CHAPTER 4

IMPALA

GENERAL INTRODUCTION

Integral to any study of predator-prey relationships is a study of the prey species itself. No justifiable generalizations can be made to replace actual observations on the prey animals at the site of the predator study. Of general consequence is some attempt to obtain an indication of prey abundance. While this cannot always be directly related to prey availability, it provides at least some measure of the contribution made by the prey species to the dynamics of the system being studied.

The catholic diet of the jackal results in a wide range of potential prey animals which should be studied. As the focal prey species in the present study was the impala, particular attention was paid to the population of this species occurring in the Reserve. From the outset I speculated that if the jackal were indeed capturing adult impala, they would probably be selecting for individuals somehow easier to capture than the average in the population. No attempt was made to study the dynamics of other prey species as this did not fall within the terms of reference of the study. However, any relationship between the jackal predator and the impala prey is subject to influences from other components within the ecosystem, as was illustrated in Chapter 3 in the diet switching by the jackals which was closely related to rainfall and insect abundance.

Certain information on the impala in the NTGR was already available.

Lind (1974) estimated that the Reserve contained a population of approximately 14 000 impala. Subsequent estimations by Walker (1983) placed the impala population at between 11 000 and 22 000. A comprehensive aerial survey conducted in 1984 (Joubert 1984) gave an estimate of 6 000 impala in the NTGR. Despite discrepancies in total number, all of the above reports indicated that the population of impala is far higher in the south-central region of the Reserve than in the northern areas. Furthermore, calculations using Joubert's data indicate a density of approximately fifteen impala per km^2 in the south-central region and approximately five impala per km^2 in the northern areas. The area selected for the study of the jackals was thus known to carry a relatively high density of impala.

In addition to a necessity to study the population parameters of the impala population of the Reserve, I had a separate interest in another aspect of the population from a veterinary perspective. Mange had been reported in the impala in the Reserve as early as 1974 (Lind 1974), and subsequent sporadic reports were received of impala with mange in the southern areas of the Reserve. A regional Veterinary Officer had examined some of the specimens and had diagnosed sarcoptic mange (Devine, pers. comm.). A study, which originally was not linked to the jackal project, was launched to obtain more information on the reported mange condition. It was, however, cautiously speculated that if mange did occur in the impala, it was perhaps these animals which were being preyed upon by the jackals.

The investigations on impala described in this chapter were aimed at determining baseline parameters of the population and the cause of the reported mange and its significance in the population. This chapter is divided into four sections, each dealing with a specific investigation into

aspects of the impala population in the Reserve. Initially the study was comprised of the collection of baseline data as well as casual observations of animals to note the presence of mange. Observations made during the baseline study - Section 1 - indicated the need for the collection of a specific sample to determine the cause of the mange - this forms the subject of Section 2. This preliminary investigation led, for reasons that will become apparent, to the undertaking of a quantitative assessment of external parasite levels - Section 3. In parallel to the the other studies, the temporal and spatial occurrence of the "mange" was determined - Section 4.

Each of the sections, while separated in this thesis, were inextricably linked through the study. The specific investigations were not planned from the outset; as the need for specific data was indicated, so another investigation was added to the project. By the very nature of the results obtained, the study could not have been planned in advance. In retrospect it may thus appear that certain aspects could have been covered in more detail, or in a different way. However, what is reported here is a reflection of how the study evolved as new and important facts came to light.

SECTION 1 - BASELINE PARAMETERS

Introduction

As data were available on the density of impala in the south-central region of the Reserve (Joubert 1984), and as impala are a water dependent and therefore relatively sedentary species (Murray 1982), it was not considered necessary to conduct a specific census to determine impala abundance in the

study area. Baseline material was, however, required on age structure and condition for comparison with impala killed by jackals during the study. Observations on parasites were at this stage regarded as of interest value only.

Materials and Methods

In order to obtain reliable information I undertook to do the shooting of impala required by Mashatu Game Reserve for ration and lodge purposes as from February 1986. Due to time constraints this was only done for six months. A total of 114 impala were shot between 15/02/86 and 16/08/86. In order to compare impala from different regions of the Reserve all impala were shot within two circumscribed areas as depicted in Fig. 20. Male impala under two years of age were not shot. Apart from this criterion, all the animals were shot in a random manner - the animal which presented the best target was shot. The date, sex and location were recorded for each animal shot, and the presence of external parasites was noted. The mandibles of all shot impala were cleaned and retained for age determination as described below. Approximately once a week two of the impala were transported to Kgwedi research base where they were processed as follows:

1. Mass and standard body measurements (Ansell 1965) were determined.

2. All viscera were examined for signs of parasitism;

3. The warm carcase mass was determined.

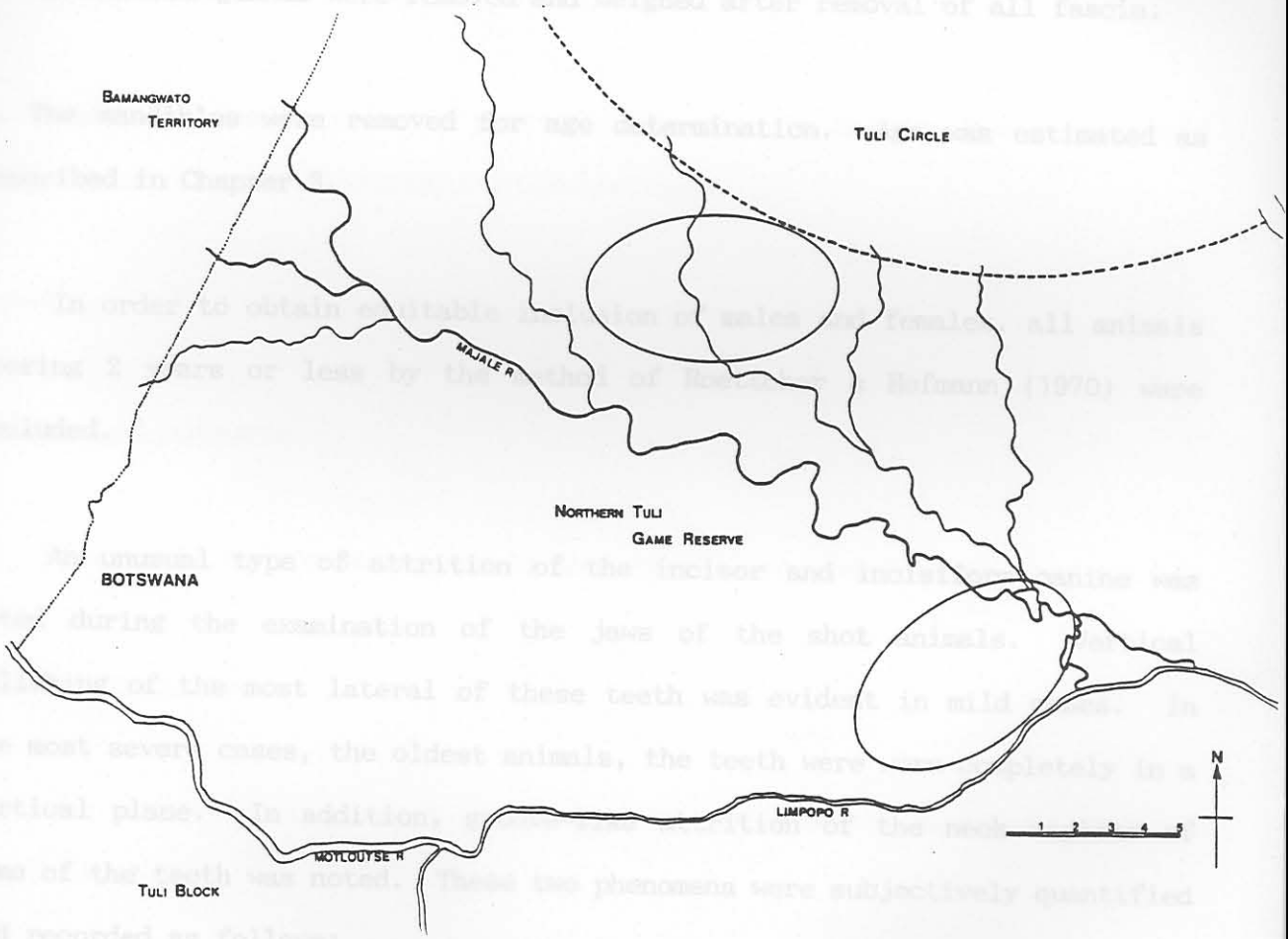

Figure 20. Northern and southern impala baseline data collection zones.

4. The kidneys were individually removed together with their perinephric fat caudally to the internal iliac arteries. Fat and kidneys were separated and weighed on a triple beam balance. Kidney Fat Indices were calculated as described by Riney (1955) (KFI = mass of perinephric fat/mass of both kidneys x 100).

5. The adrenal glands were removed and weighed after removal of all fascia.

6. The mandibles were removed for age determination. Age was estimated as described in Chapter 3.

In order to obtain equitable inclusion of males and females, all animals scoring 2 years or less by the method of Roettcher & Hofmann (1970) were excluded.

An unusual type of attrition of the incisor and incisiform canine was noted during the examination of the jaws of the shot animals. Vertical polishing of the most lateral of these teeth was evident in mild cases. In the most severe cases, the oldest animals, the teeth were worn completely in a vertical plane. In addition, groove-like attrition of the neck regions of some of the teeth was noted. These two phenomena were subjectively quantified and recorded as follows:

Vertical wear: 0 = none;
1 = tip of tooth rounded;
2 = tip of tooth substantially flattened;
3 = Tooth worn to mid-crown;
4 = Only stump of crown remaining; and

5 = Total vertical attrition - level with or below gingiva.

Grooves: 0 = none;

1 = slight indication of groove;

2 = well defined groove; and

3 = deep groove - half or more of tooth diameter.

The most advanced value was used for each pair of teeth.

Ages of animals collected as control samples in Section 3 and Section 4 were included for age structure determinations.

Results

Weights and measures

Masses and body measurements of shot impala are presented in Appendix A7.

External parasites

The subjective assessment of the presence of external parasites revealed the following:

1. Numbers of ticks observed on the impala were generally low compared to the values reported by Horak (1982). Only adult ticks could be evaluated by subjective appraisal, but nevertheless absolute numbers did not appear to be very high except in occasional animals;

2. There was a marked difference in the number of ticks on impala from the two

areas. Some impala from the south central region carried large numbers of ticks, but invariably they had at least some ticks on their bodies. In contrast, adult ticks were encountered on only two of the 61 impala shot in the northern region.

Necropsy notes

Thirty-four impala were necropsied.

Tape worm cysts in muscle tissue were only occasionally encountered. Calcified cysts, probably originally the hydatid cysts of *Echinococcus sp.*, were encountered in the lungs and viscera of 11 of the the 34 impala necropsied.

Tape worms (*Stilezia sp.*) occurred in the bile ducts and livers of four of the impala. This infestation was accompanied by variable thickening of the bile duct walls and the accumulation of a yellow purulent exudate.

Condition

Kidney Fat Index

Perinephric fat and renal masses and calculated kidney fat indices are presented in Appendix A8. Frequency distribution of KFIs is shown in Fig. 21.

Adrenal glands

Masses of adrenal glands are presented in Appendix A8.

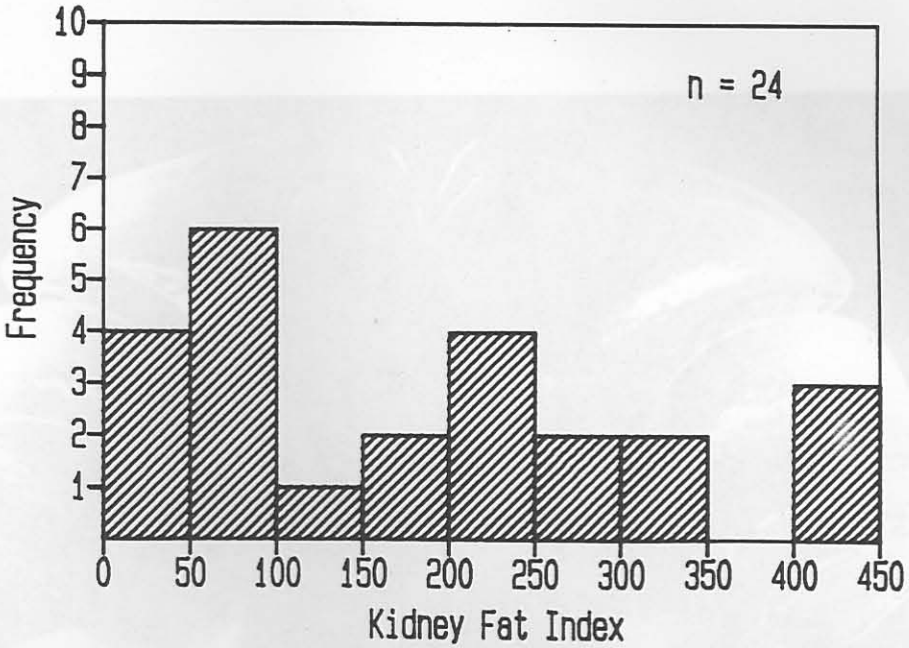

Figure 21. Frequency distribution of Kidney Fat Indices of impala: Section 1, baseline data.

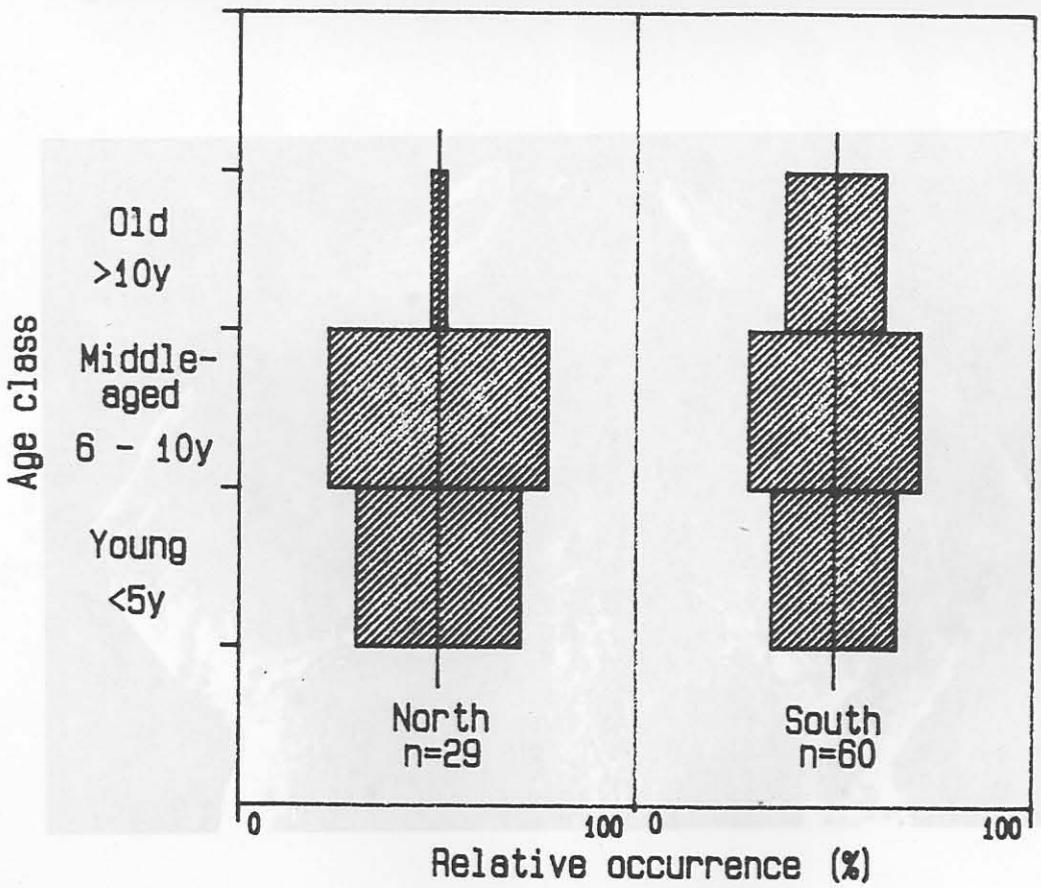

Figure 22. Age group distribution of impala over two years old from northern and southern regions of the NTGR.

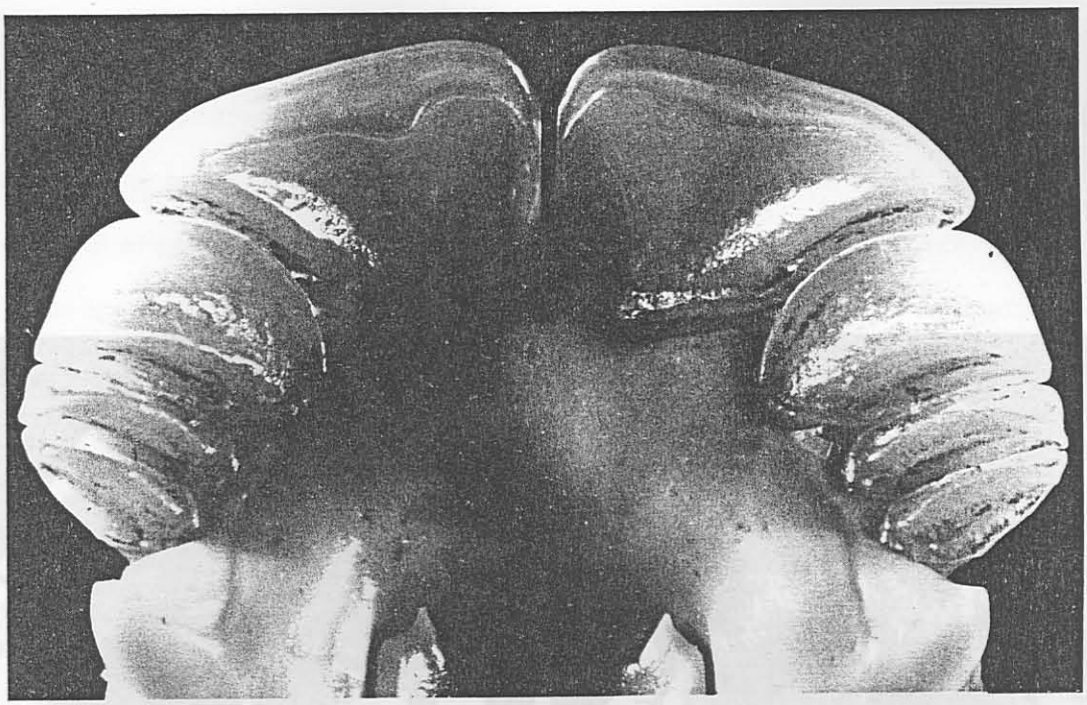

Figure 23 a. Normal impala incisor-canine complex.

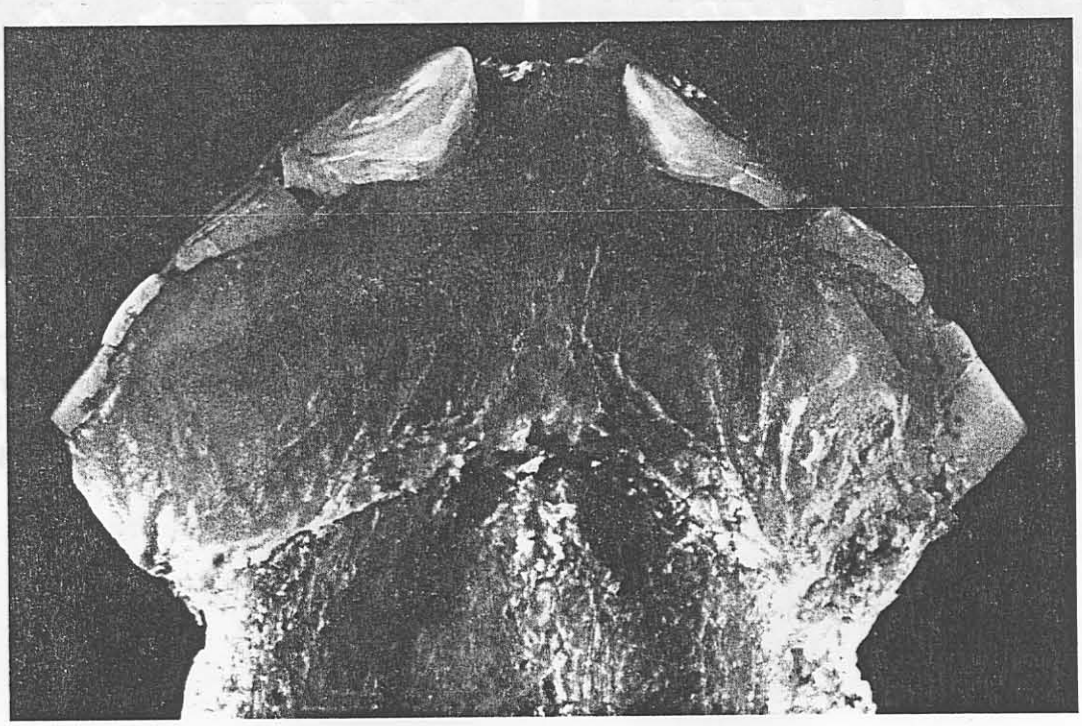

Figure 23 b. Total vertical attrition of an impala incisor-canine complex.

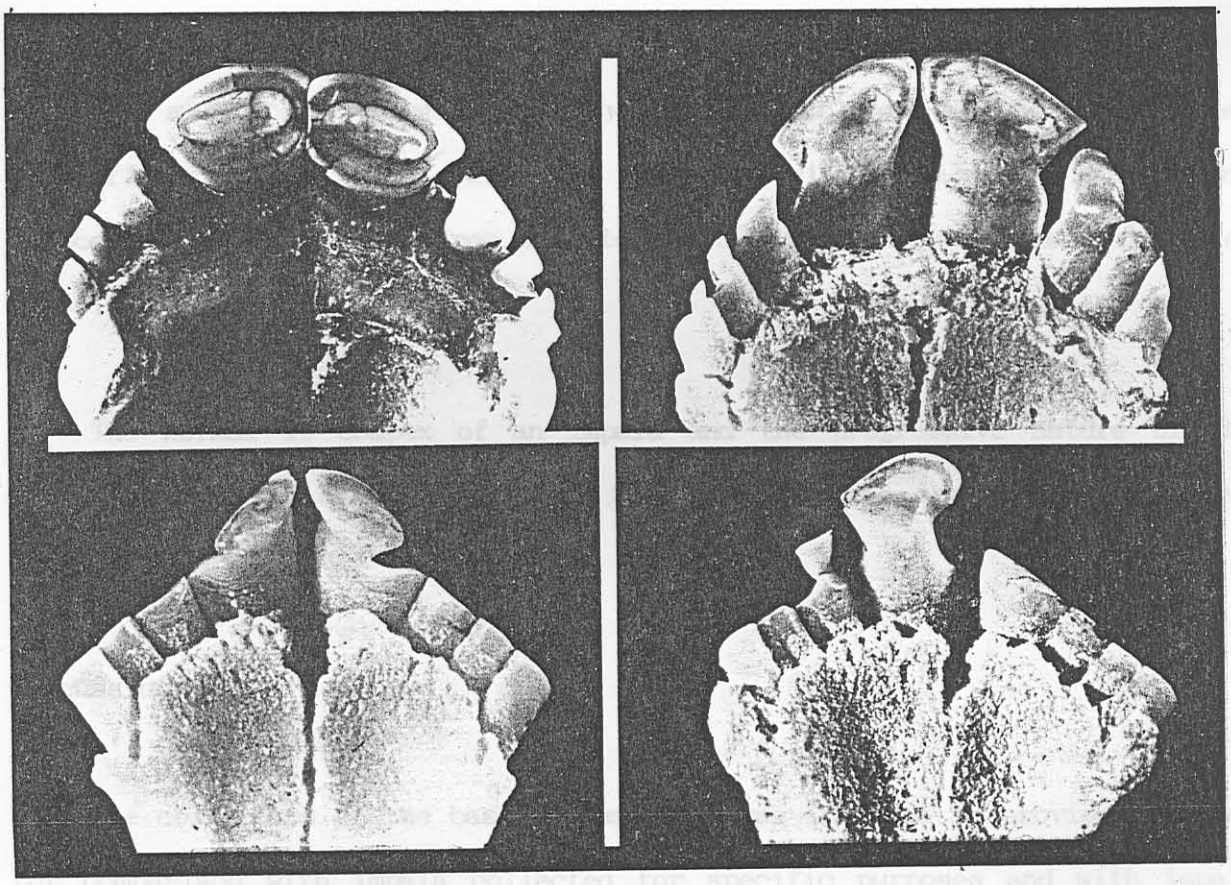

Figure 23 c, d, e & f. Intermediate attrition of impala incisor- canine complexes showing vertical attrition and grooves in the neck regions of the teeth.

Age

Ages as determined by the three described methods are presented in Appendix A9. Age distributions of impala older than two years from the two collection areas are presented in Fig. 22. Vertical and neck attrition of incisors and canines is presented with the age categories in Appendix A9.

The age structures of the two impala sub-populations differed significantly (X^2=6,13, d.f.=2, p<0,05), with a highly significant preponderance of animals from the old age class in the south-central region (X^2=6,16, d.f.=1, p<0,025).

The normal IC compex of an impala and the progressive nature of the notching and vertical attrition is illustrated with some representative examples in Fig. 23.

Discussion

The collection of the baseline material was intended to provide material for comparison with impala collected for specific purposes and with impala killed by jackals during the study. As such, the data collected are recorded here as they may be of some use in future studies of ungulate populations in the NTGR. In the context of the present study, two aspects of the baseline study were of immediate interest, although at the time their full implications were unknown.

External parasites

The dichotomy in external parasite abundance between the two sample areas indicates environmental differences between the two regions. Although parasite numbers in the southern area did not appear to be excessive in comparison with results from other areas of southern Africa (Horak 1982), the almost total absence of ticks on the impala from the northern areas of the Reserve raises the question of what the determining factor is which has led to this considerable disparity. Two classical answers to this *status quo* immediately spring to mind. First, the density of animals in general , and of impala in particular, is higher in the south central region than in the north (Lind 1974, Joubert 1984, pers.obs.). This alone could lead one to intuitively expect that parasite numbers may be higher in this region simply due to the higher biomass of potential host animals (Norval & Lightfoot 1982).

Second, the south-central region consists largely of a floodplain on alluvium, with good stands of perennial grass along some of the rivers. while the northern region consists of mopane scrub on basalt interspersed with valley bush (Joubert 1984). This habitat difference could again account for a greater abundance of ticks, which thrive in better vegetated areas and infest their hosts by ascending and waiting on the vegetation (Norval & Lightfoot 1982.)

The combination of these two factors would thus appear to be sufficient to explain the relative abundance of ticks on impala from the south central region, and were it not for the other aspects of the present study this may well have remained the the final conclusion based on classical knowledge of tick ecology (Barnard 1986, Hair & Bowman 1986). However, taking other

aspects of the present study into consideration, this classical explanation may not provide the real answer. As indicated, the baseline study served only to indicate an interesting trend. A comprehensive discussion must thus follow the other sections of this chapter, and is thus included in the chapter on Ecosystem Processes - Chapter 7.

Age

The incisor wear index of Roettcher & Hofmann (1970) was used to compare the two sub-populations as it provided an index of relative physiological age which is of importance in a study of selective predation.

Following exclusion of impala two years old or less from the shot sample' samples of 29 impala from the northern area and 60 from the southern area remained. These data are insufficient for the construction of life tables for the two regions, but do suggest some interesting trends in the two sub-populations. The significant preponderance of old animals in the sample from the south-central region - i.e. 25% of the sample - indicates possible differences in population level processes in the two areas of the Reserve.

In addition to the differences in age related dental attrition , the vertical attrition of the incisor teeth and the associated canine (hereinafter referred to as the incisor-canine (IC) complex) was enigmatic as it could not be explained by normal patterns of tooth wear. This vertical attrition is quantified in Appendix A9. Essentially what was observed was a progressive vertical attrition of the lateral elements of the IC complex. This was first observed in animals 2 - 3 years of age on the canine and 3rd incisor. In

older animals, this attrition was more severe, and progressed to involve the 2nd and later the 1st incisors. The ultimate outcome of this attrition was represented by total attrition of these teeth in the vertical plane, with the surfaces of the stumps actually lying below the surface of the gingiva. The notching of the neck regions of the teeth also progressively increases with age, and was most severe in the oldest animals - those that still had some remaining teeth. During the baseline data collection phase the worn incisor teeth were of novelty interest only. The true importance of these early observations only became apparent later, and is discussed in the appropriate sections below.

The obvious explanation of the occurrence of the very old animals in the southern region is that there may be some difference in the mortality factors present in the two sub-populations. An alternative hypothesis is that old animals from the entire region move to the south central region when they become old. The latter can be rejected on the grounds that impala are known to occupy limited home ranges, only undertaking extensive movements under unusual circumstances (Murray 1982). The limited movement of a herd of impala in the NTGR was confirmed by the telemetry study - Section 2 below.

The baseline data thus raised the question of what difference there was, if any, in mortality factors between the two sub-populations and how, if at all, this could explain the disparity in age structures. Again this question becomes relevant in the light of other aspects of the study, and is discussed further in Chapter 7.

Condition

Kidney Fat Index

The Kidney Fat Index of impala is markedly influenced by factors such as age, sex, pregnancy, season, nutrition and the annual rut (Anderson 1965, Cowley 1975, Hanks, Cumming, Orpen, Parry & Warren 1976, Brooks 1978, Dunham & Murray 1982). The sample of 24 impala in the present study therefore can only provide an indication of the range of KFIs within the NTGR population. As seen in Table 9, KFIs range from 8,3 to 448,2, similar to the wide range recorded by Dunham & Murray (1982), except that the peak values are higher in the present study (possibly due to a different definition of perinephric fat). These results indicate that while, for whatever reason, some of the impala in the population may be in poor condition, there is ample evidence that this is due to individual variation and not to malnutrition of the entire population. This finding is of particular relevance to Chapter 3.

Adrenal Glands

Mean adrenal masses are $1,46 \pm 0,30$ (left) and $1,42 \pm 0,27$ (right)(n = 12) (Table 9). Excluding one of the male impala from the sample (no. 641) which had exceptionally heavy adrenal glands (the only territorial male shot in the peak rutting season), a significant negative correlation (r= -0,77) (Fig. 24) was found between total adrenal mass and KFI, as has been reported in California deer (Hughes & Mall 1958). As with the Kidney Fat Index, variables exclude interpretation of these results beyond their value as a baseline parameter. However, the correlation recorded here suggests that use of adrenal mass as an index of condition in impala should be investigated.

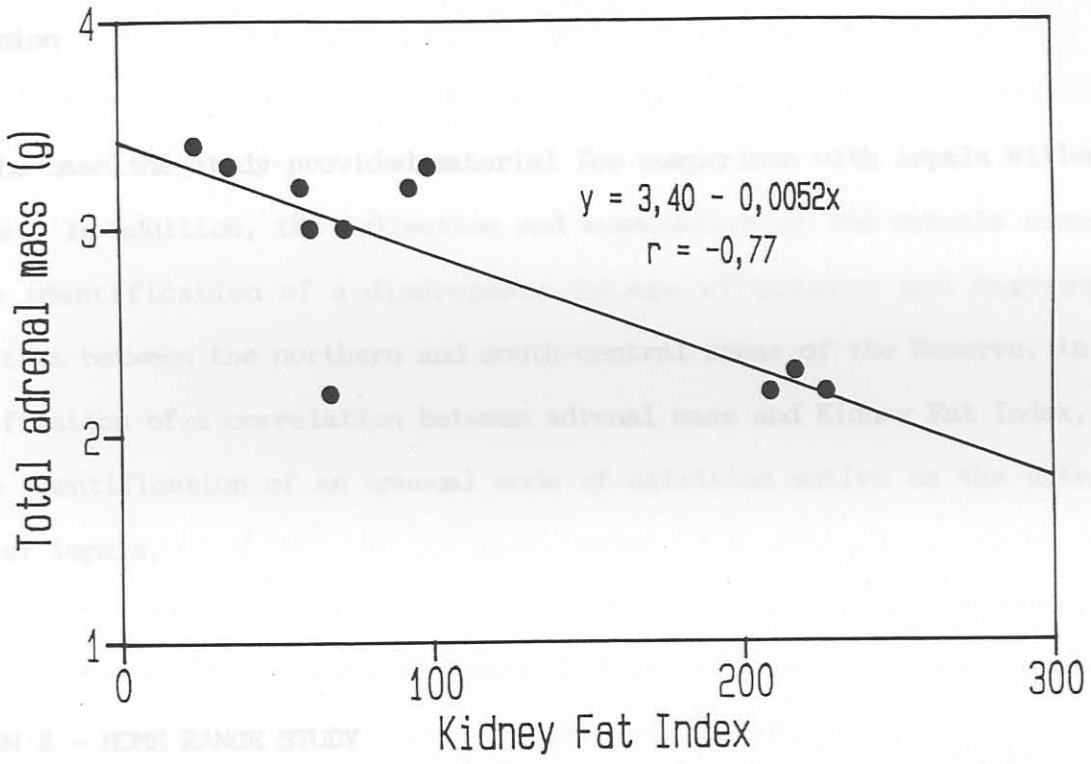

Figure 24. Relationship between total adrenal mass and Kidney Fat Index in impala.

Weights and measures

The weights and measures obtained in the baseline study comply with those obtained in other studies on this species to date (Smithers & Wilson 1979).

Conclusion

The baseline study provided material for comparison with impala killed by jackals. In addition, the collection and examination of the animals resulted in the identification of a discrepancy in age structures and degrees of parasitism between the northern and south-central areas of the Reserve, in the identification of a correlation between adrenal mass and Kidney Fat Index, and in the identification of an unusual mode of attrition active on the anterior teeth of impala.

SECTION 2 - HOME RANGE STUDY

Introduction

Impala are considered to remain within relatively restricted home ranges except when exceptional environmental events occur (Murray 1982). One assumption of the present study was that impala in the NTGR comply with this general rule, thus implying limited movement of animals between the northern and central areas of the Reserve, which are separated by some 15 km. All observations made over the three-and-a-half years of residence in the Reserve indicated that impala in the NTGR do move over restricted ranges.

One radio collar was available from the jackal study. As telemetric and radio tracking was being conducted for the jackal study, it was decided to fit the radio collar to a female impala in order to monitor the range use of her and her clan.

Materials and Methods

A female impala was darted using the equipment described in Chapter 3. The drug mixture consisted of 1 mg etorphine hydrochloride (M99, Reckitt & Coleman, Pinelands, RSA) and 10 mg xylazine hydrochloride (Rompun, Bayer SA, Isando, RSA). A radio collar of the type described in Chapter 3 was fitted, and an antidote (diprenorphine hydrochloride, M5050, Reckitt & Coleman) was administered intravenously.

The impala was located using the telemetry equipment and regime described in Chapter 3. Additional direct observations were made by radio tracking on a sporadic basis and recorded as described in Chapter 3. Home range was calculated using the minimum convex polygon method (Mohr 1947).

Results

563 telemetric and 24 direct locations were obtained over a 65 day period from 10-04-1988 to 15-06-88. The total range covered by the impala during this period was 7,22 km^2.

Discussion

The area used by the impala and her clan of approximately thirty females

and their offspring was 7,2 km^2, which which is considerably larger than the range of 0,40 - 1,20 ha recorded by Murray (1982) for this species. Nevertheless, in relation to the total area of 650 km^2 covered by the Reserve, the movements of the impala and her clan are relatively localized, and there was certainly no indication of movement to or from the northern areas during this period. Observations indicated that the impala utilized open habitats at night, and entered the dense valley vegetation only during the day. This observation was not quantified.

Conclusion

The limited movements of the tagged impala and her clan, coupled with all the casual observations made during the course of the study, provide some indication that NTGR impala do comply with the general home range utilization patterns of this species. As there is no indication to the contrary, it is concluded that an assumption that the northern and southern sub-populations of the NTGR can be regarded as separate, at least in the short term, is justified.

SECTION 3 - MANGE PILOT STUDY

Introduction

Observations made during the Baseline Study indicated that "mangy" animals were indeed present in the Reserve. With the background knowledge that general body condition may influence the predisposition to mange (as reviewed by Nelson, Keirans, Bell & Clifford (1975), the Mange Pilot Study was

designed to:

1. Provide a general qualitative impression of the pathology associated with the mange reported to occur in the Reserve;

2. Quantitatively determine parameters which may influence predisposition to the mange, such as age, condition and internal parasite burden; and

3. Provide an indication of how a quantitative study of the mange should be undertaken.

Materials and methods

In November 1986 a sample of five visibly mangy female impala were shot in the vicinity of the Pontdrift border post, an area where mangy animals were noted to be particularly abundant at that time. A control sample of five females also was shot in the same area. As in the baseline data section, the first animal (in this case only female impala) which stood still for long enough to provide a clear shot was taken. If, however, the animal was visibly "mangy" it was not shot. The control sample thus represents a random sample of non-mangy female impala. As the impala were shot out of the hunting season, a permit from the Department of Wildlife and National Parks was obtained prior to commencement of the study. All these animals were processed as described in Section 1 above. In addition:

1. All animals were photographed from the left and right sides;

2. A drop of liquid paraffin was applied to areas of affected skin on the

"mangy" animals and the skin was scraped with a glass slide. The debris in the liquid paraffin was then transferred to a clean slide, covered with a cover slip and examined for the presence of mites;

3. Detailed examination for signs of pathology was undertaken; and

4. The left femur was sawn in half along its length and examined for signs of erythropoeisis and atrophy of the adipose tissue.

Results

Weights and measures

Masses and body measurements of shot impala and foetuses are presented in Appendix A10.

Condition

Kidney Fat Index: Perinephric fat and renal masses and calculated kidney fat indices are presented in Table 9.

Table 9. Impala Kidney Fat Index and adrenal mass - Section 3.

	Fat	Kidneys	KFI	Left adrenal	Right adrenal	Total adrenal
"Mangy" group.						
M0186	14	170	8,2	2,3	2,1	4,4
MO386	24	140	16,9	1,9	1,4	3,3
MO486	38	146	26,0	1,8	1,4	3,2
M0586	22	136	16,0	2,3	2,3	1,7
M0686	21	147	14,4	2,1	1,7	3,8
Mean (std. dev.)			16,3(6,4)			3,3(1,0)
Control group						
M0286	140	139	101,0	1,4	1,3	2,7
M0786	29	122	23,8	1,7	1,3	3,0
M0886	15	130	11,8	2,1	1,5	3,6
M0986	76	143	53,0	2,1	1,5	3,6
M1086	59	111	53,0	1,8	1,7	3,5
Mean (std. dev.)			48,5(34,5)			3,3(0,4)
			t=2,13 n.s p>0,05			t=1,60 n.s. p>0,1

All masses in g.
KFI = Kidney Fat Index = Mass of perinephric fat/Mass of kidneys x 100.

Adrenal Glands — Adrenal gland masses are presented in Table 9.

Age

Ages determined from the mandibles of sample and control animals, and vertical attrition of incisors and canines, are presented in Table 10.

Recorded wear on molar teeth was low in relation to incisor attrition in older animals.

Table 10. Impala ages and vertical dental attrition - Section 3.

	Age			Vertical wear			
	Murray *	Spinage **	R&H ***	C	I3	I2	I1
					****		
"Mangy group							
MO186	8.5	f	3	5	5	5	5
M0386	8.5	f	3	5	5	5	5
M0486	8.5	f	3	5	5	5	5
M0586	8.5	f	3	5	5	5	5
M0686	8.5	f	3	5	5	5	5
Control group							
M0286	7.5	d	3	4	4	2	2
M0786	2.0	2	1	2	2	0	0
M0886	7.5	f	3	3	3	2	1
M0986	7.5	d	3	4	4	4	2
M1086	2.5	d	1	0	0	0	0

* Murray (1980). Age in years.
** Spinage (1971). 2= 1-2 years; d= 5-6 years; f= >8 years
*** 1= young, < 5 years; 2= middle aged, 5-10 years; 3= old, > 10 years. Based on incisor wear, Roettcher & Hofmann (1970) .
**** 0=none; 1=tip of tooth rounded; 2=tip of tooth substantially flattened; 3=tooth worn to mid-crown; 4=Only stump of crown remaining; 5=total vertical attrition.

External parasites

The subjective assessment of the level of external parasites revealed the following:

Mites

Repeated scrapings of apparently mangy skin failed to reveal the presence of any mites. There was also no external manifestation of mite infestation such as scaling, inflammation, thickening or crusting.

Ticks and lice

Body Numbers of external parasites were far higher on the "mangy" animals than on the controls, as evidenced by close inspection of the entire body. Large numbers of ticks were found on the lower legs and neck region, and occasionally under the tail. No ticks were found in the areas affected by the "mange".

Ears Large numbers of tick larvae, nymphs and adults were found in the hairy fringes and ridges on the insides of the pinnae. There were noticeably less ticks in the ears of sample animals than in the ears of the control animals - see Fig. 25.

Tail and Fetlock Glands Inspection of the tails and fetlock glands of the sample animals revealed a high level of louse activity in these long-haired regions of the body. Large numbers of lice and their eggs were visible, and there was considerable accumulation of debris (Fig. 26). This was in stark contrast to the low level of louse activity in these regions on the control animals.

Necropsy notes

Mange: The "mangy" areas of the body were in fact devoid of hair without any macroscopic evidence of pathology associated with mange. The smooth, hairless skin is illustrated in Fig. 27. The lack of hair exposed the skin which is naturally black in colour, imparting the "mangy" appearance at a distance. This alopecia was total or partial in severity, and affected larger

Fig. 25a

Fig. 25b

Figure 25 a,b. Ticks in the ears of an old (a) and a young (b) impala.

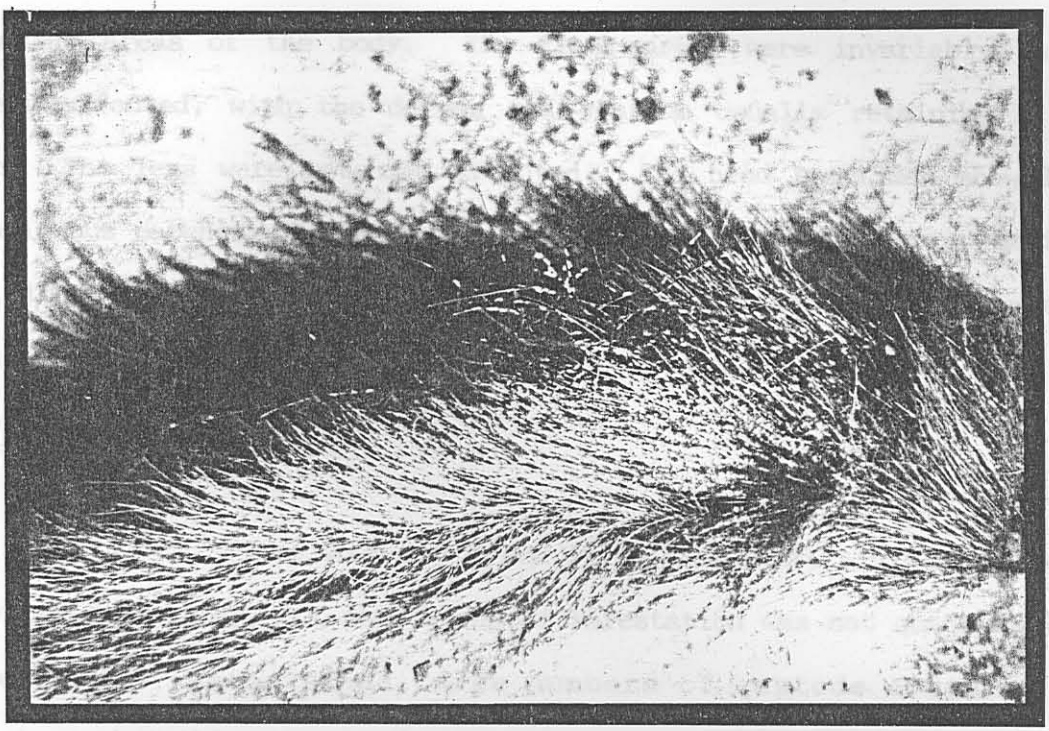

Fig. 26a

Fig. 26b

Figure 26 a,b. Lice and debris in the tail (a) and a metatarsal gland (b) of an impala with a totally worn incisor-canine complex.

or smaller areas of the body. The flank areas were invariably the most severely affected, with the dorsum and ventrum usually retaining a better pelage. The legs were patchily affected. The head sometimes showed small discontinuous patches of alopecia. A distinctive feature observed during the pilot study was that the pelage cranial to a line parallel to the scapula spine, at the level of the shoulder, was invariably totally unaffected by the alopecia Fig. 28.

Parasitism: Tape worm cysts and liver tape worms were encountered as in the baseline study, but the degree of infestation was not quantified. Some of the "mangy" animals had large numbers of cestode cysts in their musculature, but this was not observed in all the sample animals.

Musculature: Several of the sample animals exhibited a pale coloured musculature which had a strange rancid smell even on the fresh carcase. The pale muscles were also abnormally friable.

Body condition: All the impala were in poor condition. Little or no fat reserves were present in the body cavities of most of the animals, and serous atrophy of adipose tissue was evident. The fat in the femurs was jellylike and a pale pink colour indicating a complete absence of fat. Although some animals were in slightly better condition, there was no apparent difference between the sample and control groups.

Haemopoiesis: Although again there was little to differentiate the two groups, there was evidence of haemopoeisis in the head region, and in some cases even the shaft region, of the femurs of sample and control animals.

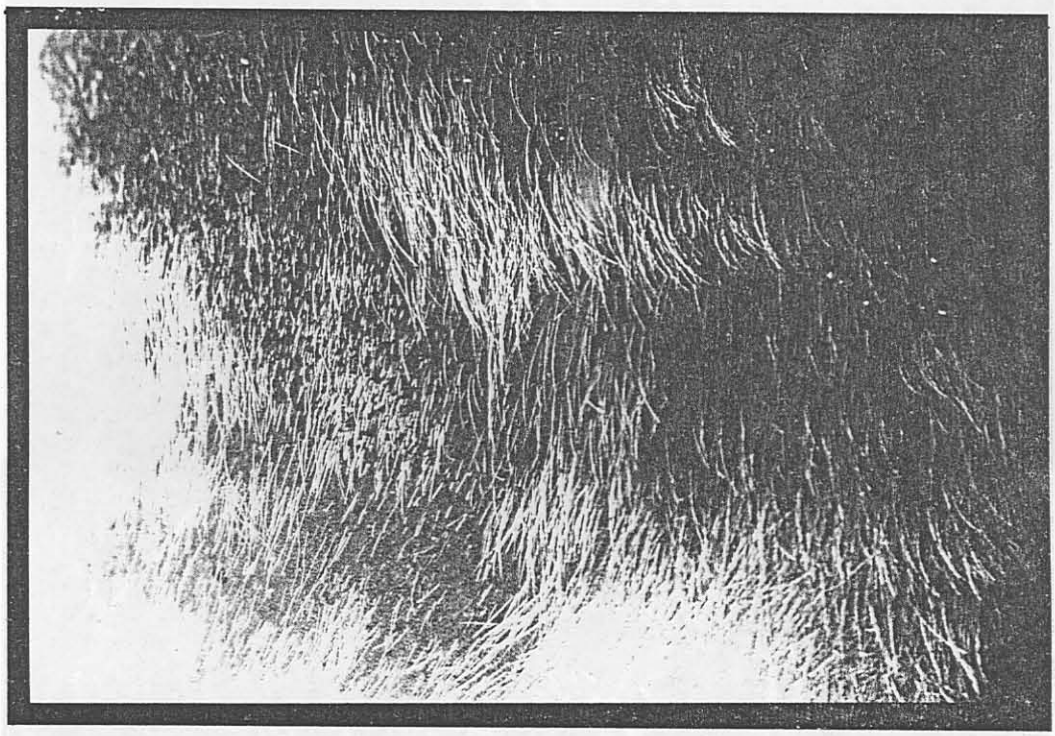

Figure 27. A typical area of alopecia on an impala with a totally worn incisor-canine complex.

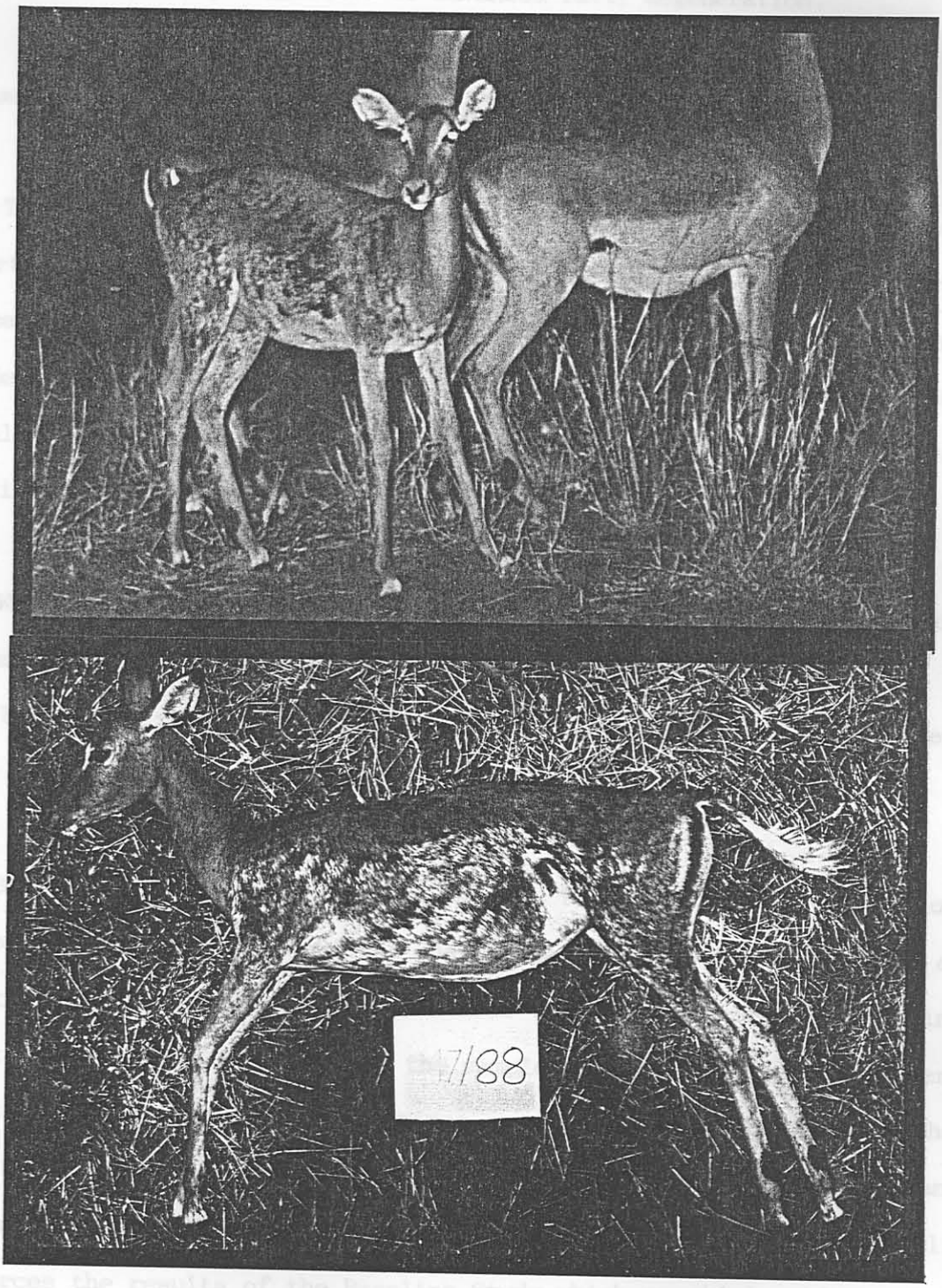

Figure 28 a,b. Impala with advanced alopecia demonstrating the black colouration and the abrupt termination of the alopecia at the shoulder.

Liver: The livers of the animals in the worst condition were swollen and friable, suggestive of advanced fatty degeneration.

Discussion

The intention of the pilot study was to determine the cause of the reported mange in the impala population of the NTGR, and to provide an indication of a suitable protocol for a detailed study of the mange syndrome so identified. The fact that there was no trace of mange in any of the study animals at first was a source of consternation, but this later led to even more interesting discoveries.

What was highlighted by the pilot study was the fact that a quantitative determination of external parasites, other than mites, was essential. This thus became the task of the following section which deals with a detailed study of the syndrome identified by the study.

Before discussing the results of the Pilot Study, the nature of the control animals reqires attention. As can be seen from Table 10, three of the five control animals are from the oldest age category according to incisor attrition. However, while all of the sample animals exhibited total vertical attrition of the incisors and canines, even the old sample animals had at least some of their teeth remaining. The fact that three of the five randomly shot animals were from the oldest age category is highly exceptional, and reinforces the results of the Baseline Study which provided evidence that the age structure of the southern impala population is skewed towards the older age categories.

While the mean Kidney Fat Indices of the two groups did differ (sample $16,3^{\pm}6,4$ (n=5) vs control $48,5^{\pm}34,5$ (n=5)), the difference was not significant (Table 9). However, it should be noted that the KFI values of less than 16 in Table 9 represent a total absence of fat, the value being due to the fascia which is normally weighed with the fat. Four of the five sample animals thus had no perinephric fat, while only one of the five control animals had no perinephric fat. In addition, as it is known that older impala lose condition more markedly in winter (Dunham & Murray 1982), the low KFI values of the control group is likely to be due to the predominance of old animals in the control sample.

Adrenal masses also did not differ significantly between the two groups - Table 9. However, the adrenal masses of the animals in the poorest condition were also the highest, confirming the correlation between KFI and adrenal mass found in the Baseline Study, and also confirming that all the animals were in poor condition. Because of the similarity in age structures between the two groups, the study does not provide a comparison between ages or condition. The only dramatic difference between the two groups was therefore that the incisors of the sample group were all totally worn down in the vertical plane, while the control animals, even those that were old, had relatively unworn incisors - Table 10.

Given the above limitations on statistical comparisons, the pilot study did reveal results which were interesting in themselves. What is apparently "manginess" in the impala is in fact alopecia. There are no macroscopic signs of any skin pathology other than the lack of hair. That true mange may well occur in the impala population of the NTGR is not in doubt - through circumstances that prevailed at the time no truly mangy animals were

encountered during the present study. The animals with advanced alopecia have a higher tick and louse burden in the remaining pelage on the body. Tick numbers in the ears appear, however, to be lower in the affected animals. At the time of collection the sample animals were in extremely poor condition, although this did not differ significantly from the randomly collected animals.

The most striking finding of the pilot study was that, without exception, all the animals exhibiting advanced alopecia had incisor canine complexes which were worn to below the gumline in the vertical plane. Conversely, all the control animals had unworn or mildly worn teeth, and did not exhibit alopecia. Although this unusual pattern of attrition had been observed during the baseline study it had not, at the time of collection, been correlated with the alopecic condition. This unusual form of attrition has, therefore, a direct relationship with the bald impala syndrome which has been described here.

As can be seen in Appendix A10, all 10 impala shot for the study, including the old animals, were pregnant. Despite their lack of incisor teeth, all the old females had conceived and had carried their foetuses almost to full term. If lack of food was ever to be proposed as a potential population regulating mechanism in this species, these results should be noted as an indication that, acting alone, such a mechanism would only come into effect if the ewes were in a worse condition than in the present study.

The pale musculature and excess erythropoeitic tissue of the affected animals indicated that, in such a debilitated state, the level of parasitism could be responsible for anaemia and a resultant responsive change in the bone

marrow. The strange smell associated with the pale carcases was possibly due to tissue changes induced by the anaemia and accompanying ketosis. In this state, tape worm cysts and liver parasites apparently proliferated under conditions of reduced immune response - a state of chronic stress is indicated by the adrenal hypertrophy (Table 9).

Conclusion

A superficial conclusion of the Pilot Study is that there was no mange present in the impala population of the NTGR at the time of the study, and that a comprehensive study of the alopecia syndrome identified in its place would require quantification of external parasite abundance.

So much for the answers provided by the Pilot study. As is so often the case, however, it is the questions generated, not so much the answers, which played a pivotal role in the progress of the present study. The question remaining is of course "Why is the vertical attrition of the incisor-canine complex so closely associated with the alopecia syndrome?"

A few short paragraphs cannot do justice to the convoluted pathway that led to the answer to this puzzle. In an attempt to do so, the rest of this section is so constructed as to simulate that journey of contemplation.

The teeth of the old impala with alopecia are worn down to, or even below, the gumline in a vertical plane. What could cause such attrition? Eating? No, that would result in a flat plane of attrition parallel to the maxillary dental pad (Fig. 23a). How about geophagia? - A suggestion that the impala may eat the bases of termitaria to ingest essential trace elements.

Surely the teeth would be rough, the gums lacerated, and the front teeth more worn than the lateral teeth, not vice versa. How about accidental geophagia? - a suggestion that the impala may scrape their teeth on the ground in cropping the short vegetation of the Tuli Block. The same reservations as above would apply, and this does not correlate with the observed grazing behaviour of this species. What if ..... what if they scrape their teeth against their own bodies. What for? To remove parasites and groom the pelage! But how can the skin wear down the teeth? I don't know! - but if you watch impala you will notice that they do appear to lick themselves fairly often, and maybe they are in fact combing themselves with their teeth instead.

Indeed, close observation did eventually confirm that impala do use their teeth for grooming purposes - Fig. 29. Leuthold (1977) has also noted that antelope do make use of their teeth for grooming purposes. Further development of implications of this phenomenon is published in McKenzie (1990) (Appendix B3). For the purposes of the conclusion of this chapter we require the factual observation that impala do indeed rub their teeth against their skin with an upward sweeping motion of the head.

So, given that impala do rub their teeth against their skin, is there any real proof that it is in fact this action which results in the vertical wear of the teeth?

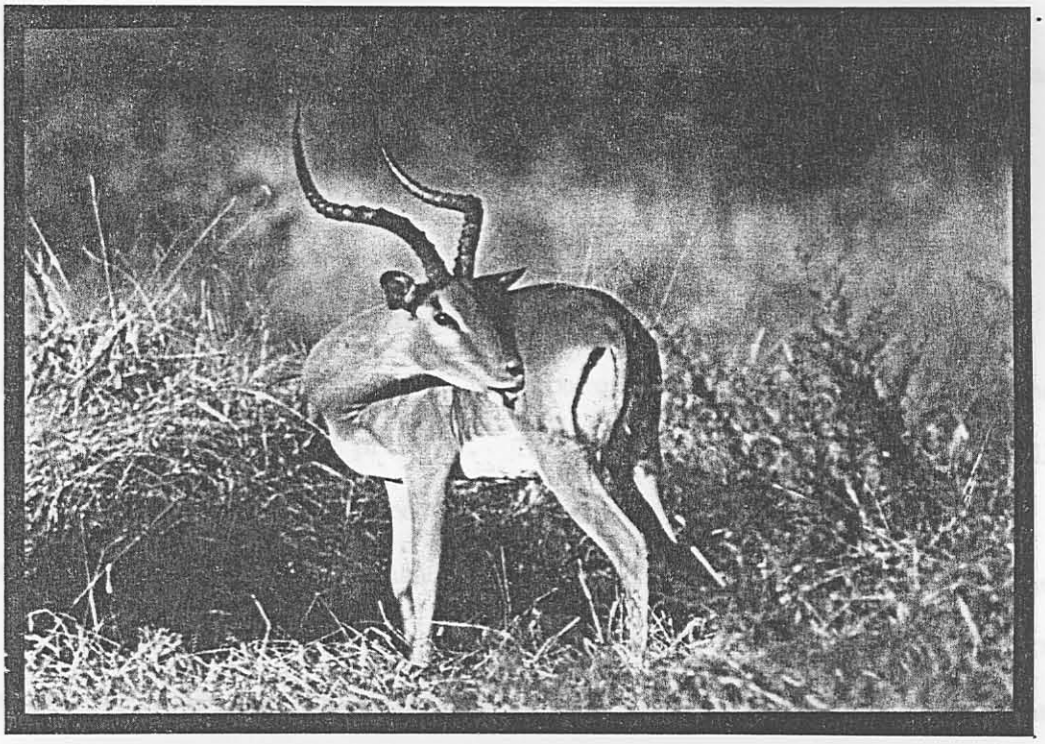

Figure 29. Use of the incisor-canine complex in grooming by an adult male impala.

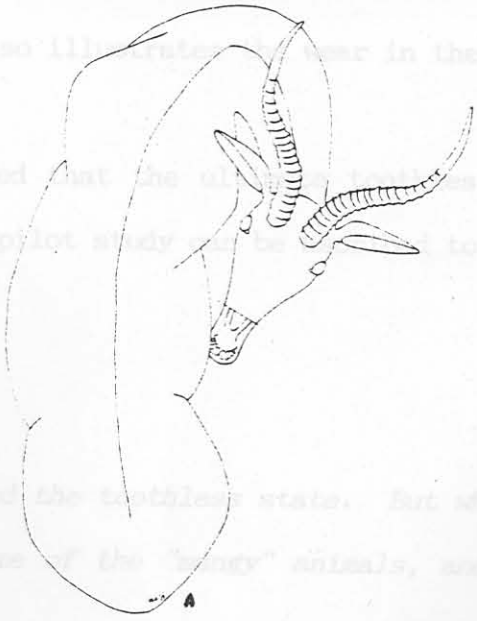

Figure 30. Alignment of components in a typical grooming posture of an impala. (Artwork: A.F. van Rooyen)

Inspection of the IC complexes of old impala from the baseline collection, pilot mange study and from jackal kills did indeed reveal a very interesting pattern of attrition:

Fig. 30 illustrates simulated grooming action by upward movement of the IC complex through the pelage. It is apparent that there are two places where wear will occur during this process. The first is the tips of the needle-like lateral IC elements as they are rubbed against the skin. The second is the neck region of these teeth as hairs are pulled between the crowns of the teeth in the upwards grooming action - Fig. 31. Fig. 23 illustrates the progressive changes in the shape of the elements of the IC complex which can be ascribed to these two modes of attrition. Progressive flattening of the tips of the teeth is accompanied by undercutting in the neck region. Which wear surface results in the final disappearance of the crown varies between elements of the IC complex, and between individuals, as can be seen in Fig. 23. The radiograph in Fig. 32 also illustrates the wear in the neck region.

It is thus concluded that the ultimate toothless state observed in the sample animals from the pilot study can be ascribed to the use of the teeth in grooming.

So we have explained the toothless state. But why are the teeth worn to <u>below</u> the gumline in some of the "mangy" animals, and how is this linked to the observed alopecia?

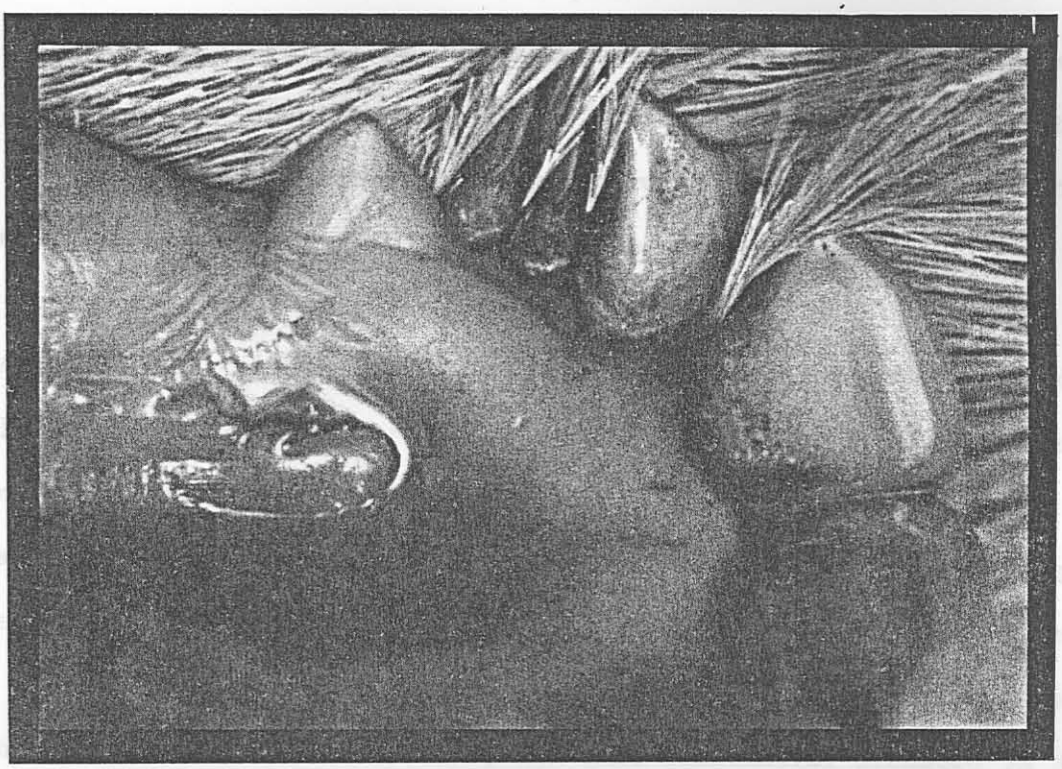

Figure 31. Simulated upwards combing action of the impala incisor-canine complex.

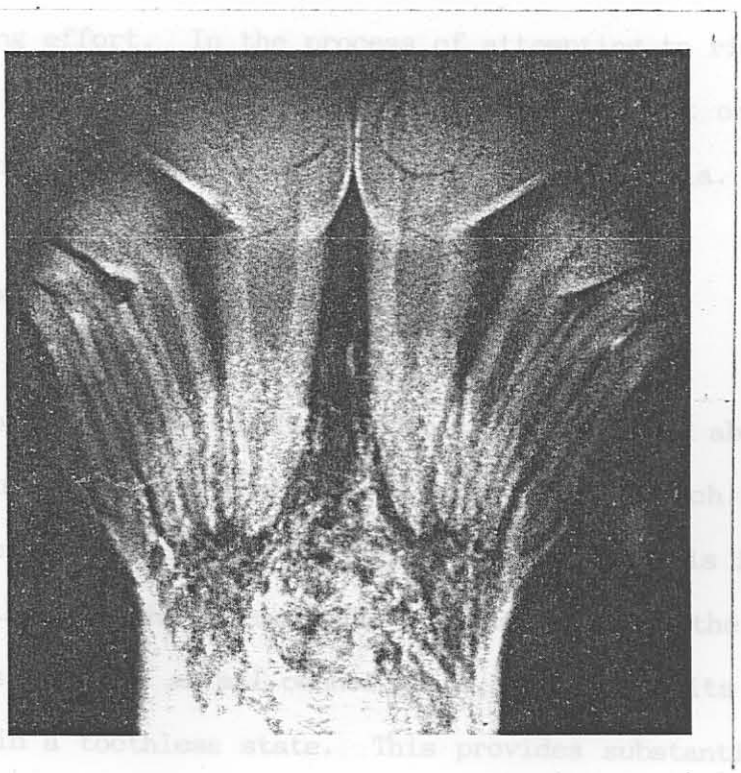

Figure 32. Radiograph indicating macroscopic grooves in the neck regions of the elements of an impala incisor- canine complex.

Assuming the toothless state has been reached, what happens thereafter? It is apparent from the prevalence of these old animals in the population, and from the fact that they are apparently otherwise healthy when shot, that the IC complex is not essential to eating, nor to survival.

Although not quantified, this pilot study did indicate that the toothless animals apparently carry a far higher burden of ectoparasites than those with unworn teeth, indicating that the loss of the IC complex renders the impala incapable of effectively removing the parasites which infest their pelage. However, the attrition of the IC element stumps to below the gumline, and their polished appearance, indicates that the grooming efforts persist even though the organ is now ineffective, and that substantial pressure is applied during this grooming effort. Now if impala are normally sensitive to the presence of parasites in their pelage, then such large numbers as were present on the old animals must drive these animals to distraction, causing an increased grooming effort. In the process of attempting to rid the pelage of parasites, loose and even normal hairs would be pulled out or broken off by the repeated rubbing action, resulting eventually in alopecia.

Is there anything to support this hypothesis?

Referring to Fig. 28, it can be seen that, as described above, there is a disctinct, abrupt line at the shoulder, cranial to which the pelage is effectively intact. Alopecia is only apparent caudal to this line. The line corresponds exactly with the accessibility of the pelage to the grooming teeth - cranial to this line the animal cannot groom itself with its teeth, nor rub out its hair if in a toothless state. This provides substantial support for the hypothesis that the baldness is induced by protracted grooming efforts

directed towards those parts of the body which can be reached.

In conclusion, the Pilot Mange Study has led to the identification of a syndrome unrelated to mange. Because the only apparent pathology is alopecia, and because this is induced by the action of the animals themselves, I have dubbed this syndrome 'autogenous alopecia' (Auto (from Greek *auto* = self) and -genous (from Greek *gen-* = produced)). The pilot study also determined that a quantitative determination of external parasite abundance would be required to confirm this hypothesis. This is the subject of the next section.

SECTION 4 - QUANTITATIVE PARASITOLOGICAL STUDY

Introduction

From the results of the Pilot study it became apparent that a quantitative collection of external parasites from "mangy" and randomly selected animals was required. The hypothesis to be tested was that animals without an effective dental grooming organ should carry higher external parasite burdens than animals with unworn teeth.

Quantitative studies of external parasites of African ruminants have been undertaken by several authors using different methods. As quantitative data were of primary importance, it was decided that the method described by Hopkins (1949), whereby the hair is dissolved with a strong alkali solution thus exposing all the external parasitic arthropods, would be the method of choice. However, because Spinage (1969) had stated that species identification is made difficult by this method, and that processing of one

skin could take up to two days, a combination of the alkali method and the scrubbing method described by Horak, de Vos & Brown (1983) was chosen.

Between the 5th and the 18th of September 1988 a collection of impala in the NTGR was undertaken as described below.

Materials and Methods

Field

Six "mangy" female impala and six randomly selected female impala were shot the in lower Majale floodplain area of the NTGR in September 1988. In addition, two randomly selected impala were shot on Naledi Ranch in the northern part of the Reserve. Time considerations did not allow the processing of more impala from the north. The shot animals were immediately suspended by the hock joint from an elevated structure on the rear of the vehicle. The fetlock glands were removed and the tail and ears were severed at their bases. All these parts were stored separately in sealed plastic bags. The hind legs were severed at the hock joint and the forelegs at the carpus. The legs were placed in a large strong plastic bag. The rest of the skin was then removed and also placed in a strong plastic bag. 1-2 l of 1% Triatix (Coopers SA, Johannesburg, RSA) was added to the bags containing the hide and legs as a tick detatching agent (Horak *et al.* 1983). The contents were agitated to ensure complete wetting and then sealed. Upon returing to the base camp, the carcases were processed as in Section 2 above. In addition, a sample of approximately 10 g of fat from the central shaft of the left femur was collected, stored in an airtight plastic container and frozen.

The digestive tracts were removed and the contents processed as described by Reinecke (1984) for the quantitative determination of internal parasites.

Skins were processed as follows:

1 Tail, Glands and Ears. These parts were placed separately in 500 ml plastic containers. The containers were then filled with a 10% solution of NaOH at room temperature. The containers were agitated from time to time. When the hair was completely softened it was scraped from the skin with a knife. The skin was rinsed in the NaOH until clean and then discarded. The contents of the bottle were repeatedly agitated until the hair had almost completely dissolved. The contents of the bottle were then sieved through a 150 um sieve until clear and then transferred back to the bottle. Formalin (10%) was added in a 1:10 ratio and the bottle retained for later analysis.

2 Legs The bag containing the legs was emptied into a large plastic tray (350x600x200 mm deep). The bag was thoroughly rinsed with water into the tray. The legs were then thoroughly scrubbed in the direction of the hair with a steel brush, ensuring that every part of the leg was scrubbed. The leg was then rinsed in the water. The entire leg was then rubbed hard with the fingers in the direction of the hair. Any parasites thus located were scraped into the water. This process of scrubbing and checking was repeated three times. Following a final thorough rinsing in running water, the legs were discarded. The contents of the tray were then sieved and stored as described in 1 above.

3 Hide The hide was emptied into the tray and the bag rinsed as described above. The skin was then cut into sections approximately 200x200 mm in size.

A wooden cutting board was placed at an angle into the tray. Each piece of skin was scrubbed and rinsed three times as in 1 above. After the final rinse the skin was discarded. After the entire hide had been scrubbed in this manner the remaining water was sieved and stored as in 1 above.

A 20x20 mm sample of skin was removed from the flank of each animal and stored in 10% formalin for later histological examination.

Laboratory

1 Internal parasites were identified and counted by J. Boomker, Faculty of Veterinary Science, Medical University of South Africa, Medunsa.

2 The Bone Marrow Fat Index was determined following the technique decribed by Brooks, Hanks & Ludbrook (1977), with the exception that the Soxhlet extraction was over 24 h and not 8 h, as suggested by Shackleton & Granger (1989).

3. External parasites. The scrubbed hide and leg samples were rinsed through a 150 um sieve to remove the formaldehyde and were then replaced in the bottles with 10% NaOH at room temperature. The bottles were agitated at intervals until all the hair had dissolved, and the contents were again sieved, rinsed and stored in 10% formalin.

The parasites in all the samples were counted and identified under a stereo microscope, and were transferred to small bottles containing 70% ethanol.

4. Ages and degree of vertical dental attrition were determined as described in Section 1.

5. Skin samples were sectioned, stained and examined by B.R. van Rensburg, Department of Pathology, Faculty of Veterinary Science, University of Pretoria.

Results

The impala collected for the study were numbered as follows:

M0188, M0288 - Random, northern region. (Northern control)

M0388, M0488, M0588, M0688, M0788, M0888 - Alopecic, south-central region. (Southern sample)

M1088, M1188, M1288, M1388, M1688, M1788 - Random, south-central region. (Southern control)

Weights and measures Foetal sexes and masses are presented in Appendix A11.

Condition Kidney Fat Indices and Bone Marrow Fat Indices are presented in Table 11. Southern sample animals did not have lower BMFI's than the southern control group, but did have significantly lower KFI's (Table 11).

Age Ages determined from mandibles, and vertical attrition of incisors and canines, are presented in Table 12. All animals in the southern experimental

Table 11. Impala Kidney Fat Index and Bone Marrow Fat Index - Section 4.

	Fat	Kidney	KFI	BMFI
Northern control group				
M0188	388	103	378,4	84,6
M0288	528	111	475,7	94,2
Southern sample group				
M0388	194	145	133,4	87,6
M0488	41	184	22,5	74,0
M0588	169	189	89,3	88,8
M0688	124	145	85,3	67,9
M0788	96	146	66,1	87,2
M0888	128	224	57,3	87,4
Mean (std. dev.)			75,7(37,1)	82,15(8,9)
Southern control group				
M1088	471	171	275,9	87,2
M1188	406	155	262,1	90,7
M1288	769	138	557,8	82,1
M1388	154	163	194,7	87,5
M1688	753	146	516,8	85,4
M1788	433	167	259,7	89,1
Mean (std. dev.)			344,5(152,5)	87,0(3,0)
			t=4,19 p<0,002	t=1,26 n.s., p>0,1

Fat and kidney masses in g.
KFI = Kidney Fat Index = Mass of perinephric fat/Mass of kidneys x 100.
BMFI = Bone Marrow Fat Index = % fat in bone marrow of mid-shaft of femur.

Table 12. Impala ages and vertical dental attrition - Section 4.

	Age			Vertical wear			
	Murray *	Spinage **	R&H ***	C	I3	I2	I1
					****		
Northern control group							
M0188	3.5	b	1	0	0	0	0
M0288	4.5	d	1	0	0	0	0
Southern sample group							
M0388	6.5	d	3	4	4	4	2
M0488	8.5	f	3	5	5	5	5
M0588	8.5	f	3	5	5	5	5
M0688	7.5	d	3	5	5	5	5
M0788	8.5	f	3	5	5	5	5
M0888	6.5	d	3	5	5	5	5
Southern control group							
M1088	5.5	d	2	2	1	0	0
M1188	5.5	d	1	1	1	0	0
M1288	2.5	a	1	0	0	0	0
M1388	4.5	b	1	2	2	2	1
M1688	3.5	b	1	1	0	0	0
M1788	4.5	d	1	1	0	0	0

* Murray (1980). Age in years.
** Spinage (1971). 2= 1-2 years; d= 6-8 years; f= >8 years.
*** 1= young, < 5 years; 2= middle aged, 5-10 years; 3= old, > 10 years. Based on incisor wear, Roettcher & Hofmann (1970).
**** 0=none; 1=tip of tooth rounded; 2=tip of tooth substantially flattened; 3=tooth worn to mid-crown; 4= Only stump of crown remaining; 5= total vertical attrition.

group exhibited advanced or total attrition of the incisors and canines.

As recorded in Section 3, wear of molar teeth in older animals was mild relative to incisor attrition.

Impala nos M1488 and M1588 were shot as part of the control sample in the south-central region, but were found to have severely worn incisors-canine complexes and were thus not used for the study.

External parasites External parasite numbers from the different body regions are presented in Appendix A12. Summarized data on total parasite numbers are presented in Table 13. Total parasite numbers from the legs, fetlock glands and tails are presented in Table 14.

Table 13. Impala total external parasites Section 4.

	Ticks					Lice	
	B.dec				R. zam	Lino.	Dam.
	A	EA	N	L	N		
Northern control							
M0188	0	0	1	3	0	2	0
M0288	0	0	5	11	0	3	9
Southern sample							
M0388	78	17	63	39	15	20	3
M0488	86	9	111	105	5	209	0
M0588	110	2	195	171	5	73	24
M0688	192	24	257	329	2	111	23
M0788	131	7	137	274	4	142	2
M0888	165	14	209	268	24	703	2
Southern control							
M1088	51	1	159	304	1	38	37
M1188	120	10	187	338	3	31	4
M1288	80	3	185	74	4	4	13
M1388	80	1	175	224	2	70	4
M1688	38	1	79	89	3	3	1
M1788	58	4	182	44	1	11	16

B.dec = *Boophilus decoloratus*; R.zam = *Riphicephalus zambesiensis*; Lino = *Linognathus sp.*; Dam = *Damalinia sp.* A= adult; EA= engorged adult; N= nymph; L= larva. Damalinia sp.

Table 14. Impala external parasites-legs, fetlock glands and tails. Section 4.

	Ticks			Lice	Total
	Adult Engorged females	Adult Total	Larvae & Nymphs		
Northern control group					
M0188	0	0	4	0	4
M0288	0	0	16	3	19
Southern sample group					
MO388	17	88	70	10	168
M0488	9	76	108	6	190
M0588	1	100	198	67	365
M0688	23	190	217	77	484
M0788	7	125	231	101	457
M0888	13	129	151	614	894
Mean (std. dev.)	12(8)	118(41)	163(64)	146(232)	426(264)
Southern control group					
M1088	1	32	64	28	124
M1188	5	62	99	30	191
M1288	0	23	35	8	66
M1388	0	16	37	57	110
M1688	1	23	24	1	48
M1788	1	23	75	6	104
Mean (std. dev.)	1,3(1,9)	30(17)	56(29)	22(21)	107(50)
	t=3,28 p<0,01	t=4,89 p<0,001	t=3,73 p<0,01	t=1,25 n.s. p>0,05	t=2,91 p<0,05

The numbers of adult engorged female ticks, total adult ticks, and larval and nymphal ticks on the legs, fetlock glands and tails were very significantly higher on the southern sample group than on the southern control group. Differences in louse numbers were not significant. Total parasite numbers were marginally different ($p<0,05$) (Table 14). All tick infestation data differed significantly between the two groups, and it was only the louse data which made total parasite burdens only marginally different, and in particular it is the single large louse burden (M0888) which is resposible for this. Tick infestation is of greatest significance in parasite problems in wildlife (Lightfoot & Norval 1981), and the significant tick data are regarded as the most notable result of this section.

Both northern control animals carried significantly fewer total parasites

than the southern control group (d=2,69 and 2,60 respectively, p<0,01). Neither of these animals carried any adult ticks.

Internal parasites Total internal parasite numbers are presented in Table 15. Total internal parasite numbers did not differ significantly between the southern control and southern sample groups (Table 15).

Skin histology The histopathologist's report is presented in Appendix A13.

Discussion

All of the sample animals shot had worn incisor-canine complexes, while all the control animals had unworn teeth - Table 12. The results of the present study thus constitute a comparison of parasite burdens and condition between animals with intact IC complexes and animals without intact IC complexes.

Total external parasite numbers from the legs, fetlock glands and tails differed significantly between the two groups - Table 14.

Total parasite numbers from the ears did not differ significantly between the two groups, although there was a trend towards less parasites in the ears of the old animals, as observed in the pilot study - Appendix A12. Visible ticks in the ears were far fewer in number than observed during the pilot study.

Total parasite numbers on the hides did not differ significantly - Appendix A12.

Table 15. Impala internal parasites - Section 4.

Number	Coop	C.des	C.ham	C.hep	C.hun	Imp.	Long	L.nam	Oeso	Tric	T.def	Total (Adult)	Coop L	Total
MOI88	0	0	180	0	0	0	0	0	0	0	90	270	190	460
M0288	0	0	490	0	0	0	0	0	0	0	200	700	80	780
M0388	0	0	30	30	40	0	0	0	0	0	730	830	0	830
M0488	0	1420	680	0	20	0	0	40	0	580	420	3160	820	3980
M0588	0	90	0	10	10	0	0	0	0	500	520	1130	5080	6210
MO688	0	480	160	0	0	0	0	0	0	220	160	1020	940	1960
M0788	0	120	80	0	10	20	80	40	0	0	0	350	0	350
M0888	0	480	140	0	0	0	0	0	60	430	350	1460	420	1880
												1358(966)		2535(2193)
M1088	0	360	300	0	20	0	0	0	0	80	0	760	420	1180
M1188	0	120	20	0	0	0	0	0	0	20	10	170	140	310
M1288	0	10	0	0	0	0	0	0	60	80	90	240	0	240
M1388	0	340	300	0	0	0	0	0	0	200	0	840	820	1660
M1688	20	200	80	0	90	20	0	0	20	0	0	430	20	450
M1788	60	920	740	20	140	0	10	40	0	200	200	2330	0	2330
												795(798)		1028(847)
												t = 1,10 n.s.		t = 1,57 n.s.
												p>0,1		p>0,1

Coop = Cooperia sp.
Coop L = *Cooperia sp.* larvae
C.des = *Cooperoides sp.*
C.ham = *Cooperoides hamiltoni*
C.hep = *Cooperoides hepatica*
C.hun = *Cooperoides hungi*

Imp = Impalaia sp.
Long = *Longistrongylus sp.*
L.nam = *L.namaquensis*
Oeso = *Oesophagostumum sp.*
Tric = *Trichostrongylus sp.*
T.def = *T.deflexus*

The ears are not accessible to grooming by the teeth, and thus do not fall within a discussion of the effectiveness of the dental grooming organ. The fact that the ears of younger animals have a tendency to carry more ticks (Appendix A12, see also Section 3) is, however, of interest. The ears of young animals from the south-central region carry very large numbers of ticks, and the persistence of this situation over several years is a plausible explanation for the scarred, uneven appearance of the ears of the old animals. This scarring may result in the lower numbers of ticks in the ears of old animals via several possible avenues:

1. The scar tissue may simply be physically unsuitable for tick attachment;

2. The scar tissue may be poorly vascularized and thus unattractive for tick attachment;

3. The prolonged infestation may give rise to local immune responses which can be responsible for reducing tick attachment (Allen 1984); and

4. The absence of hair on the scar tissue reduces protection of the ticks from scratching action and allogrooming. Impala scratch the insides of their ears with the sharp tips of the hooves of their hind legs. The prediliction by ticks for the hairy areas of the ears (see Fig. 25b) may be in response to, or as a result of, this scratching activity.

Statistical analysis of the parasite burdens of the hides is subject to two major limitations. First, it has been noted that ticks do not occur on the bald areas of the old impala. This is probably due to the lack of protection afforded by hair. With the bald areas devoid of ticks and lice,

the hide of a bald animal cannot be compared with the hide of a normal impala. Second, in the author's opinion, the scrubbing method does not remove all the parasites from the pelage. This observation is based on the fact that, despite repeated scrubbing, ticks had to be manually removed from the legs - this despite the relatively ideal conditions of firm immobilization and tight stretching of the skin, and a short, sparse pelage. This is of importance in a comparative study where some skins with a sparse pelage are easier to scrub than normal skins. Furthermore, some regions of the body, particularly the neck region, are difficult to scrub thoroughly due to their thick pelage. While the NaOH method may make species more difficult to identify (Spinage 1969), it does provide an absolute count of parasites. This method was not used on the hides in the present study because of the published details on the time required to treat one complete hide (Spinage 1969). Experience gained in the present study showed that materials stored in formalin can subsequently be successfully treated with NaOH, and that identification of species was not hampered by the NaOH treatment. Thus if time in the field is limited, formalinized hides can be returned to the laboratory for later digestion. In retrospect, therefore, I agree with Spinage (1969) that this is the method of choice when the overriding consideration is quantitative determination of parasite burdens.

Given the above limitations, the total parasite number on the hides are not considered to provide a reliable indication of the effectivity of the dental grooming organ.

The remaining portions - the lower legs, tail and fetlock glands- were analysed in a quantifiable manner, and are accessible to the grooming organ. A comparison of the parasite burdens for these regions shows that there is a

significant increase in the number of parasites on animals without an effective grooming organ. Most significantly, the number of engorged adult ticks is considerably higher on the old animals (Table 14).

While the results of the parasitological study provide *prima facie* evidence to support the hypothesis that impala use their teeth for the removal of parasites from their pelage, there is a possible limitation to an unequivocal conclusion in this regard. An alternative hypothesis could be that the older animals are in poor condition and immuno-incompetent, and thus destined to carry more parasites irrespective of the intactness of the dental grooming organ. The other results of the present study will be discussed in the light of this alternative hypothesis.

The Kidney Fat Indices (Table 11) indicate that the older animals are in significantly poorer condition than the controls. This result may be intuitively expected, as the lack of front teeth is likely to have some effect on the foraging ability of these animals. Dunham & Murray (1982) also reported that older animals lose more condition in winter. However, the absolute value of the KFIs indicate that, while in poorer condition than the controls, the older animals were not in as poor a condition as the animals used in Section 3. The BMFI's did not differ between the groups, and comparison with values from other areas (Brooks, Hanks & Ludbrook 1977., Brooks 1978, Monro 1981) comfirms the above statement that the old animals were not in poor condition, with the possible exception of no. 0488. Thus poor condition *per se* cannot account for the discrepancy in parasite burdens. In addition, while the sample animals did have worn incisor teeth, and were thus classified as "old", the wear on their cheek teeth was not indicative of extreme old age. In fact, wear on their molar teeth was mild in comparison

with that described for old animals from other areas (Spinage 1971, Murray 1980). Thus extreme old age also cannot reasonably be claimed to be the cause of the higher parasite burdens, for whatever reason.

The attainment of old "incisor age" before old "molar age" is discussed further in Chapter 7.

Further evidence for the fact that the sample animals were not totally debilitated is the fact that they were all pregnant and carrying healthy foetuses.

High parasite burdens on sick or old animals, of whatever species, may be due partly to poor condition and concomitantly reduced immuno-competence (Allen 1984), but is also due to a cessation in grooming activity (Lightfoot & Norval 1981, pers. obs.) which may be partly ascribed to the energetic costs of grooming which become too high in the debilitated animal (Lightfoot & Norval 1981). The alopecia of the sample animals indicates that they had not reached a stage where they were no longer able or willing to groom themselves, thus further emphasising that debilitation did not account for the differences described here.

Internal parasites are also subject to immune mediated responses by the host animal (Wakelin 1984). The number of internal parasites did not differ significantly between the two groups (Table 15), and there was no correlation between external and internal parasite abundance ($r<0,001$). The slightly higher burdens in the older animals could be due to several factors. The absolute numbers of internal parasites encountered in the present study was not particularly high. Levels of up to 14 000 internal parasites have been

recorded in impala (Horak 1978). Thus, whatever reason there may be for the slightly higher parasite numbers in the older animals, there is no indication of an uncontrolled level of internal parasitism in these animals or in the population as a whole, and therefore no indication that the high external parasite numbers could be ascribed to a state of immuno-incompetency.

Together with the possibility of condition induced hyperparasitism, the possibility that poor condition alone was a cause for the alopecia was studied through histological sections of skin samples. A large percentage of telogen (resting) hair follicles were observed in all samples, and also in sections from impala collected in Pilanesberg National Park. The difference between sections from animals displaying autogenous alopecia and the control animals is that the hairs in the former are absent from the follicles, or are broken off at or below the surface of the epidermis. An interesting observation was that there was thickening of the walls of the sub-epidermal blood vessels, with an accompanying eosinophil infiltration, in all the samples from Botswana. An infiltration of eosinophils is indicative of a hypersensitivity response, and is often seen in conjunction with chronic parasitic infestation (Smith, Jones & Hunt 1972). The thickening of the blood vessel walls indicates that this is indeed a chronic condition. As indicated in the pathologist's report (Appendix A13), this supports the hypothesis that the hair is removed in response to parasitic irritation. The similar response in the skin of the control animals indicates that they too are exposed to the parasitic agent. While the low levels of ticks and lice present on these animals may well explain this observation, it is probable that biting flies and mosquitoes could also contribute to the development of this situation. These parasites are unfortunately not quantified in a study of this nature, but observations on impala confirmed that these parasites are responsible for

irritation of impala in the NTGR. It is thus not possible to determine the precise cause of the pronounced chronic reaction in the normal animals of the central region of the NTGR. However, the contrast between this situation and the mild reactions seen in the Pilanesberg animals does provide an indication that external parasitism, of whatever type, is more pronounced in the central region of NTGR than in Pilansberg NP.

The fact that two out of the eight impala randomly shot in the south-central region exhibited advanced attrition of their incisor-canine complexes (nos 14 & 15) reinforces the indications from Sections 1 and 3 that there is an abundance of impala from the oldest age-groups in the south-central region.

Northern animals. The two animals shot in the north were required to confirm the observation made during the Baseline Study that very few parasites were present on animals from the northern regions. As can be seen from Table 14, the animals from the north had one to two orders of magnitude fewer external parasites than the animals randomly shot in the south-central region. The results from these two animals do independently confirm the observation that far fewer ticks, particularly adult ticks, are present on animals in the northern areas both carried significantly fewer total parasites than the southern control group (d=2,69 and 2,60 respectively, $p<0,01$), and neither carried any adult ticks at all. Based on observations on 61 animals and the quantitative analysis of these two animals, it is readily apparent that a real and significant difference in the numbers of ticks on impala from the two areas does exist.

Factors such as host availability, vegetation cover, climate etc. may all influence absolute abundance of ticks (Norval & Lightfoot 1982) and possibly

other external parasites. The relationship between autogenous alopecia and the confirmed dichotomy in tick abundance is discussed in the chapter on Ecosystem Processes - Chapter 7.

Conclusion

The results of the quantitative study successfully demonstrate that impala without functional front teeth carry more external parasites than normal individuals. Horak (1982) reported high numbers of lice on an old impala, but unfortunately did not document the condition of this animal's front teeth. While the present study has indicated the need for further experimental evidence, I feel that the evidence that the dichotomy is not due to old age or poor condition is sufficiently strong to conclude that the main function of the dental comb is the removal of external parasites.

Histological evidence has supported the conclusion that the alopecia is self-induced, and that there is no microscopic evidence of mange in the alopecic or control animals. The dichotomy in tick numbers between the northern and south-central areas was confirmed by the present study.

The identification of autogenous alopecia as a well defined syndrome raises many questions: Why does it occur in the NTGR? What factors restrict its occurrence within the NTGR? Does it occur elsewhere? Why do the incisors wear out before the molars? What are the implications for the ecosystem?

Some of these questions will be addressed in Chapter 7, but others will require further investigation before the picture is finally complete.

SECTION 5 - DISTRIBUTION OF AUTOGENOUS ALOPECIA

Introduction

It was apparent from observations made during the Baseline Study that "manginess" in impala is not evenly distributed throughout the Reserve. In order to determine the spatial and temporal incidence of the syndrome in the NTGR, two distinct periods were used in which the occurrence of alopecia in impala was determined. The two periods were within the hot/wet season of 1985/86 and the hot/dry season of 1986. Sampling was such that the same herds of impala were not repeatedly counted, and it was ensured that the south/central and north/north-western areas of the Reserve were well covered, with occasional observations from other areas.

Materials and Methods

Impala were counted from a vehicle using binoculars, and were classified as adult/juvenile and normal/mangy. Juvenile was taken as any animal less than two years old. Mangy animals were any which exhibited alopecia, crusting, exfoliation of the skin or matting of the hair on any part of the body. Small black spots sometimes observed on the face or lower legs did not result in classification as mangy if limited to these areas.

Observations were recorded on a casette recorder and later transcribed. Two methods of location of impala for counting were used:

1. Encounter. Herds of impala were encountered while driving through the Reserve, either while specifically searching for impala or while out for

another purpose;

2. Waterhole watches. Vehicles were parked at waterholes on 7 occasions to facilitate observations of impala coming to drink. All observations were made in the early morning or late afternoon.

Impala were not counted in cold or windy weather as under these conditions pilo-erection may occur which can be confused with manginess or a staring hair coat, particularly if the animal is viewed from behind.

Results

The distribution and abundance of "mangy" impala in the hot/wet and hot/dry seasons of 1985/86 are presented in Figs. 33 and 34 respectively.

It was observed that the "mangy" animals regain a normal pelage in early summer after the first green flush, and are then indistinguishable from other impala. This regrowth of the pelage is already apparent within 10 - 14 days of the first green flush, and imparts a velvety appearance to the previously bare skin. This is due to remarkably sudden, synchronized emergence of hair on the affected body regions - Fig. 35. Within a further two weeks the pelage attains a normal appearance.

Discussion

It is apparent from the results obtained that autogenous alopecia was entirely absent from the Reserve in the hot/wet season. This was confirmed in

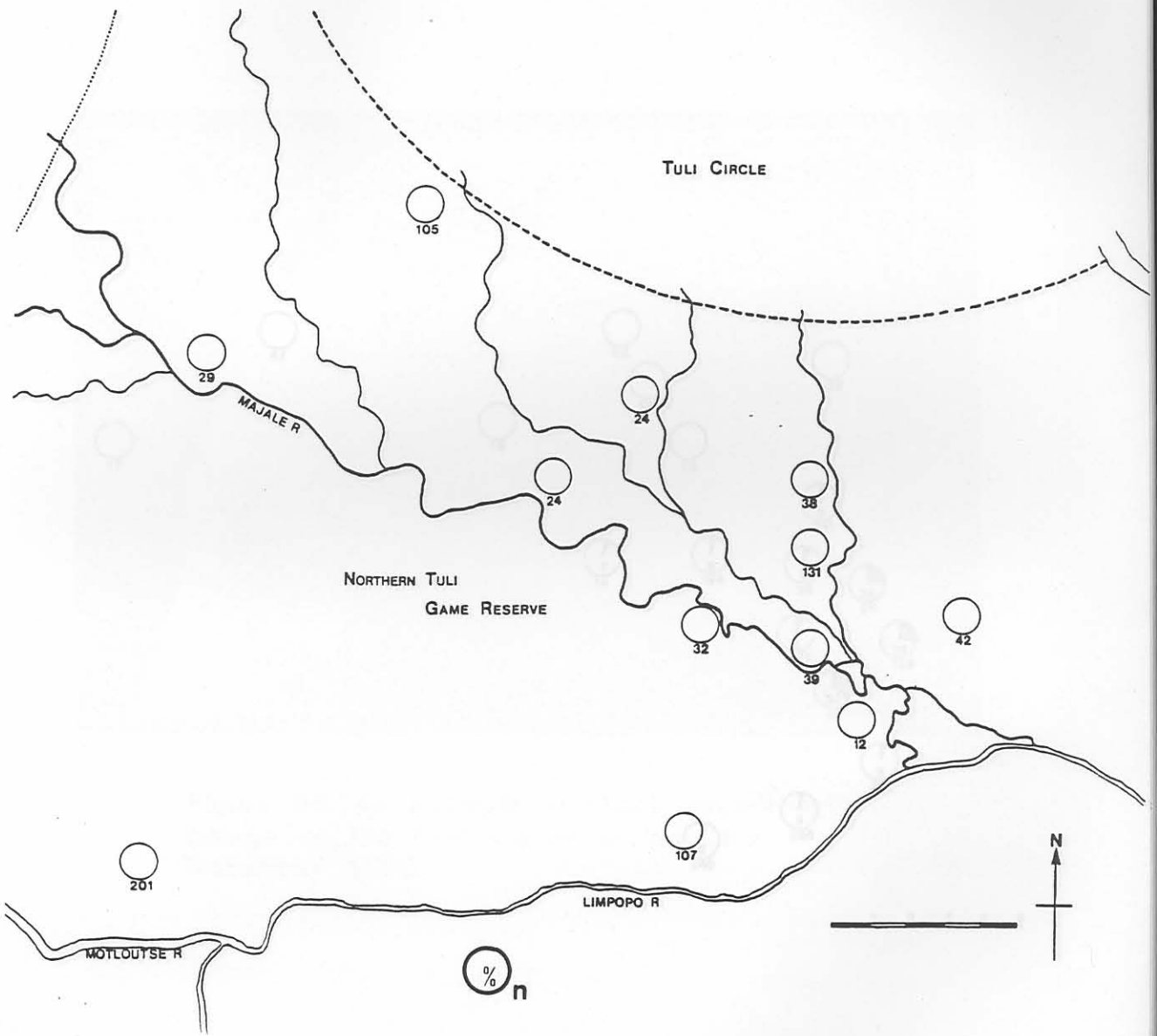

Figure 33. Incidence of autogenous alopecia in adult female impala in the NTGR: hot/wet season, 1986.

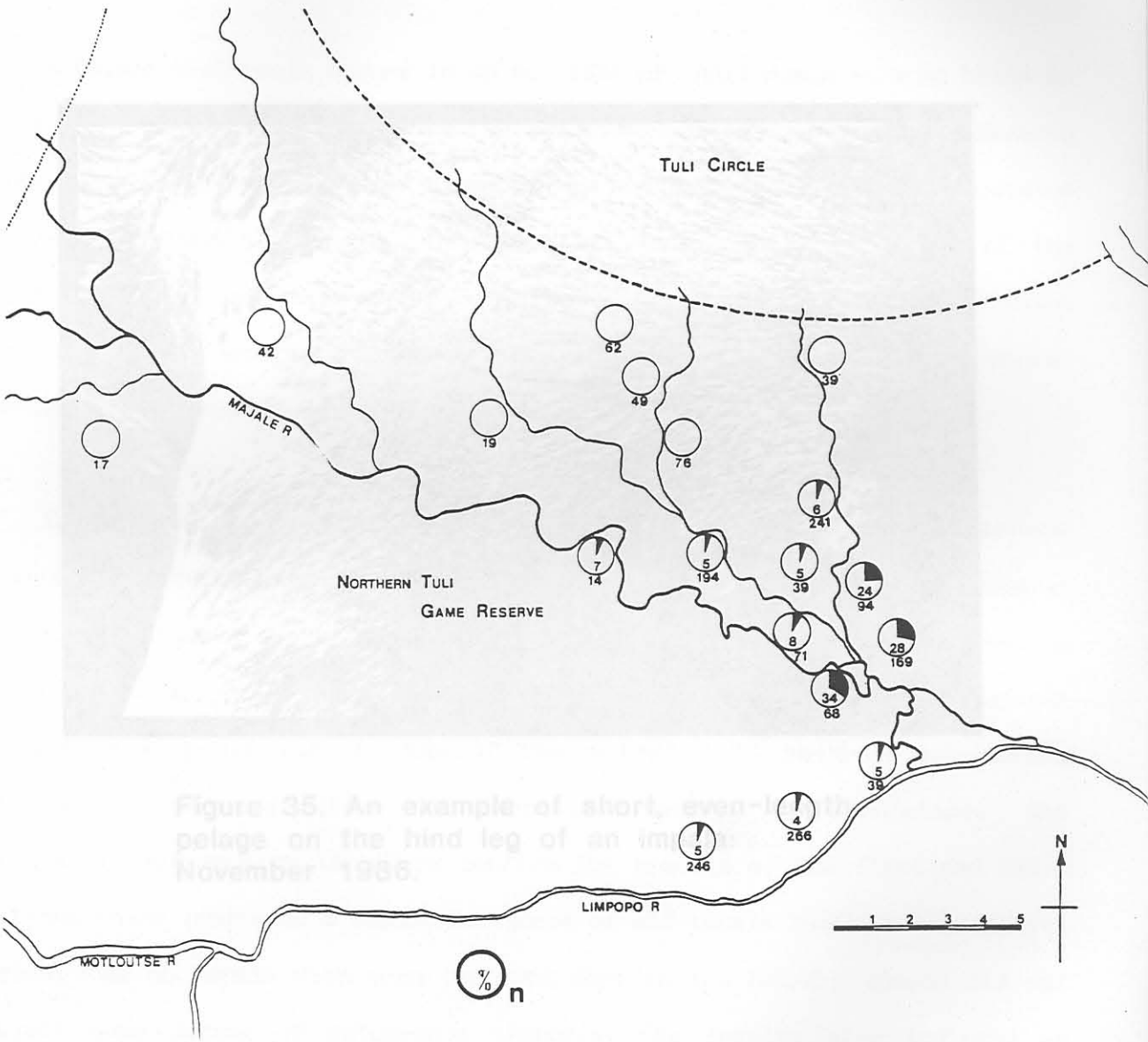

Figure 34. Incidence of autogenous alopecia in adult female impala in the NTGR: hot/dry season, 1986.

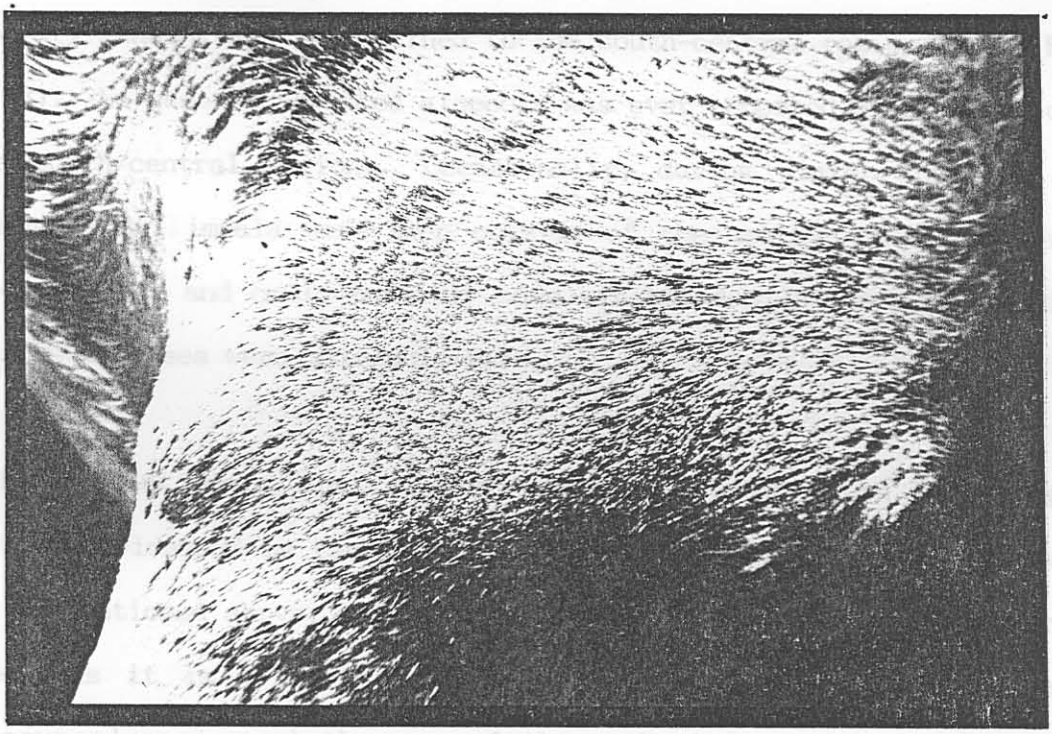

Figure 35. An example of short, even-length pelage on the hind leg of an impala: November 1986.

subsequent summer seasons of 1987 and 1988 when numerous impala were observed without ever recording a case of autogenous alopecia anywhere in the Reserve in the hot/wet season. Alopecia was observed during the hot dry seasons in these years, but animal counts were not conducted.

Autogenous alopecia occurs in up to (33%) of individuals in some herds in the hot/dry season, and is confined to the south-central region of the Reserve (Fig. 33). No case of advanced alopecia was ever reported or observed outside of the south/central region. Occasionally, during winter, outside of the incidence study, impala were seen outside of the south-central region which appeared scruffy and could possibly have exhibited mild autogenous alopecia. However, such cases were extremely rare.

The discontinuous spatial and temporal distribution of autogenous alopecia as evidenced by the present study raises several questions, some of which, as mentioned above, will be discussed in Chapter 7. From the previous two sections it is evident that there is an absolute correlation between autogenous alopecia and the age of the animal: all animals exhibiting autogenous alopecia are from the oldest component of the population. The results of this section therefore confirm the results of the first and third sections which indicated a higher incidence of old impala in the south/central region. As no impala with worn incisors shot in the hot/dry season did not exhibit some degree of autogenous alopecia, the results also indicate an absence of old impala with worn incisors outside of the south/central region. As the absolute correlation with age exists, the factors underlying the distribution of the autogenous alopecia must be correlated to the factors affecting the differences in age structure of the two sub-populations.

Conclusion

This section of the study showed that autogenous alopecia is almost totally confined to the south/central region of the Reserve, and is strictly seasonal in occurrence. The number of animals exhibiting severe autogenous alopecia, and the length of time during which autogenous alopecia is apparent are likely to vary from year to year depending on the prevailing environmental conditions.

The cyclical disappearance of the autogenous alopecia further confirms its non-malignant nature, and highlights its strong links to other factors operating within the ecosystem. As a full discussion of this syndrome thus requires a holistic perspective, final conclusions are left to Chapter 7.

GENERAL CONCLUSION

What was intended as a baseline study to provide material with which to compare jackal prey resulted in an entirely independent facet to this project.

The baseline material was useful in its own right in providing material for use in the chapter on jackal predation (Chapter 3). The other material has resulted in a new hypothesis on the functional biological role of the ruminant IC complex (McKenzie 1990, Appendix B3), and in the identification of a specific "disease" syndrome in wildlife, namely autogenous alopecia (McKenzie, in prep.). In identifying these two fields of enquiry, it is to be expected that the study has generated more questions than answers. To await unequivocal resolution of all the aspects uncovered in the present study would have placed an unacceptable burden on the completion of the thesis. This

chapter is thus concluded without finality in many aspects, but with specific identification of where further investigation is required.

As this chapter is devoted to impala, and the results of studies on this species, conclusions on the implications emerging from this chapter which are of a more general nature are left to the chapters on Autogenous Alopecia (Chapter 6) and Ecosystem Processes (Chapter 7).

A profound *caveat* emerges from the results of the present study. Parasite abundance, as a measureable entity, is attracting the attention of an increasing number of parasitologists and ecologists alike. Sufficient numbers of animals are relatively easily obtained to produce an "average" number of ticks, lice etc., and such averages, being statistically robust, could be extrapolated to other areas or other times without due cognizance being taken of the underlying processes giving rise to a particular pattern of parasite abundance. Caughley (1977:199) states " We must be cautious of values that summarize neatly as numbers. They may be insubstantial." As demonstrated by the present study, collection of animals from within the same physical location but separated by just a few kilometres, can result in differences in parasite abundance of an order of magnitude in size. All such studies should, therefore, record the site of collection to a considerable degree of precision. This is of ever increasing importance as fragmentation of formerly pristine wilderness by fences creates innumerable islands, each of which has its own peculiar combination of process which can give rise to totally different parasite abundance patterns.

Of equal importance to spatial variation, and as highlighted by the present study, the age of all sample animals used in parasitological studies

needs to be carefully recorded. This is of particular relevance in ruminant animals where, in addition to chronological age, the degree of wear of the incisor-canine complex should be independently assessed. Failure to do so, in the light of the results of the present study, could render even the most carefully determined parasite counts and resultant "averages" meaningless.