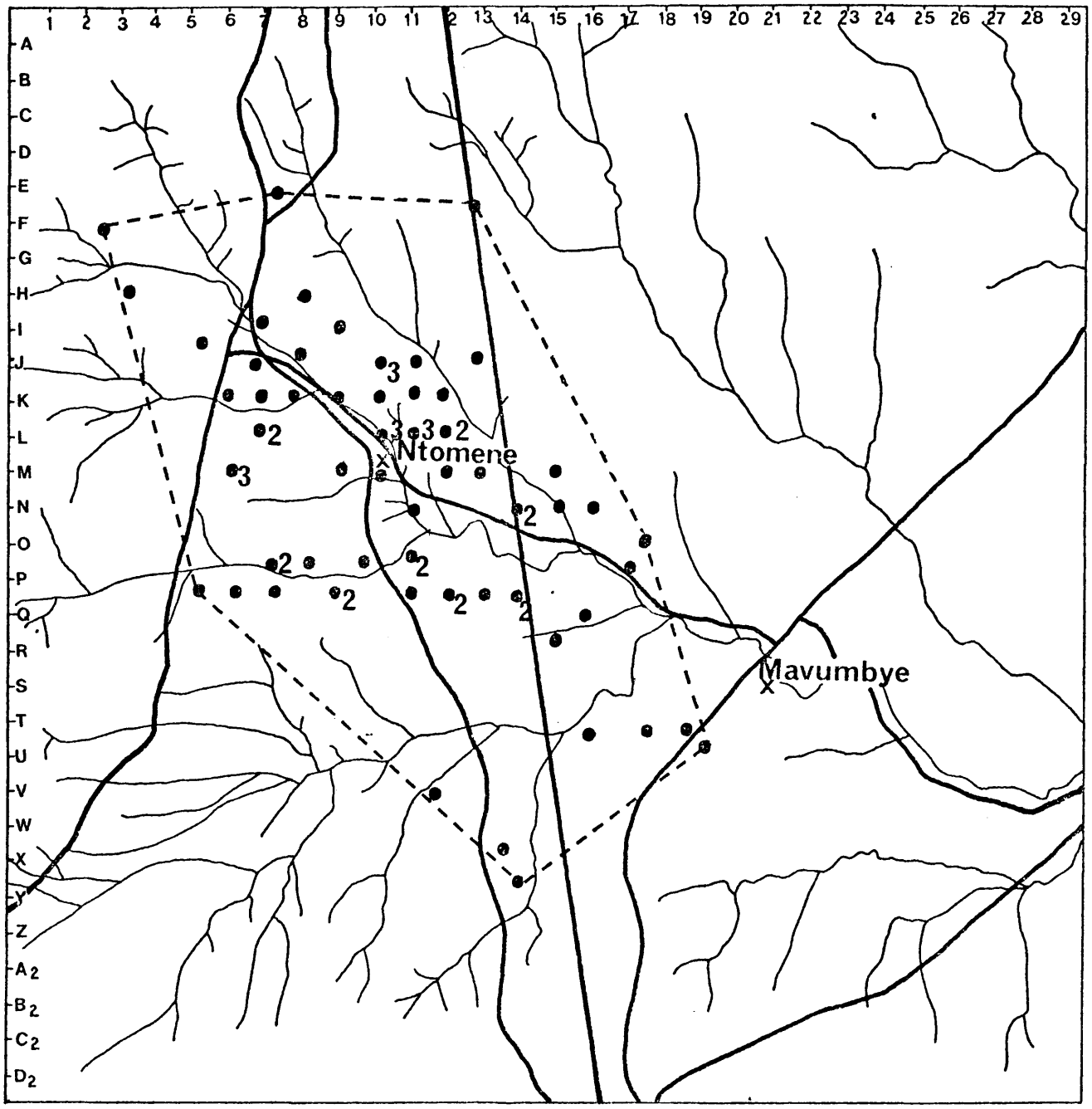

Fig.8a. Daily positions with number of recorded sightings per grid of a pride of lions as recorded during the rainy season in the Satara area of the Kruger National Park.

LEGEND

- Sightings
- Activity zone
- Roads
- Rivers
- X Windmills

0 1 2 Km

N

individual killed once every 28 days, compared to wet season frequency of once every 30,8 days.

In comparing these results it must be remembered that there were cubs in this pride and they could not be accurately fitted into the predation scheme. As the intake of several cubs was equated to one adult lion, this could lead to variations in the results obtained. It would, however, appear that there is no significant difference in predation rates during the wet and dry season.

RESULTS OF KILL FREQUENCY IN THE NORTHERN LEBOMBO FLATS (BOYELA AREA)

This area is broadly classified as mopani shrub savannah and is a preferred roan antelope habitat. Zebra, buffalo and tsessebe also occur in the area.

Table 9. gives the kill frequency of 60 randomly distributed days of observation on a single lion pride in this area. This pride was so wild that it was impossible to identify individual animals that did not wear transmitting collars. The pride will be regarded as consisting of one adult male, two adult females and three juveniles.

Discussions Of Tabulated Results (Table 9.).

In a period of 60 days this pride made a total of 11 kills, giving a frequency of one kill every 5,5 days.

This pride was wild and therefore very difficult to approach, even while on a kill. It was thus very difficult to determine the exact number of lions on a specific kill. It was found that the male of this particular

.. / 38.

pride was always the first to flee. This could account for him not being recorded at nearly 50 per cent of the kills. For the analysis of the data he will be regarded as being with the pride at all the kills. This is done on the following grounds:

No kills in the area were indicated by vultures at which at least one of the marked animals, both young females, were not present, i.e. there were no other lions active in the area at the time of the study.

It would therefore appear that the lion which at times was seen with this pride was either one of a few transients or an extremely nervous resident male.

Using similar criteria to that which was used in the first two sections of the study for young animals, these three juvenile animals will be regarded as three adult lions, their body mass being approximately equal to that of an adult at the end of the study, making a total of:

1 Adult male,

2 Adult females,

3 "Adult" (3 juveniles).

Using these figures, six lions kill one prey animal every 5,5 days. Each individual kills one animal every 33,0 days or 11,1 animals per year.

Carcase Mass Of Kills Made

Table 10. gives the mean carcase mass of lion kills recorded in the Boyela area.

In the 60 day period of observation on this particular pride, 11 kills were recorded, representing a carcase mass of 2 329 kg (Table 10.).

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Table 9: Kills made by a single pride of lion, found in 60 randomly distributed days of observation in the Boyela area

Day No	Species	Sex	Age	Lions present		
				F	M	J
6	Zebra	M	10 years	4	1	3
11	Roan	M	-	2	1	3
14	Buffalo	F	3 years	2		2
18	Giraffe	-	Young	2		3
20	Warthog	-	-	1		3
27	Waterbuck	F	Adult	2	1	
34	Impala	M	1 year	1	2	
40	Zebra	F	$4\frac{1}{2}$ years			@
44	Zebra	-	13 years	1	3	3
52	Zebra	-	8-9 years	1	2	2
59	Buffalo	-	3 years	2	1	2

@ : Unknown
M : Male
F : Female
J : Juvenile

Table 9a: The date and corresponding day number on which observations were made during the dry season on a single pride of lions in the Boyela area.

Date	Day no.	Date	Day no.	Date	Day no.
72/07/01	1	72/08/11	21	72/09/05	41
/02	2	/12	22	/06	42
/03	3	/13	23	/07	43
/04	4	/14	24	/08	44
/05	5	/15	25	/09	45
/06	6	/17	26	/10	46
/07	7	/18	27	/11	47
/08	8	/19	28	/12	48
/09	9	/20	29	/14	49
/10	10	/21	30	/15	50
/11	11	/22	31	/16	51
/12	12	/23	32	/17	52
/13	13	/24	33	/19	53
/14	14	/25	34	/20	54
/15	15	/26	35	/23	55
/16	16	/27	36	/24	56
/17	17	/28	37	/26	57
/18	18	/29	38	/27	58
72/08/07	19	/30	39	/28	59
/10	20	/31	40	/29	60

Because of the shyness of the pride it was impossible to obtain the remains of the carcase on the day of the kill, for fear they would not return once disturbed. In three cases necessary parts for sex and age determination and hence the estimation of carcase mass, could only be collected the following day. Many of these structures were by then destroyed by hyaenas. As a result three of the carcase masses given in Table 10 were roughly estimated as follows: The mass of the buffalo was taken as being the mean for that particular age class regardless of sex. The remains of the giraffe were massed and regarded as representing 25 per cent of the carcase mass. An upper and lower canine indicated that the warthog was approximately two years old. The mass of live animals this age was obtained from records kept of animals destroyed and captured in testing various immobilizing drugs.

RESULTS OF KILL FREQUENCY IN THE CROCODILE BRIDGE AREA

This area is on the southern boundary of the Park, which is formed by the Crocodile river. The latter is fenced on its south bank. These two factors combine to give a barrier to animal movement to the south. Numerous impala, zebra and herds of buffalo are found along the river.

Table 11 gives the kill results of 60 days randomly distributed observation on a single pride, in this area.

Discussion Of Tabulated Results (Table 11.).

The interpretation of results for this section is made difficult by the lack of uniformity in the pride size as found on the kills. This is to a large extent probably due to the linear nature of the pride's activity zone,

.. / 40.

Table 10: Carcase mass of 11 lion kills, by a single pride, in the Boyela area

Species	Age	Sex	Carcase Mass in kg
Zebra	13 years	F	220
	8-9 years	M	220
	8-9 years	M	220
	$4\frac{1}{2}$ years	F	200
Buffalo	3 years	-	265
	3 years	F	265
Giraffe	$\pm$ 2 years	-	400
Roan	Adult	M	270
Waterbuck	Adult	F	200
Impala	18 months	M	39
Warthog	-	-	30
		TOTAL :	2 329

M : Male
F : Female

Table 11: Kills made by a single pride of lion, found in 60 ramdomly distributed days of observation in the Crocodile Bridge area

Day no	Species	Sex	Age	Lions present		
				F	M	C
1	Waterbuck	M	Adult	5	2	7
3	Buffalo	-	± 14 months	4	1	7
7	Buffalo	M	Adult	5	2	7
13	Buffalo	M	Adult	4	2	7
21	Giraffe	F	Adult	4	3	
23	Buffalo	F	Adult	5	2	7
29	Wildebeest	F	8-12 years	5	2	
34	Waterbuck	F	Sub-adult		2	
34	Impala	M	Adult	5		7
39	Waterbuck	F	Adult	4	2	3
44	Buffalo	-	5 months	3	1	4
50	Waterbuck	M	Adult	3	2	6
52	Impala	M	Adult	3		5
56	Buffalo	M	5 months	3		5

M : Male
F : Female
C : Cubs

Table 11a: The date and corresponding day number on which observations were made on a single pride of lions in the Crocodile Bridge area.

Date	Day no.	Date	Day no.	Date	Day no.
72/10/02	1	72/10/28	21	72/11/26	41
/03	2	/29	22	/27	42
/04	3	72/11/01	23	/30	43
/05	4	/02	24	72/12/03	44
/07	5	/03	25	/04	45
/09	6	/04	26	/05	46
/10	7	/05	27	/06	47
/12	8	/06	28	/07	48
/13	9	/07	29	/10	49
/14	10	/08	30	/12	50
/15	11	/09	31	/13	51
/16	12	/13	32	/14	52
/19	13	/14	33	/15	53
/20	14	/15	34	/16	54
/21	15	/16	35	/17	55
/22	16	/18	36	/18	56
/23	17	/19	37	/19	57
/24	18	/23	38	/20	58
/26	19	/24	39	/23	59
/27	20	/25	40	/24	60

the southern boundary line being the Crocodile river, along which four different prides were known to be active during the study period. This overlapping of activity zones could possibly have led to a mixing of the individuals of a pride with those of another. In so doing, an individual may be absent from its home pride for varying lengths of time.

The pride is considered as consisting of:

2 Adult males,

4 Adult females,

2 "Adults" (7 cubs, ranging in age from ± 3-10 months).

The 14 kills were recorded in a 60 day observation period, therefore the pride of eight killed every 4,3 days. Each individual lion killed once every 34,4 days or 10,6 prey animals per year.

Carcase Mass Of Kills Made By The Pride

Table 12. gives the mean carcase mass of kills made by a single pride of lions in the Crocodile Bridge area.

In the 60 day period of observation on this particular pride, 14 kills were recorded, representing a carcase mass of 3 606 kg (Table 12.).

CALCULATION OF THE MASS OF PREY ANIMALS KILLED BY A LION IN ONE YEAR

From the four sections of the study an average daily kill requirement per lion was obtained. This figure does not represent the actual mass of food eaten by a lion per day, but represents the mean daily quantity of carcase mass killed by lion over an extended period. Table 13. thus gives the

.. / 41.

Table 12: Carcase mass of 14 lion kills, by a single pride, in the Crocodile Bridge area

Species	Age	Sex	Carcase mass in kg
Buffalo	14 months	-	207
	Adult	M	440
	Adult	M	440
	Adult	F	277
	5 months	-	98
	5 months	-	98
Waterbuck	Adult	M	200
	Sub-adult	F	130
	Adult	F	150
	Adult	M	200
Impala	Adult	M	44
	Adult	M	44
Giraffe	Adult	F	1 100
Wildebeest	8-12 years	F	178
		TOTAL :	3 606

M : Male
F : Female

Table 13: Average daily carcase mass required by a lion in each of the four study sections and the yearly carcase mass killed per lion

Section No	Daily carcase mass requirement (kg)	Yearly carcase mass requirements (kg)
1	6,3	2 339
2	6,8	2 485
3	7,5	2 638
4	6,7	2 434

average daily carcase mass required by a lion in each of the four study areas and the yearly carcase mass killed per lion.

The mean food requirement for a lion over a period of one year was worked out using the kill frequency and mass of the prey killed (Table 13.).

The results of the four sections of the study were averaged to give mean requirement for the intake per lion for the entire Park. This mean requirement amounts to 2 498 kg per lion per year.

Daily Food Intake Per Lion

For purposes of comparison the average daily food intake of lions will be compared with those obtained by Schaller (1972) in East Africa and Eloff (1973) in the Kalahari Gemsbok National Park.

The daily food requirements for lions in this study were not directly calculated, but will be taken as being equal to 75 per cent of the daily carcase mass requirement. This is done on the ground that approximately 25 per cent of the carcases of large prey animals is not consumed by lions. Therefore the lions in the study area have an average daily food intake of 5,1 kg . Eloff (op. cit.) found a daily food intake of 4,7 kg for females and 7,2 kg for males.

The present study made no distinction between the sexes and used the "lion unit" as representing adult lions of both sexes.

Averaging Eloff's results a daily intake of 5,9 kg per lion is obtained. Schaller (op. cit.) estimated a daily intake of five kg for females and seven kg for males. This gives an average of six kg per lion per day,

which is very similar to the figures obtained by Eloff and approximately one kg more per day than found in the present study.

Prey Unit

For interpretation of results a basic prey unit is required. For this purpose a prey unit equivalent to ± 200 kg was chosen. This figure was arrived at as an approximate average carcase mass for the major prey species, relative to the percentage of each species killed by lions per year.

Using the prey unit as a basis the equivalents were worked out for the various prey species according to their average carcase mass (Table 14.).

Carcase mass in this instance refers to live mass of the animal minus mass of stomach contents.

Food Requirements Of A Lion Using The Prey Unit As A Basis

A lion's food requirement for one year is 2 498 kg . Therefore a lion requires approximately 12 prey units per year.

Taking the lion population as consisting of the equivalent of 1 000 adult animals, the food intake for this population of lions is 12 000 kill units per year.

If the percentage kills recorded for each species are expressed in kill unit equivalents, an approximation to the number of that species which are expected to be killed by lions per year is obtained.

Table 14: Equivalent prey units for major prey species

Species	Prey unit equivalent	No of prey = 1 Prey unit
Giraffe	2-3	$\frac{1}{2}$
Buffalo	2	$\frac{1}{2}$
Zebra	1	1
Wildebeest	1	1
Waterbuck	1	1
Kudu	1	1
Impala	,25	4
Warthog	,25	4

Table 15. gives the expected number of lion kills for each species as worked out according to the percentage kills recorded and prey unit equivalents.

Possible Causes For Variation Of Numbers Of Animals Killed By Lions Per Year

Various factors could influence the expected number of kills for each of the major prey species as listed in Table 15.

(i) Mass of prey:

The proportion of young animals caught will greatly affect the number of a particular species caught by lions. For example, if 50 per cent of the kills of a species were young animals, with a mean mass approximately half that of the adult, it would be expected that the number of kills for that species would increase by a factor, in this case 50 per cent, which would again bring it to the expected yearly carcase mass kill for that species.

(ii) Fluctuation in the number of lions:

The numbers of lions in the study area could vary rapidly and considerably. This could also bring about changes in the numbers of prey killed annually. These fluctuations in the number of lions need not necessarily be spread over the entire Park, but could be local. Local fluctuations along the boundaries, especially the southern boundary, are common. Lions leave the Park and are shot outside. During the eighteen months starting at the beginning of 1973, at least 26 lions have been shot south of the Crocodile river.

Fluctuations could also result from disease. The very nature of the lion's social system make them susceptible to diseases, such as mange and possibly infectious feline enteritis.

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Table 15: Expected number of lion kills in the Kruger National Park, for each species, as worked out according to percentage kills recorded and prey unit equivalents, for a lion population equivalent to a 1 000 adult lions

Species	Percentage of recorded kills	Prey unit equivalent	Expected no killed/year
Impala	22	,25	10 560
Wildebeest	21	1	2 520
Zebra	18	1	2 160
Buffalo	13	2	780
Kudu	9	1	1 080
Waterbuck	8	1	960
Giraffe	6	2	180
Warthog	2	,25	960

Favourable conditions could lead to decreased mortality of both adults and cubs, which in turn could cause substantial population increases in a relatively short period.

CHAPTER 5. FACTORS AFFECTING THE SUCCESS OF A HUNT, HUNTING TECHNIQUES AND BEHAVIOUR AT A KILL

DEFINITION OF A HUNT

Schaller (1972) regards a hunt as taking place only once the prey is within 60 metres of the stalking lion. This, it is felt, only takes into consideration the final part of the hunt.

Schaller (op. cit.) found that 88 per cent of hunts consisted of a combination of stalks and runs, which are in effect used together.

For the purpose of this study the hunt will be defined as taking place from the time a lion assumes a stalking posture and approaches a potential prey animal, provided the stalk lasts for at least 100 metres.

FACTORS AFFECTING THE SUCCESS OF A HUNT

There are several factors which may contribute to the success or failure of a hunt, among which are the following: cover, i.e. the height and density of vegetation, time of the day and wind direction.

Cover

The large animals preyed on by lions are much faster than the lions themselves. So of necessity the lion must use the available cover to get as close as possible to the prey.

The first, second and fourth sections of this study were done in areas roughly classed as maroela (Sclerocarya caffra) and knoppiesdoring (Acacia nigrescens) savanna. Here the presence of scrub vegetation was almost

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absent and the lions had to rely on grass for cover.

The effectiveness of grass cover in the efficiency of lion predation is clearly demonstrated by the spatial distribution of kills after the start of the rain in the central district. Prior to the start of the rains the prey animals all had to go to one of two waterholes in the area. It was here that they were preyed on by the lions (66,2 per cent of the kills were within a two kilometre radius of the water). Here cover was minimal, but the concentration of potential prey animals was high.

As soon as the rains fell and veld pans began to fill, prey animals did not need to go to permanent watering points. The concentration of potential prey at these points ceased to exist.

Between days 84 and 88 (Table 5.), 100 mm of rain fell. This was enough to fill some of the numerous natural depressions in the area and subsequently also resulted in the dispersal of prey animals. From the start of the rains it took nine days for the lions to make a successful kill and a further six days before they made another, thus demonstrating the effect of lack of cover coupled to dispersion of prey animals. Dispersion, when considered on its own, is not an important factor. This is shown by a fairly regular kill rate after the first three to four weeks discussed on page 44, the grass having attained its maximum height.

When the grass had reached its maximum height ($\pm$ 0,75 m), the lions were observed to make two kills in broad daylight, before 0800 hours. In both cases the animals concerned were wildebeest. In one case a wildebeest herd was lying in the long grass on a slight rise. Here a lioness crept up to the herd and bit a 15 month old wildebeest on the throat before it

had a chance to rise, no charge being made. The second instance was observed under similar conditions.

Time Of Day

Lions were observed to hunt mainly at night. This could be coupled to the advantage that the darkness gave them. Schaller (1972) arrived at similar conclusions.

Contrary to what Schaller (op. cit.) found about lions hunting just after dark, it was found during the present study that they were inactive until the early morning when temperatures dropped. This was particularly apparent in winter. The majority of successful hunts took place in the early morning between 0200 hours and 0500 hours, but kills were observed at all times of the day, as were unsuccessful stalks.

The radio marked lions in the Satara area were the only ones that could be observed continuously for 24 hour periods. About 90 per cent of the kills were made between the times stated.

Lions do, however, hunt any time of day and night, if conditions are suitable. Schaller (1972) quotes a communal day-time hunting success for wildebeest and zebra being 27 per cent, and for night-time as being 42 per cent.

Wind Direction

Guggisberg (1961), Stevenson-Hamilton (1954) and Denis (1964) stated that lions when stalking prey, approached them from a down-wind direction. The present study gave no indication that this was the case. Schaller (1972) who noted the wind direction in 300 hunts, mentions that in 28 per cent of observed stalks, one or more lions started the stalk from an up-wind

position, 28,3 per cent from down-wind and 43,7 per cent from one or the other side.

Number Of Prey

The next most important factor affecting the success of a hunt, is the number of prey animals being stalked.

Solitary animals are more successfully hunted than are herd animals. It is for this reason that adult male wildebeest and lone buffalo bulls form such a large percentage of recorded kills. Schaller (1969) found that 81 per cent of kills were buffalo bulls. In the course of this study nine hunts were recorded on solitary animals of the above species. Eight of these (88 per cent) were successful.

Sex Of Lions Relative To Hunting Success

Solitary males and prides of males were seen to hunt on 29 occasions. Seventeen of these attempts (59 per cent), were successful. Schaller (1972) quotes that two or more lionesses hunting together had a success rate of 30 per cent.

The figures obtained in this study may be biased, because males were radio marked in preference to females. They were therefore easier to locate regularly and to maintain contact with. Schaller (op. cit.), however, spent more time with females.

It is popularly believed that lionesses do all the killing while the male does nothing, or very little. This is not really the case. The bias is easily explained when the sexes of adult animals are examined. Of the

2 748 lions seen by the author in the course of the study, 25,5 per cent were adult males, 36 per cent adult females, 13,7 per cent sub-adult animals and 24,8 per cent cubs.

A sub-adult lion as classified in this study is almost the same size as an adult female and could easily be mistaken for the same by an inexperienced observer. This, in addition to the fact that young lions are known to have killed at the age of 17 months, goes a long way to explain this misconception. The adult female and sub-adult sections of the population make up 49,7 per cent of the population.

Schaller (1972) found that in 71 hunts by single lions in groups of mixed sex, males took the initiative only twice. He also stated that only three per cent of 1 210 lions observed stalking were males.

The results of this study seem to indicate that his figure is a bit low, even though the results of this study were biased towards males. Conditions in the two study areas, however, differ markedly. Of 188 hunts observed, the following was noted with regard to the percentage occurrence of males and females in hunts:

Males and females: 61 per cent

Females only, or solitary females: 23 per cent

Males only, or solitary males: 16 per cent

In the last two instances there may have been animals of the other sex present which were not seen.

Age Of Lions Relative To Hunting Success

The young lions already described in Chapter 4., made their first known

successful kill at the age of 17 months. The animal killed was a 10 month old zebra.

To effect a kill, a lion is almost completely reliant on its teeth especially the canines, and physical condition. When the canines become worn down with age, or broken, the lion's chances of killing will decrease. One very old female (No. 2), was caught and marked. At the time of capture, her canines were no more than stumps. She was seen a year later in the same area in good condition. It is quite possible that she could not kill anything herself, but lived at the expense of the rest of the pride, who killed mainly wildebeest and zebra.

The presence of many lions under one year of age appear to affect the success of hunting. When a stalk starts, the young animals invariably follow one or more of the adults, with no apparent attempt at concealment.

No successful hunts were observed when the cubs followed the adults after the hunt had begun.

Location Of Prey

Vision appears to be the main method used in prey location. Lions were observed to be walking apparently randomly through an area until a prey animal was seen. They then changed course if necessary and proceeded to stalk the prey. On other occasions, while resting, lions were seen to rise on apparently seeing a herd of animals appear nearby and to initiate a stalk-hunt procedure.

The stalk seems to be completely visually orientated, the lions approaching only when the prey is not looking in its direction. This is done in typical

fashion: head, tail and body almost in straight line, with stops in mid-stride where necessary.

The lion often apparently fixates on a few animals in a herd, and in so doing spoils its chances, since other animals in the herd, which may be separated from the intended prey see the lion and give the alarm.

Lions appear to make little use of their sense of smell when hunting, but could well do so when following herds of game. On numerous occasions for example, lions were seen to be moving behind a herd of buffalo in its tracks. This could, however, also be visual as buffalo leave a distinct path in areas through which they have moved.

Tree climbing in Lake Manyara National Park is presumably for better observation (Makacha and Schaller 1969). In Gorongoza National Park, lions climb a disused lookout tower to survey the plains below. During the present study lions were frequently seen standing up on their hind legs in long grass so as to survey the area for prey. This was noted in the lions in the northern area of the Park, as well as in the southern area. On one occasion lions were seen to be walking through grass which was about one metre high. One or more of the lions stopped at irregular intervals and stood for a few seconds on their hind feet. It was difficult to make a clear observation, but it appeared as if the hind legs of the lions were bent, resembling a dog begging. Both males and females were seen to assume this posture.

Hunting By A Pride

Once the individuals of a pride become aware of the potential prey, their

reactions differ markedly. For example, some individuals may immediately start stalking, while others may take no notice, or even lie down on the spot.

Even though the pride as a unit may all be moving in a certain direction they need not necessarily all be together, they could be spread out over a few hundred metres or more. The same applies to a pride resting during the day.

The individual lions then stalk the prey, sometimes from various points and sometimes as a group. In one case, eight lions, two males and six females, were seen to be stalking a herd of resting buffalo as a group. Here, each lion made use of the best available cover and in so doing outflanked or even got behind the prey. Individual lions then tried to approach as close as possible to the prey before making a final charge, which is normally less than 20 metres, in successful charges. The above description is typical for hunts by prides and also applies to hunts by individuals.

Often before a lion charges, the prey may become aware of the lion and flee in any direction, provided that it is away from the sighted lion. In so doing the prey may run into other lions and subsequently be pulled down and killed. Kruuk and Turner (1967) have made similar observations.

The phenomena of multiple killings by lions may be described as occurring by the above mentioned method, where more than one of the lions successfully pull down a prey animal.

Opportunistic Kills

Into this category, all the cases where lions killed an animal without

actually going through the entire hunt procedure have been placed.

In the present study, an adult male lion came upon a hare (Lepus sp.), which it immediately killed and started eating. A further instance was observed when a lioness flushed some warthog. The warthogs fled and disappeared into a hole. The lioness then went to the hole and started clawing at the entrance. After a while, she partly entered the hole and then emerged with a young warthog, held in her mouth.

Killing

Stevenson-Hamilton (1954) and Guggisberg (1961) maintained that a prey animal is killed by having its neck broken. In none of the kills observed, could it be said with certainty that the neck of the animal had been broken and in so doing, causing the animal's death. This could well, however, have been the case in impala, as the animals were usually killed very quickly - before the dust had time to settle.

In larger animals, not one animal could have died from a broken neck as they invariably continued to struggle after being pulled down, frequently attempting to rise, or in the case of buffalo, sweeping the ground with the lion.

Killing Of Smaller Prey Animals

Impala were the animals observed to be killed most frequently. Although the method varied, it was always essentially the same. The prey was either knocked down by a single blow of a forepaw, or caught with both forepaws and then bitten in the neck or throat region.

Schaller (1972) recorded the following data concerning 26 small antelope kills for the site of fatal bite:

Back of neck: 16,

Throat: 6,

Head: 2,

Back: 1,

Chest: 1.

Killing Of Larger Prey Animals

The final charge at a prey animal usually brought the lion alongside the prey or slightly behind it. Almost invariably the lion would then leap onto the back of the animal, and grasp it with its forepaws in the shoulder and neck region. It was, however, not always possible to see if the lion actually bit the prey at this point. From this point, one of two things happened:

(i) The animal lost its balance and fell to the ground, the lion falling with it. The lion then immediately went for a bite hold on the neck or muzzle, but the throat seemed to be bitten into more often - 75 per cent of the times (n = 142). The lion then maintained this position until the prey stopped struggling. Other lions often obtained bite holds on the downed prey.

(ii) In other instances, the lion would slip off the animal retaining its hold on the neck and pulling it down almost on top of it. Once down, the animal was again bitten in the throat. The lion held the animal until it ceased to move.

The former method is used extensively by lions that prey on buffalo. For

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example, an adult male buffalo was attacked and killed by a single lion, using a similar method. This buffalo was walking down to a watering point near which the lion was lying. The lion rose and walked towards the buffalo which paid no attention at all to the lion. When the lion was about 20 metres from the buffalo it charged. The lion struck the buffalo slightly from behind, just ahead of the shoulder, and in doing so knocked it down. The lion immediately seized hold of the buffalo's throat and held on. The buffalo tried to shake the lion off, but was unable to do so. The buffalo stopped struggling after 45 minutes.

Once an animal has been pulled down by lions it struggles only a short while. Probably a shock factor, coupled to suffocation.

Of the 142 wildebeest, zebra and buffalo killed, 107 were bitten in the throat and neck and 35 on the muzzle.

In cases where more than one lion attacked an adult buffalo, the achilles tendons were bitten into. In one case, the tendon on one leg was actually severed.

Once the animal is down, the lions don't necessarily wait for it to die but often start eating immediately. The animal can, therefore, die as a result of loss of blood, in combination with suffocation, which is the cause of death in the majority of lion kills.

Behaviour At A Kill

After a stalk-hunt procedure by two males and two females, a territorial wildebeest bull was pulled down and killed by male F. Male F then lay, apparently resting, next to the wildebeest while the females started

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eating immediately. After 11 minutes, male E approached the carcase and both F and E started eating. The cubs, at this stage 12 months old, arrived 37 minutes later. They crawled over the adult lions to get to the carcase. No irritation, however, was shown by the adults.

The lions stayed at the carcase for $\pm 9\frac{1}{2}$ hours before leaving. The remains consisted only of bones and skin, which were later consumed by hyaenas, jackals and vultures.

The above is typical of the behaviour observed at a kill.

Moving The Kill

After having made a kill, lions often drag it under a tree or bush. This is more common during the day than at night, possibly for one of two reasons:

(i) To be able to eat in the shade,

(ii) To protect the kill from scavengers.

Large animals are usually grabbed by the nape or neck and dragged in the appropriate direction by a single lion, simply by moving backwards, forwards or by dragging the animal to one side. On no occasion were other lions seen to help in the moving of a carcase. The contrary was often observed. When one lion made a definite effort to move the carcase, the other lions often pulled in the opposite direction, apparently in fear of losing their food. This often resulted in the dismembering of the carcase, particularly if it had already been partly eaten.

Smaller carcases are bitten on the neck and lifted partially off the ground by the lion, holding its neck up and walking, or trotting to the selected

spot. On one occasion a lioness was seen to run over 200 metres carrying an uneaten adult impala ram in this manner.

Time Lapse Prior To Feeding

Lions often begin eating an animal before it is dead and in so doing speed up its death. On three occasions, however, lions were observed to lie panting near the carcase. No definite cause for this time lapse between killing and eating could be found. The lions in all cases ate all the edible parts of the prey, so hunger or a lack thereof can be disregarded. The only possible explanation is that the lions were too tired after the struggle to start eating immediately.

Once the lions lay around the carcase, some even resting their heads on it, while on another occasion two of the lionesses lay on the carcase, while the males played with the cubs about 20 metres away.

The longest of these periods from death to eating was an interval of 23 minutes, the other two intervals being seven and 13 minutes.

On one occasion an adult male was seen to lie on an impala for 23 minutes before he started eating it. There was another male present who kept trying to get at the carcase. He eventually ended up half under the first lion chewing at the neck. The start of this episode was accompanied by much growling and slapping, but the intensity abated when the first male rose from the carcase and started eating.

Feeding

Lions were often seen to lick the skin of a kill, especially large kills,

before biting into the area. This was particularly evident in the areas covered with blood. Schaller (1972) also found this, and stated that lions tended to pull out the long hair, such as the beard of wildebeest, on their kills.

It often takes the lion considerable time to open a carcase. In one instance, five lions took nearly nine minutes to open the visceral cavity of a wildebeest. This is an exception rather than the rule, as the lions spent most of their time fighting amongst each other. The carcase is normally bitten open in the groin region, with the insides of the thighs being the first parts to be eaten, followed by the chest, forequarters, head and neck. Fig. 9. shows lions on a kill.

In the present study no preference for parts of the viscera could be determined, as these were normally eaten while still inside the visceral cavity.

Stevenson-Hamilton (1954) and Guggisberg (1961) stated that lions disembowel an animal and hide the intestines under dead leaves and grass, before starting to eat their kill. Only one similar instance was seen in this study, when a lioness scratched dry grass and sand over the rumen contents with her forefeet. Schaller (1972) has also noted that his type of behaviour is rare.

On occasions where lions were seen to eat the rumen and large intestine, the contents were either shaken out, or removed as follows: a forepaw was placed on the intestine and then pulled through under the paw. In doing so, most of the contents were squeezed out at the distal end.

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Fig. 9: Lions on a kill.

Schaller (1972) mentioned that lions may eat the viscera to obtain vitamins and fats which are not found in the skeletal muscles of their natural prey.

Foetuses, especially those of zebra, seemed to be favoured by lions. On opening the abdominal cavity, the foetus, if present, was immediately removed and consumed by one or more of the lions. This was accompanied by a greater amount of growling and grunting than was found with any other part of the carcase.

The lions on larger kills either stood, lay or crouched around a carcase and eat wherever they can. This is accompanied by growling and slapping until the carcase is dismembered, or each lion has had its fill.

The meat is cut by the carnassials and swallowed in large lumps. The forepaws are used to hold the carcase away from the lion in its efforts to tear pieces off the carcase. They are also used to hold bones which are licked clean by the rough tongue.

After having eaten their fill, lions often move a short distance from the carcase and feed again a few hours later. An adult male lion was seen to stay with a wildebeest he had killed for three days.

For the quantity of meat consumed, see Chapter 4..

Pecking Order

During this study no evidence was found of a pecking order at a carcase. In certain cases, however, males were seen to eat first and even to chase females away from kills. On another occasion, in the same pride, the females were seen to eat first, accompanied by the cubs, while the two males

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were repeatedly chased off by the females.

Remains Of Lion Kills

The remains were always somewhat scattered around the kill site. This was not so apparent where only one or two lions were present at a kill. The carcase remains tended to be more scattered if there were many lions, especially so when cubs were present. The spinal column of large animals was seldom dismembered and only rarely was the head detached from the spinal column. Wildebeest jaws, however, tended to become detached from the skull. If there were lots of lions present the facial muscles were nearly always eaten in zebra, but very seldom in wildebeest.

Female and young impala were often devoured completely, except for the upper and lower jaws, hooves and spinal column.

An impala ram killed by three adult male lions, was almost completely eaten in seven minutes. All that remained was the spinal column, pelvis, larger leg bones, horns and hooves. The brain case was opened and the brains eaten.

Relationship Between Lions And Other Predators And Scavengers At A Kill

Very few interactions were noted between the various predators in the course of this study.

Only one case of lions scavenging from other predators was noted. In this particular case a kudu was scavenged from three cheetah. Schaller (1972), however, quoted numerous instances of lions scavenging.

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Hyaenas were invariably chased by lions when they approached too near their kill, but no actual physical damage ever resulted from these chases.

Black-backed jackals were tolerated by lions and were in fact even seen to dart in between lions at a carcase, snatch some meat and retreat to eat a small distance away. Jackals were also seen to follow lions and even to bark at a lion's approach.

Vultures were seldom found on the ground at a kill, while lions were still in possession. Lions did, however, often chase vultures off a kill if they found the vultures on it.

Hooded vultures in the Msassane area of the central district were often to be found resting in trees near a pride of lions that was resident in that area. This was such a common occurrence that this pride of lions could regularly be found by just looking for the vultures.

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CHAPTER 6. TERRITORIALITY AND MOVEMENTS

Most mammals show some form of territoriality or defence of an area which is capable of supporting the needs of the individual or group. The territorium, or protected area, is demarcated by various means, either visual, oral, olfactory, or by a combination of these. The concept of territoriality has led to various viewpoints being expressed by different authors. So much so, that the meaning of territoriality is now somewhat obscure. But for the purpose of this study a territory is defined as an area inhabited by an animal or animals who derive their basic needs from this area, and which protect this area from intrusion by other animals of the same species.

TERRITORIALITY IN LIONS

Schenkel (1966) and Guggisberg (1961) state that lions do have distinct territories. Schaller (1972) used the term "pride area" to indicate the area in which a pride were known to move, in preference to "territory", on the grounds that even though lions did act aggressively towards intruders, this could be explained as a general animosity towards strange lions. Secondly it was difficult to demarcate an area which the lions regarded as their territory because few pride interactions were seen. Strict delineation of a territorium would serve no purpose in an area where lions move about a large area in search of prey animals. It stands to reason that the lions would be in that part of their range which most easily supplies their needs. Schaller (op. cit.) stated that certain prides showed more aggression towards intruders than did other prides. In one case a particular pride invariably chased intruders off its "pride area" even in an area where there was very little game.

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The size of the area which a pride occupies is determined by the number of prey animals in the area as well as the number of lions in the pride.

Schaller (op. cit.) arrived at the conclusion that lions did in certain instances defend a territory within the pride area, but that this territory is not clearly demarcated, its demarcation changing with conditions.

Lions possess all the means to successfully demarcate a territorium and observations show that certain marking methods are used.

Roaring is probably the lion's most effective "marking" method, as it has the greatest range. While observing a resident pride, two young males were seen to approach a water hole near which the resident pride was feeding on a wildebeest carcase. One of the pride males left the carcase, walked a small distance, and roared repeatedly for about four minutes. The two young males stopped on hearing the first roars, lay down, and after a while left in the direction they had come from. It is doubtful that the male that roared saw the approaching lions.

Olfactory marking: A male spraying urine into bushes was seen on one occasion. This is probably a form of marking, as suggested by Schaller (1972). This, however, was seen in the centre of this particular lion's activity area, so its usefulness as a marking means for territority as a unit is unknown. The lion in passing is almost certain to leave a scent trail as well as faeces and urine, which could also be marking.

Visual marking: The mere presence of a lion in an area is probably an efficient method of demarcating a territory.

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Activity Zone

In view of the large areas that lions cover in their wanderings, an area up to 1 290 sq. km as recorded in the present study, it is doubtful if lions do in fact demarcate a territory.

An activity zone which encompasses the normal area in which the pride as a unit moves, would be a better concept.

If territoriality is accepted in lions, then a distinction would have to be drawn between:

(i) territoriality of the males in the pride,

(ii) territoriality of the females in the pride,

(iii) territoriality of the pride.

This is done on the following grounds: the pride as a unit confines itself to an area for long periods. The present study revealed that the well known pride, studied in parts one and two, remained in the same area for four years. Individual males of the pride did, however, leave the pride on occasions for up to nine days, and joined, or followed neighbouring prides.

Individual females were also found to leave their prides for unknown lengths of time and wander over large areas.

From the above it would appear that lions do show some preference for a certain area, but are not bound to it. Transient lions of either sex are admitted into this area and may join the pride for lengths of time.

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Pride Interactions

In one instance, a male joined a pride consisting of two males, two females and seven cubs, and stayed with the pride for over a year. No conflict between any of the lions was seen at the start of this union.

Females in oestrus were readily accepted into a pride temporarily. Schaller (1972), stated similar instances.

Interactions between prides from neighbouring areas is rare and was never witnessed. Known individuals from neighbouring prides did occasionally leave their prides for a few days and joined other prides. This was noted on six occasions in the Satara area, in four cases by solitary males who joined the pride, once by a non-oestrus female that joined the pride for two days and once by a non-oestrus female that entered the pride's activity zone for an unknown period, but did not join the pride.

Figure 10. shows the activity zones of the various prides around the Satara rest camp. The overlap between the various activity zones is apparent and is probably greater than shown in the figure. This would become more obvious, if it was possible to obtain more sightings from each of the prides concerned.

The activity zones not completely enclosed indicate incomplete knowledge of the lions' activity in the area.

Size Of Activity Zone

The size of the activity zone of a lion or group of lions appears to vary with the density of potential prey. For example, in the central district

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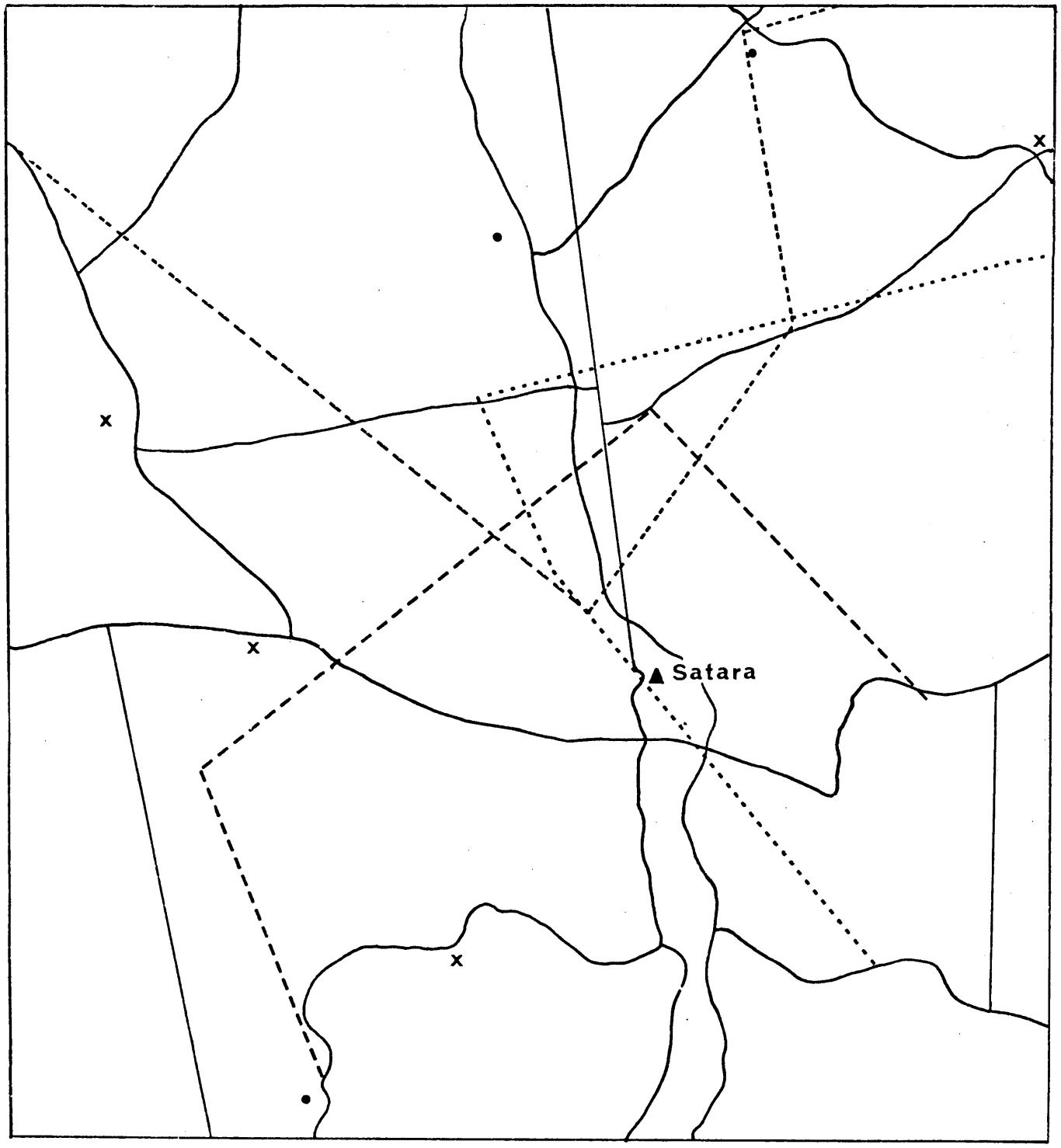

Fig.10. Activity zones of various prides of lions around the Satara rest camp in the Kruger National Park.

LEGEND
Roads
Windmills
Waterholes
Activity zones

0 1 2
Km

N

during the first and second parts of the study, the activity zone of the pride increased from 63 sq. km in the dry season to 142 sq. km in the wet season. There was no apparent emigration of prey animals from the area, just a wider distribution as a result of more watering points.

An adult female, marked between the Sabie and Sand rivers, an area with a high prey density was found to have an activity zone of ± 100 sq. km , over a period of two years.

In contrast to this, the pride studied in the northern area had a dry season activity zone of ± 400 sq. km . This area could, however, have been much larger, as the pride could not be located every day. It is possible that the pride moved further west than recorded, giving an appreciable extention to their activity zone. The prey density of this area was calculated as being four prey animals per sq. km .

Nomadic lions have very large activity zones. One female, for example, was recorded as having moved 100 km north and 29 km south of her point of capture. This lioness was resighted only six times in three years, and none of these sightings showed any significant east west movement. If, however, east west movement of only 10 km took place, which seems most likely, then the lion had an activity zone of 1 290 sq. km . This large activity zone can not be attributed to low prey density as the almost entire activity zone fell in the central district, with a prey density of 20,7 prey animals per sq. km , where prides of lions were found to have activity zones seldom exceeding 200 sq. km .

Certain prides of lions are known to follow migratory wildebeest and zebra herds. The activity zones of these prides would then be determined by the

extent of the movement of the prey, whose movements in turn are dictated by weather conditions.

Daily Movements Of A Pride

Prides were seldom found lying up on consecutive days in the same place, except in cases where a large kill had been made. As soon as the pride had devoured the kill, it generally moved away from the area.

No pattern of movement or distinct hunting pathways could be determined. But it did appear as if the daily movements decreased immediately after a kill was made. Table 16. shows the average distance in km between lying up spots for a single pride on the night immediately preceeding and following a kill, for dry and wet seasons in the Satara area. The apparent decrease in distance travelled by the pride in the wet season on the third and fourth days, is probably due to the fact that it was not always possible to trace the animals on consecutive days. Only in two instances was it possible to trace the pride for four consecutive days after a kill was made.

The pride would normally move away from their lying up spot just after sunset and walk for varying distances up to a few kilometres. This walk would be interspersed by long periods of rest and with occasional roars being made by the pride members. This procedure would carry on till after midnight, from which point in time the pride seemed to start hunting more seriously. Rest periods were shorter and playing seldom noticed except in the case of cubs. Soon after sunrise the pride would nearly always be found in a sunny spot. They would later move from this spot to a shady position once it started getting warmer.

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Table 16: Table showing the average distance in km between lying up spots for a single pride of lion, on the nights immediately preceeding and following a kill, for dry and wet seasons in the Satara area

	Mean distance in km between lie up points				
	Day before kill	Number of days after kill			
		1	2	3	4
Dry season	3,1	2,4	3,6	5	8
Wet season	4,5	4,6	4,8	4	3

ACTIVITY PATTERNS OF THE PRIDE

Figure 11. shows the typical activity pattern of a pride of lions for a 24 hour period.

The greater part of each day is spent resting. Schaller (1972) found that lions spent up to 20 hours a day resting. The present study showed similar results.

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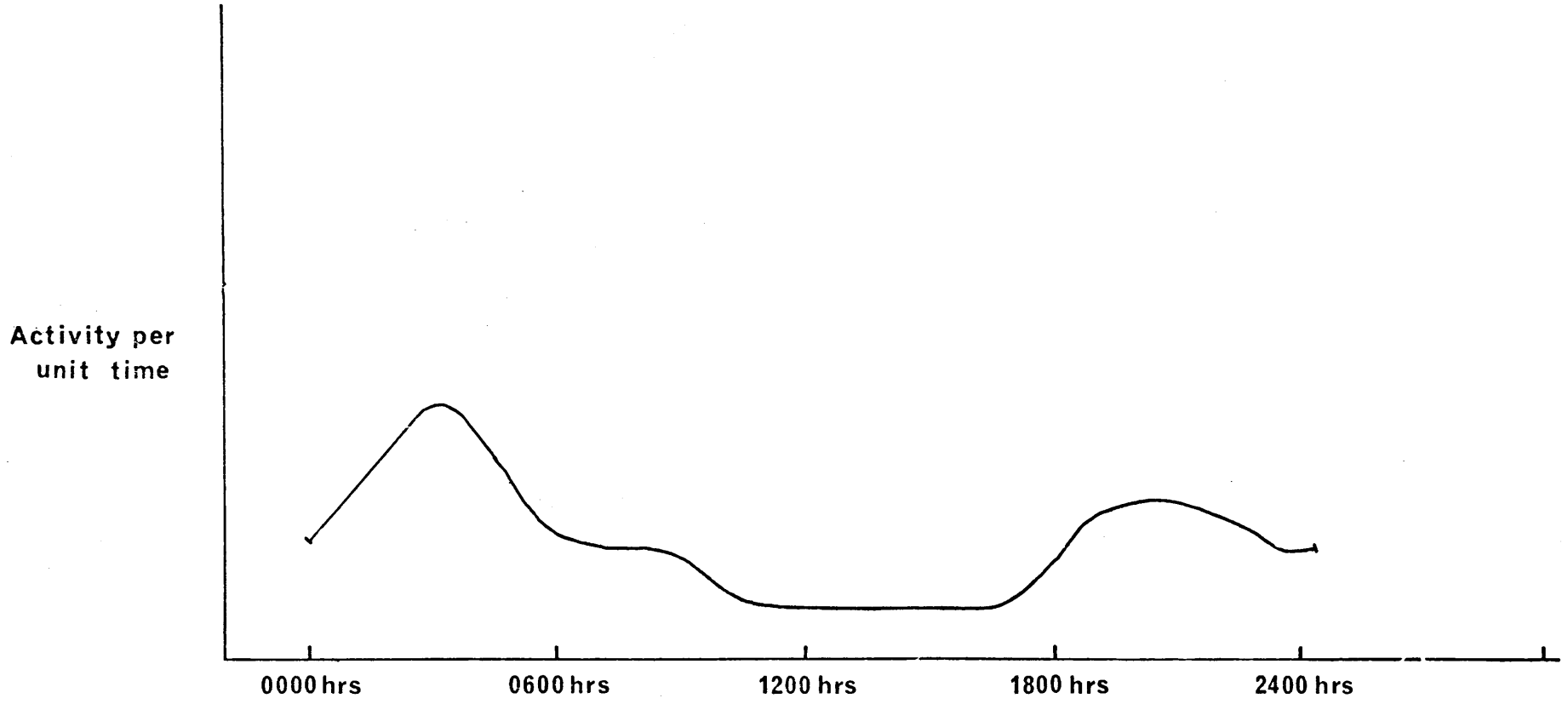

Fig.11. Typical activity pattern of a pride of lion over a 24 hour period.

CHAPTER 7. POPULATION DYNAMICS

In the management of an area such as the Kruger National Park, the population dynamics of the lions is of some considerable importance. It is unfortunate, that in this instance, the most important aspect is also that for which it is the most difficult to obtain data.

Population Size

Using the block method as described in Chapter 2., the lion population of the Park was estimated at 651 adults. Using a minimum of 651 adult lions as a basis for representing 61,5 per cent of the total population, see Table 17, the following figures are arrived at for the juvenile and cub sectors of the population:

Juvenile 146 animals,

Cub 265 animals.

For the interpretation of the predation results, these two sectors of the population must be converted into lion units representing adult animals by using similar criteria to those in Chapter 4., i.e. two juveniles equal to one adult and 3-4 cubs equal to one adult, depending on the size of the cubs. The 146 juvenile lions therefore represent 73 adults and the 265 cubs, 88 adults, which adds up to a total of 151 adults. Therefore, the total minimum number of lion units in the park is equal to 651 plus 151, or 802 lion units.

In the densely populated central district, the various Rangers have estimated the lion populations on their sections as being much greater than those depicted in Fig. 4., in many cases, more than double (Smuts pers. comm.).

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Table 17: Percentage occurrence of the different age and sex groups in a sample of 2 748 lions counted in the Kruger National Park

Age group	Percentage
Adult males	25,5
Adult females	36,0
Juveniles	13,7
Cubs	24,8

In an area densely populated with lions, as in the central district, two or more different prides could easily have been regarded as being a single pride. This error may have resulted in an underestimation of the population. Similarly in areas of low lion density two prides of similar size could have been regarded as being a single pride with a very large area, again resulting in an underestimation. If a 25 per cent error is assumed because of this method for the entire Park, then a total of 1 000 lion units is obtained.

The method used, is the only method available for censusing the lions in the study area. For economical and aesthetic reasons the various statistical methods, and aerial census are ruled out.

Population Structure

During the study 2 748 lions were classified, many of them more than once, into three age group classes:

(i) Adult males and females,

(ii) Juvenile animals,

(iii) Cubs.

This classification was done according to the size of the animals concerned:
Small cubs: animals up to one year, with maximum height approximately that of the adult's chest.
Large cubs: animals up to two years with a maximum height of less than that of an adult's shoulder.
Juveniles: animals older than two years old, with height that of the adult's shoulder.

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Table 17 gives the percentage occurrence of the different age groups in a sample of 2 748 lions counted in the Kruger National Park.

It is difficult to make sex ratio and age structure comparisons with other workers' results, since the criteria used by them are not known. Cubs and juveniles are both very difficult to sex in the field. This is owing to their shyness, coupled to the concealment offered by the long grass found in most of the study area.

Certain differences are noted when comparing the percentage occurrence of the various sectors of the population studied, with those obtained by Schaller (1972).

The adult male sector of the Park's lion population showed an increase of seven per cent relative to Schaller's population. Similarly the adult female population showed an increase of 4,5 per cent. The cub percentage for this study was also 12,5 per cent higher than that obtained by Schaller.

Conversely the percentage occurrence of juveniles, Schaller used sub-adult, was 11,55 per cent lower. These differences could be partly explained for the cub and juvenile sectors by comparing mortality of these sectors in the two areas. A mortality rate of 29 per cent was calculated from the data in Table 18, as compared to the 87,4 per cent calculated by Schaller.

Lions at birth have equal ratios (Sadleir 1966). Brand (1963) recorded 131 male and 130 female births in a total of 261 births at the National Zoological Gardens, Pretoria, which supported what Sadleir (op. cit.) had found. Schaller (1972) found that this held true for cubs up to one year of age and also probably for his sub-adult class which extended from 18 months of age to maturity.

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Differential Male Mortality

Examination of the data given in Table 17 indicates a deviation from the expected adult male to female ratio of one to one. Territorial strife between males could be the cause of this difference, but reports of lions being killed by other lions reveal that approximately equal numbers of both sexes are killed in such encounters (Rangers reports).

Reproduction

Lionesses are polyoestrus, with a gestation period of ± 108 days (Schaller 1972). It is theoretically possible that a lioness could conceive within a few weeks of having lost a litter. Schaller found that this potentiality was only reached in three out of 13 cases.

The one lioness in the Satara pride had a litter of four, 22 months after the birth of her previous litter, which have all reached maturity. The other female from the same pride, is not known to have conceived again.

A female, No. 2, was caught and marked in the central district. Two years later she was seen again, this time accompanied by cubs approximately two months of age. At the time of capture her canines were worn-down stumps, which indicated old age. Schaller also recorded very old females having cubs.

Sexual Maturity

Schaller (1972) estimates that females come into oestrus for the first time at about the age of 42 months. Males are thought to reach maturity at $3\frac{1}{2}$ to four years, at which stage a sudden increase in mane length and change of colour and body size is apparent.

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One particular lion estimated to be three and a half years old, had a very distinctive orange mane. He was caught and marked with a radio collar. Three months later his mane was black.

Litter Size

The number of cubs in a litter normally vary from one to six. Van Hooff (1965), however, recorded the birth of seven cubs from one female in the Arnhem Zoological Gardens. Brand (1936) found an average of 3,1 in captive prides.

In the study area it was very difficult to determine litter size accurately unless a long time was spent with a particular female. This was particularly so where two females from the same pride had cubs at more or less the same time.

Cubs are rarely seen before they reach two months of age. The mortality in this period is thus unknown.

Mating Season

No distinct mating or parturition seasons were observed, but further study could indicate that they may well occur. According to Fairall (1968) most lion cubs are born in winter and autumn.

Mortality

This is a difficult parameter to measure, as are its causes. Animals may leave an area and be recorded as dead, or loose their markers and similarly be falsely recorded dead.

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Cause of death is in most cases hard to determine. In cubs mortality often passes unnoticed.

Causes Of Mortality

In the study area, man as a mortality factor has little or no effect on the lion population, except on the borders where lions leave the Park and are shot outside.

Starvation: This is the main mortality factor of lions in the study area. This is not a sole factor, but is the proximate factor, brought about by a primary factor, which includes injury and accidents.

Lions have, however, been known to survive serious injuries. One particular lion marked with a radio, had at some stage broken a forelimb and a jaw, though not necessarily at the same time. He was in perfect condition when caught. In fact, these old injuries only showed up under close examination. It can only be presumed that he parasitized on the rest of the pride during his convalescence.

A notable example of this was seen, when an adult male broke a forelimb while killing a buffalo. For three months after this he never participated in a hunt, but followed the pride at a distance until he could keep up.

If either of these lions had been solitary animals, they probably would have starved.

The first lion mentioned eventually died of starvation as a result of a fight with another who forced him to leave the pride after having severely

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injured him. It is not uncommon however for lions to be killed instantly in these fights.

During the course of the study three lionesses were found to have been killed after being bitten immediately anterior to the pelvis. There were no drag marks made by the hind quarters where the lionesses were found, so it is presumed that death was almost instantaneous.

Males killed in fights were recorded on four occasions during the study. In only one case death was not instantaneous. All animals had been severely bitten. In one case the jugular vein and carotid arteries were severed. In the other two cases it was impossible to ascertain where the fatal injury had been sustained, but it was presumed to be in the head and neck region, as both regions were severely bitten. In one case the skull had been crushed. Numerous other instances are recorded annually by Rangers throughout the Park.

Other factors, apart from intraspecific competition, limiting the population of lions in the Kruger Park, according to Pienaar (1969), include: (i) hyaenas, which devour old individuals and young cubs temporarily abandoned by their mothers; (ii) flash floods during the rainy season which may overwhelm young cubs in their lair; (iii) severe bush fires, which may have the same effect (even adults have been burnt to death); (iv) the injuries inflicted by larger or aggressive prey species which may cripple or even kill their attackers (kicks by zebra and giraffe; goring by the horns of buffalo, sable, roan and even kudu; the quills of porcupines penetrating the paws, mouth and throat); (iv) army ants, which sometimes

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attack very young cubs; (vi) infectious disease such as anthrax and cat flue; (vii) the bites of poisonous snakes, such as mambas; (viii) the imbedding of thorns or other foreign bodies in paws, hampering movements and (ix) parasitic infestations such as Dirofilaria desjardinesii and Trichinella spiralis, which may cause severe emaciation and paralysis.

Young (1975) recorded that lions have died after feeding on carcases of animals which have died of anthrax. Also that in certain parts of the study area, 100 per cent of older lions are infested with Linguatula serrata, this parasite may be responsible for necrotic rhinitis in affected lions.

Cub Mortality

Stevenson-Hamilton (1954) estimated that 50 per cent of lion cubs die before they are two years old. During the course of the study, cubs were studied in three prides in the Satara area. A total of 17 cubs were used as a sample. These cubs were first seen when they were approximately five weeks old. Table 18 gives the number of cubs which reached an age of 24 months, from the initial sample of 17.

Young (1975) found experimentally that lion cubs developed rickets when solely fed on boneless meat. Rickets has been observed in wild lions. This condition could perhaps be found in prides that killed, for example, mainly buffalo, where no fine bones would be avaialable to the cubs. Further investigation is, however, required.

Young (op. cit.) states that in a certain pride in the study area, all the cubs died from sarcoptic mange caused by Sarcoptes scabiei.

Both male and female lions have been known to eat cubs, and one hyaena destroyed had the remains of two cubs ± three months old in its stomach.

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Table 18: Mortality table of 17 lion cubs from three prides, in the Satara area, recorded up to two years of age.

Pride No	Number cubs	Number of cubs surviving			
		6 months	12 months	18 months	24 months
1	7	7	7	7	7
2	5	5	5	3	3
3_1	3	3	3	3	2
3_2	2	2	0	0	0

CHAPTER 8: SUGGESTIONS FOR FUTURE RESEARCH AND MANAGEMENT

Because of problems encountered in the interpretation of results, the writer feels that for efficient future management of the area, an accurate census of lions in the area should be made. An accurate census is essential for the correct interpretation of the number of animals killed by lions per year. This census should not only provide data on the number of lions in the Park, but also give details of population structure.

SUGGESTED CENSUS METHODS

Marking and Resighting

This method for censusing could be used, if suitable marking techniques were applied, i.e., collars, or small coded brands consisting of symbols. This technique has the disadvantage, however, of only being useful after a long period of observation, during which the number of lions in the area may have varied. As it is essential to be able to determine the number of lions in the Park at a given time, this method is not entirely suitable.

Calling

A more suitable method would be to "call" lions to a point by using recorded roars, or by placing bait in the area. If these two methods are combined, it is almost certain that most of the lions in the immediate vicinity will be attracted to the observers. This would have to be repeated over a period of a few days in each area. Single points of observation would not be sufficient, so observers should be spread over the area to cover all possible prides. Once a reliable estimate of the lions was obtained in one area, the observers could move to another and in so doing, the entire Park could be censused in a matter of months.

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To avoid duplication a suitable marking technique would have to be applied. This could be in the form of small inconspicuous brands applied to the lions under sedation. Ear tags could also be used as in this case it is not important that the lions remain marked for long periods of time.

The above method would give a very accurate total for the number of lions in the Park, and would also supply accurate details of population structure. Secondly the extent of activity zones and movements of nomadic animals could be accurately recorded.

THE EFFECT OF PREDATION ON ABUNDANT PREY SPECIES

An attempt, should be made to determine to what extent the lion population is limiting the population growth of the two major prey animals, namely wildebeest and zebra.

This could be done as follows. Three areas where wildebeest and zebra occur should be selected and their boundaries demarcated using possible migration routes as a guide to forming boundaries. Certain prey animals in these areas should be caught and marked to indicate possible migrations to and from the areas. These areas should be far enough from each other that movement of both prey and predators between these areas should be virtually ruled out.

The areas should be treated as follows:

1. Control area - no extra management technique should be applied to this area but regular counts of the prey animals and predators should be made. In this instance lion and hyaenas should both be counted.

2. Lion control area - all lions should be removed from the area, and periodic checks made that lions from surrounding areas have not moved into the area.

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3. Lion and hyaena control area - All lions and hyaenas should be removed here and again periodic checks should be made that the area has not been repopulated.

The prey animals should be counted in the area, with the most important counts being made just before the peaks in the calving season and at regular intervals there after, particular emphasis must be placed on the number of calves in each area.

This technique if applied over a period of two or three years should show to what extent the lions are limiting these populations.

THE EFFECT OF LION PREDATION ON THE RARER PREY SPECIES

The Lebombo flats of the northern part of the Park have been set aside as a sanctuary for roan and sable antelope and eland. There has been no appreciable increase in the population in recent years. A study of the effect of predation as a limiting factor should be instigated in this area, following similar lines as that suggested for wildebeest and zebra.

The effect of buffer species should be given particular attention, particularly with an eye to spatial distribution of buffer species in the dry season, as a result of artificial water points in the area.

PREDATION AT ARTIFICIAL WATER POINTS

In recent years the Park has embarked on an extensive drilling programme and boreholes have been sunk throughout the Park. These boreholes provide water throughout the year in areas where there previously was no water. The effect of these new water points has been to disperse the game over a wider area in the dry winter months. Where previously large herds of wilde-

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beest and zebra, numbering several hundred, were seen at a single water point, there are now small herds to be found, seldom exceeding fifty animals at most of these new water points.

A detailed study of the effect of this fragmentation of large herds relative to predation should be made. This could be done by forcing the small herds together in the dry season by closing certain water points in an area, thereby forcing the herds together. The lion prides in the area would then be forced to move after the prey to the water, or to move out of the area. These movements could be followed and the interactions between the various prides studied. Predation figures for these circumstances could be compared with those for smaller herds, at artificial waterholes in similar areas. These data could then indicate what effect these "new" water points are having on the prey population growth curves.

The results of these two techniques could then be taken together with the results of this study to give a more complete picture of lion predation

COLLECTION OF DATA FROM LIONS DESTROYED IN CONTROL AREAS

Data on parasites and reproduction potential could be collected.

An age determination technique could be worked out using either cementum layers in the canines, or using skull measurements compared to known age animals.

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SUMMARY

The lion (Panthera leo, Linn, 1758), has always been regarded as the most dominant predator of the African continent. It is now, however, confined to small areas set aside as game reserves and wilderness areas, whereas its previous range covered the entire African continent and parts of Europe and Asia.

The lions in the Kruger National Park were previously subjected to control measures, following public pressure. These measures appeared to have had little effect on the lion population, which continued to increase in number, as did the herbivores. This increase in the number of herbivores is probably the direct result of application of management practices applied in the area.

For the efficient management of an area it is essential to determine the effect of predation on the various prey species. Lions have been credited with 51,2 per cent of the kills recorded in the period from 1966 - 1972.

Additional data has been collected on mortality, reproduction, territoriality and movements with a view to determining the factors limiting growth and spatial distribution of the lion population.

The number of lions in the Park was estimated as being a 1 000 plus, by using a grid map of the area, onto which were plotted prides, as recorded in the monthly reports sent in by Rangers. These data were used in conjunction with known activity zones of marked animals, to establish the approximate activity zone of each pride. The number of animals in each pride were then summated.

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Lions were caught and marked to determine the most effective marking methods. Hot branding and coloured "stercolite" collars were found to be the most suitable techniques.

Lions in selected prides were caught and fitted with radio transmitter collars, to facilitate daily location.

The study was divided into four sections to investigate the predation rates by lions in the three major prey habitats. The first and second parts of the study were done in the Satara area to evaluate possible differences in predation rate during the dry and rainy seasons. No apparent difference was found.

The lions in each section of the study were followed for varying periods of time and the following recorded: all kills made; the age and species of each prey animal; the number and sexes of lions at each kill. The approximate mass of each kill was estimated using the average mass for that particular age-group of prey animal, as found in the data obtained from animals destroyed in control operations.

The total mass for the kills of each section of the study was calculated and the yearly kill requirement for the lions in that area established. The results of all four sections of the study were averaged to give the mean yearly kill requirement for lions in the whole study area. This mean requirement amounted to 2 397 kg per lion per year.

For interpretation of the results a "prey unit", equivalent to a carcase mass of 200 kg was defined. This unit was used as the basis for calculations of the yearly requirement of a known number of lions in the study area.

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The number of kills recorded for each species were expressed as a percentage of the total number of kills recorded. The figure so obtained was converted into prey unit equivalents to give the expected number of a species killed by lions per year. Possible causes for variation of numbers of animals killed by lion, are mass of prey and fluctuations in the numbers of lions in the study area.

The behaviour of all major prey species was studied in relation to their susceptibility to predation.

A general study of the hunting behaviour was made, as well as the factors which may contribute to the success or failure of a hunt and the relationship between lions and other predators and scavengers.

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OPSOMMING

Die leeu (Panthera leo, Linn. 1758) is nog altyd beskou as die mees dominante roofdier op die vasteland van Afrika. Waar dit voorheen voorgekom het oor die hele Afrikaanse kontinent en gedeeltes van Europa en Asië, is die verspreiding daarvan nou beperk tot wildtuine en wildreservate.

Leeus in die Nasionale Krugerwildtuin was voorheen onderhewig aan getalleuitdunning as gevolg van publieke aandrang. Dat die uitdunning min invloed gehad het, blyk uit die feit dat ten spyte van beheermaatreëls, die leeubevolking in getalle toegeneem het. Terselfdertyd het die getalle van herbivore ook toegneem, waarskynlik as gevolg van die toepassing van beheerpraktyke.

Om 'n gebied doeltreffend te kan beheer, is dit noodsaaklik om die effek van predasie op die verskillende prooidiere te bepaal. Gedurende die tydperk 1966-1972 was leeus verantwoordelik vir 51,2 persent van die totale aantal vangste.

Data oor mortaliteit, voortplanting, territorialiteit en bewegings is versamel met die oog daarop om die faktore wat groei en ruimtelike verspreiding beperk, te bepaal.

Die hoeveelheid leeus in die Park is geskat op ± 1 000 individue, deur gebruik te maak van 'n kaart van die gebied waarop verskillende afgebakende gebiede in die vorm van 'n roosterpatroon aangebring is. Die verskillende troppe en hul groottes, soos verkry uit die maandelikse verslae van die veldwagters, is op die kaart aangedui in kombinasie met bekende aktiwiteits-

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sones van gemerkte diere, om naastenby die groottes van die verskillende aktiwiteits-sones te bepaal. Die getal leeus in elke trop is toe bymekaar getel.

Leeus is gevang en gemerk. Brandysters en gekleurde „sterkolite" nekbande het geblyk die mees effektiewe merkmetodes te wees. Om daaglikse opsporing te vergemaklik is leeus in bepaalde troppe gevang en toegerus met nekbande wat radiosenders bevat.

Die projek is ingedeel in vier afdelings om die tempo van leeu-predasie in die drie hoof prooihabitatte te bepaal. Die eerste en tweede gedeeltes van die projek is uitgevoer in die Satara-gebied, om moontlike verskille in predasie gedurende die reën- en droëseisoene te bepaal. Geen waarneembare verskille kon gevind word nie.

Die leeus van elke afdeling van die projek is vir verskillende tydperke gevolg en die volgende is opgeteken: alle vangste; die ouderdom en spesies van die prooi; die hoeveelheid en geslagte van leeus by elke vangs. Die massa van elke prooidier is geskat deur gebruik te maak van die gemiddelde massa vir die spesifieke ouderdomsgroep en spesies soos verkry uit gegewens van diere wat vernietig is gedurende uitdunningsprogramme. Die totale massa van alle vangste vir elke spesifieke afdeling is bepaal en van lg. is die jaarlikse hoeveelheid vleis wat leeus in daardie gebied nodig het, bepaal. Die gemiddeld van die resultate van al vier afdelings is bepaal. Die getal gee die gemiddelde jaarlikse massa benodig deur leeus in die Park en daaruit is die gemiddelde vangsbenodigheid per leeu vasgestel op 2 397 kg per leeu per jaar.

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Om die resultate te interpreteer is gebruik gemaak van 'n „prooieenheid", wat gelyk is aan 'n karkasmassa van 200 kg . Die hoeveelheid vangste vir elke spesies is uitgedruk as 'n persentasie van die totale hoeveelheid vangste en die resultate is omgesit in „prooieenheid-" ekwivalente.

Variasie in die aantal vangste deur leeus kan veroorsaak word deur verskille in massa van prooi en fluktuasies in die leeu se bevolkingsgetalle.

Die gedrag van die belangrikste prooispesies is bestudeer, veral met die oog op hulle kwesbaarheid vir predasie.

'n Algemene studie van leeus se jaggedrag is gemaak, asook faktore wat die sukses of mislukking van so 'n jag bepaal. Bykomend hierby, is die verhouding tussen leeus en ander roof- en aasdiere bestudeer.

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APPENDIX

SCIENTIFIC NAMES OF ANIMALS MENTIONED IN THE TEXT

Mammals:

Buffalo *Syncerus caffer*

Zebra *Equus burchelli*

Wildebeest *Connochaetes taurinus*

Impala *Aepyceros melampus*

Roan antelope *Hippotragus equinus*

Sable antelope *H. niger*

Tsessebe *Damaliscus lunatus*

Eland *Taurotragus oryx*

Elephant *Loxodonta africana*

White rhinoceros *Ceratotherium simum*

Black rhinoceros *Diceros bicornis*

Hippopotami *Hippopotamus amphibius*

Waterbuck *Kobus ellipsiprymnus*

Giraffe *Giraffa camelopardalis*

Kudu *Tragelaphus strepsiceros*

Warthog *Phacochoerus aethiopicus*

Spotted hyaena *Crocuta crocuta*

Leopard *Panthera pardus*

Cheetah *Acinonyx jubatus*

Caracal *Felis caracal*

Serval *F. serval*

Wild dog *Lycaon pictus*

Black-backed jackal *Canis mesomelas*

Porcupine *Hystrix africaeaustralis*

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Reptiles: Crocodile *Crocodylus niloticus*

Land Tortoises *Testudo pardalis*

Birds: Ostrich *Struthio camelus*

Hooded vulture *Necrosyrtes monachus*