MCKENZIE A A

CO-OPERATIVE HUNTING IN THE BLACK-BACKED
JACKAL CANIS MESOMELAS

PhD UP 1990

Co-operative hunting
in
the black-backed jackal *Canis mesomelas* Schreber

by

Andrew Alec McKenzie

Submitted in partial fulfilment of the
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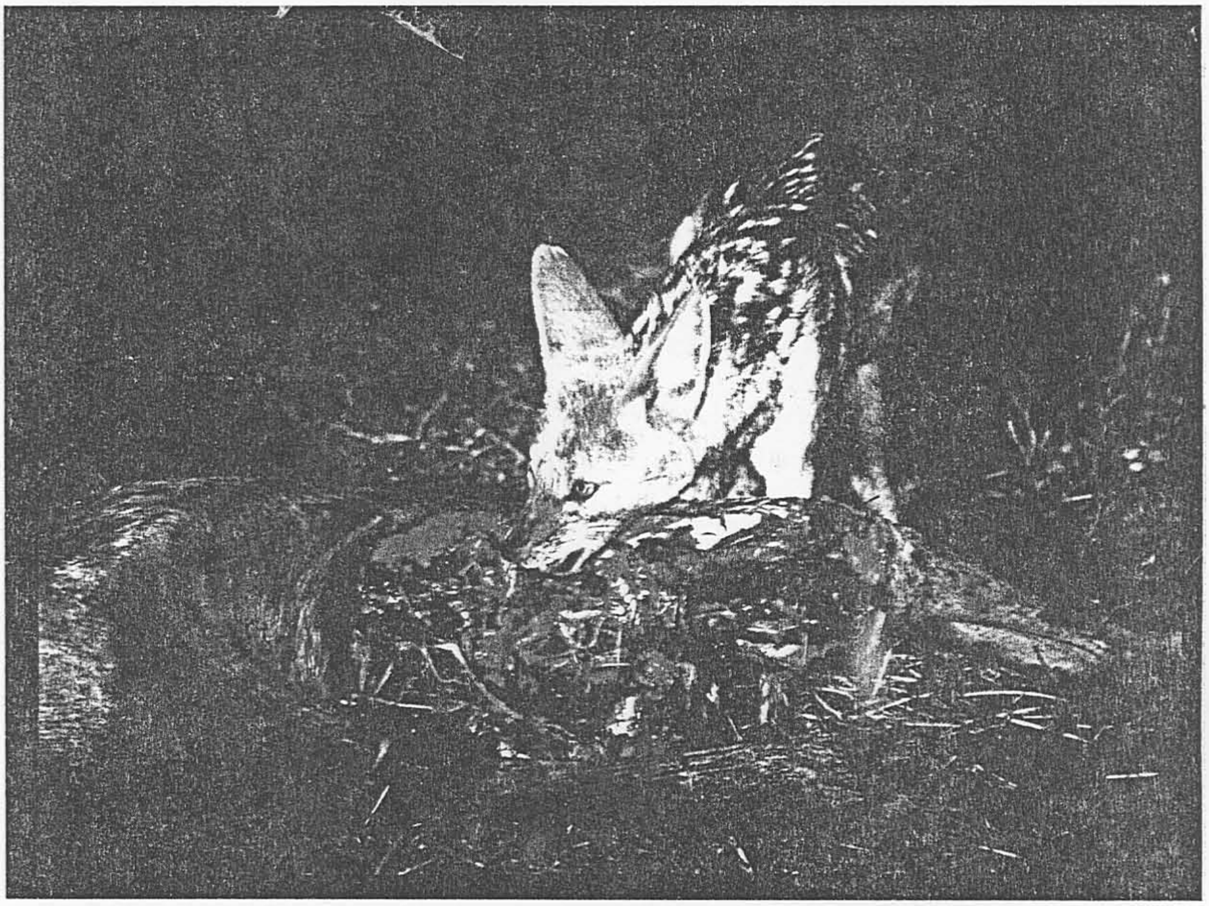

"Premeditated control of animals is a prerogative that only man can exercise.... If man takes this responsibility lightly, he may alter the natural order and indirectly threaten his own place in the unnatural world thus created."

(McCabe & Kozicky 1972:393,394)

Dedicated to all those who gave
so generously of themselves

Co-operative hunting
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by

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Abstract

Black-backed jackals *Canis mesomelas* prey regularly on adult impala *Aepyceros melampus* in the Northern Tuli Game Reserve, N.E. Tuli Block, Botswana. This predation was found to be highly selective - eight of eleven impala killed were old and in extremely poor condition, one other had a fractured leg; opportunistic - a high percentage of old impala was present in the population where the predation was recorded; co-operative - groups of six to twelve jackals temporarily co-operated in killing and consuming impala; and seasonal - frequency of hunting of impala was highest under dry conditions, and was non-existent following good rainfall when jackals subsisted almost entirely on insects.

Testing of impala by putting resting herds to flight was recorded; this was undertaken by one or two jackals only. Selected potential prey were cornered in thick bush and harassed by an increasingly larger group of jackals. A single throat bite was administered by one of the jackals - no laceration, severing of major vessels or crushing of the trachea was recorded. The prey was dispatched by other jackals which entered the abdomen cranial to the hind leg and severed the major abdominal blood vessels.

Minimum seasonal home ranges of mature jackals were approximately 1 km^{-2}, 10% of total home ranges. Male jackal home ranges increased during winter; this was accompanied by an increase in trotting behaviour and an increase in excursions into adjacent areas. Jackal population density was between four and seven km^{-2}. Signs of a predator trap with respect to several less common prey species was evident.

Extensive use of anterior teeth by impala and other ruminants during grooming was discovered. The teeth are arranged in a comb-like array, and in old animals exhibit wear patterns which are due to the grooming function. Older impala without functional front teeth carried significantly more ectoparasites than other impala. Repeated grooming attempts by these old animals removed the hair resulting in partial baldness named "autogenous alopecia".

Preponderance of old impala, the resultant high jackal population, and autogenous alopecia were ascribed to ecosystem stress induced by the absence of large selective predators.

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CHAPTER 1

INTRODUCTION

> "Further research, or rather re-search, is needed for more understanding not only of the canids but also of man's place in nature, the two being intimately related. We must strive to preserve and foster this relationship, this unity and interrelatedness of all things and at the same time reduce man's alienation from nature as well as from his fellow beings. The dynamically balanced intrinsic complexity of life, of ecosystems, of species, of individuals, and of the cells of the body must be appreciated; for man, it must also be understood. Why? In order to predict, control, modify, or manipulate and exploit? I hope simply for the sake of awareness and also for the possible necessity of intervention in times of an ecocatastrophe, as well as to avert such an eventuality."
>
> (Fox 1975:460)

As a group of animals, the Canidae display a remarkable adaptability to environmental extremes. Representatives of this family occur from the Artic tundra to sub-tropical deserts. They subsist on animal and vegetable matter, the former ranging in size from insects weighing less than one gram to large ungulates weighing over 800 kilograms. Canids may lead a solitary existence, or may form part of large cohesive packs of up to 36 individuals. Some depend for their existence on a certain social structure, while others, such as the jackal and coyote, can adapt their social system to suit prevailing conditions. The symbiotic relationship between man and the earliest domestic dogs may be seen as an example of the flexibility and adaptability of this highly successful group of carnivores (Eaton 1969). And the ability of certain species to flourish and take advantage of man's ineptitude despite heavy persecution - again the coyote and the jackal serve as excellent examples - indicates that in some way or another the canids will continue to adapt despite the accelerating rate of global change induced by man.

This study of the predatory habits of the black-backed jackal *Canis mesomelas* has a rather fortuitous origin. During my early acquaintance with the Northern Tuli Game Reserve (NTGR) in Botswana, the then manager of Mashatu Game Reserve, part of the NTGR, mentioned to me that the jackals in the region were responsible for killing adult impala *Aepyceros melampus*. This intrigued me - an adult impala weighs between 32 and 66 kg, while an adult jackal weighs only between 6 and 10 kg (Smithers 1983). The killing of such large prey by jackals would thus constitute a spectacular feat. In addition, the jackal is often accused of killing domestic stock, and the possibility that this reputation could be based on a predatory role in natural areas is an intriguing one. The study was thus launched, not without some scepticism, to determine whether or not the local folklore had some foundation in fact.

Jackals have sporadically been reported to hunt and kill medium-sized antelope (van Lawick Goodall 1970a, Kruuk 1972, Schaller 1972, Sleicher 1973, Lamprecht 1978a, Moehlman 1983, Goss 1986). All of these reports merely served to fuel speculation as to whether this was an integral part of jackal biology, or whether these were freak incidents of curiosity value only. Most studies on the diet of jackals have utilized the indirect techniques of stomach-content or faecal-content analysis (Grafton 1965, Bothma 1971, Smithers 1971, Rowe-Rowe 1976, Stuart 1976, Hall-Martin & Botha 1980, Rowe-Rowe 1983). This is hardly surprising, as the jackal is a small, largely nocturnal carnivore - traits which make direct observation of feeding habits a difficult and time-consuming task. Furthermore, much of the motivation for earlier studies was the perceived impact of jackal predation on stock farming enterprises (van der Merwe 1953, Rowe-Rowe 1975). Surviving jackals in farming areas are even less likely to allow close observation after years of relentless persecution. The outcome of these practical difficulties was that the source of individual prey items could rarely be unequivocally determined - i.e. was it hunted or was it scavenged. This most important question was therefore not answered by such early investigations. Even the extensive study of the black-backed jackal by Ferguson (1980) did not yield a large amount of direct observational data.

Some other aspects of jackal (hereinafter used to refer to the black backed jackal *C.mesomelas*) biology have been well studied, although much basic work remains to be done. Black-backed jackals occur sympatrically with the two other jackal species - the golden jackal *C. aureus* and the side-striped jackal *C.adustus* - in parts of Africa. In southern Africa *C.mesomelas* and *C.adustus* occur, the latter occurring only in the moister eastern and northern extremities of the subregion while the former occurs throughout the subregion with the exception of these extremities. There is only a small area of overlap in the north-eastern sector (Smithers 1983).

Jackals are monogamous and exhibit a long-term pair bond (Moehlman 1983). Between one and six young are born between June and September in southern Africa (Smithers 1971, Rowe-Rowe 1974 in Rowe-Rowe 1975). Some of the young jackals may remain with the parent pair for more than a year, and may assist in raising the next litter of young (Moehlman 1979, 1983). Dispersing young jackals move over larger areas than adults or younger jackals (Ferguson, Nel &

de Wet 1983). Adult jackals may display territorial behaviour (Moehlman 1983) or may have an overlapping home-range system (Rowe-Rowe 1982, Ferguson *et al.* 1983, Hiscocks & Perrin 1988). Home-range size is highly variable between geographical areas (Ferguson *et al.* 1983).

Jackals may become strictly nocturnal when persecuted, but otherwise are most active at dawn and dusk (Ferguson, Galpin & de Wet 1988). Activity consists largely of foraging and hunting, with social interactions, marking of territories with faeces and urine, and maintenance behaviour of lower frequency (van Lawick Goodall 1970a, Lamprecht 1978a, Ferguson 1980, Moehlman 1983). Jackals prey on anything from termites to adult antelope (Lamprecht 1978a). Predation on larger prey is more successful if undertaken by more than one individual (Wyman 1967, Lamprecht 1978a, Ferguson 1980). Jackals are most renowned as scavengers. This reflects the opportunistic nature of the species - individuals will move far from their normal home-range and will form large aggregations when large scavengeable resources are available (Ferguson *et al.* 1983).

Jackals emit a wailing call which can be heard over a considerable distance. Frequency of calling is greatest during the breeding season (Skead 1973).

The answer to the question posed by the present study lay in direct observation. The fact that many, many hours of frustration, exasperation and boredom would accompany this mission was evident from the paucity of comparable information. Even studies on coyotes *C. latrans* (White 1973, Bowen 1981, Bekoff & Wells 1985) and wolves *C. lupus* (Mech 1966, Peterson 1977, Allen 1979, Gasaway, Stephenson, Davis, Shepherd & Burris 1983, Carbyn &

Trottier 1987, Peterson, Woodlington & Bailey 1984) have yielded frustratingly few direct observations of predation after many hundreds of cumulative man-hours of study. The need to make-do with available equipment together with a complete lack of experience in dealing with the wiles of the jackal also yielded a unique set of frustrated ambitions. The fact that the study was successful is due to a considerable amount of good fortune, coupled with a degree of dogged determination.

The outcome of the present study has a far broader scope than is indicated either by the title of this thesis or by the original question. As a highly adaptable, opportunistic carnivore, the habits of the jackal are likely to reflect the underlying processes at work within the particular system in which it is being studied. The broad scope of the present study is, therefore, a reflection of the fact that in studying the predators within a system the system itself is being studied - the predator merely provides the window through which to view the intricate workings of its environment.

As in the system itself, each part of the present study stands on its own as an entity with its own peculiar characteristics. Yet each part supports, is supported by, and interacts with, all the other parts. An appreciation of the interactive nature of the various parts can only follow the detailed description of the parts themselves. This thesis is, therefore, divided up as follows:

Chapter 2 describes the context of the present study - the history and geography of the study area;

Chapter 3 describes the study of jackal predation;

Chapter 4 describes the study of the impala population in the study area;

Chapter 5 describes attributes of other large carnivores - wild dogs *Lycaon pictus* and spotted hyaenas *Crocuta crocuta*- which are of relevance to the study;

Chapter 6 describes the pathology of a syndrome of hairlessness in impala - autogenous alopecia - discovered during the study, and

Chapter 7 describes the relationships between the different parts of the study and places these in context.

The many cross-references used in the text are a reflection of the holistic nature of the study. It is strongly recommended that the summary at the end of this thesis be read first to obtain a synthetic overview before reading the individual chapters.

Ockham's Razor is the mantra of science which states that "One should choose the simplest hypothesis fitting the facts" (Brynum, Browne & Porter 1983). The study of ecosystems is a complex task indeed, and the application of Ockham's Razor can simplify the conclusions to a few short sentences. Yet the emergent mathematical formulation of natural systems is showing what ecologists have known all along - that ecosystems, and other natural systems, are governed by chaotic forces (May 1989). And what is the simplest description of chaos? Chaos!

Study of an ecosystem yields a pattern. Can any conclusions be drawn from a pattern? The pattern is merely a reflection of the temporal and spatial matrix of processes at work within the system, many combinations of which could potentially yield the identical pattern (Cale, Henebry, & Yeakley 1989). I believe that it is the task of the ecologist to employ all the faculties at his disposal to identify the processes responsible for the patterns he observes - it is the ecologist who, after all, will be charged with caring for ecosystem health and "In ecosystems as in organisms, what constitutes health is not (despite the popular view) based on objective scientific criteria, but rather involves judgement" (Rapport, Regier & Hutchinson 1985). The true sequence of events is unlikely to follow the simplest route, and the ecologist must, of necessity, trample on Ockham's toes, limited only by his own caveat that he is merely doing his best. At least, by using his judgement, something of substance is generated which can be compared to future patterns to determine if indeed the true processes have been identified. The present study is thus a record of my attempts to identify the processes that gave rise to the patterns that I observed in the ecosystem of the Northern Tuli Game Reserve. I believe that it is only the identification of these processes which has led to a meaningful outcome to this study. Yet the conclusions I have reached must always be viewed in the context of my inability to ever fully understand a system far older and more complex than myself.

CHAPTER 2

STUDY AREA

Introduction

The study was undertaken in the Northern Tuli Game Reserve (NTGR), a private game reserve in eastern Botswana. A general description of the Reserve is given for reference purposes. Only a small portion of the Reserve was utilized as the jackal study area and, where appropriate, specific reference is made to the characteristics of this circumscribed area.

Location

The NTGR is located in eastern Botswana between 21°55'S and 22°15'S and between 28°55'E and 29°15'E. The Reserve constitutes the north-eastern extremity of a 350 km strip of private agricultural land known as the Tuli Block (Fig. 1). The Reserve is bounded in the east by the Shashe River and in the south by the Limpopo River. The former constitutes the border between Botswana and Zimbabwe and the latter the border between Botswana and South Africa. The south-western boundary is bordered by the Motloutse River, while the remainder of the western boundary consists of a double foot-and-mouth disease control fence. The northern boundary is comprised of a semi-circular unfenced cut-line which demarcates the Tuli Safari Area in Zimbabwe (Fig. 2).

The Reserve consists of nine original farms, some of which have been subdivided into several portions. With the exception of the fences shown on

Figure 1. Location of the Northern Tuli Game Reserve.

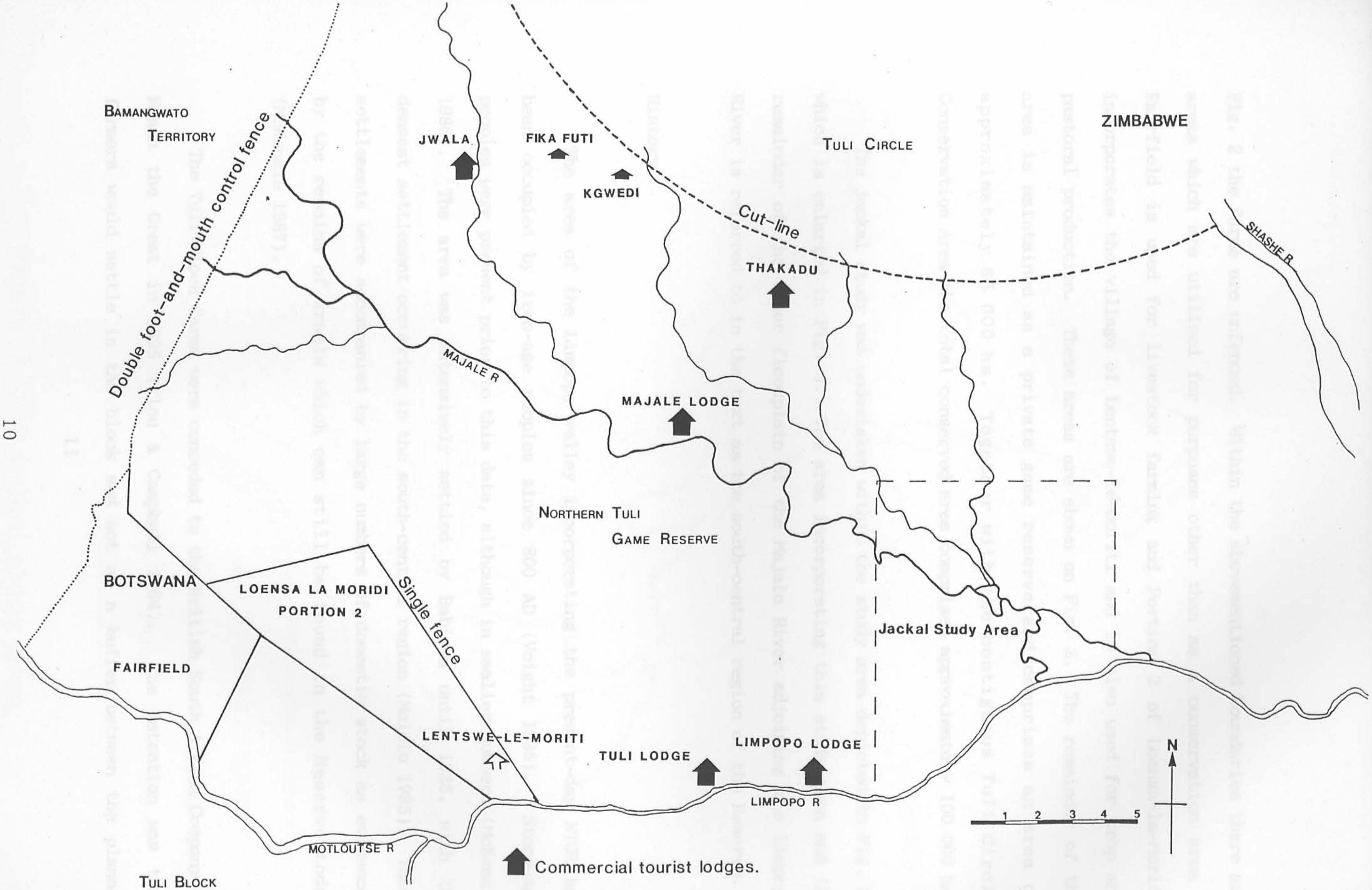

Figure 2. The Northern Tuli Game Reserve.

Fig. 2 the farms are unfenced. Within the abovementioned boundaries there are areas which are utilized for purposes other than as a conservation area - Fairfield is used for livestock farming and Portion 2 of Loensa-la-Moridi incorporates the village of Lentswe-le-moriti and is also used for crop and pastoral production. These areas are shown on Fig. 2. The remainder of the area is maintained as a private game reserve and comprises an area of approximately 65 000 ha. Together with the contiguous Tuli Circle Conservation Area the total conserved area comprises approximately 100 000 ha.

The jackal study was undertaken within the study area depicted in Fig. 2, which is enlarged in Fig. 3. The area incorporating this study area and the remainder of the lower floodplain of the Majale River adjoining the Limpopo River is referred to in the text as the south-central region of the Reserve.

History

The area of the Limpopo valley incorporating the present-day NTGR has been occupied by iron-age peoples since 800 AD (Voight 1985). Stone-age peoples were present prior to this date, although in smaller numbers (McKenzie 1986). The area was intensively settled by Babirwa until 1926, with the densest settlement occurring in the south-central region (Molelu 1985). These settlements were accompanied by large numbers of domestic stock as evidenced by the remains of kraals which can still be found in the Reserve today (McKenzie 1987).

The Tuli Block farms were conceded to the British South Africa Company by Khama the Great in 1895 (Tlou & Campbell 1984). The intention was that farmers would settle in the block and act as a buffer between the planned

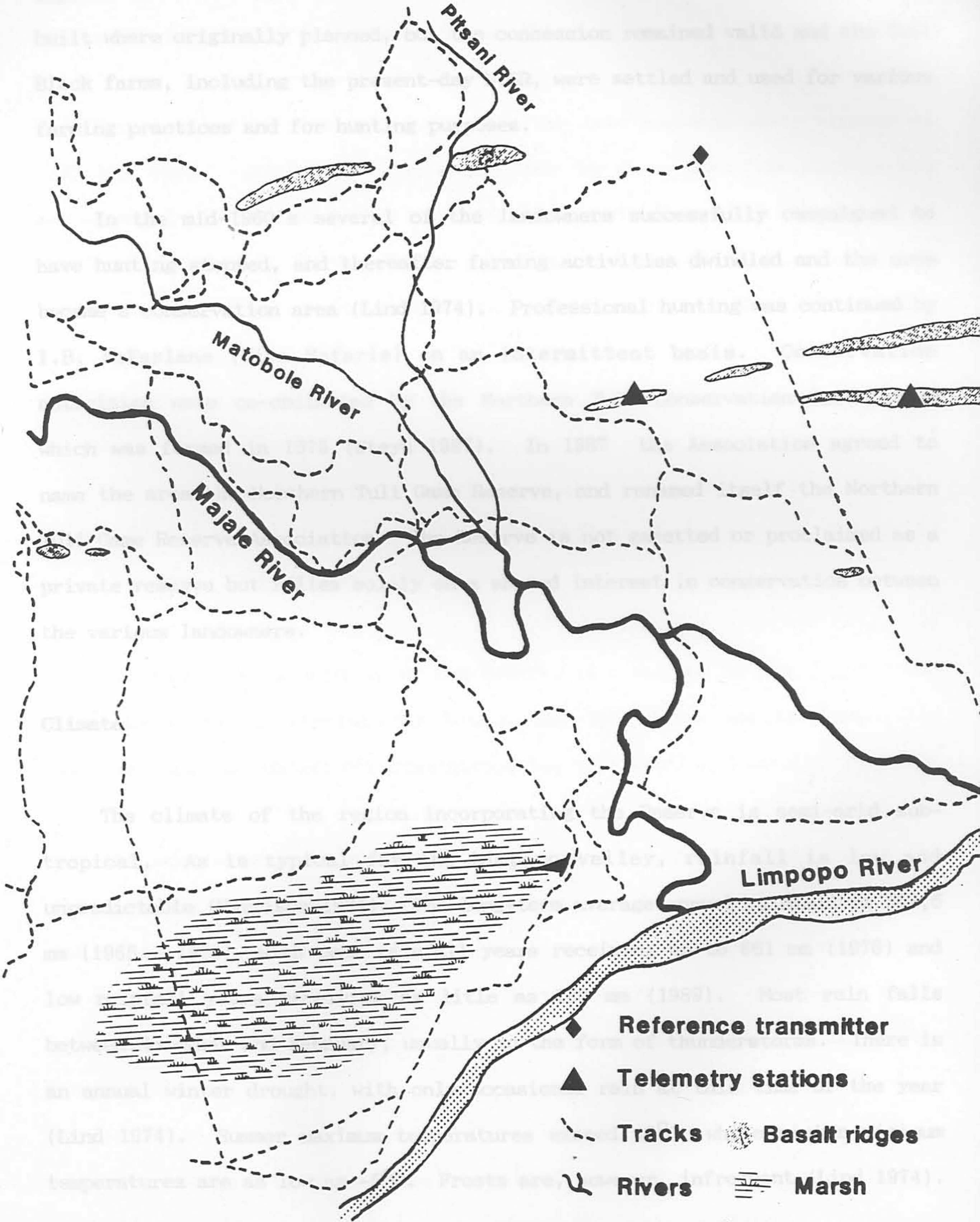

Figure 3. The jackal study area.

Cape-to-Cairo railway and the boer Transvaal Republic. The railway was not built where originally planned, but the concession remained valid and the Tuli Block farms, including the present-day NTGR, were settled and used for various farming practices and for hunting purposes.

In the mid-1960's several of the landowners successfully campaigned to have hunting stopped, and thereafter farming activities dwindled and the area became a conservation area (Lind 1974). Professional hunting was continued by I.B. McFarlane (Vira Safaris) on an intermittent basis. Conservation activities were co-ordinated by the Northern Tuli Conservation Association which was formed in 1975 (Steyn 1987). In 1987 the Association agreed to name the area the Northern Tuli Game Reserve, and renamed itself the Northern Tuli Game Reserve Association. The Reserve is not gazetted or proclaimed as a private reserve but relies solely on a shared interest in conservation between the various landowners.

Climate

The climate of the region incorporating the Reserve is semi-arid sub-tropical. As is typical for the Limpopo valley, rainfall is low and unpredictable (Harrison 1984). The long-term average annual rainfall is 369,5 mm (1965 - 1989), with peak rainfall years receiving up to 661 mm (1976) and low rainfall years receiving as litle as 180 mm (1989). Most rain falls between November and February, usually in the form of thunderstorms. There is an annual winter drought, with only occasional rain at this time of the year (Lind 1974). Summer maximum temperatures exceed 42^{o}C, while winter minimum temperatures are as low as -5^{o}C. Frosts are, however, infrequent (Lind 1974).

The prevailing wind is south-easterly. Whirlwinds are common in the hot-dry season from August to December (Lind 1974).

The jackal study was concentrated in the late summers/ early winters of 1987 and 1988. Rainfall in the study area in the preceding summers was approximately 190 mm and 284 mm respectively (Pontdrift records, Department of Transport, Pretoria, South Africa. A single storm of 92 mm recorded at Pontdrift on 16-01-87 is excluded as this did not extend to the study area.)

Geology and Soils

Two differing descriptions of the geology of the Reserve are given by Alexander (1984) and Joubert (1984). The geological description summarized here is derived from Joubert (1984).

The geological substratum of the Reserve is comprised of the deep Clarens Sandstome Formation overlain by Letaba and Sabi River Basalt Formations. Numerous east-west dolerite dykes intrude the abovementioned strata.

The sandstone is only exposed along the southern extremities of the Reserve along the Limpopo and Motloutse rivers. The rest of the Reserve is dominated by the basalt formations. Extensive alluvial plains occur along all the major rivers, including the lower Majale River. Old, undulating plains are flanked by the younger alluvial deposits along the rivers and by the basalt hills.

The jackal study area is comprised almost entirely of alluvial floodplains. The riverine areas represent the younger alluvium, while the fringe areas are the older flood-plains. Weathered basalt ridges intrude the edges of the study area, and the telemetry stations indicated on Fig. 3 were situated on two of the highest of these ridges.

Extensive accelerated erosion has followed over-utilization of the herbaceous layer (Lind 1974, Joubert 1984). Both sheet and donga erosion were evident in the study area, giving rise to areas devoid of vegetation within the otherwise well vegetated river valley. Riverine soils are deep, while the basalt areas have a very thin layer of remaining top-soil.

Topography and Drainage

The Reserve is extensively dissected by incisive drainage lines. Most of the Reserve is drained via the Majale River which terminates in the south-central portion of the Reserve where it enters the Limpopo River (Fig. 2). Other minor rivers flow directly into the Motloutse, Limpopo and Shashe rivers. All of these rivers flow only sporadically in summer and are dry, with the exception of isolated pools, during winter.

The incised topography of the basaltic regions is abruptly replaced by the undulating older flood-plains along all the major rivers. The floodplain is interrupted by the sandstone formations in the south and west and by the dolerite dykes in other parts.

The study area is bisected by the Majale River. Due to recent flooding and siltation the young floodplain is dissected by deep dongas and exhibits a case of river capture and a case of ox-bow formation (Fig. 3). The topography is gently undulating except for the flatter young floodplain, the recent dongas (which are up to 3 m deep) and the incised basaltic terain on the fringes.

Vegetation

The vegetation of the Reserve falls within the broad classification of Mopani Veld (Acocks 1975). The following more detailed classification follows Joubert (1984).

The vegetation of the Reserve comprises three major landscapes - the Floodplains on Alluvium, the *Colophospermum mopane/Terminalia prunoides* Rugged Veld on Basalt, and the Karoo Sandstone landscape. The latter occurs only along the south-western fringes, the Floodplain landscape occurs along all the major rivers, and the rest of the Reserve is comprised of the various elements of the Rugged Veld on Basalt landscape.

The study area is dominated by the Alluvial landscape. The triangular portion between the three rivers (Fig. 3) consists lagely of *Acacia tortilis* savanna. The remainder of the riverine areas consist of a mozaic of *Acacia albida* Gallery Forest and *Croton megalobotrys* Thicket. Fringing these communities is a thin, variable zone of *Salvadora angustifolia/Acacia tortilis* Brushveld which is replaced by the open *Boscia foetida* savanna on the old, undulating floodplain.

The Rugged Veld landscape is represented on the fringes of the study area by the *Colophospermum mopane/Terminalia prunoides* Middleslopes, and on the ridges by the Basalt Outcrop community.

The woody communities mentioned above form a complex mozaic in the study area. A consistent difference is however apparent between the herbaceous vegetation of the young floodplain on the one hand and the old floodplain and basalt elements on the other. The former is covered by a dense stand of tall, largely perennial grasses - mostly *Cenchrus ciliaris, Chloris gayana, Panicum maximum, P. meyerianum and Urochloa mossambicensis.* The latter is covered largely by short annual species. The most common forb, which forms a dense yellow and green carpet in summer, is the dubbeltjie *Tribulis terrestris.* The most common grasses on the old floodplain are the short *Enneapogon brachystachius* and *Oropetium capense.* These are replaced by the taller but sparse *Aristida spp.* and *Enneapogon cenchroides* in the basaltic areas.

An exception to the above is the large *Sporobolus consimilis* marsh which occurs in the south-western corner of the study area. This marsh, or vlei, consists of a homogeneous stand of the tall "elephant grass" *Sporobolus consimilis*, is an important component of the south-central region, but was not utilized by any of the study jackals.

Fauna

A comprehensive faunal list for the Reserve is given by Lind (1974).

Large mammals which occur within the study area are listed below, with the most recent estimates of total abundance in the Reserve shown where available (le Roux 1989). Calculated densities within the NTGR are shown. A subjective indication is also given of the relative abundance of all the species within the jackal study area.

Carnivora

Acinonyx jubatus	Cheetah	common
Canis mesomelas	Black-backed jackal	very common
Civettictis civetta	African civet	common
Crocuta crocuta	Spotted hyaena	scarce
Felis caracal	Caracal	scarce
Felis lybica	African wild cat	common
Genetta genetta	Small-spotted genet	common
Genetta tigrina	Large-spotted genet	common
Ichneumia albicauda	White-tailed mongoose	scarce
Mellivora capensis	Honey badger	scarce
Mungos mungo	Banded mongoose	common
Panthera leo	Lion	common
Panthera pardus	Leopard	common
Proteles cristatus	Aardwolf	scarce

Artiodactyla

			Total	density no/km^2
Aepyceros melampus	Impala	very common	5800	8,9
Connochaetes taurinus	Blue wildebeest	common	223	0,34
Giraffa camelopardalis	Giraffe	scarce	26	0,04
Kobus ellipsiprymnus	Waterbuck	scarce	15	0,02
Phacocoerus aethiopicus	Warthog	scarce	90	0,14
Potomachoerus porcus	Bushpig	scarce		

Raphicerus campestris	Steenbok	common		
Sylvicapra grimmia	Common duiker	common		
Artiodactyla (cont.)				
Taurotragus oryx	Eland	common	110	0,17
Tragelaphus scriptus	Bushbuck	scarce		
Tragelaphus strepsiceros	Greater kudu	common	540	0,83
Perissodactyla				
Equus burchelli	Burchell's zebra	common	187	0,29
Others				
Cercopithecus pygerythrus	Vervet monkey	common		
Hystrix africae-australis	Porcupine	scarce		
Lepus saxatilis	Scrub hare	common		
Loxodonta africana	African elephant	common	451	0,69
Orycteropus afer	Aardvark	scarce		
Papio ursinus	Chacma baboon	common		
Pedetes capensis	Springhaas	scarce		

Gibson (1989) states that only *C. adustus* occurs in the Tuli Safari Area in Zimbabwe. As this area is directly contiguous with the NTGR, and as many *C. mesomelas* have been recorded in the Reserve without a single record of *C. adustus* (Lind 1974, present study), Gibsons' statement is regarded as questionable.

The following ungulates have become extinct in the Reserve within historical times:

Alcelaphus buselaphus	Red hartebeest
Damaliscus lunatus	Tsessebe
Hippotragus equinus	Roan
Hippotragus niger	Sable
Oryx gazella	Gemsbok
Redunca arundinum	Reedbuck
Syncerus cafer	Buffalo

Human Activities

The Reserve is utilized for photographic safaris - both private and commercial. The most intensively utilized area is the south-central region which is utilized by the commercial enterprise of Mashatu Game Reserve as well as by visitors to the Gilfillan properties in this area. This is reflected in the extensive road network in this area (Fig. 3). Utilization is almost exclusively in the form of game-drives in open four-wheel-drive vehicles. Extensive night-spotting is undertaken using spotlights. Up to seven vehicles may be active within the south-central area at times of peak utilization.

Hunting by Vira Safaris ceased in the Reserve in 1987. The only remaining consumptive activity is the utilization of impala and kudu by the commercial lodges and for staff rations. Very little of this shooting is undertaken in the south-central region to avoid increased wariness by the game animals.

CHAPTER 3

JACKAL PREDATION

Introduction

The study on the jackals of the Northern Tuli Game Reserve commenced on the 1st of September 1986. Glen Devine, then manager of Mashatu Game Reserve, reported that the local Batswana people believed that the jackals in the area were responsible for killing adult impala on a regular basis. In informal discussion he urged me to conduct the study on the jackals of Mashatu as he felt they would prove very interesting. The observations of Lind (1974), Devine, myself and many others that there were large numbers of jackals in the Reserve certainly indicated that they may be important predators in the region. The project was so launched, but I don't think that any of us suspected just how interesting the story would be.

Jackals have achieved notoriety in Africa as avid predators of small domestic stock (van der Merwe 1953, Lombaard 1971, Rowe-Rowe 1975, Ferguson 1980). In many cases this reputation may be justified (Rowe-Rowe 1975, 1976). However, all the studies on the diet of this species (van der Merwe 1953, Grafton 1965, Bothma 1966, 1971, Wyman 1967, Smithers 1971, Rowe-Rowe 1976, 1983, Stuart 1976, Lamprecht 1978, Stuart & Shaughnessy 1984, Avery, Avery, Braine & Loutit 1987, Hiscocks & Perrin 1987) have demonstrated unequivocally that the black-backed jackal is an opportunistic feeder, preying on animals ranging in size from termites to 40 kg antelope and sheep, is not averse to feeding on vegetable foodstuffs, and will feed on carrion of any origin if available. Such demonstrably opportunistic behaviour understandably is

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extended to those large packages of food that are almost totally defenceless against even the weakest predator - sheep. If reason were to prevail, the blame would fall not on the jackal but rather on inappropriate husbandry practices. Of course the reverse is true, and the merciless persecution of jackals has had devastating consequences for this species as well as for the other small carnivores and scavenging birds of Africa.

The adaptability and opportunistic nature of jackals means that they manage to survive under the harshest of conditions, even the intensive persecution by man. This opportunistic nature has been taken to explain the sporadic cases where jackals have been observed killing adult gazelles (van Lawick-Goodall 1970a, Kruuk 1972, Schaller 1972, Sleicher 1973, Lamprecht 1978a, Moehlman 1983, Goss 1986). The ratio of the mass of an adult jackal to an adult gazelle is approximately 1:5, and these remarkable observations have therefore been important in documenting the killing ability of this small predator. However, three of the five reports cited here noted that the victims were sick or behaving unnaturally, and one is tempted to speculate that perhaps the ever-oportunistic jackal will sieze any opportunity to prey on animals which are most easily killed.

Like the jackal, the North American coyote *Canis latrans* is a monogamous small canid. The coyote is almost twice as large as the jackal (coyote males 13,4 kg, females 11,4 kg (Andrews & Boggess 1978) cf. jackal males 7,9 kg, females 6,6 kg (Smithers 1983). Coyotes prey regularly on cervids, both adult and young (Berg & Chesness 1978, Hilton 1978, Bowen 1981, Smith, Neff & Woolsey 1986). Moreover, as shown by Hilton (1978), the predation on adults may be selective for animals in poor condition, and in all studies predation increased in winter, thus demonstrating the kind of opportunism one could expect from other medium-sized canids such as jackals. Indeed, there are remarkable similarities in the behavioural ecology of these two species which will be demonstrated by the present study, and much could be learned about the jackal by applying a comparative approach to future studies on jackals. For this reason, extensive reference is made to the coyote literature in this thesis.

To direct the study on the reported predation by jackals on adult impala the following questions were posed:

1. Do jackals indeed hunt and kill adult impala in the Northern Tuli Game Reserve?.

2. If they do hunt and kill adult impala,
    a. How is this achieved?
    b. How regularly is it undertaken?
    c. How many jackals participate in a kill?
    d. Are any changes in socioecology associated with any such predation?
    e. Is there any selectivity in the predation?

3. What space and time utilization patterns are associated with predation by jackals on adult antelope?

From the outset it was known that jackals prey on young antelope (Wyman 1967, Pienaar 1969, van Lawick-Goodall 1970a, Kruuk 1972, Stuart 1976, Lamprecht 1978a, Ferguson 1980, Rowe-Rowe 1983, Stander 1987), that jackals are monogamous, live in small family groups, and give birth to one to six pups in early spring (Ferguson 1980, Moehlman 1983, Smithers 1983). As the scope of the present study was not broad enough to cover all aspects of jackal ecology, those about which much is already known were not included. The primary goal of the study was to document as many kills of adult antelope as possible, and to relate these to the other aspects, both known and observed, of the behavioural ecology of this species.

The study had to proceed with certain constraints. First, the heterogeneous habitat resulted in jackals often being lost to sight. Radio collars were therefore an essential prerequisite, and jackals had to be captured for the purpose of fitting the collars. Second, as the Reserve was utilized for tourism purposes, impact on these activities had to be minimized. Thus a minimum number of animals could be collared, and offroad vehicle activity had to be minimized. The latter, as well as the fact that much of the habitat in the Reserve was not suitable for following and observing an animal as small as a jackal, meant that continuous behavioural observations were impossible. The questions addressed by the study thus remained brief and specific. Other information gleaned during the course of the research is recorded to supplement what little is known about the jackal rather than as a complete record of events.

Location and observation of jackals was designed to record the presence or absence of any indication of predation on adult impala. To make locations and observations as feasible as possible, the central lower floodplain of the Majale River was chosen as the site for the study - this area has sections of open, short-grass plains which fringe on the riverine bush, thus making at least some of the travelling and observation relatively easy. In addition, this area has the best developed network of tracks in the Reserve. This site was also suitable in that it included several prominent hills which would be useful for radio tracking and telemetry.

While it is generally well known that jackals are wary of human persecution, Shortridge (1934) reported that jackals in remote areas are among the easiest animals to catch. In presuming that I was dealing with a relatively unpersecuted population in a game reserve, I proceeded to select the most ethical capture technique without being too concerned about the possible wariness of the jackals.

From the outset there were significant constraints on the capture operation for the project. First, only adult jackals resident in the selected study area would be suitable - there were not enough radio-collars to mark young animals, which could be expected to range over a wide area (Ferguson 1980). Second, as the area had a population of leopards and lions it was considered undesirable to use methods which would expose trapped jackals to possible predation by these larger carnivores. As jackals had been closely approached on many occasions during the run-up to the project, it was concluded that darting would be the most feasible, selective and ethical method of capture. However, although a darting system was developed to a state of sophistication in which a 100 mm diameter target could be hit with 95% certainty at 15 m, the approachability of the jackals had been overestimated. Furthermore, the more attempts that were made to approach jackals within the study area, the more wary they became of the study vehicle. It thus became essential to experiment with other methods. In retrospect it is regrettable that the final solution - foot-hold traps - was not tried first.

Eventually an adequate number of animals were collared in March 1987.

Unfortunately, due to managerial commitments in the Reserve, the study was suspended completely between 7th July 1987 and 15th February 1988. Thereafter, intensive observations and telemetry proceeded until 15th June 1988 and again from 4th to 18th September 1988.

As the jackal study relates intimately to the subjects contained in Chapters 4 and 5, a complete discussion of the implications of the results of the jackal study are reserved until Chapter 7.

Materials and Methods

Capture

Darting

Darting was undertaken using a modified Vario 1 Telinject dart pistol (Telinject SA, Randburg, SA). The pistol was modified so as to have quick-release trigger, stock and telescopic sight. Accurate darting required a range of approximately 15 m. Close approach to jackals was attempted by: 1. Baiting with impala, wildebeest, zebra and elephant carcases were moved to suitable sites within the selected study area; 2. Driving after sighted jackals - both during the day and during the night - in an open landcruiser; and, 3. Calling jackals to a brush hide with recordings of a distressed scrub hare and with varmint callers. Reflective tape was attached to darts to facilite the following of darted jackals as well as the recovery of darts that missed their targets, as described in McKenzie (1988a) (Appendix B1)

Foot-hold traps

Foot-hold traps were used as a last resort. My reticence to use steel foot-hold traps was due in the first instance to the reported injuries caused even by padded traps (Drewek 1980, Olsen, Linhart, Holmes, Dasch & Male 1986, Olsen, Linscombe, Wright & Holmes 1988) and, in the second instance, to the fact that the numerous lions and leopards present in the study area were likely to kill trapped jackals if they were left in open traps overnight. In order to solve the first problem, the traps obtained ("Jackal",Brock-Tuchten, Johannesburg) were modified as recorded in McKenzie 1989b (Appendix B2). The modified padded traps could safely be set off against one's fingers, and I was thus satisfied that injuries would be reduced to a minimum. The second problem was overcome by complementing the bait at the trap with sounds of a distressed scrub hare to encourage immediate investigation by any nearby jackals, and thus hopefully maximize chances of capture without having to wait overnight or longer.

Trapping was finally successfully undertaken as follows:

1. Padded traps were set in one track of the road transecting the study area, at a site away from any thick bush. Traps and equipment were treated in plant extract, handled and set as described by Bodicker (1980). The set traps were then left for 1 - 2 days with a log over the trap to prevent vehicles from setting off and damaging the trap.

2. Impala meat was minced in a standard meat mincer (approximately 500 g per trap), using plastic gloves to avoid contamination with human odour.

3. One hour after sunset the vehicle was driven next to the trap. Without alighting or switching off the engine, the log was lifted and placed in the vehicle. While still in this position, the minced meat was evenly spread on the ground over approximately 1 m^2 centred on the buried trap.

4. Recorded sounds of a distressed young scrub hare were played at maximum volume from a portable cassette tape recorder for 10-15 sec while turning the recorder to cover all directions.

5. After playing was completed the vehicle was slowly driven away to a nearby hill where calls of a jackal in the trap were awaited.

6. Upon hearing a jackal in the trap, I drove rapidly to the scene, threw a blanket over the jackal and administered the immobilizing drug.

Apendix A1 is a short account of the various methods used in an attempt to capture the ostensibly unaffected jackals, together with the shortcomings of the various methods. In total, four months of nightly effort were expended trying different techniques. In general, the methods failed to yield mature jackals from within the selected study area. Only as a last resort did I turn to using steel foot-hold traps, and only then after developing an acceptably humane modification.

Immobilization and handling

Trapped jackals were injected intramuscularly with 30-60 mg of Zoletil(50:50 tiletamine hydrochloride/zolazepam hydrochloride mixture, Virbac, Carros, France) (based on mean of 5,6 mg/kg for Canidae: Boever, Holden & Kane 1977). After injection the jackal was left in the blanket until the drug took effect. Once immobilized, the jackal was released from the trap and inspected for any injuries. One ml Compropen (150 mg procaine penicillin, 142,5 mg benethamine penicillin/ml, Centaur, Johannesburg) was administered intramuscularly.

Standard body measurements and masses (Ansell 1966) were determined. The age class of the jackal was determined from tooth eruption and attrition according to Lombaard (1971), and age group was assigned according to Ferguson *et al.* (1983).

Once fitting of the radio collar had been completed, the jackal was placed on a blanket and observed until fully recovered.

<u>Radio Collars</u>

Manufacture: Radio collars were manufactured as described in Appendix A2.

Fitting: Initially collars were fitted so that they could not be pulled off by pulling at the transmitter compartment (ventral) or side of the collar. This method was used as some of the first jackals captured were young, and tightening of the collars had to be minimized. Later collars were fitted so that they could not be pulled over the head. Once the correct size had been determined, the collar was secured with two pop rivets, and excess belting was cut off.

<u>Reflectors</u>

Reflectors were manufactured and fitted to collars as described in Appendix A3.

Radio Tracking

Technique: Radio tracking equipment consisted of a Yaesu FT290R Mark II 2m transceiver (Yaesu-Musen Co. Ltd., Tokyo, Japan), a RT58U co-axial cable, and a four element Yagi antenna constructed as described by Ferguson (1980). The co-axial cable was trimmed for maximum gain as described by Parish (1981).

The transceiver was mounted in an open LWB Land Rover. An overhead shelf was used to secure a swivel mount with handle as described in Appendix A4. The Yagi antenna was strapped to the swivel mount by means of a strip of car inner tubing in such a manner that it would swing free if struck by a branch, and in such a way that it could be rapidly removed and remounted when the antenna was to be held by hand.

At the beginning of a tracking session, the approximate position of each jackal was determined from one of the several high hills in the study area. For these locations, the Yagi was removed and held by hand in a standing position in order to maximize gain and directionality. After transmitter signals had been located, the Yagi was remounted. Upon nearing the approximate location of a particular jackal, the antenna was swept from side to side using the swivel-mount with the left hand while driving. This facilitated accurate location of the jackal's position. Once a clear signal was received, a roof spotlight, also operated by the left hand, was used to search for the jackal until visual location was achieved. A hand held spotlight was used to supplement the latter from a standing position if the jackal could not be located immediately.

Hills were used whenever a jackal could not be re-located during a session.

Data Collection: Upon sighting, time, identity number, group size, habitat, activity and location were noted.

Activity was grouped into the following categories:

Resting	Social activities
Active, unclassified	Other intraspecific interaction
Zig-zag foraging	Interspecific interactions
Hunting - impala	
- other	
Feeding - own kill	
- scavenge	
- cache	

Habitat was recorded as follows, according to the classification of Joubert (1984):

01 *Boscia foetida* savanna
02 Valley bush
03 *Acacia tortilis* savanna
04 *Croton megalobotrys* thicket
05 *Colophospermum mopane/Terminalia prunoides* middle slopes

06 Erosion plains - areas of valley bush and/or *Acacia tortilis* savanna which have been denuded by sheet and donga erosion, and which have little or no ground cover.

07 *Colophospermum mopane* scrubveld (a subdivision of the above found on alluvial soils, predominated by short, stunted *C.mopane*)

08 *Salvadora angustifolia/Acacia tortilis* brushveld

Location was recorded as follows: A two-times enlargement of the aerial survey map of the study area was obtained (Department of Surveys and Lands, Gaborone, Botswana). A strong plastic overlay was adhered along the top edge of the photograph. A 1 km^2 grid was drawn onto the plastic overlay. Each square was further divided into a 12x12 grid. Fine grid size was thus equivalent to 83x83 m. Due to prominent features of the terrain (trees, rivers, hills, roads), and substantial acquaintance with the study area, the locality of the jackals could be pinpointed on the photograph to within the 83x83 m grid. The position was temporarily marked on the photograph with an adhesive pointer while the overlay was held in place and the grid reference read off.

All data were recorded on a tape recorder and later transcribed onto a data sheet.

If the located jackal was not engaged in hunting or associated activity, searching for the next jackal commenced. If the jackal was engaged in interesting behaviour, additional notes to the above were made. Detailed continuous behavioural observations were not undertaken because of the unsuitability of much of the terrain other than the open plains, and because vehicle damage to the habibat had to be minimized.

Once each jackal had been located, the process was repeated. In this way it was attempted to locate each jackal at least once every three hours. As the consumption stage of impala kills lasts 2,5-4 h, and the hunting up to 4 h (pers. obs.), this interval provided an assessment of whether or not a jackal was involved in an impala hunt on a particular night. This method was used to determine the number of jackal-nights on which impala were consumed, and was considered more productive in this regard than observing a single jackal for a prolonged period.

If a jackal was located while feeding on an impala kill additional data were collected on the prey as follows:

Sex was noted

The mandible was collected for age determination. Age was determined from attrition patterns as described by Roettcher & Hof mann (1970), Spinage (1971) and Murray (1980). Cementum annuli were not used for age determination as this method has been singularly unsuccessful in this species (Spinage 1973, Reich 1981). As dental attrition varies markedly between different geographical areas (Roettcher & Hofmann 1970, Spinage 1971) none of the ageing techniques could be used to provide a precise record of true chronological age. As the study dealt with selective predation, an index of relative physiological age was required. "Age is generally meant to be an index of the passage of time, but to a demographer it also indexes probability of death." (Dapson 1980:544). In order to obtain such an index, the technique of Roettcher & Hofmann (1970) was selected as this method allows identification of animals in which physiological function is affected by advanced or total incisor attrition. Advanced or total incisor attrition represents a situation in which ingestive processes are compromised. A similar index of advanced senescence is not evident from molar attrition, except possibly the eventual total attrition of M_1 (Spinage 1971). Such advanced molar wear was not encountered in the impala collected in the study area for baseline age structure purposes (Chapter 4, Section 1), and incisor wear was thus the only index through which the (physiologically) oldest animals could be identified. Because of the lack of precision in extrapolating from other areas, the age data as determined using the method of Roettcher & Hofmann were classified into age classes as follows:

Age class 1/Young: <5 years. Less than 50% of enamel of occlusal surface of I_1 lost.

Age class 2/Middle-aged: 6-10 years. 50 - 100% of enamel of I_1 lost.

Age class 3/Old: >10 years. Attrition of I_1 advanced beyond occlusal surface, with reduction in size of surface of I_1 and other incisors. Most extreme case represented by total absence of all incisors and canines.

One femur was collected for determination of the Bone Marrow Fat Index as described in Chapter 4.

An autopsy was performed to ascertain the presence of any pathology, and to determine the exact cause of death. The distance between canine bite marks were measured if found.

The number of jackals observed in the vicinity of the kill was recorded.

Weather and phase of the moon were noted.

Telemetry

Stations: Two six-element Yagi antennas and two telemetry stations were constructed as described in Appendix A5.

The telemetry stations were located on elevated hills within the study area. A radio transmitter was placed at a site equidistant from the stations at a point which could be located on the 1:50 000 map of the study area (see Fig. 3).

Location: Each session began and ended by taking the bearings of the fixed transmitter. All bearings were taken by determining the point of fade-on of signal strength, which was sharply demarcated with the apparatus used. For jackal bearings, each cut-off point was confirmed at least twice before recording. Bearings on all jackals were taken every 20 min throughout the tracking session. Relative bearings of jackals were calculated as the perpendicular bisector of the two cut-off bearings. Actual bearings were calculated relative to the bearing of the reference transmitter. In using this method, errors in tower conformation, movement of the compass rose and bias in the antenna were nullified. Positions were plotted at the point of intersection of bearings from the two towers. Positions thus plotted were converted to grid references and entered onto a data sheet.

Telemetric tracking sessions were undertaken between 28-3-1988 and 15-06-1988. Evening sessions were from 18h00 to 23h00, and morning sessions from 06h00 to 08h30.

Calibration: Precision of the tracking apparatus was tested using stationary transmitters, the bearings of which were recorded until a total of 41 recordings were obtained. To eliminate observer bias, the audible fade-off was determined without looking at the compass rose. Once the point was identified, the pointer was stabilized and the reading was noted.

Activity: Together with each location it was recorded whether or not the jackal was active, as determined by the activity collar (one jackal) or changes in signal strength (Ferguson 1980, Fuller, Biknevikius, Kat, van Valkenburgh & Wayne 1989).

To supplement the activity recordings between sessions, an automatic activity recording device was constructed as described in Appendix A6. This device was located at the highest station, and was activated at the end of each tracking session. Recorded data were transcribed onto data sheets.

Data Analysis: All radio-tracking and telemetry data were entered into dBase III+ files for analysis. Files were formatted for use in SEAS (Spatial Ecology Analysis System, John Cary, Department of Wildlife Ecology, 226 Russel Labs, University of Wisconsin, Madison, WI, USA.) for the determination of home range sizes and movement patterns. Using SEAS, home range was calculated using the minimum convex polygon method (Mohr 1947), and the centre of activity was determined using the harmonic mean method (Dixon & Chapman 1965).

Faecal analysis

To supplement direct observations, fresh jackal faeces were collected within the study area during April, May, June and September 1988. The scats were macerated and sieved as described by Stuart (1976).

Identification of remnants was undertaken with a dissecting microscope, and observations were recorded as follows:

Mammalia: Rodent hair and/or bone fragments were classified as 'Rodent', and were not identified further. Hair from mammals other than rodents were retained. These hairs were then later sectioned and identified as described by Keogh (1983).

Aves and Reptilia: bird and reptile remains were identified to the level of order only.

Invertebrata: Insects and arachnids were recorded separately. Insects were further separated into Isoptera and 'Other Insects', the latter including all insect remains other than Isoptera. Arachnida were separated into Scorpiones and Solifugae.

All fruit remains were classified as food items, but were not identified.

Grass and leaves were recorded, but were not considered as food items for analysis. This is contrary to Bothma (1971), but is in agreement with Grafton (1965) and Rowe-Rowe (1983).

Data were analysed to yield the relative percent occurrence of items in the diet - i.e. the occurrence of each item is expressed as a percentage of the total occurrences. This method closely approximates the proportions actually consumed (Rowe-Rowe 1983), within the limitations of faecal analysis, and facilitates comparison between the four monthly collection periods.

Population Estimation

1. Mark-Recapture Estimate: Resightings of marked animals may be used to estimate population size if certain conditions are met (Caughley 1977). During radio-tracking, numerous jackals were encountered within the study area. Date, location, group size and presence of identifying marks (i.e. radio collars) were recorded. Jackals located by radio tracking were not recorded, nor were other jackals with a jackal located by radio tracking. If, however, the jackal being tracked was located on a road, or within the arc of the vehicles's headlights in the vicinity of the road, it was recorded as a random location. Data thus obtained were analysed to determine whether or not they were suitable for population estimation (Caughley 1977).

2. Home Range Size: The mean of the minimum seasonal home range sizes derived from the home range calculations were used to determine the density of jackal family groups within the study area. A conservative estimate of two adults, one current offspring associated with the adult pair, and one juvenile jackal covering a larger area, based on the results of Ferguson (1980) and Rowe-Rowe (1982), yields a minimum of four jackals active within each adult home range. Rowe-Rowe (1982) estimated that up to eight jackals could be active within the home range of an adult pair of jackals. These estimates were used to determine minimum jackal density based on the minimum seasonal home range size.

3. Known Jackal Groups: Through extensive travelling throughout the study area the centres of activity of jackals other than the study animals were identified. These observations were used to determine the number of jackal families within the most intensively traversed part of the study area and, using the above estimate of numbers per family, to estimate jackal density within the study area.

Results and Discussion

Capture

Darting

Three jackals were captured by darting (Table 1). Darting was unsuccessful as a method for capturing adult jackals in the selected study area. This was due to wariness by the jackals upon being purposefully approached, extremely fast reaction by jackals to the sound of the dartgun being fired, and difficulty in accurately estimating range at night. In addition, only younger jackals stayed at carcases when approached, and large carcases attracted adult jackals from outside the selected study area. Jackals were attracted by varmint callers and tape recordings, but would not approach to within range of the dart gun. Two jackals were killed and one was injured by darts. Use of reflective tape facilitated the following of darted jackals as well as the recovery of many darts that missed their target as recorded in McKenzie (1989a).

Trapping

The use of padded foothold traps was extremely successful. Time from baiting traps to capture varied from 10 min to 2 h. No fractures or excessive swelling were recorded, and only a single laceration , due to self traumatization, was recorded. Mild lameness was observed for a variable period after capture, as recorded in McKenzie (1989a). One trapped jackal was attacked and killed by lions within 7 min of capture - an inherent risk in using this method in the Reserve which was taken only as a result of failure of all other methods.

Immobilization

Times to tractability, first attempts to rise and ambulatoriness are recorded in Table 1. The relatively high doses of Zoletil used could have been reduced for the trapped individuals. These doses were initially used to achieve rapid induction during darting. However, even the high dose given to animal no. 3 did not guarantee rapid induction. Intramuscular injection was guaranteed when injecting the trapped animals, thus avoiding prolonged induction.

Generally, induction and recovery proceeded smoothly, and Zoletil proved to be a useful drug for the immobilization of jackals. The only disadvantage encountered was that once the solvent is added to the dry powder, the drug expires within 4 to 5 days. Thus capture of a single jackal in the field

Table 1. Immobilization dosages and response.

ID	DATE	CAPTURE	DOSE 1	TRACTABLE 2	MOVE 3	WALK 4
01	29/10/86	Dart	50	3	47	67
02	29/10/86	Dart	50	7	59	107
03	01/11/86	Dart	70	16	84	105
04	23/11/86	Trap	90	-	140	160
05	11/04/87	Trap	70	-	-	-
07	06/03/87	Trap	60	2	52	130
17	01/03/88	Trap	50	9	84	144
18	22/04/88	Trap	50	3	50	75
19	22/04/88	Trap	50	3	63	93
20	02/03/88	Trap	40	4	56	66

1 Zoletil (Virbac, Carros, France). Total dose in mg.
2 Time till sufficiently anaesthetized for safe handling without physical restraint.
3 Time till first purposeful movements.
4 Time till successfully rises and walks.

All times in minutes.

resulted in wastage if further jackals were not caught within a few days thereafter.

One jackal, no. 15, did not recover from anaesthesia. *Post mortem* examination was inconclusive, and it was concluded that shock had resulted in the death of the animal, which died during the recovery phase.

Radio Collars

Transmitters functioned satisfactorily for a minimum of 8 months, and in one case for 16 months. The only failure experienced was due to crack in the potting fluid which admitted moisture.

Loose fitting collars were removed by the first two jackals at 4 days and 3 weeks after fitting. In both cases, the removal was as a result of snagging of the dorsal side of the collar on small branches when the jackals inserted their heads into bushes, presumably to forage. Upon pulling against the snag, the collars were pulled over the occiput and off the animals - a feat which would otherwise have been impossible. Subsequent collars were fitted with less free play so as to avoid this problem.

Reflectors

The reflectors constructed from number-plate material were extremely useful in assisting in the location of jackals with a spotlight, particularly in dense vegetation. While occasionally a reflector was lost from an animal, the majority stayed in place. Reflectors were not fitted to later collars as they were so effective that they increased the visual impact of the collars, which was undesirable from the point of view of the tourist activities in the Reserve.

Radio Tracking and Telemetry

The radio tracking and telemetry systems functioned satisfactorily, with the exception of the automatic activity recording system. While the automatic data recording device worked extremely well, wow and flutter in the recorded signals from the ordinary collars made it difficult to discriminate activity from inactivity with absolute certainty. These data were therefore discarded.

The measured precision of the telemetry towers yielded a standard deviation of $0,37^{\circ}$ (n=41). As a fixed transmitter was used as the reference bearing during tracking, the telemetry stations were thus accurate to within less than one degree. While tests on stationary transmitters are commonly used to determine accuracy of telemetry systems (Ferguson 1980, Fuller *et al.* 1989) it must be realized that acccuracy is somewhat less than that determined by this method when one is tracking moving animals. This is due both to movement of the animals relative to the observer during tracking, and to fluctuating signal strength caused by movement of the collar on the animal.

Morphometric data

Masses and measurements of the study animals are presented in Table 2.

Table 2. Jackal measurements, masses and ages.

ID	SEX	TL	E	HF	T	G	N	MASS (kg)	AGE CLASS •	AGE GROUP ••
01	M	1030	105	150	305	355	210	6.0	4	2
02	F	1030	100	155	300	360	-	6.0	4	2
03	F	990	105	155	280	390	220	6.5	5	3
04	F	950	97	148	290	-	220	-	4	2
05	M	1020	105	145	290	-	235	7.0	5	2
06	F	--	-	165	290	-	200	5.5	4	2
07	M	1040	100	-	300	370	205	6.0	5	3
08	F	960	100	145	280	340	200	5.8	5	2
09	M	1120	110	145	350	420	235	8.0	6	3
10	F	1010	95	140	270	-	190	5.8	5	3
15	F	1030	105	135	285	-	225	6.5	5	3
16	M	1040	105	145	300	390	220	6.5	5	3
17	M	1110	105	155	320	420	-	8.0	5	3
18	F	920	95	142	260	380	210	5.8	5	2
19	F	1050	105	145	300	390	220	6.0	5	3
20	M	1020	100	150	280	375	225	6.5	5	2

TL = Total length, along the curve. E = Ear. HF = Hind foot. T = Tail. G = Girth. N = Neck. All measurements in mm.

• Age class according to Lombaard (1971). ④ = 6 months - 1 year. ⑤ = 1 - 7 years. ⑥ = >7 years.
•• Age group according to Ferguson *et* al (1983). 1 = young. 2 = sub-adult, fully grown, < 3 years old. 3 = Adult.

Feeding ecology

Direct observations

Predation on Impala

The study confirmed that jackals in the south-central region of the NTGR do prey on adult impala. Predation by jackals on impala older than 6 months was recorded on 11 occasions. Jackals were identified as the hunters responsible by direct observation on two occasions, by autopsy results on seven occasions, and by spoor and carcase remains on the other two occasions. Autopsies revealed the site, depth and canine spacing of any bite wounds on the carcase received prior to death. The canine spacing cannot conclusively discern between the bite of a caracal *Felis caracal* and a jackal (Roberts 1986). However, the shallower nature of jackal bites, the distribution of bite wounds on the body, and the pattern of consumption, beginning with the abdomen, facilitate the identification of jackals as the responsible predator. Moreover, caracals were only seen on two occasions during three-and-a-half years of intensive nocturnal activity in the Reserve, and thus the likelihood of misidentification of the responsible predator through thorough *post mortem* examination is assessed as minimal.

If a kill was located too late to conduct a meaningful autopsy, other characteristics indicated that jackals were the responsible agents. The kills of jackals were located in moderate to dense bush cover, in contrast to the open areas where cheetah kills were observed. The skeleton was always intact, as described below, eliminating lions and spotted hyaenas as possible agents. The absence of the spoor of other carnivores also assisted in determining the responsible agent. Finally, a frenzied activity was noticed when jackals had made their own kill, as opposed to where they were scavenging remains from other predators.

Kills located and their characteristics are recorded in Table 3.

In addition to kills located, jackals were seen to run after impala on seven occasions, and on another occasion a group of five jackals was observed unsuccessfully attempting to kill an impala over a period of more than four hours.

Out of a total of 186 jackal-nights monitored, five involved killing or consuming of an adult impala.

Several facets of the recorded predation of are particular interest:

Selectivity

In discussing the selectivity of predation it is pertinent to review the method of age estimation used on impala in the present study - i.e. incisor wear was used to provide an index of relative physiological age of the prey animals. Predators, with the possible exception of man, cannot make use of chronological age as a selection criterion for predation - rather, old age represents a physiological state which may increase the likelihood of death (Dapson 1980), particularly vulnerability to selective predation. Partial or complete absence of incisor teeth, as represented by Age class 3 impala in the present study, represents a condition - related to but not necessarily exclusively the result of old age - which compromises feeding ability,

Table 3. Details of impala killed by jackals.

Date	Est. time of kill	Circumstances *	Sex	Age Class **	Habitat density ***	No. of jackals seen	Bone Marrow Fat Index	Notes
04/06/85	20h00	Feeding	F	3	Moderate	7	-	
05/11/86	19h15	Feeding	F	3	Low	8	2,70	Extensive alopecia
26/11/86	19h00	Feeding	F	3	Moderate	6	3,24	Extensive alopecia
04/12/86	20h00	Feeding	M	1	Moderate	7	-	Mild alopecia
27/02/87	20h00	Remains	F	3	Moderate	-	0,50	
20/03/87	20h00	Harassing	M	1	Moderate	6	-	Compound #, r. metacarpus
27/04/87	21h00	Harassing	F	3	Moderate	12	2,14	
23/06/87	21h00	Feeding	M	3	Dense	5	0,25	
03/07/87	20h00	Feeding	F	3	Moderate	8	2,10	Moderate alopecia
15/09/88	01h00	Feeding	M	1	Dense	12	-	
18/09/88	24h00	Remains	F	3	Moderate	-	19,15	
							4,29 ± 6,64 Mean (std. dev.)	

Only impala over 6 months of age included.
* Harassing = jackals harassing and attempting to kill impala. Feeding = jackals feeding on fresh kill. Remains = jackals with remains of kill.
** Age Class 1 = young, < 5 years, 2 = middle aged, 5 - 10 years, 3 = old, > 10 years.

contributing to a loss in condition and thereby increasing susceptibility to selective predation.

Chasing of impala was always seen to occur while jackals were engaged in foraging for smaller prey. While foraging on the open plains at night for small prey items, including *Hodotermes sp.*, jackals encountered herds of impala which emerge from the valley bush at sunset to rest/graze on the open plains or at the fringes of the plains during the night (See Chapter 4). The majority of such encounters seen were followed by the jackals continuing with their foraging session. However occasionally the jackal, or pair of jackals, would discontinue their foraging to observe the impala. Suddenly the jackal(s) would rush towards the resting herd, which scattered in alarm. The jackal(s) then stopped and sniffed at the ground in the vicinity of the previous position of the herd. Following this sniffing the chasing was repeated two or three times. The impala stopped after each short chase, but progressively moved into the thicker vegetation fringing the plains. On all occasions on which this behaviour was seen, the jackals resumed their previous foraging pattern. On only one occasion was a jackal heard to vocalize during this chasing process, and this vocalization was of the repeated type emitted when mobbing large predators (Bearder 1975, Goss 1986, pers. obs.).

The behaviour recorded here is strongly reminiscent of the "testing" behaviour exhibited by wild dogs (Estes & Goddard 1967, van Lawick-Goodall 1970b), spotted hyaenas (Kruuk 1972) and wolves (Mech 1970, Allen 1979, Carbyn, & Trottier 1987) when approaching herds of potential prey, and has been recorded in jackals by Lamprecht (1978a). Like these larger predators, it is likely that the jackal is far more adept than the human observer at detecting any debilitated, sick or injured animal within the group. Even jackal predation on sheep is selective for the most vulnerable individuals (van der Merwe 1953). The repeated chasing is thus likely to be the initial stages of a hunt whereby, by inducing a flight reaction, identification of potential prey animals is facilitated. Unlike the testing in wolves, however, the jackals did not invariably pursue any animal which ran. However, in all the cases observed, the entire herd of impala would flee the charge by the jackal(s), thus making such a relationship impossible.

This selection hypothesis is supported by the highly selective nature of the eventual predation. Of the eleven impala killed by jackals, condition (Bone Marrow Fat Index, BMFI) only the seven fully grown animals could be determined. The mean BMFIs of these seven adult animals killed by jackals was 4,3±6,6 (Mean ± std deviation) (Table 3), significantly less than the mean value of 87,0±2,74 ($t=28,3$, $p<0,001$, d.f.=11) obtained from the control sample of six impala shot in September 1988 (Chapter 4). All of the full-grown impala killed by jackals had extremely worn incisor teeth and belonged to the old age class. Of the three young impala killed by jackals, one had a compound fracture of the right metacarpus. No signs of pathology were detected in the other two young impala, which were also too young for BMFI determination. However, in both cases, *post mortem* examination was inconclusive as much of the carcases had been consumed by the time they were located.

Selectivity for age was tested as follows:

Hypothesis: animals from the oldest age class are selected.

Null hypothesis: there is no selection for old animals.

A complete age structure for the population under consideration was not available (see Chapter 4). The data which are available indicate that there are approximately equal numbers of impala in each age category over 3 years old in the southern impala population within the Reserve. It is highly unlikely that there would be fewer of the youngest age class than of the older age classes. If is thus assumed that the number of animals in each age class in the population is the same and that there are three age classes, then one would expect each age class to be represented in the kills in the proportion of 1:3 of the total (= 3.33 animals in 10). This assumption favours the Null hypothesis as old animals are almost always scarcer than younger animals (Caughley 1977).

The old age class in the kills was represented by 8 animals, the rest by 2 (excluding the animal which had a fractured leg). Testing for association, $X^2=28,8$, d.f.=1, $p<0,001$; with Yate's correction $X^2=24,5$, d.f.=1, $p<0,001$ - i.e. the frequency of old animals in the sample was significantly higher than expected, indicating a strong selection for advanced (physiological) age by the jackals.

From data presented in Chapter 4, it is evident that there is a relatively high proportion of old impala in the population in the study area. However, as all of the eight adult animals killed by jackals were from the oldest component of the population, it can be concluded that the jackal predation on adult impala is highly selective with respect to age.

The condition of old impala declines significantly during winter (Dunham & Murray 1982). The present study has also shown (Chapter 4) that old impala with worn incisor teeth are in poorer condition than animals with effective incisor teeth at the end of winter. Without functional incisor teeth, and with worn cheek teeth, this loss in condition is probably due to compromised ingestive and masticatory functions, as well as to increased energy expended on futile grooming efforts (Chapter 4). These factors are likely to play a critical role at times of maximum nutritional stress - during peak lactation and during winter (Dunham & Murray 1982). As all the adult impala killed by jackals were in extremely poor condition, occurrence of the selective predation may be linked to environmental conditions, such as rainfall, which influence the loss in condition by impala during these periods. Selective predation by coyotes on old deer in poor condition has similarly been shown to increase during winter (Hilton 1978).

The selective predation by jackals on impala with advanced incisor attrition, in extremely poor condition or, in one case, with severe injury, indicates an overall selection for vulnerability. As shown by Temple (1987), selectivity for vulnerability by predators is linked to the relative difficulty of subduing and killing the prey. The large size of the impala prey would suggest that jackals should be selective for vulnerability, as is evident from the data obtained in the present study.

Harassment, teamwork and joining in

Prolonged harassment of an intended prey animal was observed in detail on two occasions. On one occasion, the prey escaped after 4 h, while on the other, the animal with the broken leg, was captured and consumed.

On the first occasion, three jackals were observed harassing an adult male impala. The impala had its hindquarters backed into a low bush, and was fending off the attacks by jackals from all sides. The impala did occasionally manage to break away and move to another bush where it was again cornered and harassed. After two hours, the number of jackals had grown to five. It was observed that some of the jackals would rest while others continued to harass the intended prey. This "relay" system of harassment has also been observed when wolves corner a moose (Allen 1979).

On the second occasion (Table 3, 20/03/87) the impala was eventually killed. Over a period of approximately 2 h, the size of the jackal group grew from three to six. Resting by some of the jackals, as described above, was also observed.

On neither of the above occasions were the jackals heard to vocalize loudly, but a low "wuffing" call was heard as the jackals harassed the cornered impala.

On the first occasion, calls by nearby jackals and a lion were not followed by a response by the jackals involved in harassing the impala.

Harassment by the jackals was continuous. Individual jackals rushed towards the cornered prey which turned to fend off the charge. The jackals broke off the attack without physical contact. One or more other jackals were at this stage attacking from another angle, and the impala turned to fend of this attack. This process was repeated continuously, and was only interrupted when the impala broke from cover and ran to another bush where it was again cornered.

Wolves have been reported to harass prey prior to the kill (Mech 1970, Allen 1979, Carbyn & Trottier 1987). As both jackals (present study) and wolves select sick, weak or old animals, this harassment, by depleting the already reduced energy reserves of the selected animal, is likely to have a marked influence on the ability of the animal to fend off any physical attack when it finally occurs. The prolonged chase by wild dogs and hyaenas in open habitat (Estes & Goddard 1967, van Lawick-Goodall 1970b, Kruuk 1972) also leads to physical exertion by the prey, and would thus be most successfully applied to compromised animals.

Purposeful harassment with delayed physical contact is only likely to be advantageous if the prey in good physical condition would be difficult or dangerous to kill. This is an extension of the observation that selection by predators for old or weak animals is correlated to the difficulty with which the prey is subdued and killed (Temple 1987). Thus jackals harass adult impala (present study) and gazelles (Sleicher 1973) but not young impala (present study), young gazelles (Wyman 1967, Lamprecht 1978a) or springhaas *Pedetes capensis* (Ferguson 1980); wild dogs harass zebra and wildebeest (Estes & Goddard 1967, Kruuk & Turner 1967, Malcolm & van Lawick 1975, van Lawick-Goodall 1970b) but not impala (Reich 1981), and wolves harass moose and bison but not beavers (Mech 1970, Carbyn & Trottier 1987).

The co-operative nature of harassment by social carnivores allows the efforts of the group to exceed the stamina of the selected prey. This may be the factor alluded to when hunting ability is cited as an advantage of group living in carnivores (Kruuk 1972, 1975, Lamprecht 1981, Packer & Ruttan 1988). This is, however, the first time that mammalian predators which do not live in a cohesive group have been recorded to co-operate temporarily for the achievement of a mutually beneficial goal. The described temporary co-operation is observed under circumstances where a particular resource is available which could not otherwise be utilized.

Immobilization and Coup de grace

The method of killing of the cornered impala was deduced from two observations and seven necropsies on fresh jackal kills.

One of the jackals bites the impala on the thoat in the vicinity of the angle of the mandible. The bite is a single, holding bite without any chewing or laceration of the overlying skin. Upper and lower canines penetrate the larynx, trachea and/or surrounding fascia. On only one occasion was the jugular vein found to have been penetrated. While the bite is deep, there was never any evidence of crushing of the larynx or tracheal rings.

The throat bite immobilizes the prey, which is pulled down by the weight of the jackal. What follows is a swift penetration of the abdomen via the thin skin and abdominal wall just cranial to one of the hind legs by another jackal. One or more jackals then enter their heads via the flank wound into the abdomen. It is important to note that the animal is not disembowelled immediately. Purposefully or otherwise, the biting severs the major arteries in the dorsal part of the abdomen - aorta, hepatic artery, cranial mesenteric artery - and associated veins. The kidneys are removed in this process, but other abdominal organs remain *in situ* until after the impala is dead. After administering the *coup de grace* the heads of the responsible jackals are covered in blood. This is removed by immediately rubbing the face and head vigorously on the ground, accompanied by rolling. Signs of such behaviour at the site of coyote kills has been recorded by White (1973). This observation raises the possibility that coyotes may also use this method to dispatch large prey. As in the case of the jackal, direct observations of such kills are extremely rare.

The method used results in rapid death of the prey animal - the loss of blood pressure following the severing of these major blood vessels is certain to result in almost immediate unconciousness. The blood released into the abdomen is richly oxygenated, confirming that the throat bite does not result in asphyxiation of the prey. In one case in which the jugular vein was penetrated, there was minimal perivascular haemorrhage, confirming the short interval between the throat bite and loss of blood pressure. Minimal haemorrhage was also recorded from jackal kills by Rowe-Rowe (1975) and Roberts (1986) - nevertheless these authors assumed that the throat bite was the killing bite. These authors did, however, document that the flanks of the victims were always opened by the jackals and that this was one of the first sites of eating by the jackals. Both these authors also noted that jackals kill large prey (sheep) in a far more efficient and neat manner than do feral dogs. Whether the flank penetration method of dispatching the prey used by jackals arose for this purpose or whether it is a reflection of a preference for feeding on the abdominal organs remains to be determined.

The pattern of immobilization and killing was sufficiently consistent to indicate that the technique of killing is applied by most, if not all, jackals in the region. The organized nature of the process may be as a result of the large numbers of impala preyed upon in this region. Other reports of predation by jackals on adult antelope have suggested that the prey is disembowelled (van Lawick-Goodall 1970a, Sleicher 1973, Lamprecht 1978a). While in areas where jackals are less experienced in the killing process the *coup de grace* may not be as cleanly administered as described here, the implication of a slow and agonizing death by disembowelling may be a misrepresentation of the events. Observations in other areas may one-day indicate whether the efficient killing method described here occurs within jackal populations elsewhere in Africa.

While the throat bite does not result in the death of the animal, it does facilitate administration of the killing method. Another effect of the throat bite is likely to be inhibition of vocalization by the prey. Antelope being killed by predators emit a distinctive, loud moan which can be heard over a considerable distance. The response of lions, hyaenas, and even leopards upon hearing the sound is to run rapidly towards its source (Bearder 1977, pers. obs.), and in the case of lions and hyaenas this could result in the loss of the carcase to these larger predators, as reported by Kruuk (1972) and Lamprecht (1978a). Of the two impala killed within earshot, one emitted a single loud bleat, and the other was killed with only a slight rustling sound. The results of the study are thus inconclusive regarding the effectivity or otherwise of the throat bite in silencing the prey during the kill. However, it would be of distinct advantage to the jackals to prevent the prey's death rattle which would undoubtedly attract larger predators within earshot. The hypothesis that the immobilizing throat bite may also serve to silence the prey awaits confirmation from other studies.

Total consumption

A distinctive feature of the jackal predation is that the large group of jackals present results in the consumption of every edible part of the prey. If undisturbed, the only remains of the impala are the contents of the rumen/reticulum, some intestinal contents, and the skeleton. The skeleton is picked clean to such an extent that each individual vertebra and rib is visible. However, apart from the removal of the unattached forelegs, the skeleton remains intact and, if encountered when fresh, can be fully articulated as the ligaments remain associated with the joints. The intactness of the skeleton is a distinctive feature of a jackal kill - i.e. compared to a lion or hyaena kill where bones are crushed and the skeleton dismembered. Another distinctive feature is that the ribs are not damaged, cf. cheetah which may chew the ribs considerably (Brain 1981, pers obs.).

As jackals are disturbed by the presence of a human observer and spotlights (as also reported by Lamprecht (1978a)), one kill (27/4/87, Table 3) was observed for short periods at regular intervals to determine the rate of consumption:

Time of kill 21h04.

By 21h34 - hindquarters, lower spinal muscles and all viscera consumed.

By 22h00 - Shoulder muscles consumed and ribcage exposed.

By 23h00 - Only muscle tissue remaining is on first four neck vertebrae. Forelimbs separated from rest of body, clean. Approximately half of body skin remains.

By 23h30 - Skeleton, small scraps of skin, and forestomach contents are all that remain.

Feeding by jackals on a fresh kill was noted to be extremely rapid, in contrast to more leisurely feeding when scavenging. This was also noted by Lamprecht (1978a).

The mean mass of female impala collected during the baseline data collection (Chapter 4, Section 1) was 43,5 kg. Only the skeleton and the contents of the rumen remain when jackals are finished with a kill, as noted above. Viscera constitute approximately 20% of the body mass of impala (van Zyl, von La Chevallerie & Skinner 1969), approximately half of which consists of the rumen contents (pers. obs.). If the skeleton constitutes 15% of the carcase mass (from Buttock bone %, [Monro 1979:100], von La Chevallerie pers. comm.), then jackals obtain approximately 32,6 kg of food from an adult female impala. In the case above, as 12 jackals were present, each jackal potentially obtained 2,7 kg of high quality food from the impala kill - none of which would have been available without the co-operative hunting effort. Jackals, like many other canids, are known to be able to consume large quantities of food in a short time (Kleiman & Eisenberg 1973, Lamprecht 1978b), and are adept at caching surplus food for later use (MacDonald 1976). Thus, whether consumed immediately or later, involvement by a group of 12 jackals in an impala kill provides each individual jackal with a substantial meal equivalent to 35 to 45% of its own bodyweight, or to approximately 38 000 harvester termites *Hodotermes mossambicus* (71 mg/worker [van der Westhuizen, Hewitt & van der Linde 1985]), the main alternative food source during winter (see below). Furthermore, as 12 was the largest group recorded at an impala kill, this is a minimum estimate of the direct advantage of co-operative hunting of impala by the jackals in the NTGR.

Silence and wariness

With the exception of the low "wuffing" sound sometimes heard during harassment, and occasional bickering and yelping at the carcase, there is no vocalization by the jackals at the site of the kill. On thirteen occasions loud calls by jackals heard in the vicinity, but not at the kill, were not answered by jackals at the kill. This is in contrast to the usual response elicited in jackals by the calls of conspecifics (pers. obs.).

Jackals on an impala kill were observed to be highly excited and nervous, and were less approachable than usual, as reported by Lamprecht (1978a). After a short feeding session, individual jackals would run at a fast trot in the vicinity of the carcase before returning to feed. Feeding was interrupted by frequent pauses during which jackals would look around with an alert expression. On some of the excursions away from the carcase pieces of meat were carried off and buried as is typical of the caching behaviour of jackals (Wyman 1967, Kruuk 1972).

Group size

Group sizes of jackals at impala kills were significantly larger than observed during random observations i.e. 7,9±2,5, n=9 cf. 1.6±0.7, n=489 (t=22,5, p<0,001, d.f.=496). As observed group size during the chasing/testing phase was 1,3±0,5, n=7, the larger group accumulated during harassment and after the kill. Jackals were observed to join in during the harassment phase as well as during the feeding phase. On all occasions, the newcomers were accepted at the feeding site, and no agressive interactions were observed, nor were any signs of overt submissive behaviour by the newcomers apparent.

The method whereby group size increased between selection and the kill was never unequivocally determined by the present study. Two alternative hypotheses were, however, formulated:

1. As reported above, on one occasion when two jackals were seen chasing a herd of impala, one of the jackals emitted a call similar to the mobbing call heard when large predators are encountered (Bearder 1975, Goss 1986, pers. obs.). On the six other occasions when jackals were observed chasing impala no vocalizations were heard. A call of the type heard may be used to congregate a group of jackals once a potential prey animal has been located by one or two foraging jackals. In the case described, no additional jackals were observed to arrive, and the initiators did not continue with the hunt.

2. The process of harassment and feeding are accompanied by the "wuffing" vocalization mentioned above. The former is also accompanied by noises made by the impala in backing into a bush and fending off attacks. Feeding is also accompanied by the sounds of bickering and feeding. The sounds of these activities were audible to the human ear for up to 100 m on a still night. Jackals are very aware of any hunting or feeding activity (as evidenced by incidents recorded by Eaton 1969, Pienaar 1969, van Lawick-Goodall 1970a, Sleicher 1973, Hiscocks & Perrin 1987). Any jackals in the vicinity could thus be attracted to a hunt in progress, and would thus swell the size of the group.

If indeed the latter is the means whereby group size is increased, this may account for the observed trotting behaviour (see Activity below). The seasonal increase in home range size is largely due to excursions (see Home Range and Movement Patterns below) from the core area in the form of extensive trotting along established paths and roads. Many of these excursions were not observed to result in any feeding activity. On some of these excursions jackal no. 11 was observed to sleep before returning to his core-area i.e. he rested in an area occupied by another jackal pair. However, on five occasions, study jackals were located while participating in impala kills far outside their core area - Figs 4 and 5. In covering the vast distances at a fast trot, the jackals are without doubt exposed to a far greater possibility of encountering an impala kill in progress than if they remained within their own core area, or moved at a walk through adjacent territories. The fact that fast-trotting is only observed at the time of the year when the jackals hunt adult impala indicates that the phenomena may somehow be related.

Whilst highly speculative, the latter is felt to be the most likely explanation for the aggregation of a large group of jackals at a kill following initial selection and cornering by one or two jackals.

Seasonality

Extensive rains in February 1988 resulted in a green flush of vegetation throughout the study area which was apparent until late April. In contrast, the poor rains of 1986/1987 resulted in little greenery being seen after March.

Over the two years studied, the onset of predation was clearly linked to the rainfall and veld condition: Despite 118 jackal-nights of intensive

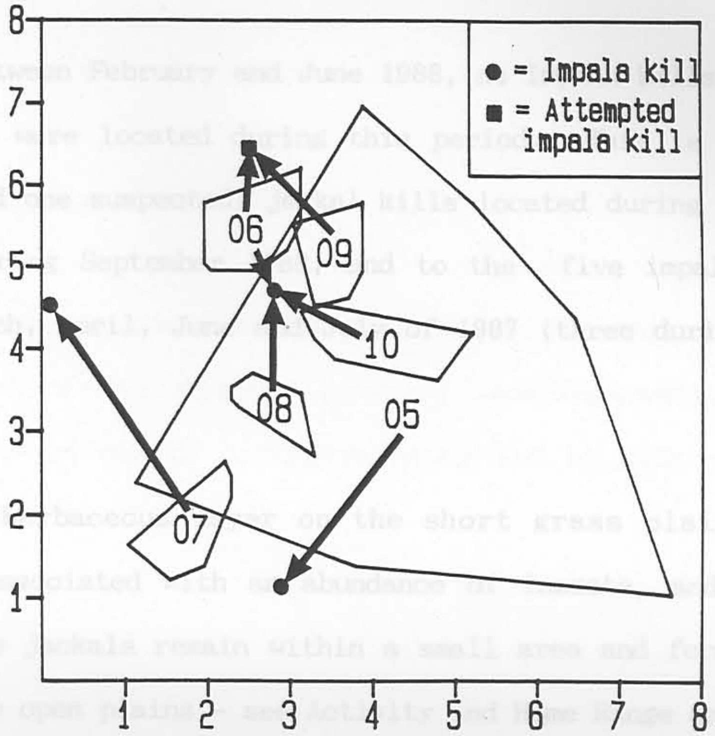

Figure 4. Location of jackals on impala kills relative to their 95% home ranges: 1987.

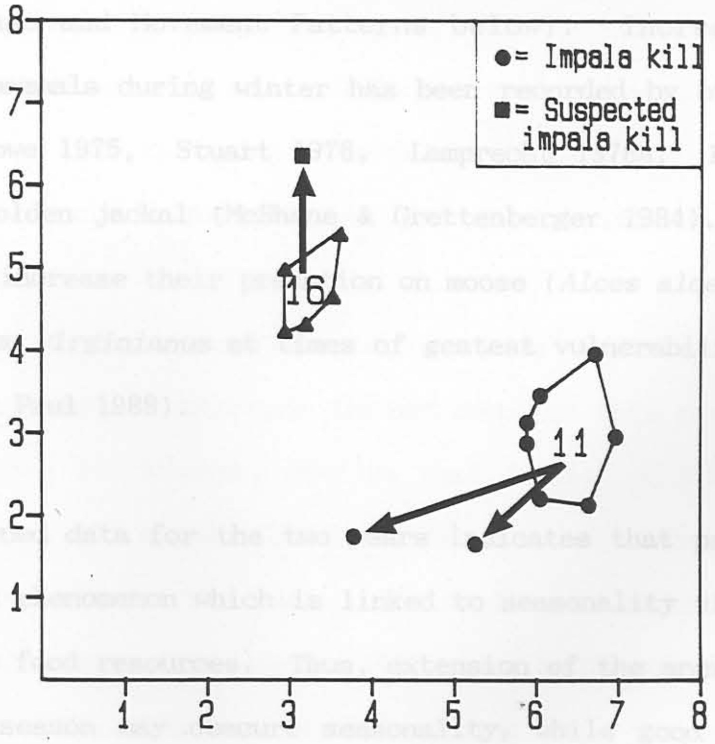

Figure 5. Location of jackals on impala kills relative to their March seasonal home ranges: 1988.

monitoring between February and June 1988, no impala kills, or even suspected impala kills, were located during this period. This is in contrast to two confirmed (and one suspected) jackal kills located during 24 jackal-nights of monitoring during September 1988, and to the five impala kills located in February, March, April, June and July of 1987 (three during 44 jackal-nights monitored).

A green herbaceous layer on the short grass plains following good rainfall is associated with an abundance of insects, and during periods of such abundance jackals remain within a small area and forage extensively for insects on the open plains - see Activity and Home Range and Movement Patterns below. Dessication of the herbaceous layer after summer is accompanied by increased foraging by jackals in the greener valley areas (See Habitat Use below). As winter progresses, jackals forage over a wider area, and eventually commence extensive excursions far outside their core activity areas (see Home Range and Movement Patterns below). Increased predation on medium/large mammals during winter has been recorded by other authors (Wyman 1967, Rowe-Rowe 1975, Stuart 1976, Lamprecht 1978a, Rowe-Rowe 1983) and also in the golden jackal (McShane & Grettenberger 1984). Wolves have also been shown to increase their predation on moose (*Alces alces*) and white-tailed deer *Odocoileus virginianus* at times of geatest vulnerability (Peterson 1977, Mech, Fritts & Paul 1988).

The combined data for the two years indicates that predation by jackals on impala is a phenomenon which is linked to seasonality via the availability of alternative food resources. Thus, extension of the annual drought through a poor rainy season may obscure seasonality, while good rains, such as in February 1988, may confine adult impala predation to the later part of the hot dry season, as was recorded by the latter part of the present study.

Other prey/food items

Quantifiable observations on utilization of other prey items did not constitute part of the study. However, some observations were made both during the two periods of intensive study and at other times. These are recorded here.

Mammalia

Impala < 6 months old Jackals were found feeding on young impala on seven occasions. Similar observations were reported by numerous other people from various parts of the Reserve. All of the occasions witnessed and reported were in December, January and February. In addition, jackals were seen actively chasing impala lambs on four occasions. On all of these occasions two jackals were involved in the chase, and on all occasions the participants were lost to sight. The latest of these incidents was in March 1988, when a particularly young impala lamb was the intended prey.

As neither of the intensive study periods coincided with the impala breeding season, the present study did not document this phenomenon in detail. These observations do, however, confirm that jackals do hunt impala lambs in the NTGR, and it would appear that the hunting is concentrated at the time of greatest vulnerability of the lambs. The ability of jackals to capture young antelope is well documented (Wyman 1967, van Lawick-Goodall 1970a, Kruuk 1972, Lamprecht 1978a, Ferguson 1980, Rowe-Rowe 1983, Stander 1987) and it is highly likely that impala lambs are an important component of the diet of jackals in the NTGR between December and February.

As pairs of jackals are considerably more successful than single jackals in hunting young antelope (Wyman 1967, Lamprecht 1978), and as group hunting is demonstrably well developed in the NTGR population (the present study), predation by jackals on young impala in the Reserve is likely to be of considerable importance in the population dynamics of the two species.

Scrub hare *Lepus saxatilis* A single jackal was found with the remains of a recently killed scrub hare in April 1987.

Small-spotted genet *Genetta genetta* Two jackals were seen attempting to capture a small-spotted genet, which escaped into a tree.

Warthog *Phacocoerus aethiopicus* In December 1987 a group of four jackals were seen harassing a female warthog with three piglets. Unfortunately the participants were surprised by the sudden appearance of my vehicle, and the interaction was disrupted. The jackals were highly excited, and the piglets were separated from the mother in their attempts to escape. Unless a suitable hole was nearby it was apparent that this attempt could have been successful if it had not been disturbed. This incident was seen during the day in the northern parts of the Reserve near Kgwedi camp (see map).

Carrion

Jackals were seen scavenging from carcases on many occasions both during the periods of study and at other times. Sources of carrion recorded in the study included: four elephants (two died of wounds inflicted by poachers, one was euthanased, and the other was shot by a landowner), one zebra (lion kill), one wildebeest (wounded by poachers, later died), two kudu (one died of old age, one lion kill), one waterbuck (victim of intraspecific agression), four impala (cheetah kills) and one impala lamb (abortus).

In February 1988 a group of six jackals were observed investigating a cheetah on an impala kill. After approximately half-an-hour, all of the jackals left the site of the kill. One of the jackals, no.11, was followed and was seen to forage for insects for several hours without returning to the site of the kill. This jackal was found with remains from the kill the next day, but the abundance of insects appeared to make scavenging a secondary activity even in the presence of such a large source of food.

Aves

Jackals were seen to snap at birds flushed from vegetation on three occasions. None of these were successful.

Reptilia

Jackal no. 5 was seen eating geckos *Pachydactylus bibroni* on three occasions. In all instances the geckos were extricated from the bases of dense bushes with considerable difficulty. On one occasion four jackals were observed unsuccessfully attempting to catch a large brown house snake *Boaedon fuliginosus*. The snake escaped into a rodent burrow.

Invertebrata

Insects Jackals were seen to consume a wide variety of insects including caterpillars, moths, ground crickets (*Hetrodes sp*, Orthoptera:Tettigonidae)(*koringkrieks*), grasshoppers, beetles, flies and maggots. After the heavy rains in February 1988 the green vegetation supported a wide variety of insects in large numbers. Jackals were seen consuming vast numbers of insects within short periods of time, as described by Lamprecht (1978a), and these observations were reflected in the predominance of insect remains in faeces observed at this time of the year (see below). Jackals were also often seen scratching open elephant dung piles and feeding on insects located within and underneath the dung.

Jackals were only observed to consume termites in winter, although faecal analysis demonstrated termites in the diet in April. On the occasions when termites were confirmed to be the source of food, inspection of the foraging site showed many harvester termites *Hodotermes mossambicus* (Isoptera:Hodotermitidae) active on the soil surface. Termites were typically fed upon in open spaces during foraging bouts which were interspersed with the wide movements typically observed in winter (see Movement Patterns and Home range below). Jackals were observed to simply lick termites off the ground while moving slowly in a zig-zag fashion. Bothma (1971) recorded 1250 termites from the stomach of a single jackal. From observations and faecal analysis (below), it is apparent that termites constitute an important part of the jackal's diet in the NTGR in winter.

Arachnida Jackals were seen successfully capturing large solifuges (Solifugae) on six occasions. Hunting invariably involved rapid movement to match the agility of the prey. On one occasion a solifuge took refuge in a hollow stick. The jackal systematically broke the stick apart with its teeth to expose the solifuge. After eight minutes of gnawing and pawing the solifuge was left to fight another day.

Coprophagia

Two jackals were seen consuming fresh baboon droppings. This behaviour was accompanied with much excitement. Only parts of the faeces were consumed.

Faecal Analysis

A total of 106 complete jackal faeces were collected and analysed. Results of the analyses are presented in Table 4.

Examinations of the diet of black-backed jackals have revealed that a wide array of food items, both of animal and vegetable origin, are utilized by this species (Grafton 1965, Bothma 1966, Bothma 1971, Smithers 1971, Rowe-Rowe 1976, 1983, Stuart 1976, Stuart & Shaugnessy 1984, Avery, Avery, Braine & Loutit 1987, Hiscocks & Perrin 1987). The conclusion reached through these various studies is that the jackal is an opportunistic feeder, making use of whatever food resource is most readily available. Large carcases are an example of a readily utilizeable source of food, and this no doubt gave rise to the early reputation of the jackal as a lowly scavenger. Utilization of carrion is, however, merely one example of the ability of the jackal to vary its diet both spatially and temporally in response to availability. The results of the analysis of the total faecal sample therefore constitute a

Table 4. Total occurrence and relative percent occurrence of remains in jackal faeces, 1988.

	April		May		June		Sept.		Total	
Mammalia	10	24	16	24	25	42	27	44	78	34
Rodentia	7	17	11	16	12	20	13	21	43	19
Impala	1	2	4	6	10	17	13	21	28	12
Scrub hare	-	-	-	-	1	2	-	-	1	.4
Unidentified	2	5	1	2	2	3	1	2	6	3
Aves	2	5	3	5	-	-	9	15	14	6
Reptilia	-		2	3	-	-	-	-	2	1
Invertebrata	26	63	45	67	35	58	26	42	132	57
Insects	26	63	30	45	32	53	21	34	109	47
Isoptera	2	5	8	12	11	18	15	24	73	32
Other insects	23	59	22	33	21	35	6	10	36	
Arachnids	-	-	15	22	3	5	5	8	23	10
Scorpiones	-	-	-	-	3	5	-	-	3	1
Solifugae	-	-	15	22	-	-	5	8	20	9
Fruit	3	7	1	2	-	-	-	-	4	2
Grass (non food)	24		18		24		30		96	
Leaves (non food)	1		-		3		-		4	
No. of scats	23		24		26		33		106	

First column: Total occurrence in sample.
Second column: Relative percent occurrence (percent of all food item occurrences).

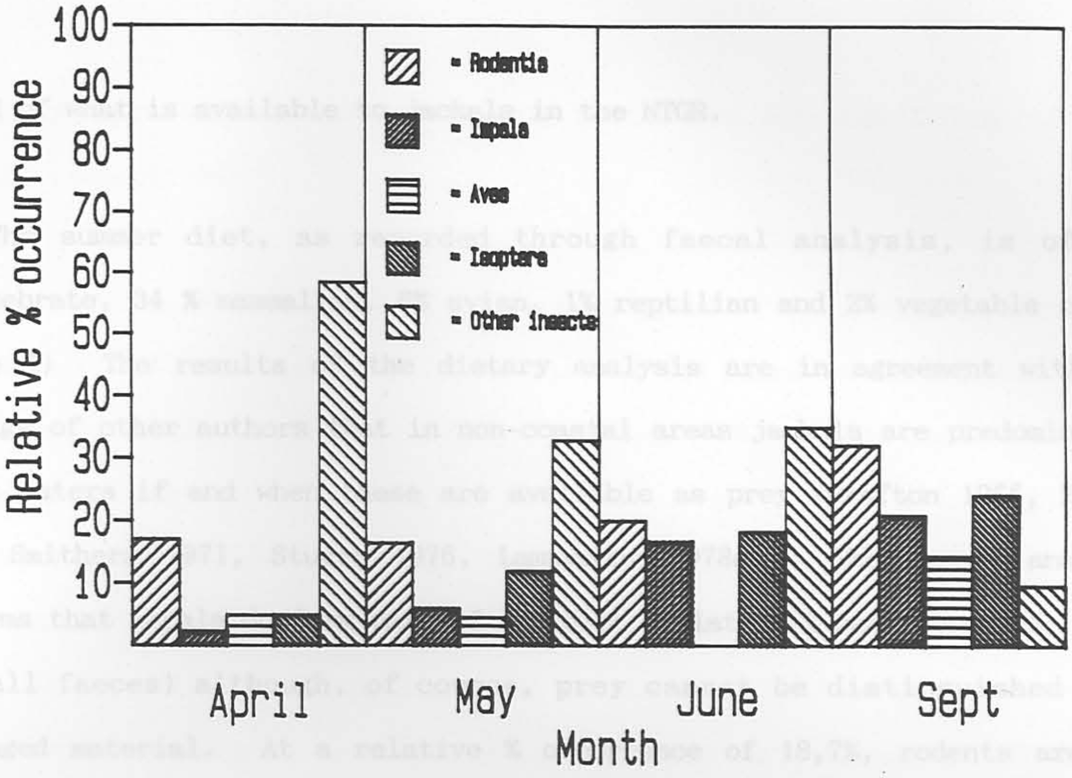

Figure 6. Relative percent occurrence of animal remains in jackal faeces: April - September 1988.

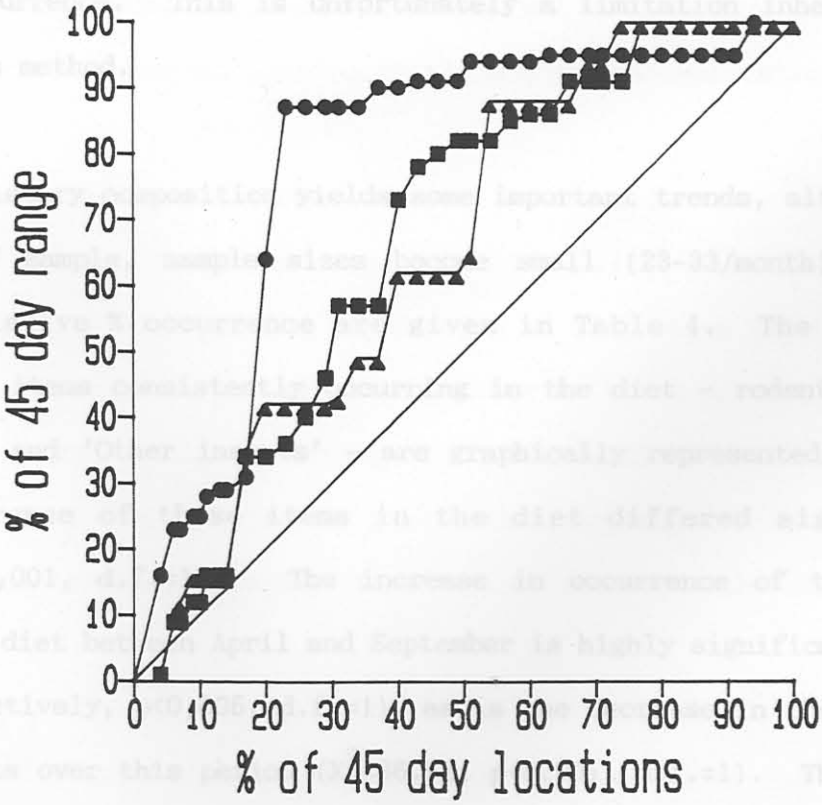

Figure 7. Relationship between the number of locations and home range size: first 45 days, 1988.

record of what is available to jackals in the NTGR.

The summer diet, as recorded through faecal analysis, is of 57% invertebrate, 34 % mammalian, 6% avian, 1% reptilian and 2% vegetable origin (Table 4) The results of the dietary analysis are in agreement with the findings of other authors that in non-coastal areas jackals are predominantly insect eaters if and when these are available as prey (Grafton 1965, Bothma 1971, Smithers 1971, Stuart 1976, Lamprecht 1978a). The faecal analysis confirms that impala do form part of the diet (relative % occurrence 12, or 26 % of all faeces) although, of course, prey cannot be distinguished from scavenged material. At a relative % occurrence of 18,7%, rodents are the mammals most commonly represented in faecal remains. If, however, the size of a meal composed of impala, whether scavenged or killed, is considered in relation to a meal of rodents or insects, the occurrence of impala in the diet represents a source of food of greater importance than is indicated by the relative % occurrence. This is unfortunately a limitation inherent in the faecal analysis method.

Monthly dietary composition yields some important trends, although in so separating the sample, sample sizes become small (23-33/month). Monthly totals and relative % occurrence are given in Table 4. The relative % occurrences of items consistently occurring in the diet - rodentia, impala, Aves, Isoptera and 'Other insects' - are graphically represented in Fig. 6. Monthly occurrence of these items in the diet differed significantly (X^2=81,69, p<0,001, d.f.=12). The increase in occurrence of termites and impala in the diet between April and September is highly significant (X^2=9,15 and 9,31 respectively, p<0,005, d.f.=1), as is the decrease in the occurrence of other insects over this period (X^2=36,62, p<0,001, d.f.=1). The increases in rodents and bird remains during this period are not significant (X^2=0,64 and 3,20 respectively).

The results of this seasonal comparison agree with the reported increase in importance of mammalian prey in the diet of the jackal during winter (Wyman 1967, Stuart 1976, Lamprecht 1978a, Rowe-Rowe 1983). In particular, the increased proportion of impala in the diet (to 40% of all samples in September) supports the conclusion made from direct observations during the present study that impala predation is associated with the annual winter dry season (see above). The impala present in the diet in June may be accounted for by either scavenging or unobserved hunting during this month. While the increased percentage of impala in faecal remains does not prove that jackals hunt impala more frequently, there was also no evidence to suggest that scavengeable resources accounted for this increase.

The only other medium sized mammal identified in faeces, a scrub hare, is also the only other mammalian prey recorded from direct observations.

The marginal increase in bird remains in September may indicate that utilization of birds increases concomitantly with mammals as winter progresses. Lind (1974) expressed the concern of landowners in the NTGR that jackals may prey heavily on ground-nesting birds in the Reserve. The present study does not record a high percentage of birds in the diet, but this does not mean that birds are not preyed upon - their appearance in the diet is likely to reflect their availability to the jackals as with the other items in the diet.

The seasonal decrease in abundance of insect remains in the faeces also confirms the results of direct observations (see above) and agrees with the findings of other authors (Wyman 1967, Stuart 1976, Lamprecht 1978a, Rowe-Rowe 1983). The increase in Isoptera (termites) also corroborates the observation that jackals did forage extensively for termites on the open plains during winter. This was also the only insect which was observed to occur in high numbers in the study area during the winter months.

Solifuges form a small part of the diet as reported by Grafton (1965), Smithers (1971) and Stuart (1976).

Grass was found in 89% of all faeces examined. The grass in some of the faeces was fresh, while in others it was dry. In many of the scats the grass appeared to have been derived from the dung of herbivores, as it was digested and finely ground. Jackals were often seen foraging in dung heaps, as recorded above and as reported by Lamprecht (1978a). These observations, as well as observations on foraging for other insects in vegetation, indicate that most grass is ingested accidentally, and thus does not comprise a food item as claimed by Bothma (1971).

Movement Patterns and Home Range

The objective of the present study was to determine the presence or absence of predation on impala by jackals in the NTGR. Data collected on movement patterns and home ranges were collected incidentally, and the data collection was not designed with detailed home range analysis in mind. Nevertheless, sufficient data are available to discern at least some trends in the home range and movement patterns of the jackals studied.

Table 5. Total home ranges of study jackals for which sufficient locations were obtained.

Age* group	ID no	Sex	Total range (sq.km.)**	Monitored From	To	Method ***	Locations
2	5	M	32,7	11/04/87	05/07/87	DIR	119
2	18	M	51,0	27/04/88	15/06/88	TEL	282
3	11	M	9,7	01/03/88	19/09/88	DIR	269
3	16	M	11,0	01/03/88	19/09/88	DIR	258
3	17	M	10,4	01/03/88	19/09/88	DIR	262
3	19	F	12,7	27/04/88	15/06/88	TEL	402

* According to Ferguson *et al.* (1983).
** Minimum convex polygon (Mohr 1947).
*** DIR = Direct observations. TEL = Telemetry.

Total Home Range

Subject to the requirement of Bowen (1982) of a minimum of 42 locations over a minimum period of 45 days, total home ranges could be determined for five of the jackals studied. These data are presented in Table 5. Note that jackal no.5 in 1987 is the same as jackal no.11 in 1988 - changing from an age Group II jackal in 1987 to a mated age Group III jackal in 1988 which is accompanied by a reduction in range size from 32,7 to 9,7 km^2. Roy & Dorrance (1985) recorded a similar reduction in home range of a male coyote from 34,0 to 6,4 km^2 upon attaining breeding status. The larger home ranges of the Group II jackals from the present study conforms to the results obtained by

Rowe-Rowe (1982) and Ferguson *et al.* (1983). While the sample size is small, the absolute size of the group II ranges (32 & 51 km^2) from the present study are closer to the values of 33 and 32,8 km^2 obtained by Rowe-Rowe than to the mean value of 85,2 km^2 obtained by Ferguson *et al.*(1983).

The size of the home ranges of the Group III jackals are approximately half of the mean of 20 km^2 obtained by Rowe-Rowe. The 95% ranges are similar to the 4,2 km^2 obtained for Group III jackals in the Kalahari Gemsbok National Park by Ferguson *et al.* (1983). While home range size of carnivores may to some extent be determined by metabolic needs and diet (Gittleman & Harvey 1982), the dispersion and abundance of resources may be expected to determine the absolute home range sizes observed within these constraints (MacDonald 1983). As speculated by Ferguson *et al.* (1983) regarding the Kalahari jackals, the small total home ranges recorded in the present study probably can be ascribed to an abundance of available food greater than in the Natal montane regions studied by Rowe-Rowe, and the Transvaal regions studied by Ferguson *et al.* This is discussed further in Chapter 7.

In the study by Hiscocks & Perrin (1988), the presence of a super-abundant food resource in the form of a seal colony probably accounts for the extremely high density of jackals recorded - 22 km^{-2}. However, under these conditions of super-abundance, the mean adult home range was found to be 27,4 km^2 (n=3). The authors concluded that "Habitat structure and prey distribution are therefore not necessarily parameters affecting home range size." (p99). However, the authors also recorded nightly fog and the use of hummocks and hills by the jackals for shelter. Without further evidence I suggest that the above conclusion is unjustified: the spatial distribution of sheltered habitat on this exposed coastline is likely to account for the relatively large home ranges in the presence of a super-abundant food resource. For example, golden jackals, in the presence of a super-abundant food source, have been recorded to remain within an area of 0,11 km^2 (MacDonald 1979).

The mean total home range of 1,8 km^2 (n=6) reported from Kenya by Fuller *et al.* (1989) is not directly comparable with the results of the present study. First, outlying points were discarded, second, only one month (June - after peak rainfall) was considered, and third, the mean number of locations used for the home range determinations was 21.

Seasonal Home Range

To date, none of the studies on jackal home ranges have addressed the possibility that home ranges may change seasonally (Rowe-Rowe 1982, Ferguson *et al.* 1983, Hiscocks & Perrin 1988, Fuller *et al.* 1989). Fortunately, sufficient data are available to compare the home ranges of the three adult jackals studied during 1988 on a monthly basis. The sizes of the respective ranges for the months of March, April, May, June and September are presented in Table 6. As can be seen from the Table, home range sizes increase steadily from March to June. The values for September must be regarded as minimum values, as the data were collected over only a 14 day period. If expressed as a percentage of the total home range, or of the September home range, Table 7, the seasonal increase is readily apparent.

Because of the study methods used, locations were only recorded every 4 - 5 h during the night. Many more observations could have been made, but it was readily apparent in March that the jackals were moving over very small areas while foraging for insects. Thus it is felt that the 48-52 observations used to obtain the initial ranges provide a true reflection of the jackal's ranges at that time. The increasing range with the seasonal changes results in a situation wherein a true asymptote (Bowen 1982) is not reached during the course of the study except in the case of jackal no. 11. However, a reasonable levelling off is achieved after 45 days (approximately 70 locations per animal) as shown in Fig. 7. Thus, the monthly increases in home range shown in Table 6 reflect a true increase in home range from summer to winter in all three of the jackals studied.

The small absolute size of the March and April home ranges in all the jackals is worthy of note.

The coyote is known to increase its home range during winter (Andelt & Gipson 1979, Laundré & Keller 1981, Bowen 1982, Springer 1982, Roy & Dorrance 1985, Parker & Maxwell 1989). For the coyote, this time of year co-incides with the breeding season as well as with changes in food availability - as it does in the case of the jackal in southern Africa. The reason for the increased winter home range could thus be related to food procurement or to the seeking of extra-pair copulations as postulated for the coyote (Laundré & Keller 1981). As all three animals in the present study were males, no comparison can be drawn between the sexes, and no unequivocal conclusion can be drawn in this regard. However, Gittleman & Harvey (1982) suggest that 10-fold increases in carnivore home range can be accounted for by changes in diet.

Feeding observations indicated that the very small ranges recorded in March, after the February rains, were linked to an abundace of insects which

Table 6. Monthly and total home range sizes, 1988.

Jackal no	Month March	 April	 May	 June	 Sept	 Total	 Total (95%)*
11	1,4 (48)	1,2 (42)	1,4 (40)	6,4 (77)	5,8 (40)	9,7 (247)	4,8 (234)
16	0,5 (53)	0,7 (46)	2,4 (34)	5,6 (83)	6,8 (42)	11,0 (258)	2,1 (245)
17	1,0 (49)	1,3 (45)	1,4 (40)	3,7 (87)	9,5 (41)	10,4 (262)	2,8 (248)

All areas in sq. km. Number of locations in parentheses.
All areas calculated by minimum convex polygon method (Mohr 1947).
* Derived by removing each point which contributes most to area until 95% of points remain.

Table 7. Home Range overlap.

	11T	113	114	115	116	119	16T	163	164	165	166	169	17T	173	174	175	176	179
11T																		
113	24,8																	
114	21,4	.																
115	25,2	.	.															
116	79,9	.	.	.														
119	75,3	23,7	19,9	23,7	110													
16T	9,9	.	.	.	.	.												
163	.	0	.	.	.	.	8,6											
164	.	.	0	.	.	.	11,7	.										
165	.	.	.	0	.	.	36,2	.	.									
166	.	.	.	.	0	.	67,2	.	.	.								
169	.	.	.	.	.	8,1	76,6	7,4	10,0	35,7	81,5							
17T	61,2	.	.	.	.	.	37,2	.	.	.	.	.						
173	.	0	.	.	.	.	.	0	.	.	.	.	17,9					
174	.	.	15,1	.	.	.	.	.	0	.	.	.	22,2	.				
175	.	.	.	2,2	.	.	.	.	.	0	.	.	23,3	.	.			
176	.	.	.	.	42,2	.	.	.	.	.	0	.	53,0	.	.	.		
179	.	.	.	.	.	40,1	.	.	.	.	.	46,2	95,7	10,6	13,6	14,4	39,3	

Vertical = Monthly range as % of total range.
Horizontal = Monthly range as % of September range.
Diagonal = % of range shared with other jackal.

11, 16, 17 = jackal nos. 3 = March, 4 = April, 5 = May, 6 = June, 9 = September, T = Total were relatively evenly distributed throughout the study area. The only other study which demonstrates such small ranges is that of Fuller *et al.* (1989) who obtained a minimum seasonal home range of 1,8 km^2 (n=6) in Kenya in June. Importantly, this period follows one of the periods of peak rainfall in that region (Fuller *et al.* 1989).

As discussed above, the hunting of impala necessitates movement over a wide area and, as this phenomenon is linked to the annual winter dry period, the change in feeding habits is certain to play some role in the changes in home range. This conclusion is reinforced by the observation that on most occasions when marked jackals were observed feeding on or harassing impala they were not within their core areas (Figs 4 and 5). Increases in coyote range - both male and female - is also accompanied by increased predation on deer (MacCracken & Uresk 1984, Andelt, Kie, Knowlton & Cardwell 1987, Parker & Maxwell 1989).

Moehlman (1983) reported a reduction in jackal territory sizes in Serengeti, Tanzania, between 1974 and 1976. This was ascribed to demonstrably increased prey abundance following a period of higher rainfall, and shows that jackal home range or territory size is sensitive to temporal changes in resource availability.

Whatever the underlying cause, the present study indicates that flexibility in home range size according to seasonal changes in prey type and availability may be an important aspect of jackal biology.

Centre of Activity and Core Area

Seasonal changes in home range could be related to changes in the centre of activity. However, as illustrated in Fig. 8, centres of activity did not change significantly despite the large changes in absolute range size. In all cases, centres of activity were located in open habitat on the short grass plains. Because of this faithfulness to a single core area, the centres of activity of the study jackals as well as of other jackal families active in the study area could be identified. These are shown in Fig. 9.

All adult jackals spent most of their time in a single core area at the centre of their range, with the single exception of no. 19 who appeared to have two distinct core areas. The relative utilization of core areas is illustrated in Figs 10 and 11. Unlike coyotes (Springer 1982), all jackals returned to their core areas after their nightly forays.

Overlap

A natural consequence of increasing home ranges through winter is that overlap of home ranges must increase. The three jackals studied resided in sub-adjacent home ranges, with at least one jackal family between nos 11 and 17, and and between nos 16 and 17 (Fig. 9). During the time of minimum home range, there was thus no overlap at all between the home ranges of the study animals. However, as winter advanced, overlap increased as shown in Table 7 to reach a maximum in mid to late winter in all cases. The overlap *per se* is a natural consequence of the increasing home range sizes. However, the fact that the study area was saturated with jackal family groups implies that overlap is an immediate consequence of any increase in range over and above the minimum summer range. Tolerance of other jackals within the home range is thus closely linked to increasing overlap in movements. Whether the tolerance is as a result of the inability to effectively exclude a large number of

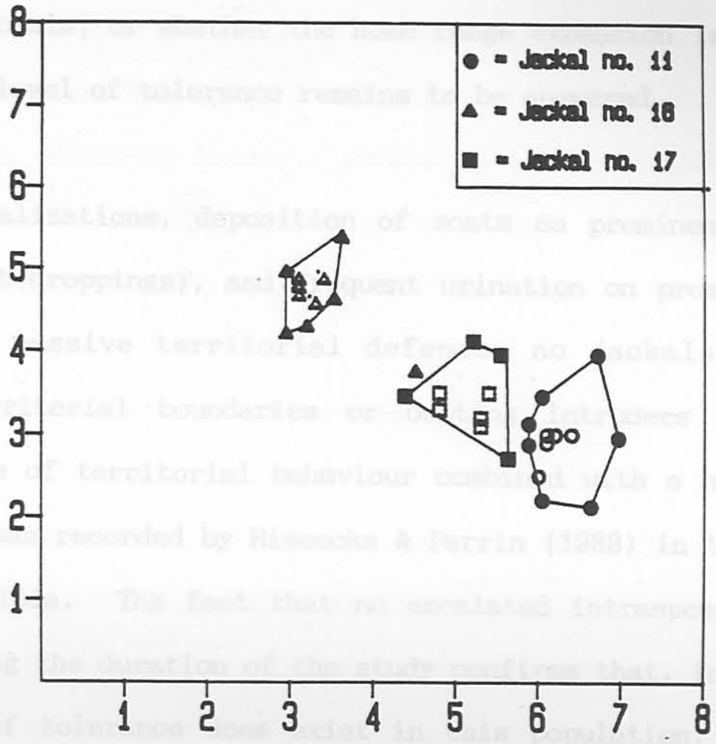

Figure 8. Monthly harmonic mean centres of activity (Dixon & Chapman 1980) relative to March seasonal home range.

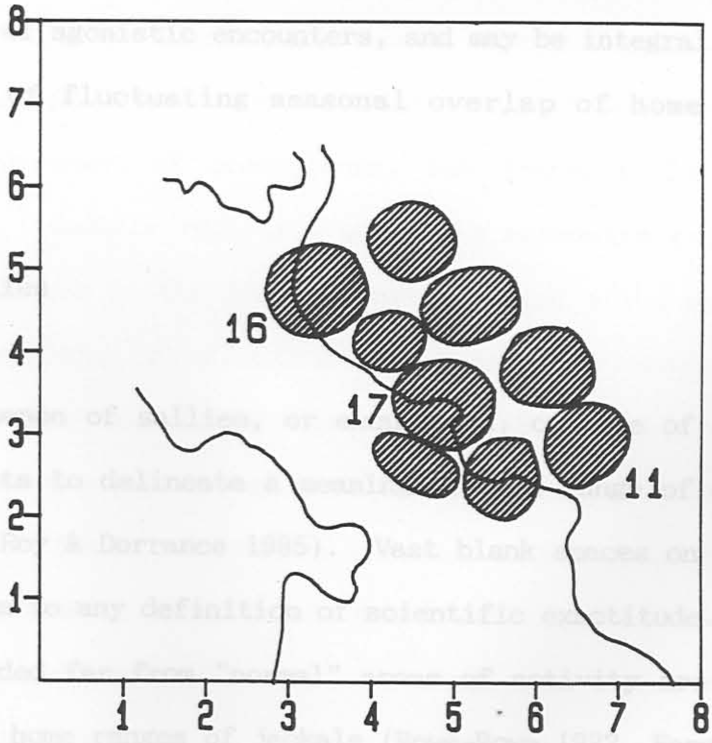

Figure 9. Jackal activity centres within study area. Sites where jackal pairs or families were regularly seen circumscribed by hand. Activity centres of nos 11, 16 and 17 indicated.

trespassing jackals, or whether the home range expansion is facilitated by an innately high level of tolerance remains to be answered.

While vocalizations, deposition of scats on prominent objects (bushes, rocks, elephant droppings), and frequent urination on prominent objects were indicative of passive territorial defence, no jackals were ever found patrolling territorial boundaries or ousting intruders during the study. Similar absence of territorial behaviour combined with a high degree of home range overlap was recorded by Hiscocks & Perrin (1988) in the Cape Cross Seal Reserve in Namibia. The fact that no escalated intraspecific agression was ever seen during the duration of the study confirms that, for whatever reason, a high level of tolerance does exist in this population. The co-operative predation recorded during the present study also reflects this high degree of mutual tolerance. As suggested by Springer (1982) for an undisturbed population of coyotes, proximity of relatives and known individuals may result in a low level of agonistic encounters, and may be integral to the maintenance of the system of fluctuating seasonal overlap of home ranges in jackal society.

Excursions/Sallies

The phenomenon of sallies, or excursions, outside of the "normal" range bedevils attempts to delineate a meaningful home range of canids (Burt 1943, Hibler 1977 in Roy & Dorrance 1985). Vast blank spaces on a map of locations does not conform to any definition of scientific exactitude. For this reason, locations recorded far from "normal" areas of activity are often excluded in calculations of home ranges of jackals (Rowe-Rowe 1982, Ferguson *et al.* 1983, Hiscocks & Perrin 1988, Fuller *et al.* 1989) and coyotes (Andelt & Gipson 1979, Bowen 1982, Roy & Dorrance 1985). Alternatively, the modified minimum area method (Harvey & Barbour 1965), which reduces the influence of outlying points, is used (Hiscocks & Perrin 1988). The methods used eliminate outlying points, or reduce their influence, until a neat group of locations remains which is then measured and is termed the home range.

As demonstrated above, the centres of activity of the three jackals remained almost unchanged between March and September. The enlarged ranges were due exclusively to sallies/excursions far from the minimum summer home range. If the 95% home range is calculated by excluding those locations which contribute most to the home range size (Ferguson 1980, Bowen 1982), resulting home ranges are 25 - 50% of the total range - Table 6.

Sequential monthly locations are plotted in Fig 10. As can be seen, the activity centres contain the highest number of locations, but the extensive sallies account for the increasingly larger winter ranges. Eliminating the 5% of the observations results in a tidier group of locations which suits the scientific requirement of orderliness, but denies a fundamental aspect of jackal biology. Jackals regularly undertake extensive excursions in winter. These excursions are in the form of fast trotting along paths and roads (see Activity below), and cover extensive areas in a short period of time. Whatever the primary reason for these forays (above), they are are a regularly observed phenomenon which should not be excluded by statistical manipulation. For this reason, total home ranges are used in the present study as opposed to 95% home ranges or some other artificial construct. Moreover, it is apparent that measurement of jackal home range size over a short period, or by using a few data points, or by lumping all data to obtain a high total number of locations does not give a true reflection of the total picture.

If indeed reduced ranges are used, the larger area should be retained as an "impact area: an area through which an animal travels and on which it impacts occasionally" (Springer 1982:196). This definition is highly suitable for the present study, with one of these impacts being predation on impala outside of the core area (Figs 4 and 5).

The progressive nature of the excursions is illustrated by the telemetric data presented in Fig. 11 a,b,c & d. Some of the zig-zagging is as a result of telemetric error, but the excursionary nature of the peripheral locations is apparent from the overall out-and-back movement pattern during excursions. These patterns are of the type defined as "ranging" movements for coyotes (Laundrė & Keller 1981).

Extensive sallies by jackals were recorded only from May onwards. The longest such excursion recorded through direct observation was by jackal no. 16, and involved a round trip of 7,1 km over 8,5 h. Jackal no. 11 was observed sleeping while out on excursions on nine occasions. However, as with the other jackals, no. 11 always returned to his core area folowing an excursion.

Mean distances moved per night should provide an indication of the increasing length of sallies through winter. However, due to the fact that only three jackals were monitored, and that continuous 24 h monitoring was not used, no comparisons can be drawn. Direct observations were spaced 3-4 h apart, and it is known from the present study, and from Ferguson *et al.* (1983), that jackals can travel several kilometres in this period. If this is of the out-and-back pattern recorded here, then part or all of the excursion could be missed. The telemetric monitoring did not reveal any significant

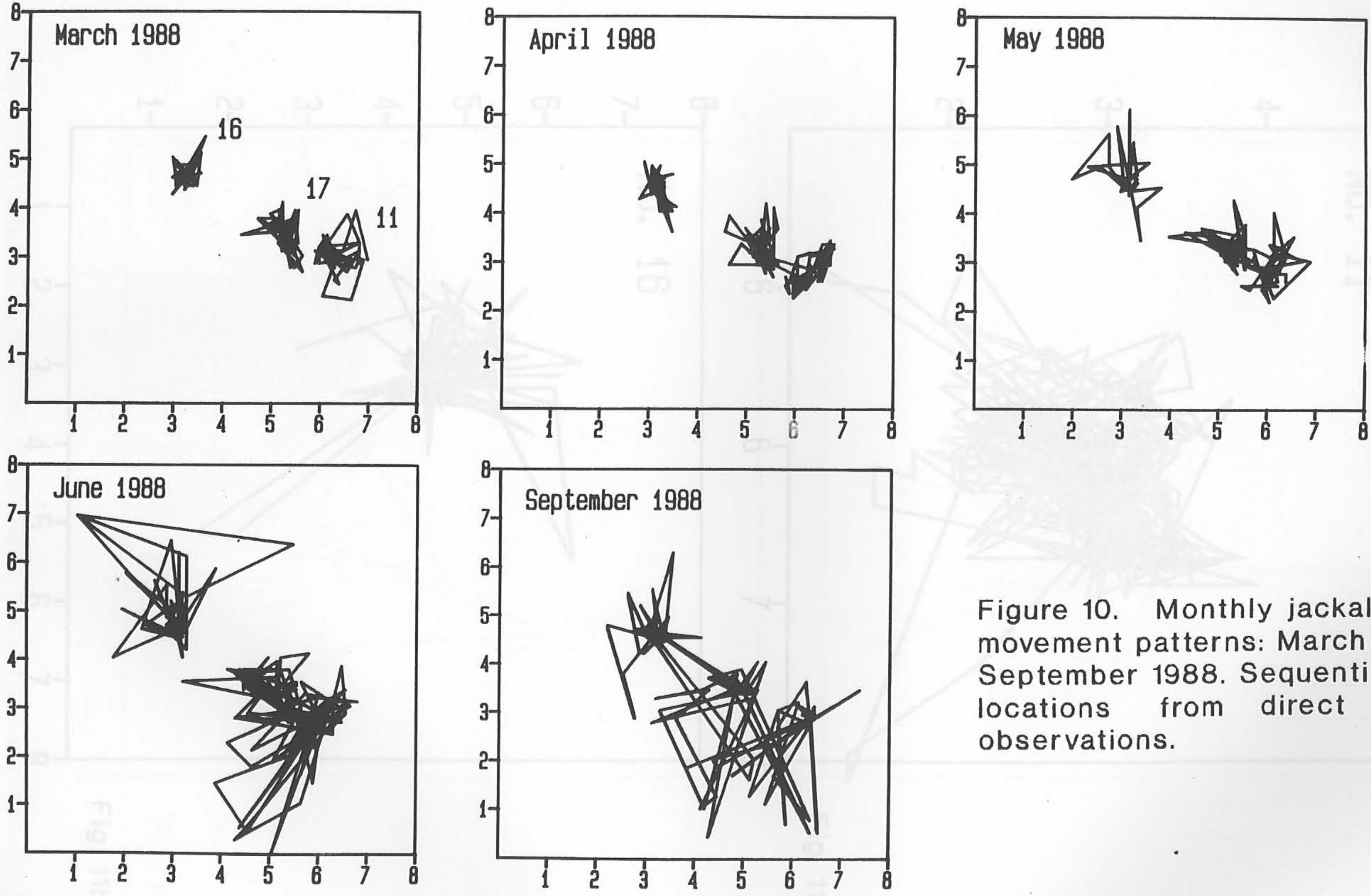

Figure 10. Monthly jackal movement patterns: March - September 1988. Sequential locations from direct observations.

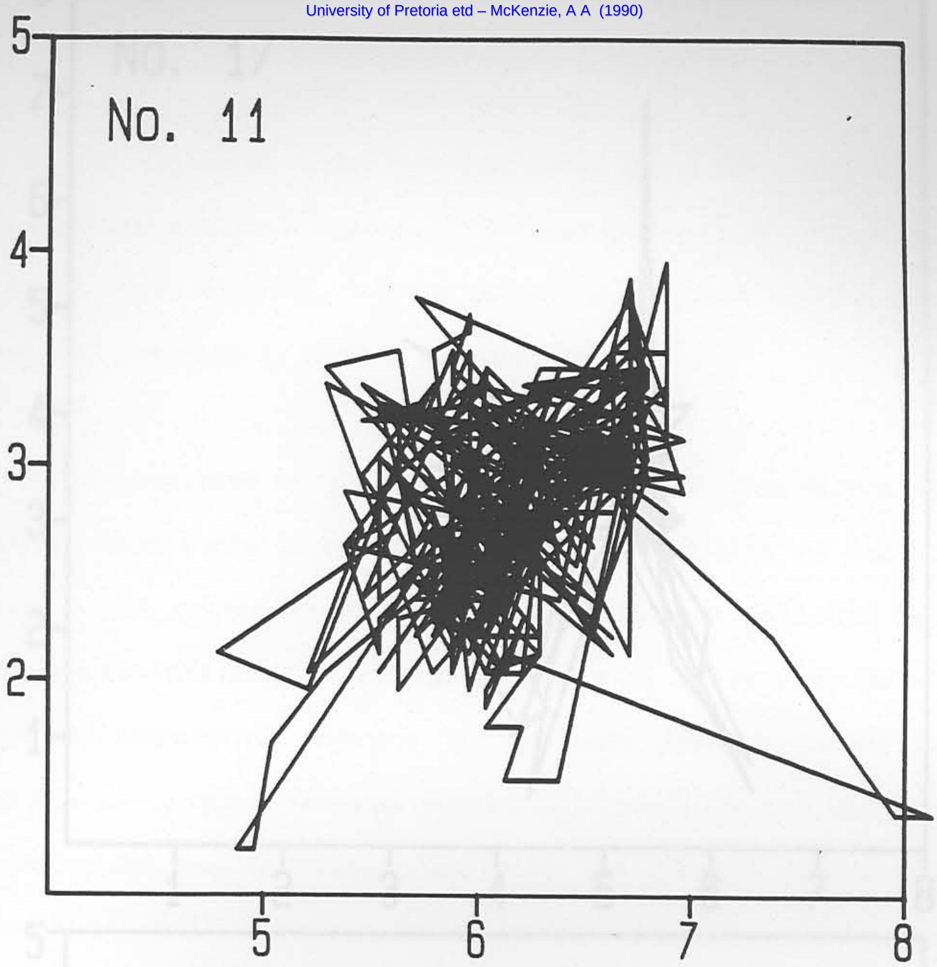

Fig. 11a

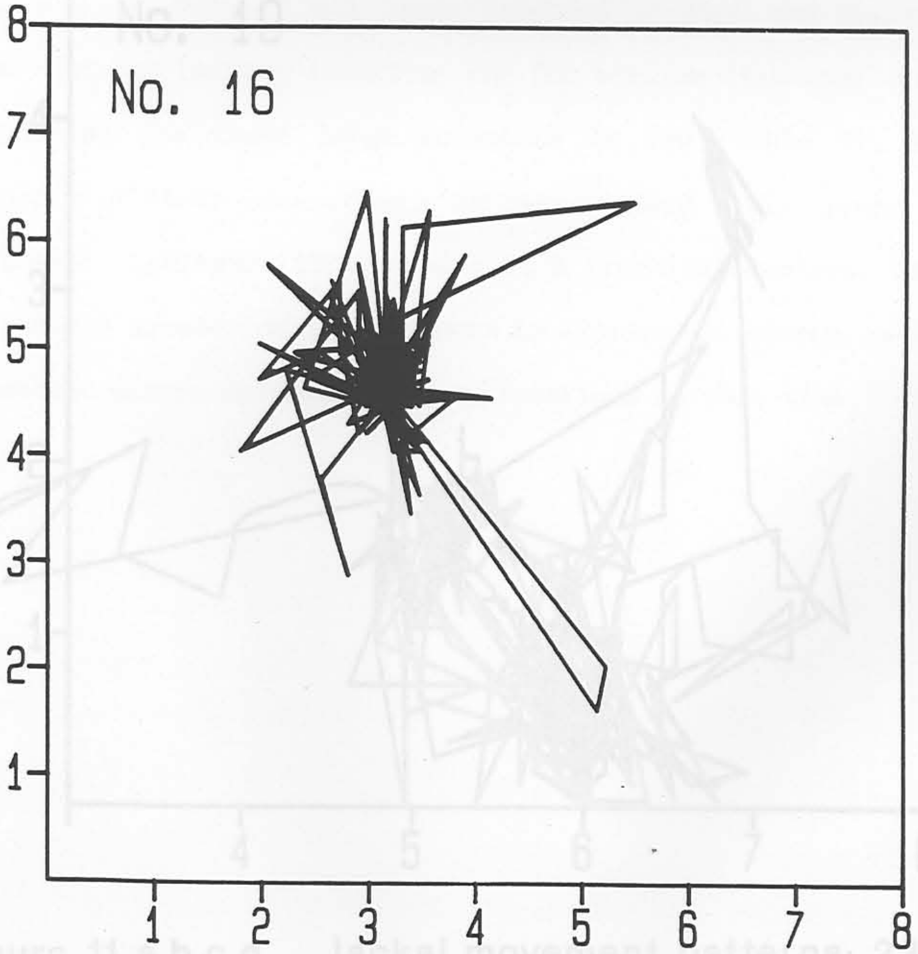

Fig. 11b

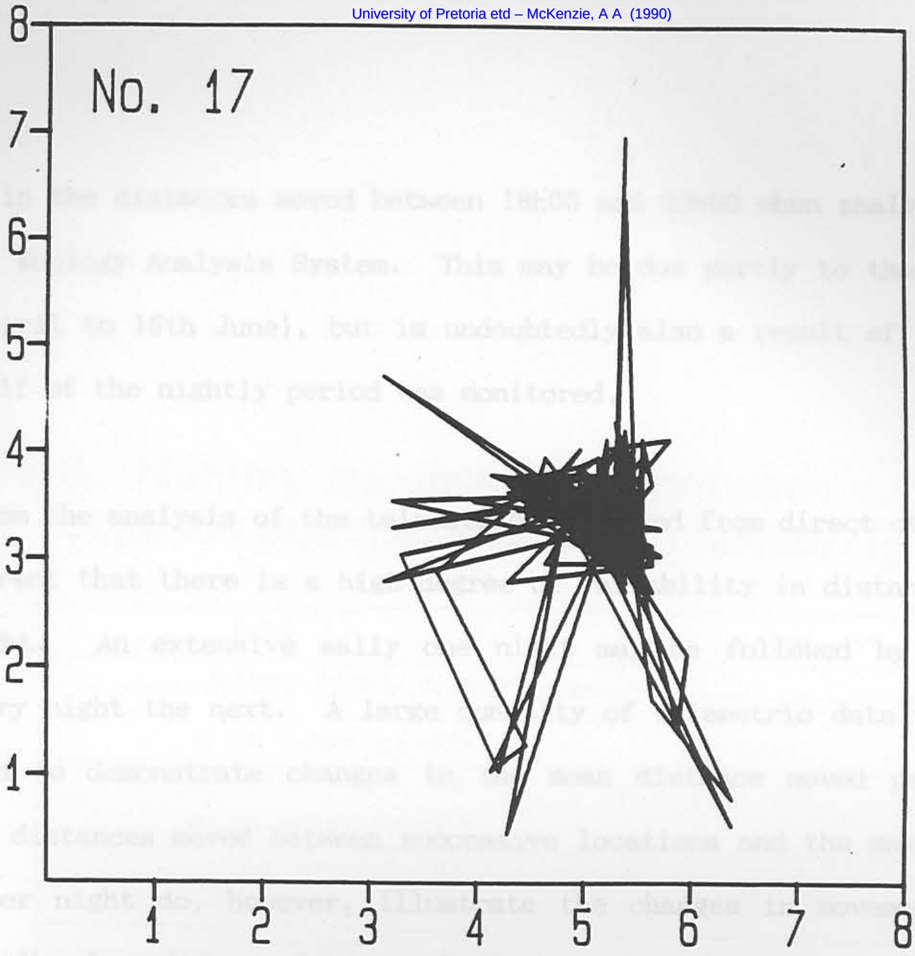

Fig. 11c

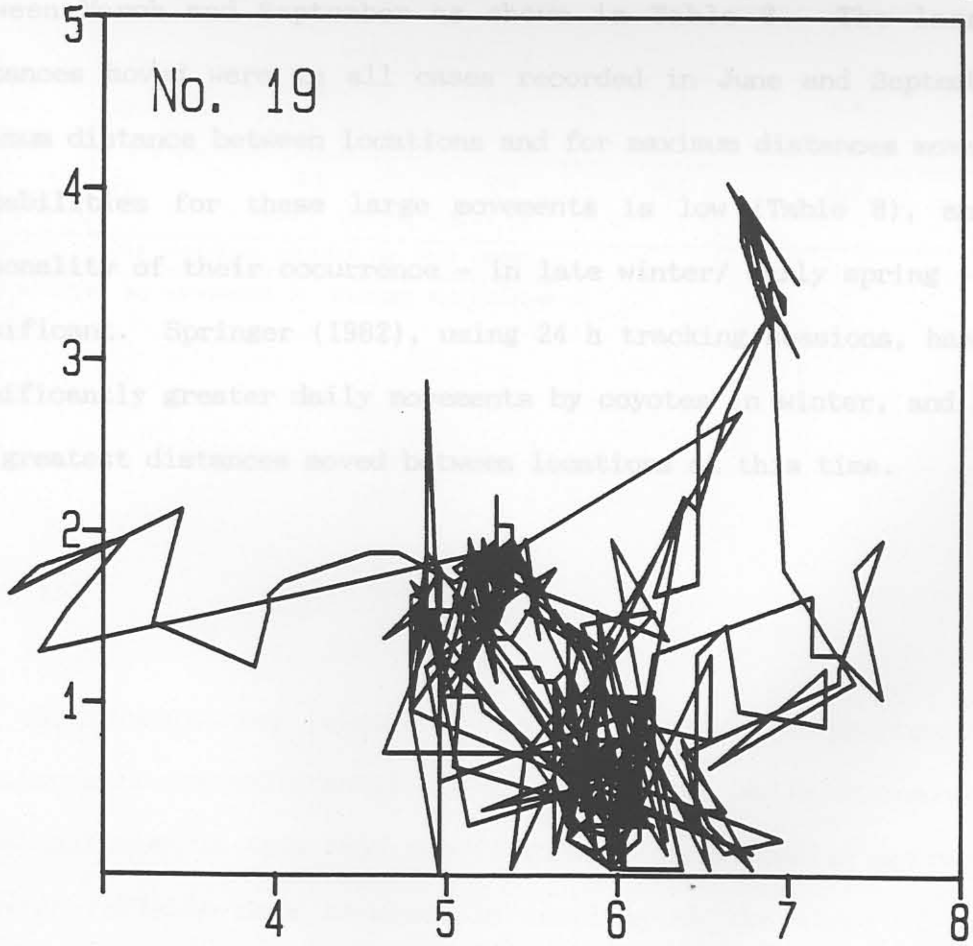

Fig. 11d

Figure 11 a,b,c,d. Jackal movement patterns: 23 April - 15 June 1988. Sequential locations, 20 min intervals, 18h00-23h00 and 06h00-08h00.

trends in the distances moved between 18h00 and 23h00 when analysed using the Spatial Ecology Analysis System. This may be due partly to the short period (23rd April to 15th June), but is undoubtedly also a result of the fact that only half of the nightly period was monitored.

From the analysis of the telemetric data, and from direct observation, it is apparent that there is a high degree of variability in distances travelled per night. An extensive sally one night may be followed by a relatively sedentary night the next. A large quantity of telemetric data would thus be required to demonstrate changes in the mean distance moved per night. The maximum distances moved between successive locations and the maximum distance moved per night do, however, illustrate the changes in movement parameters between March and September as shown in Table 8. The largest maximum distances moved were in all cases recorded in June and September, both for maximum distance between locations and for maximum distances moved/night. The probabilities for these large movements is low (Table 8), and the marked seasonality of their occurrence - in late winter/ early spring - is therefore significant. Springer (1982), using 24 h tracking sessions, has demonstrated significantly greater daily movements by coyotes in winter, and also recorded the greatest distances moved between locations at this time.

Table 8. Monthly maximum dist. between successive locations and maximum dist. moved/night.

Jackal number		March	April	May	June	Sept.
		Distance between successive locations				
	11	0,9	1,3	1,2	3,4	2,7
		n=147, x=0,66, s.d.=0,63			p=0,025	
	16	1,2	0,8	2,4	3,2	3,5
		n=135, x=0,62, s.d.=0,70				p=0,040
	17	1,1	1,1	1,8	2,0	3,3
		n=168, x=0,64, s.d.=0,60				p=0,023
		Distance moved per night.				
	11	2,0	1,5	2,3	3,8	5,4
		n=46, x=2,11, s.d.=1,42				p=0,042
	16	1,9	2,0	3,8	9,6	7,2
		n=45, x=1,84, s.d.=1,93			p=0,0001	p=0,0023
	17	2,5	2,4	2,7	3,5	5,3
		n=51, x=2,04, s.d.=1,16				p=0,038

Monthly figures represent maxima for that month.
All distances in km. Data from direct observations.
Probabilities (p) calculated for Poisson distribution of data.

Activity

While obtaining telemetric movement data, the opportunity was used to monitor activity patterns of the study jackals. While extensive activity data were collected in this way, the failure of the automatic activity recorder to provide reliable data resulted in sampling at the times of greatest jackal activity - i.e. 18h00 to 23h00 and 06h00 to 08h00. These data alone were thus of no use in determining daily activity patterns, and were discarded. However, sufficient data are available from direct observations to make some deductions concerning the activity patterns of jackals in the NTGR.

As 45% of direct observations did not detail the activity type due to limited visibility and accessibility and limited offroad travelling, detailed analysis of time-budgets falls beyond the scope of the present study.

Total Activity

The definition of total activity used here is "... the actions of an animal while it is not resting or sleeping" (Ferguson *et al.* 1983).

An analysis of the times at which jackals were found to be active reveals a bigeminus pattern of activity as described by Ferguson *et al.*, and as reported by Hiscocks & Perrin (1988) (Fig. 12). However, the results from the present study reveal a smaller trough of activity between 24h00 and 06h00 compared to the abovementioned studies. As recorded by Fuller *et al.* (1989), activity between 00h00 and 05h00 remained substantial in contrast to observations by Ferguson (1980) in the Kalahari Gemsbok National Park and as revealed by the activity graphs of Hiscocks & Perrin (1988) and Fuller *et al.* (1989). In addition, the peak of evening activity lasts approximately 4 h in the present study cf. 1-2 h in Ferguson *et al.* These differences may, however, be due to the different methods used.

Jackals appear only to become strictly nocturnal when persecuted (van der Merwe 1953, Smithers 1983, Goss 1986). The jackals in the present study were not persecuted and were often seen to be active during daylight. Times of inactivity during daylight were almost invariably spent in the shade of a tree or bush (see below), indicating that temperature plays at least some role in the maintenance of the largely nocturnal activity of the jackal.

Insufficient data are available to test for the influence of season, age, sex and light conditions on activity as reported by Ferguson *et al.* (1983). However, it was noted from observations and during telemetric tracking that peak activity, and particularly the most extensive ranging movements, occurred during nights of medium lunar intensity vs full moon and new moon, as noted by these authors.

Inactivity

Periods of inactivity, both during the day and at night, were largely confined to open habitat types (see Habitat Use below).

During daylight, jackals were observed to make use of trees and bushes for shade. However, these favoured resting places were also elevated and open, thus providing a good view of surrounding areas as observed by Ferguson (1980) in the Kalahari Gemsbok National Park. Many other non-study jackals were noted to have the same choice as regards resting places. The few occasions when jackals were seen resting within or underneath low bushes were associated with cold windy weather. The jackals would shelter in the lee of the bush as described for jackals from the coastal areas of Namibia which shelter behind sand hummocks while feeding (Avery *et al.* 1987).

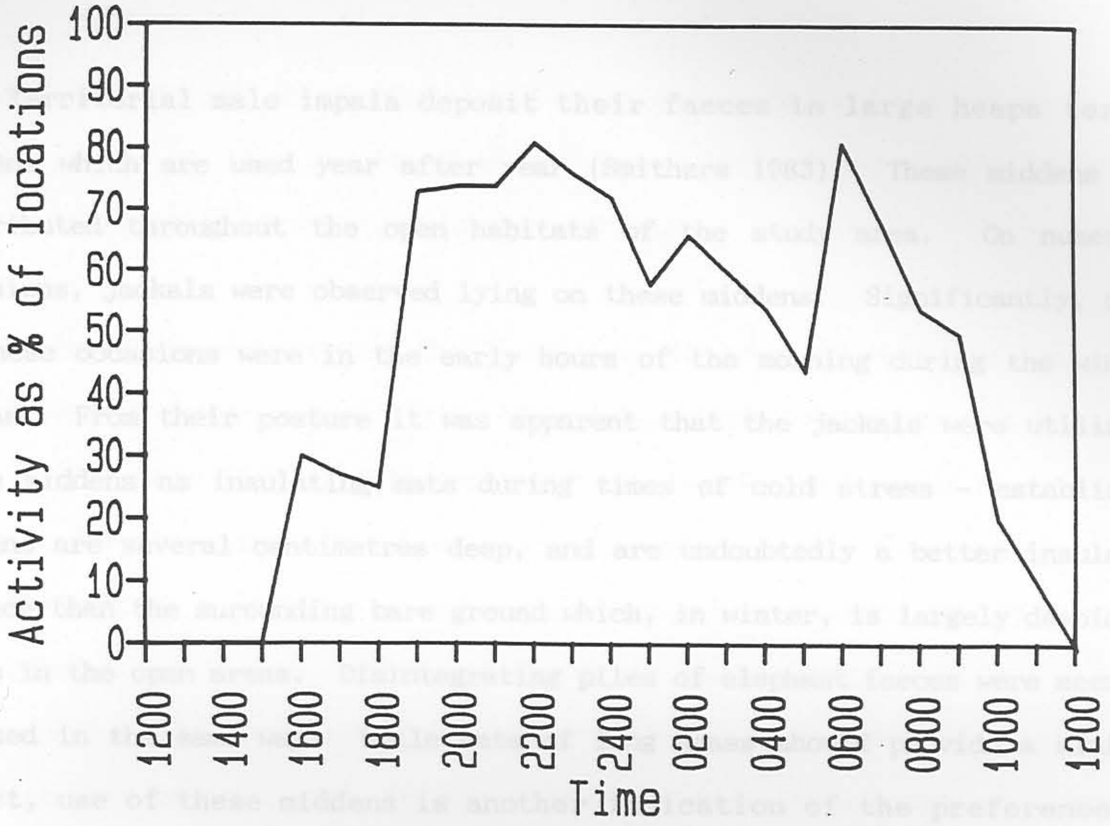

Figure 12. Hourly activity levels of jackals as determined by direct observation. n = 528.

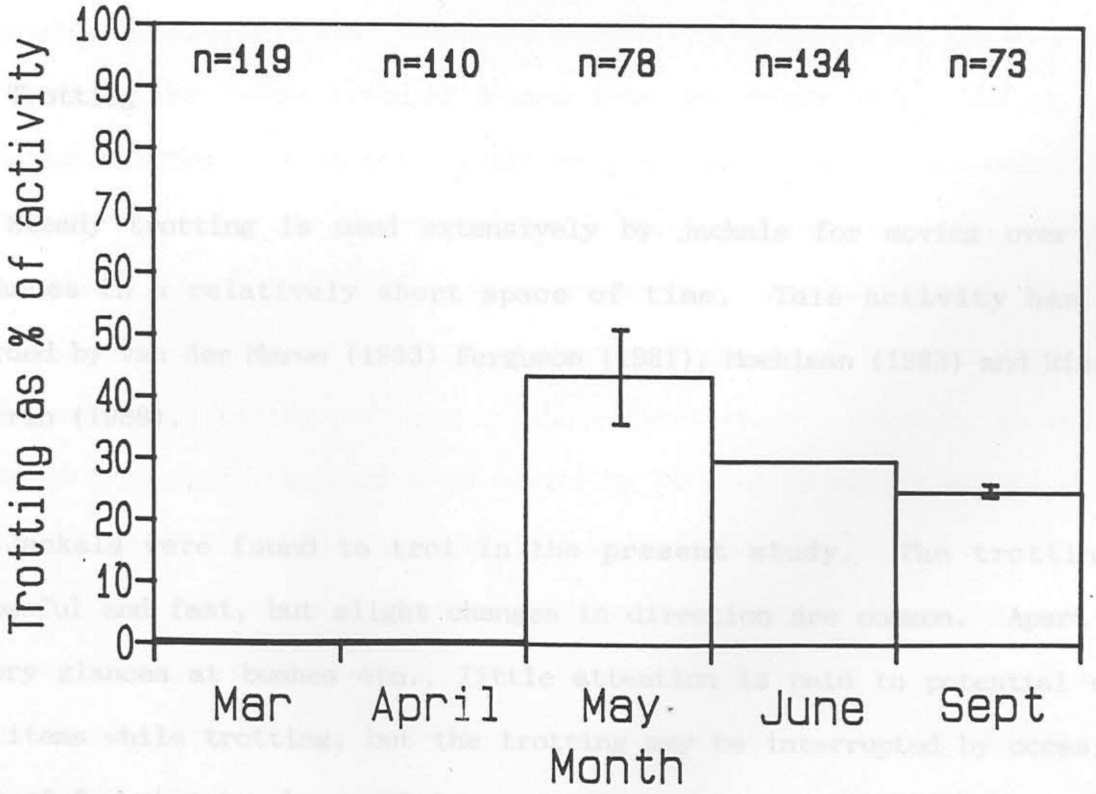

Figure 13. Relative frequency of trotting activity by jackals: March - September 1988. Vertical bars represent standard deviations.

Territorial male impala deposit their faeces in large heaps termed middens which are used year after year (Smithers 1983). These middens are distributed throughout the open habitats of the study area. On numerous occasions, jackals were observed lying on these middens. Significantly, most of these occasions were in the early hours of the morning during the winter months. From their posture it was apparent that the jackals were utilizing these middens as insulating mats during times of cold stress - established middens are several centimetres deep, and are undoubtedly a better insulated surface than the surounding bare ground which, in winter, is largely devoid of grass in the open areas. Disintegrating piles of elephant faeces were seen to be used in the same way. While mats of long grass should provide a similar effect, use of these middens is another indication of the preference by jackals for open habitat (see Habitat Use below). Extensive use of the middens by jackals is indicated by the collections of bones on these heaps (pers. obs.).

Fast Trotting

Steady trotting is used extensively by jackals for moving over large distances in a relatively short space of time. This activity has been recorded by van der Merwe (1953) Ferguson (1981), Moehlman (1983) and Hiscocks & Perrin (1988).

Jackals were found to trot in the present study. The trotting is purposeful and fast, but slight changes in direction are common. Apart from cursory glances at bushes etc., little attention is paid to potential small prey items while trotting, but the trotting may be interrupted by occasional bouts of foraging in clumps of dense vegetation. The jackal is alert, and it trots at a fast pace along established paths and roads, and the extensive use made of roads by this species (van der Merwe 1953, Bearder 1975, Ferguson 1980) can probably be ascribed to this activity.

While no seasonality in the occurrence of trotting activity was noted during 1987, a distinct seasonality occurred in 1988. Following the extensive rains of February 1988, hunting activity was largely restricted to leisurely foraging for the insects which were super-abundant during this period. Thus fast trotting as a specific activity pattern was not observed during March or April, but suddenly increased to 43,3% of all observations of active jackals in May - Fig. 13. Despite the subsequent decline to (29,7 and 24,7%) in June and September respectively, frequency of this activity remained considerably higher than in the earlier months of the year. While the decline in occurrence between May and June is significant ($t=2,86$, $p<0,05$), this cannot be ascribed to any sudden changes in environmental conditions over and above the gradual dessication with advancing winter. However, as May is known to be the onset of the jackal breeding season (van der Merwe 1953), and as jackal movements increase at this time of the year (present study), the sudden advent of fast trotting may be linked to this aspect of jackal biology. Andelt & Gipson (1979) found that wide-ranging movements by coyotes precede the onset of the breeding season. The onset of the breeding season may thus explain the initial peak in trotting activity in the present study. However, as was also discussed previously, extensive movements by jackals in winter may be related to the change in diet from insects in summer to impala in winter. With the supply of the latter in discrete, dispersed packages, trotting may be a response to the need to cover large distances during foraging excursions. Extension of coyote ranges in winter is associated with a rapid, ranging type of movement pattern (Laundré & Keller 1981, Roy & Dorrance 1985), and the winter extension of jackal home range recorded in the present study may be linked to the simultaneous change in the mode of activity recorded here.

Habitat use

The eight habitat types within the study area are so intricately interwoven that any demarcation of boundaries on a map would be contrived. Any trends or conclusions based on such an attempted demarcation would thus be of no use at all. From observations made during the study it became apparent that jackals made preferential use of open areas within each habitat type. As visual cues are important both in foraging and in predation avoidance in this species, open habitat, from a jackal's perspective, must comprise a habitat which provides good visibility. The eight habitat types cannot be clearly distinguished on this basis, as each consists of a mosaic of shorter and longer vegetation. However, each habitat type is clearly either predominantly open or predominatly closed. For the purpose of habitat preference analysis, the predominantly open habitats (*Boscia foetida* savanna, *Colophospermum mopane/ Terminalia prunoides* middleslopes, *Colophospermum mopane* scrubveld, and *Salvadora angustifolia* brushveld) and the predominatly closed habitats (Valley bush, *Acacia tortilis* savanna, and *Croton megalabotrys* thicket) were lumped together. These comprise a mean of 38% and 62% of the home ranges covered by the 3 jackals respectively (Fig. 14).

Activity and Habitat Use

In March a mean of 73% of observations on active jackals were made in the open habitats - depicting a significant selection for open habitat (X^2=25,3, p<0,001, d.f.=1). This confirms the observation that, during this time, the jackals foraged extensively in open areas for the abundant insect prey. As dessication advanced, and insect prey became noticeably scarcer in the dry open areas, jackals were seen to spend more and more time in the denser, greener parts of the respective habitats. This is reflected in the decreased overall use of open habitats as winter advanced - Fig. 15. The use of open habitat differs significantly over the period of observation (X^2=33,09, p<0,001,d.f.=4), with the preference for open habitat in March contributing most to the difference (X^2=23,09, p<0,001).

The results of the direct observations and the habitat use analysis indicate that, where possible, jackals are active in open habitat. Even when observed in dense habitat, jackals made extensive use of open areas, especially roads and paths, and a microhabitat analysis would possibly reveal an even stronger preference for open areas. Furthermore, Ferguson (1980) found that mixed bushveld habitat in the western Transvaal was used more extensively than open grassveld. This was ascribed to greater prey availability in the bushy areas. However, the persecution of jackals was noted to be a possible confounding factor, forcing jackals to remain within relatively closed habitat.

The discrepancy in findings of these two studies can possibly be ascribed to the phenomenon of risk-sensitive foraging. Jackals are preyed upon by leopards (Estes 1967, Lind 1972, Ferguson 1980, present study), and leopards were present in the study area (Lind 1974, pers. obs.). Leopards preferentially hunt in closed habitat, as they use concealment to facilitate close approach to potential prey (Smithers 1983). During the present study jackals were observed to mob leopards on many occasions (as described by Goss

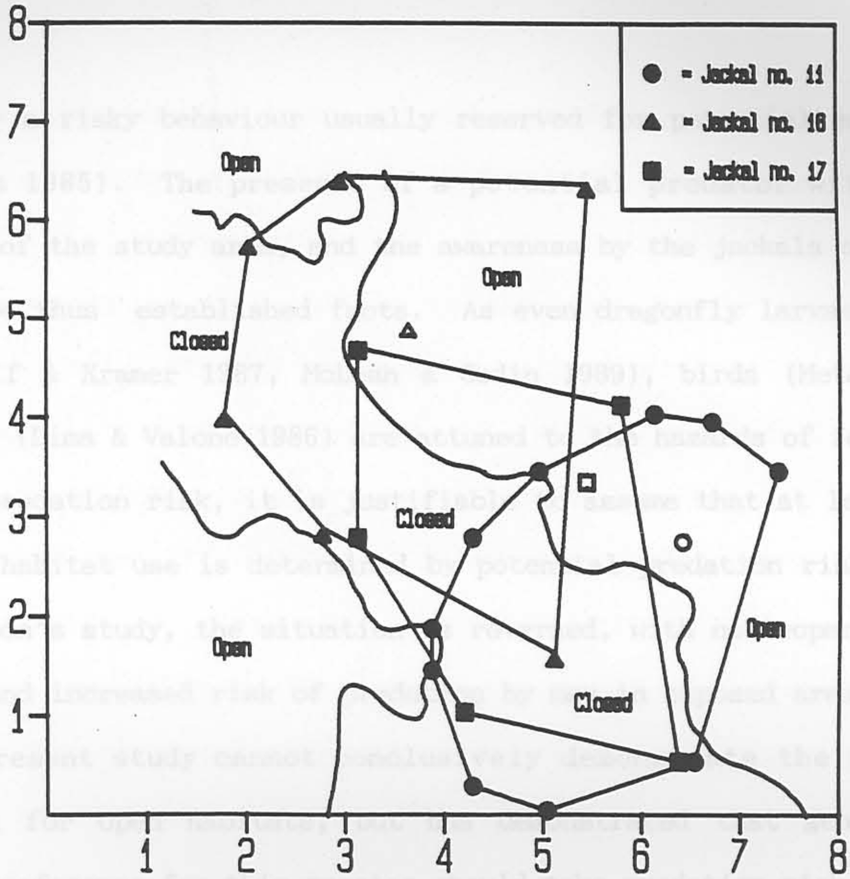

Figure 14. Total jackal home ranges relative to open and closed habitats: 1988.

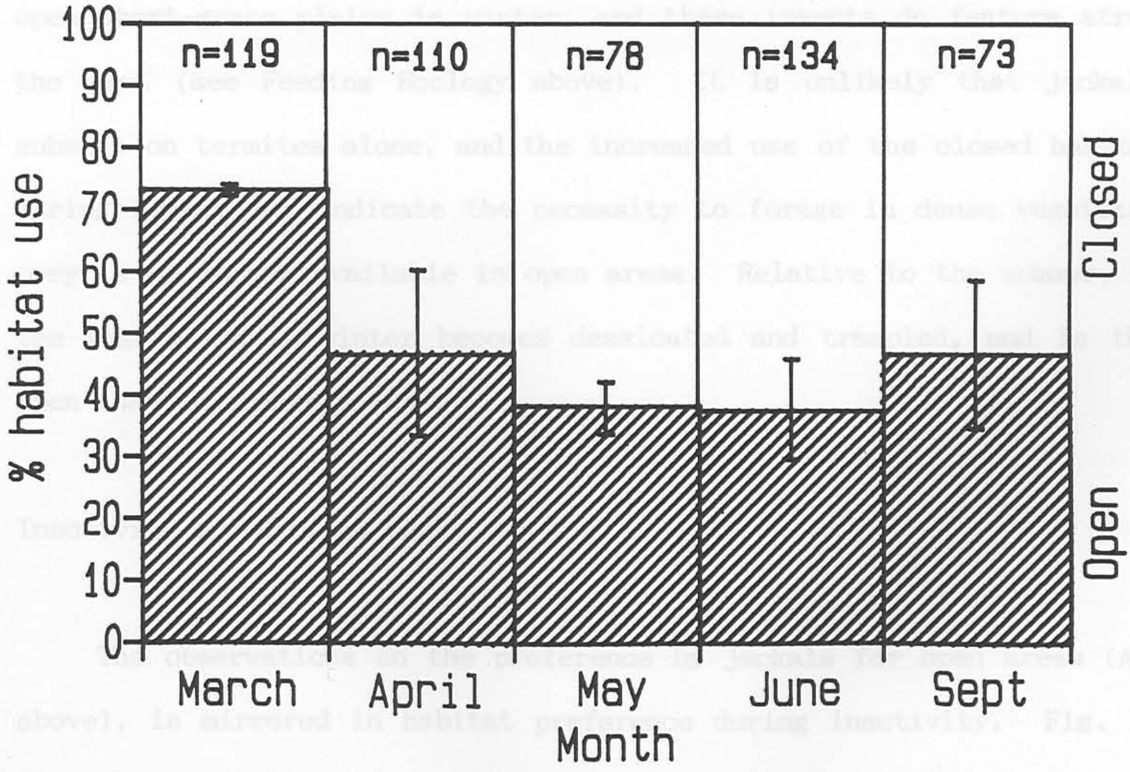

Figure 15. Use of open vs. closed habitat types by jackals during activity: March - September 1988. Vertical bars represent standard deviations.

(1986)) - a risky behaviour usually reserved for potential enemies (Curio & Regelmann 1985). The presence of a potential predator within the dense habitats of the study area, and the awareness by the jackals of the potential threat are thus established facts. As even dragonfly larvae (Pierce 1988), fish (Wolf & Kramer 1987, McLean & Godin 1989), birds (Metcalfe 1984) and squirrels (Lima & Valone 1986) are attuned to the hazards of foraging in areas of high predation risk, it is justifiable to assume that at least some of the jackal's habitat use is determined by potential predation risk. In the case of Ferguson's study, the situation is reversed, with no leopards in the dense habitat and increased risk of predation by man in exposed areas. The results of the present study cannot conclusively demonstrate the reason for the selection for open habitats, but has demonstrated that generalizations on habitat preference for this species should take predation risk into account.

Harvester termites were the only insects observed in large numbers on the open short-grass plains in winter, and these insects do feature strongly in the diet (see Feeding Ecology above). It is unlikely that jackals could subsist on termites alone, and the increased use of the closed habitat types during winter may indicate the necessity to forage in dense vegetation when prey is no longer available in open areas. Relative to the summer, however, the vegetation in winter becomes dessicated and trampled, and is thus more open than in summer anyway.

Inactivity and Habitat Use

The observations on the preference by jackals for open areas (Activity, above), is mirrored in habitat preference during inactivity. Fig. 16 shows that the most open habitat, *Boscia foetida* savanna, is preferentially selected above all other habitat types for all periods of inactivity. This habitat comprises approximately half of the open habitat utilized by the three jackals (Fig. 14), i.e. approximately 19% of the available habitat. The 76% of resting activity in this habitat is therefore highly significant (X^2=105, p<0,001, d.f.=1). Use of the open vs. closed habitats during inactivity by the jackals is illustrated in Fig. 17, with a mean utilization of 83% vs availability of 38%. In all cases, selection for open vs. closed habitat is highly significant (X^2, p<0,001). Sites where jackals were found resting are depicted in Fig. 18. As can be seen, the majority of these sites fall in open habitat and are within the March minimum seasonal range. Jackal no. 11 is the only exception in having some of his resting sites in closed habitat far away from his core area. However, these observations account for only 5% of inactivity observations on no.11.

The selection for open habitat during inactivity supports the above suggestion that risk-sensitive activities may determine habitat use by jackals in the presence of a potential predator. In the case of inactivity, habitat preference is not complicated by factors such as food abundance. The strong selection for open habitat during rest is therefore a significant aspect of jackal biology recorded during the present study. On the other hand, this contrasts with the observations by Ferguson (1980) of jackals in the Transvaal resting in dense clumps of vegetation, and highlights the impact that persecution by man has on micro- and macro-habitat use by this species.

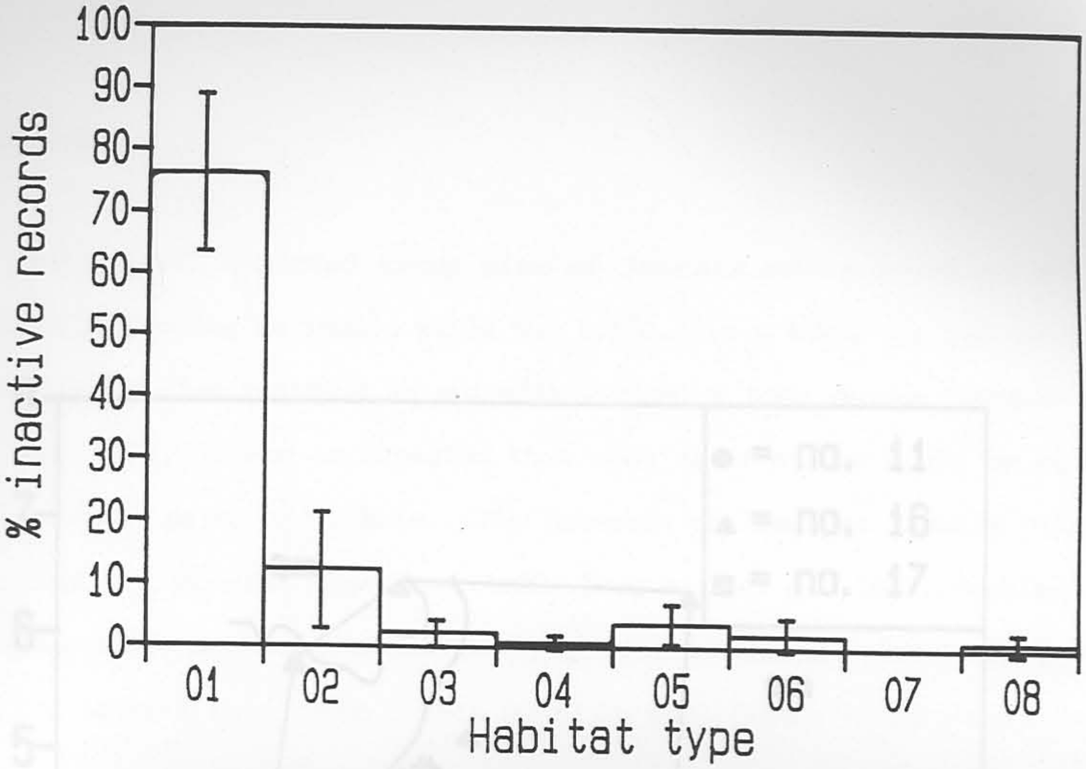

Figure 16. Use of habitat types by jackals during inactivity. 01= B.foetida savanna (O), 02=Valley bush (C), 03= *A.tortilis savanna (C),* *04=* C.*megalobotrys* thicket (C), 05=*C.mopane/T.prunoides* middle slopes (O), 06=Erosion plains (O), 07=C.mopane *scrubveld (O)*, *08= S.angustifolia / A.tortilis* brushveld (O). O= open, C= closed. Vertical bars represent standard deviations.

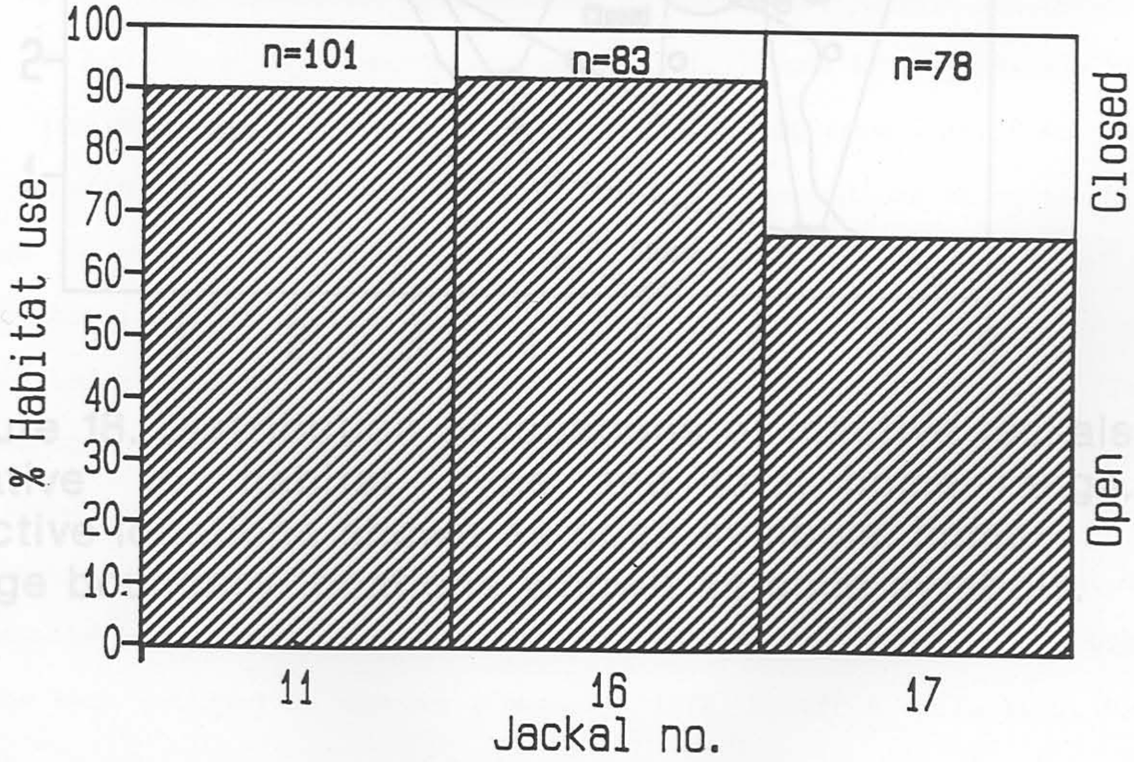

Figure 17. Individual use of open vs. closed habitat types by jackals during inactivity.

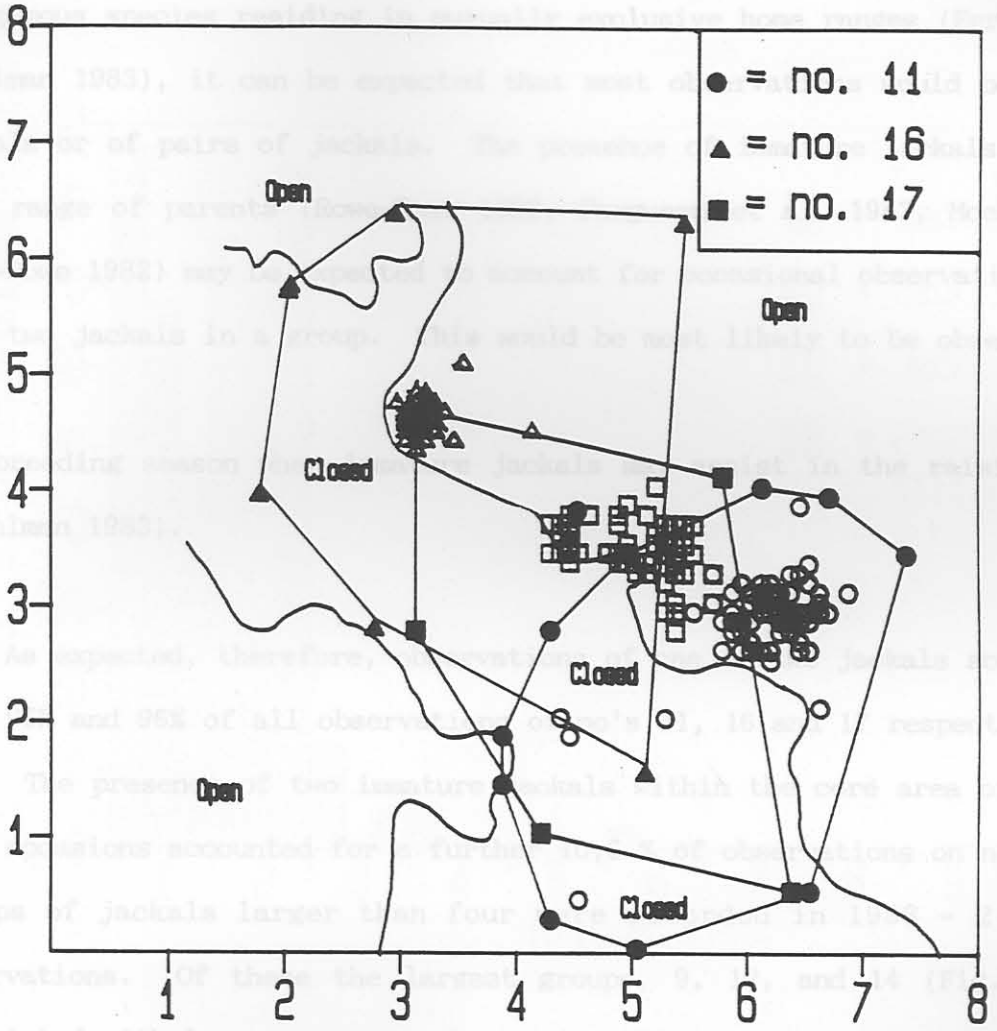

Figure 18. Distribution of locations of inactive jackals relative to habitat type and total home range. Inactive locations shown as open symbols, home-range boundary locations whown as solid symbols.

Group Size

The overall observed group size of jackals not scavenging at large carcases or feeding on impala kills was 1,6±0,7 (n = 489). As the jackal is a monogamous species residing in mutually exclusive home ranges (Ferguson 1980, Moehlman 1983), it can be expected that most observations would be of single jackals or of pairs of jackals. The presence of immature jackals within the home range of parents (Rowe-Rowe 1982, Ferguson *et al.* 1983, Moehlman 1983, Rowe-Rowe 1982) may be expected to account for occasional observations of more than two jackals in a group. This would be most likely to be observed during the breeding season when immature jackals may assist in the raising of pups (Moehlman 1983).

As expected, therefore, observations of one or two jackals accounted for 86%, 95% and 96% of all observations of no's 11, 16 and 17 respectively (Fig. 19). The presence of two immature jackals within the core area of no. 11 on many occasions accounted for a further 10,6 % of observations on no. 11. Ten groups of jackals larger than four were recorded in 1988 - 2,1% of all observations. Of these the largest groups, 9, 12, and 14 (Fig. 19), were associated with large carcases of animals killed by lions or cheetahs. Three of the groups of 6 jackals were associated with feeding on large carcases. The remaining large groups of 5, 5, 6, and 7 could not be explained by the presence of a large scavengeable resource or a jackal kill. Insufficient data are available to indicate whether the larger groups occur more often in winter as has been recorded in coyotes (Camenzind 1978, Bekoff & Wells 1980, Bowen 1981).

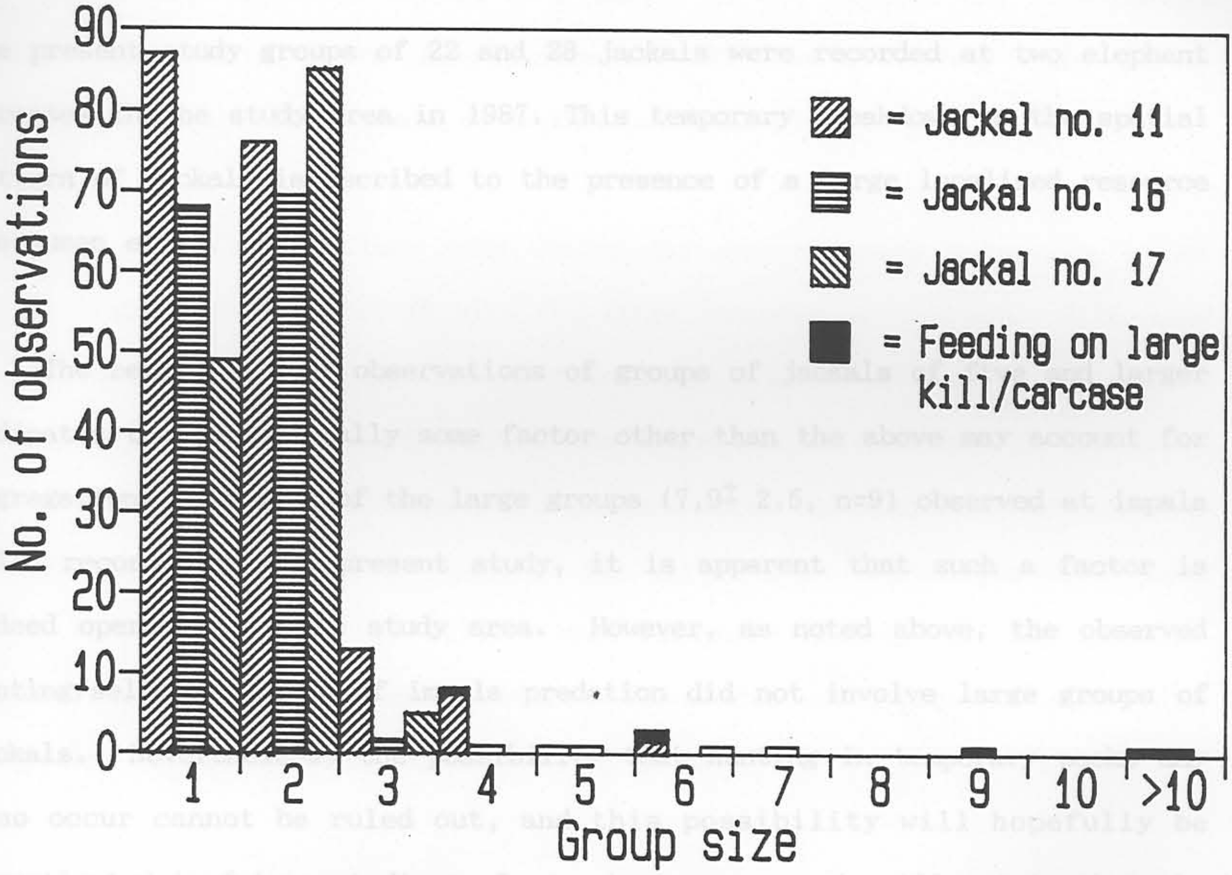

Figure 19. Group size frequency distribution. n = 489.

It is readily apparent from the predominance of observations of one or two jackals that the jackals of the NTGR do not live in packs, nor do they regularly forage in packs. Occasional aggregations of large numbers of jackals at large carcases is well known (van Lawick-Goodall 1970a, Schaller 1972, Ferguson *et al.* 1983, Moehlman 1983, Hiscocks & Perrin 1987). During the present study groups of 22 and 28 jackals were recorded at two elephant carcases in the study area in 1987. This temporary breakdown in the spatial pattern of jackals is ascribed to the presence of a large localized resource (Ferguson *et al.* 1983).

The remaining four observations of groups of jackals of five and larger indicates that occasionally some factor other than the above may account for aggregations. In view of the large groups (7,9± 2,5, n=9) observed at impala kills recorded in the present study, it is apparent that such a factor is indeed operative in the study area. However, as noted above, the observed hunting/selection phase of impala predation did not involve large groups of jackals. Nevertheless, the possibility that hunting in temporary packs may also occur cannot be ruled out, and this possibility will hopefully be investigated in future studies. I can, however, unequivocally state that the "packs" which were observed were ephemeral aggregations. There is thus no evidence that the jackals in the NTGR have resorted to pack living as has been reported for coyotes (Camenzind 1978, Hilton 1978, Bekoff & Wells 1980, Bowen 1981, 1982, Smith, Neff & Woolsey 1986) and even golden jackals (MacDonald 1979). In the light of the results of the present study and the study of Hiscocks & Perrin (1988), it would appear that black-backed jackals do not resort to living in packs in densely populated areas as observed in coyotes (Bowen 1981).

Population Density

1. Mark-recapture estimate

Resighting frequency varied by a factor of 3,3 between the five marked jackals included in random observations in 1988. The data thus could not be used for a meaningful estimate of population density.

The random observations made during the present study were made on an opportunistic basis to fit in with the other research activities. With some of the roads passing through the favoured resting areas of some of the marked jackals (eg. no. 16), biased sighting frequency was inevitable. In addition, the core area plus excursion movement pattern makes the likelihood of sighting jackals unequal at different times of the day. These limitations would have to be overcome in order to utilize mark-recapture methods on this species. Regular traversing of a fixed route at a fixed time would possibly enable the conditions for mark-recapture analysis to be met.

2. Home Ranges

From the analysis of home ranges it was apparent that the March home ranges represented minimum seasonal home ranges with minimal overlap between ranges of adjacent family groups (above). As such, these represent the area exclusively occupied by an adult pair of jackals with their associated offspring.

The mean minimum seasonal home range determined in the present study was

0,97±0,45, n=3). (This figure may appear small, but is well above the estimated minimum home range size of 0,11 km^2 estimated for golden jackals by MacDonald (1979). At an estimated minimum of 4 jackals/family, the density of jackals in the study area is thus 4 km^{-2}. If the figure of 7 - 8 jackals/adult home range used by Rowe-Rowe (1982) is applied, a density of 7 - 8 jackals km^{-2} is obtained.

3. Known Jackal Groups

The core areas of known jackal family groups within the part of the study area most intensively traversed are plotted by hand in Fig. 9. This map yields a total of 9 jackal families in an area of 10,3 km^2. Using the above estimates of the numbers of jackals/family, an estimate of between 3,5 and 7 jackals per km^2 is obtained.

Jackal population densities have been calculated by Rowe-Rowe (1982) (0,3-0,4 km^{-2}) and Hiscocks & Perrin (1988) (22±2,23 km^{-2}). The results of the present study therefore fall within the range of these data, the former from a conserved montane region of Natal and the latter from the coast of Namibia. In the case of the latter, the high densities are ascribed to the presence of a super-abundant food resource in the form of seal carcases from a nearby seal colony.

In view of the fact that the two coarse estimates used here are in close agreement, an estimate of 4 - 7 jackals km^{-2} of the study area is justified. While absolute density is thus not determined (and indeed does not exist, given the wide-ranging movements of the young jackals which can cause chaotic fluctuations in density), the estimate remains high in comparison with the results of Rowe-Rowe (1982). This author used total home ranges for his calculations, and thus may have underestimated the density. A high population of jackals was reported in the Reserve by Lind (1972). This observation was confirmed by casual observations made by myself as well as many other residents and visitors to the Reserve.

Studies by MacDonald (1979) and Hiscocks & Perrin (1988) indicate that in the presence of a super-abundant food supply, jackal population density can become extremely high. In the former study, a density of 195 golden jackals km^{-2} was recorded where abundant food was supplied at an artificial feeding point on a constant basis. The present study records the availability of an abundant food supply in the form of old impala which lose condition following the end of summer (Chapter 4). While the old impala are not a source of scavengeable food, their extremely poor condition (Table 3) indicates that they are probably relatively easily subdued by a pack of jackals, and thus consitute a reliable source of high quality food at a time of the year when food supply might otherwise be limiting. With the demonstrated ability of jackal populations to reach densities of more than 20 km^{-2}, the 4 - 8 km^{-2} estimated in the present study is acceptable. The consequences of the presence of this high jackal population in the Reserve are discussed in Chapter 7.

Conclusion

The present study has demonstrated that jackals in the Northern Tuli Game Reserve do prey on adult impala. It has shown that this predation:

1. Is regularly undertaken by jackals in the study area;

2. Is highly selective for vulnerability as reflected in advanced physiological age, poor condition, and/or injury;
3. Is opportunistic, in that the impala are preyed upon when they are most available (i.e. vulnerable);
4. Is seasonal, the seasonality depending on the abundance of other prey; and
5 Is co-operative, being undertaken by temporarily co-operating groups larger than the average social group in the population.

Opportunistic predators capture prey according to (an often unmeasurable index of) relative availability (Jaksic 1989). Old impala occur in the Reserve where the present study was conducted (Chapter 4). Old impala lose condition more markedly than other impala during late winter (Dunham & Murray 1982). Relative vulnerability is a measure of availability of prey to a predator which is selective for vulnerability - selective predators being those predators which prey disproportionately on a certain component of the available prey population (Jaksic 1989). Availability of old impala to jackals, through loss of condition, therefore increases in winter. Increased predation at a time of increased availability reflects a component of opportunism. Availability is only rarely measurable, therefore often limiting the use of the term opportunistic (Jaksic 1989). However, the results of the present study indicate that jackals are both opportunistic and selective predators.

The demonstrated ability of black-backed jackals to capture medium sized antelope is yet another parallel between this species and the coyote. Seasonal changes in home range size and movement patterns also show a strong similarity between these two species in responding to environmental cues. The wealth of information available on coyote biology could therefore be consulted to assist further research on the black-backed jackal.

In ending the speculation (Sleicher 1973, van Lawick-Goodall 1970a, Lamprecht 1978a, Smithers 1983) on the ability of jackals to regularly hunt such relatively large prey, the present study opens an array of questions which cannot be adequately adressed in this thesis. Some of these are discussed in Chapter 7. Others, based on the findings presented here, will require further specific investigations to be satisfactorily resolved.

Meanwhile, the co-operative, selective predation by black-backed jackals on the impala in the Northern Tuli Game Reserve continues. That this is the first description of regular predation on adult antelope may be due partly to the fact that little direct observation of jackal behaviour has been undertaken, particularly nocturnal observation. There is strong evidence to suggest, as discussed in Chapter 7, that this predation is the acquired result of a specific set of circumstances peculiar to the NTGR at this particular time. Therefore jackals in all regions, at all times, may not be concluded to be regular predators of medium sized adult ungulates and, in particular, the present study does not provide any evidence that jackals should be regarded as wanton or destructive predators. In fact, as is demonstrated in Chapter 7, jackals may play a pivotal role in maintaining some semblance of resilience in stressed ecosystems.

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.

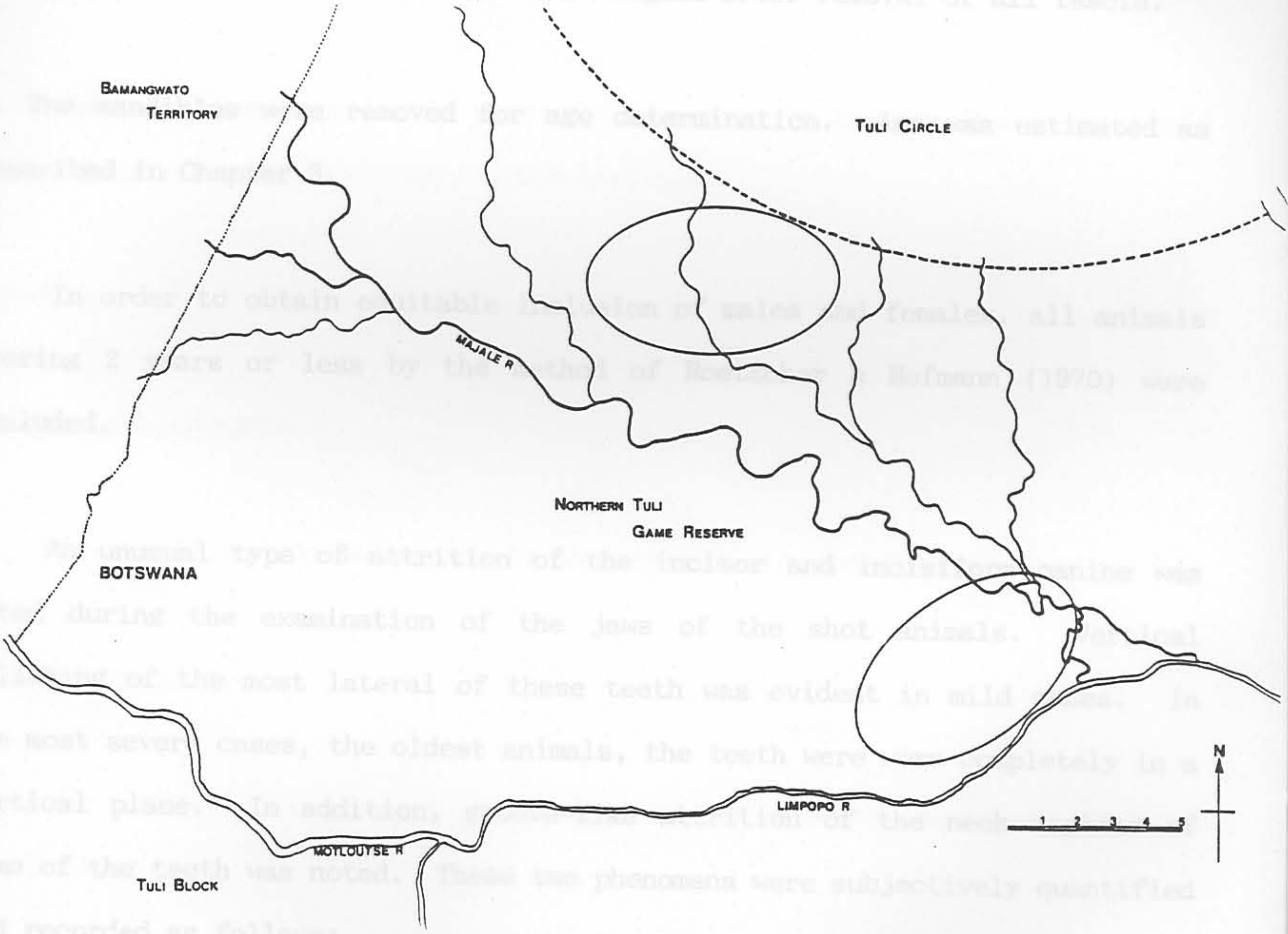

Figure 20. Northern and southern impala baseline data collection zones.

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.

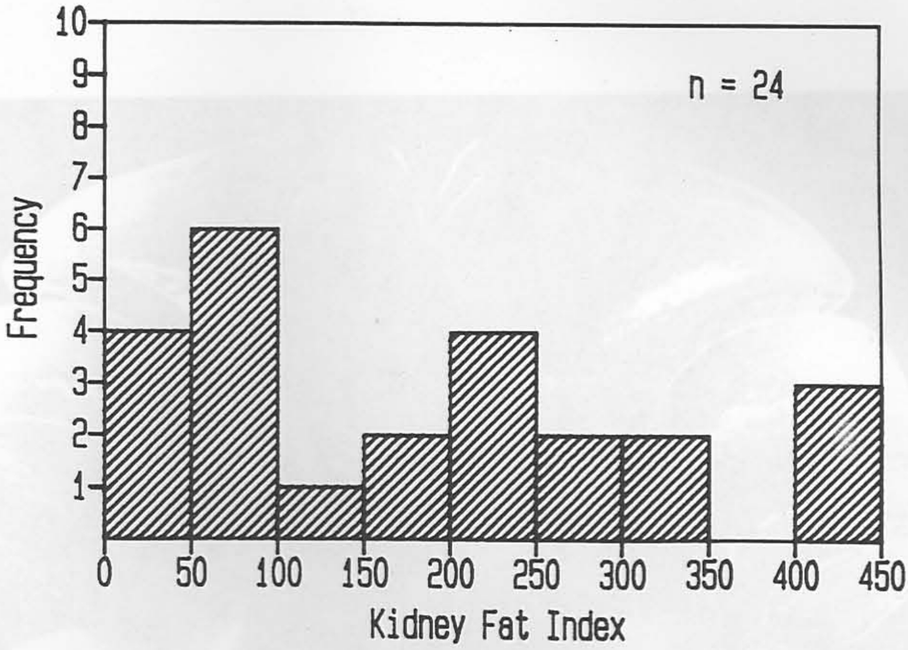

Figure 21. Frequency distribution of Kidney Fat Indices of impala: Section 1, baseline data.

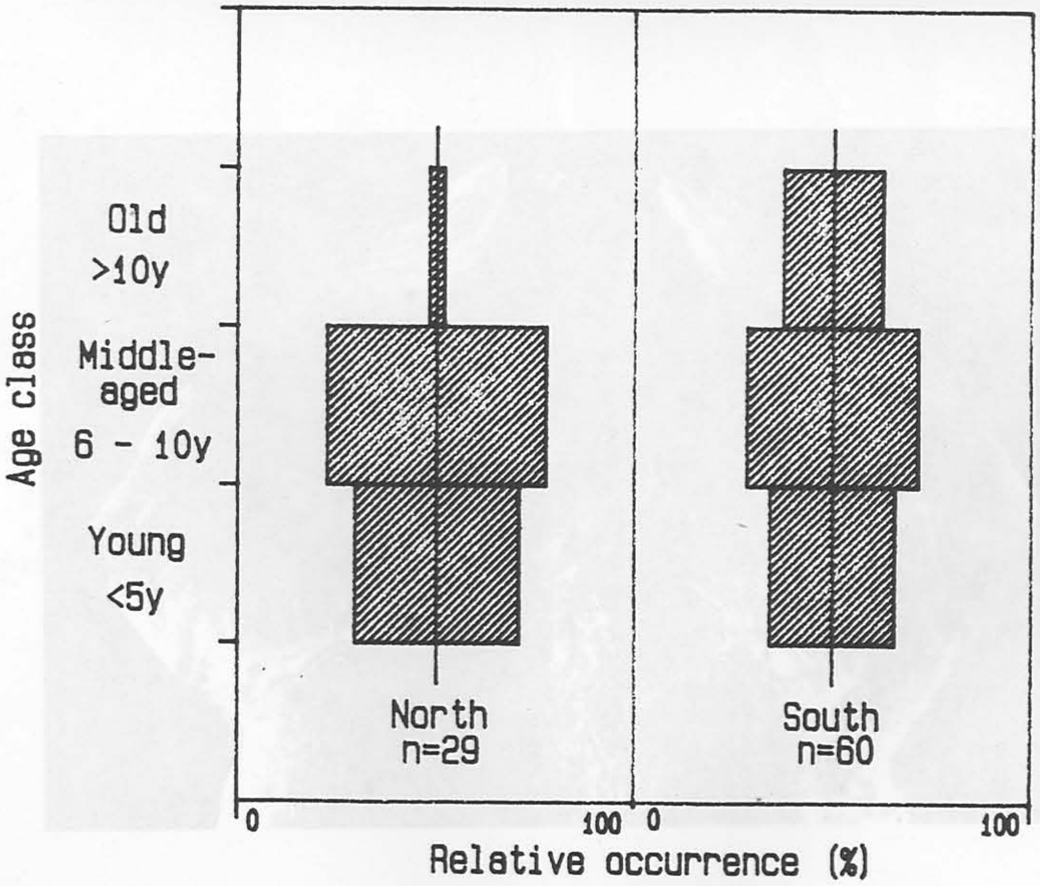

Figure 22. Age group distribution of impala over two years old from northern and southern regions of the NTGR.

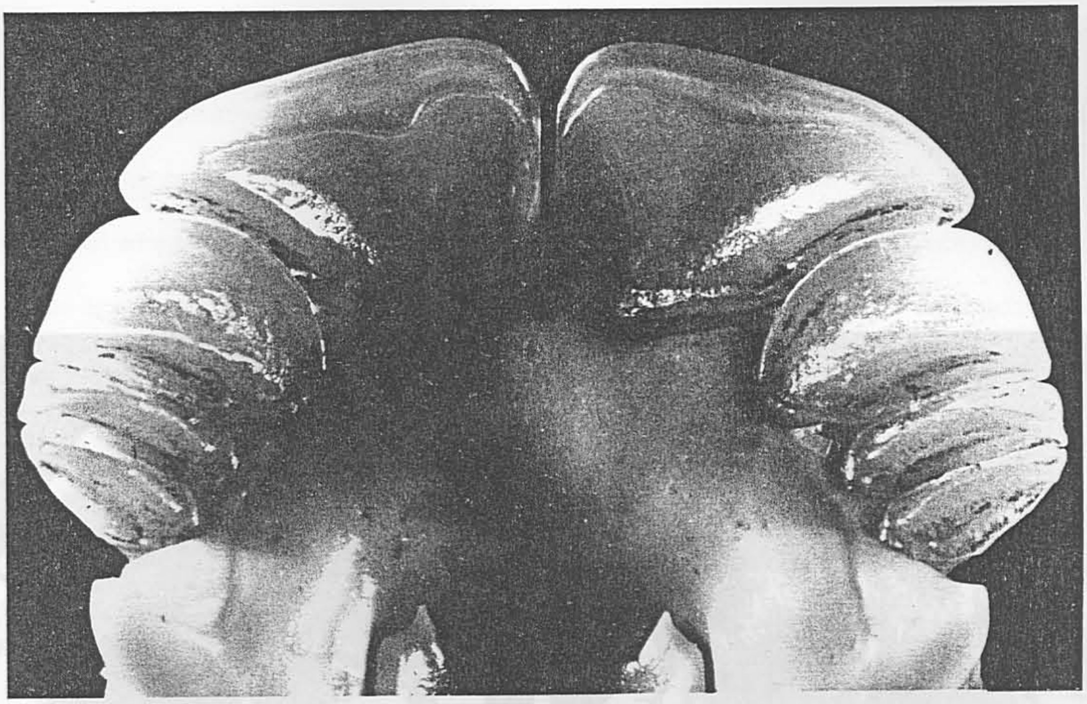

Figure 23 a. Normal impala incisor-canine complex.

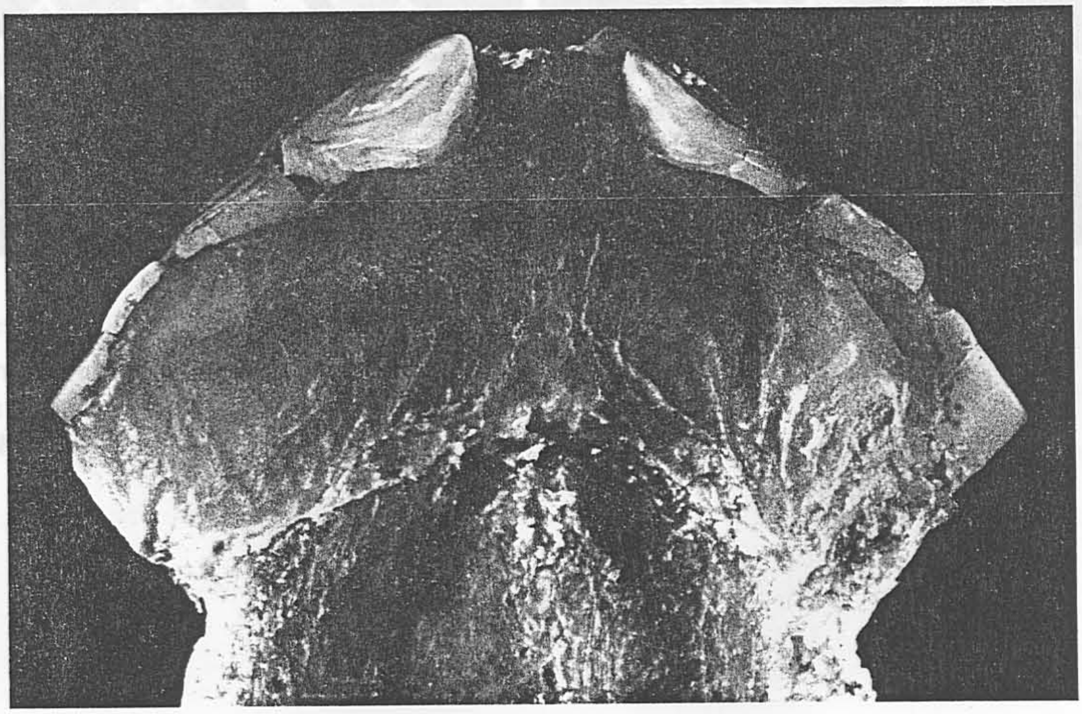

Figure 23 b. Total vertical attrition of an impala incisor-canine complex.

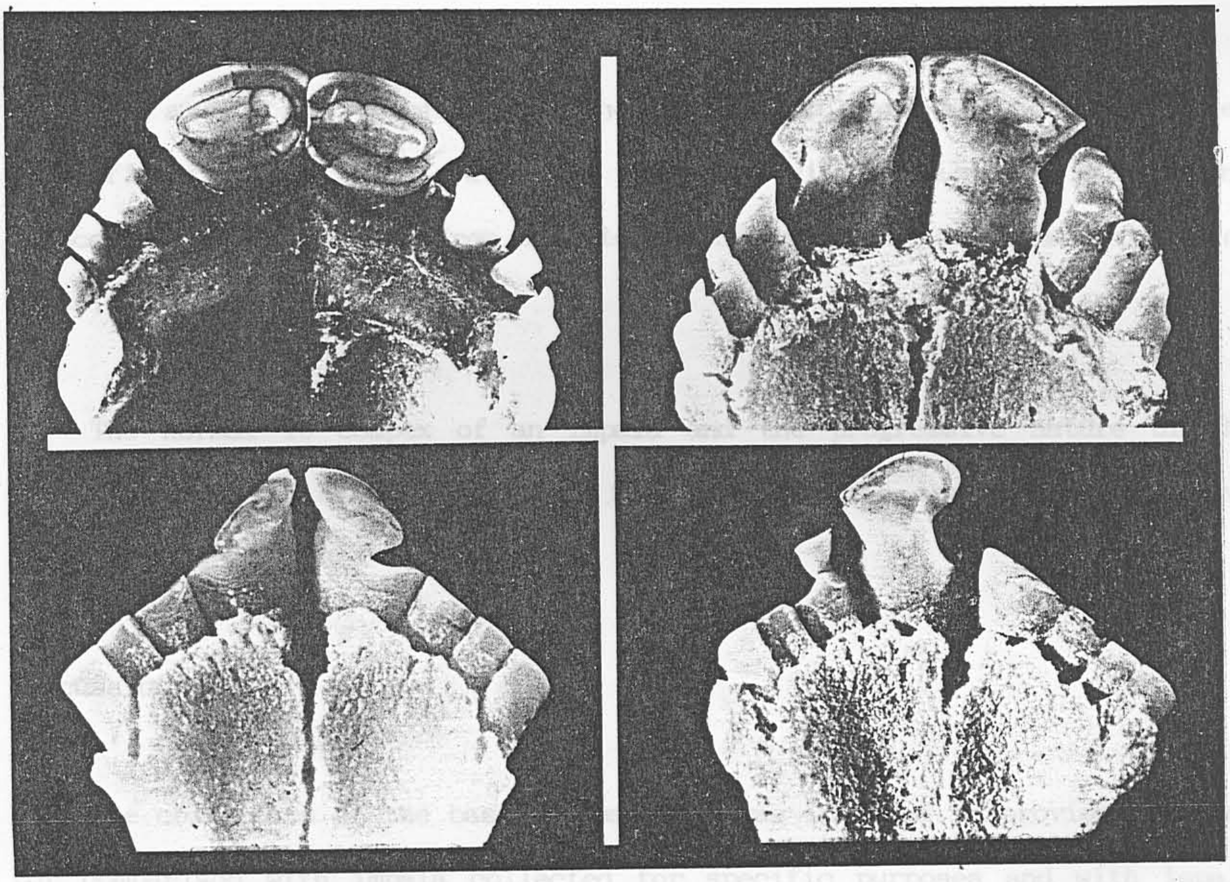

Figure 23 c, d, e & f. Intermediate attrition of impala incisor- canine complexes showing vertical attrition and grooves in the neck regions of the teeth.

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±0,30 (left) and 1,42±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.

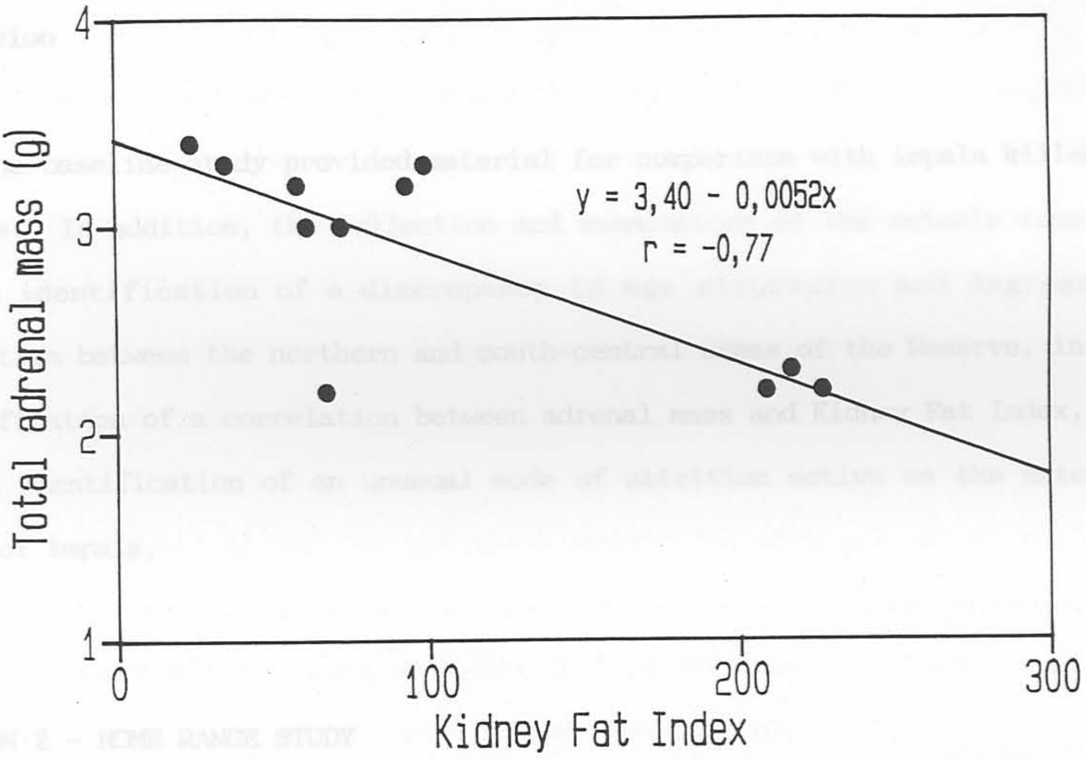

Figure 24. Relationship between total adrenal mass and Kidney Fat Index in impala.

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.

<u>Adrenal Glands</u> Adrenal gland masses are presented in Table 9.

<u>Age</u>

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.

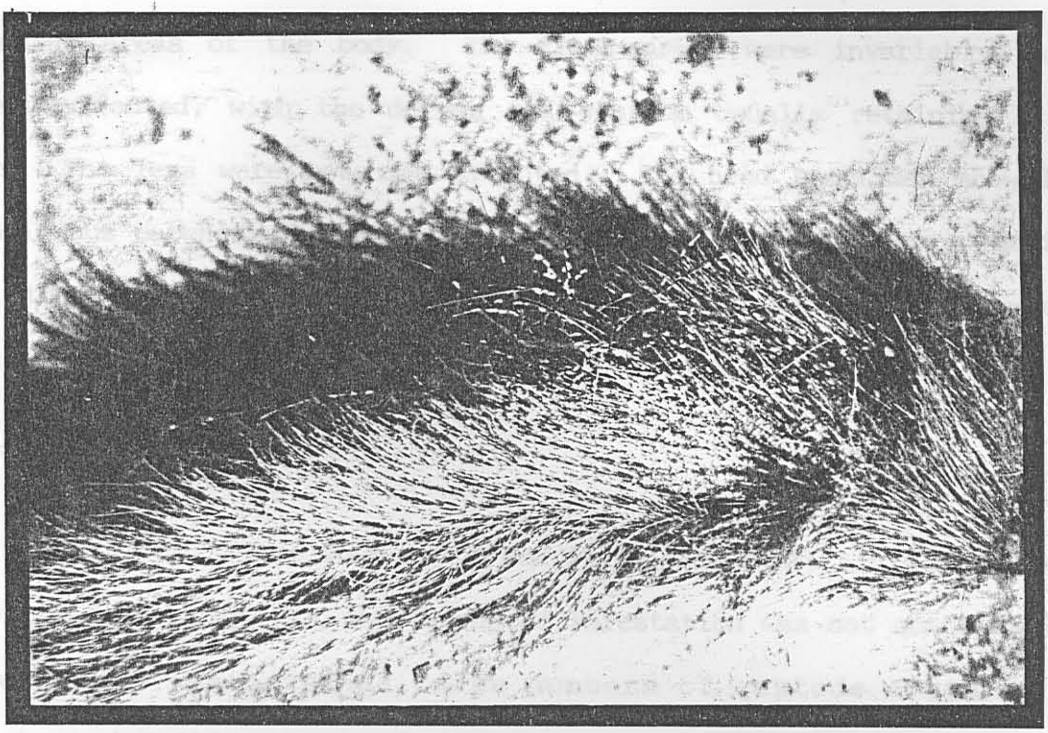

Fig. 26a

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.

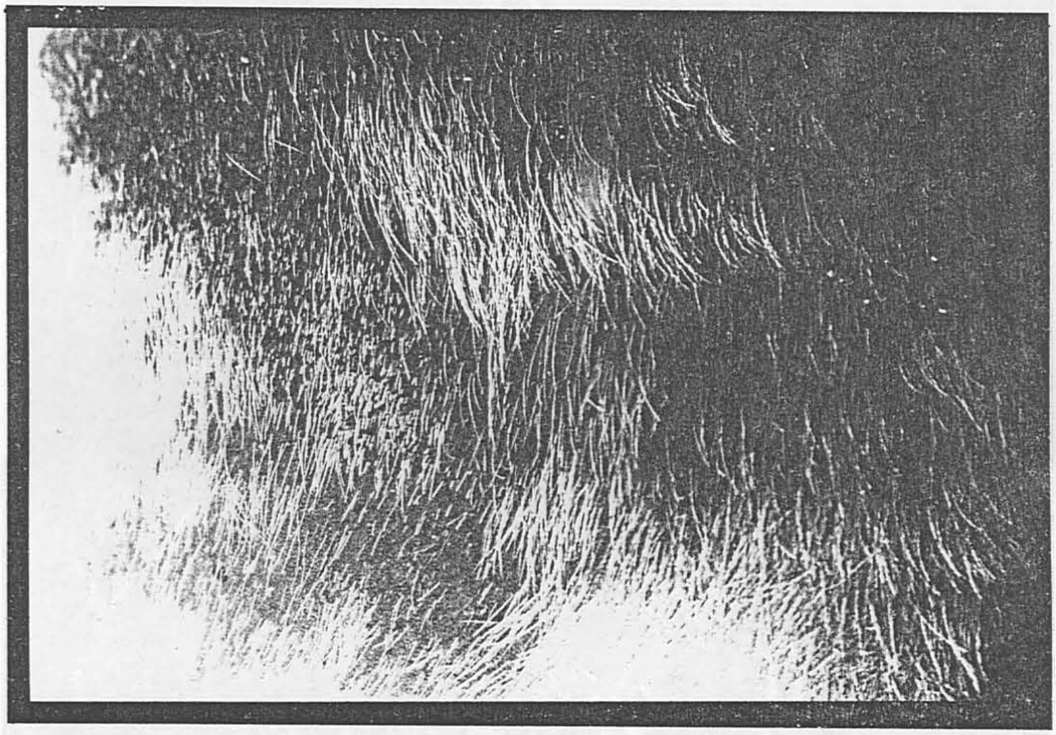

Figure 27. A typical area of alopecia on an impala with a totally worn incisor-canine complex.

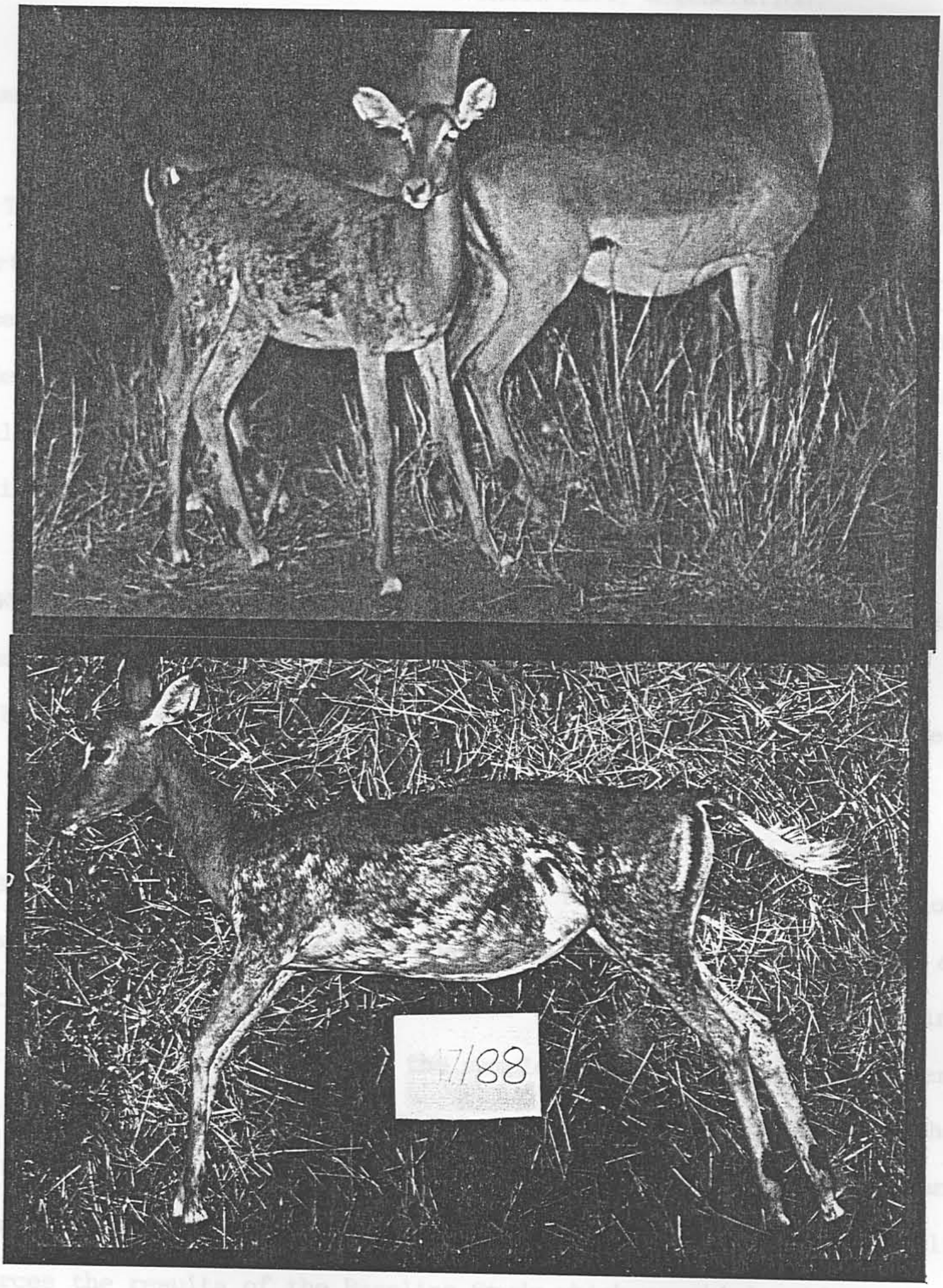

Figure 28 a,b. Impala with advanced alopecia demonstrating the black colouration and the abrupt termination of the alopecia at the shoulder.

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±6,4 (n=5) vs control 48,5±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?

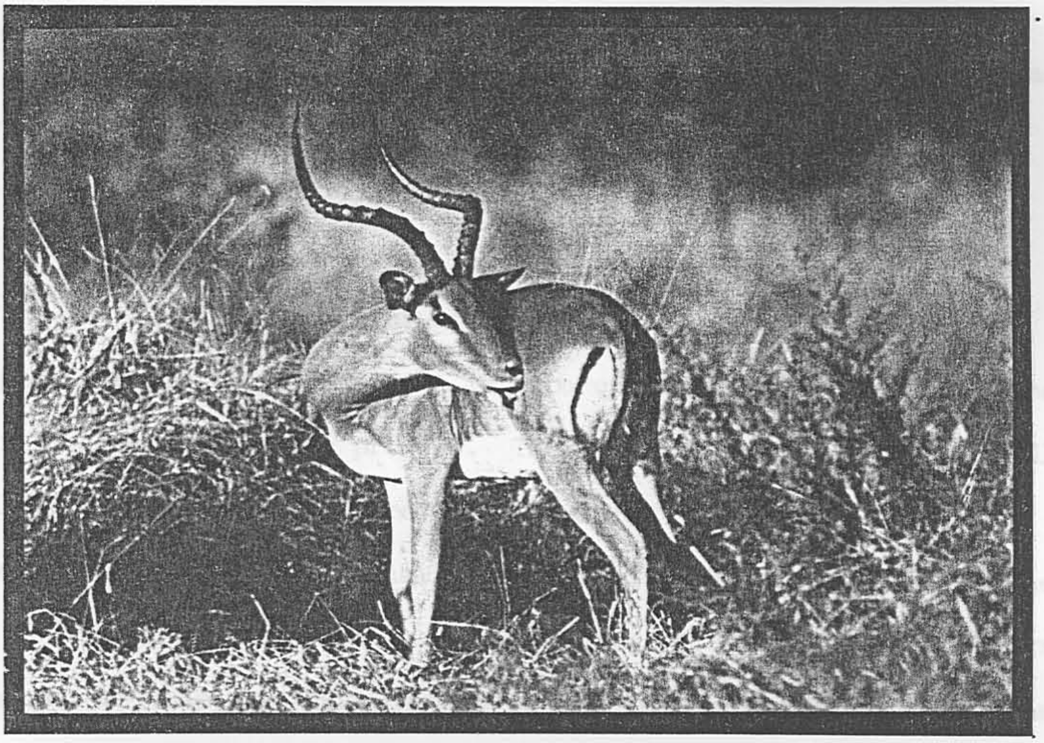

Figure 29. Use of the incisor-canine complex in grooming by an adult male impala.

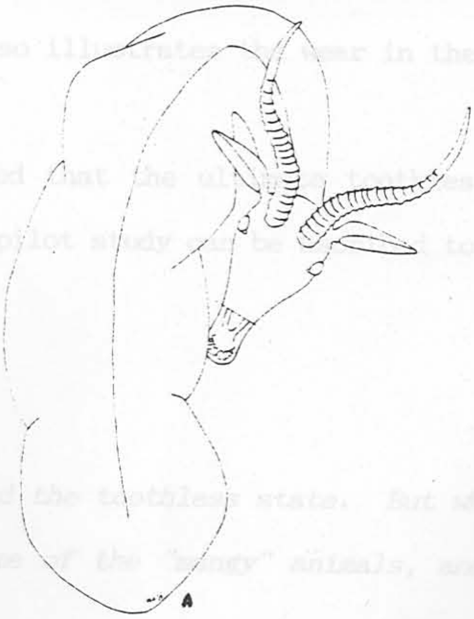

Figure 30. Alignment of components in a typical grooming posture of an impala. (Artwork: A.F. van Rooyen)

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?*

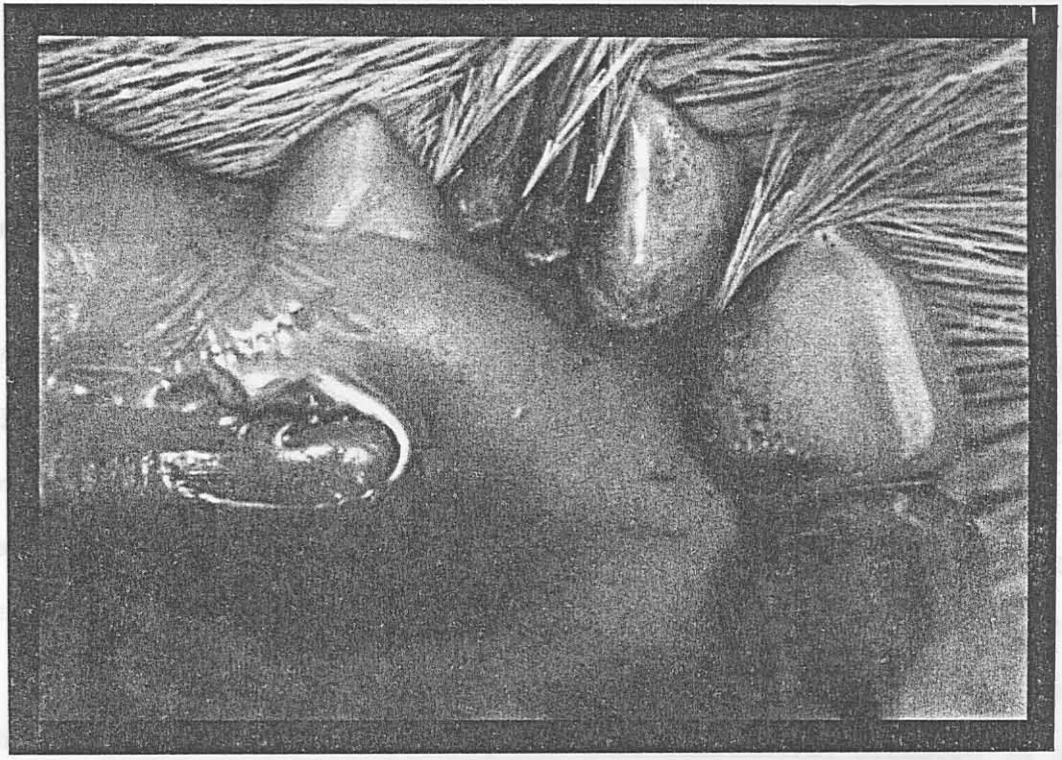

Figure 31. Simulated upwards combing action of the impala incisor-canine complex.

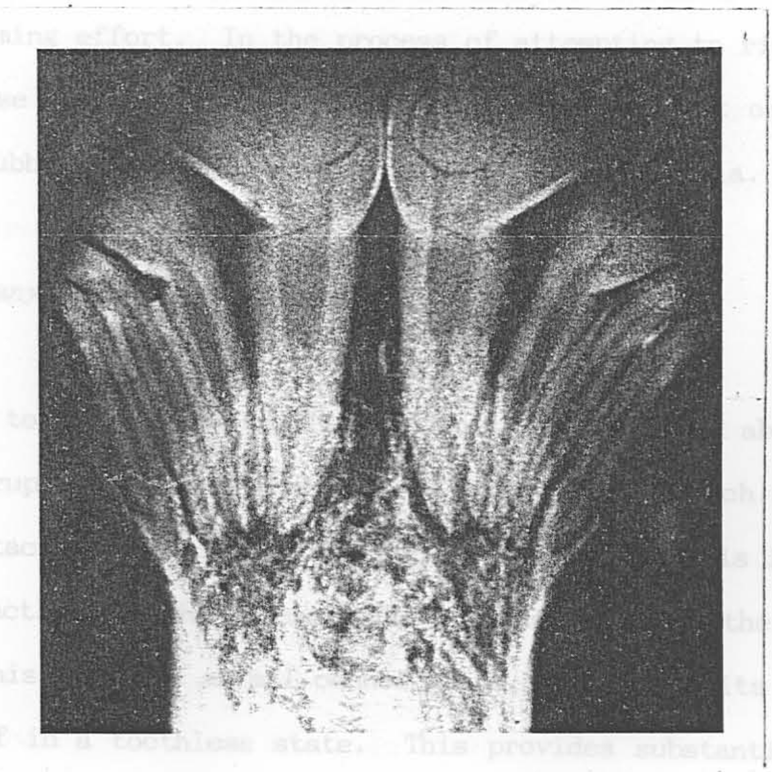

Figure 32. Radiograph indicating macroscopic grooves in the neck regions of the elements of an impala incisor- canine complex.

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	106	5	209	0
M0588	110	2	196	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	186	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
MO188	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 predilection 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

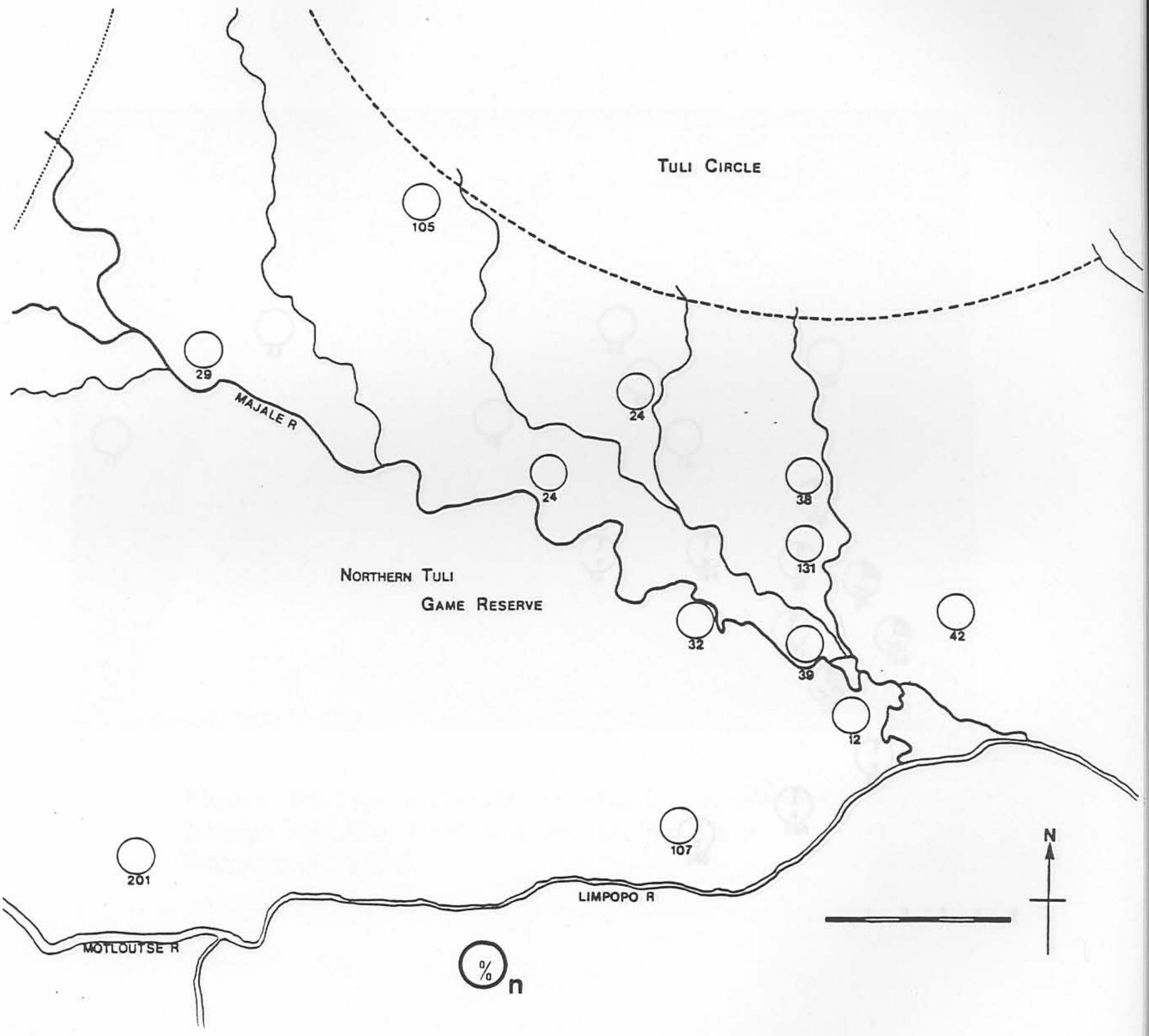

Figure 33. Incidence of autogenous alopecia in adult female impala in the NTGR: hot/wet season, 1986.

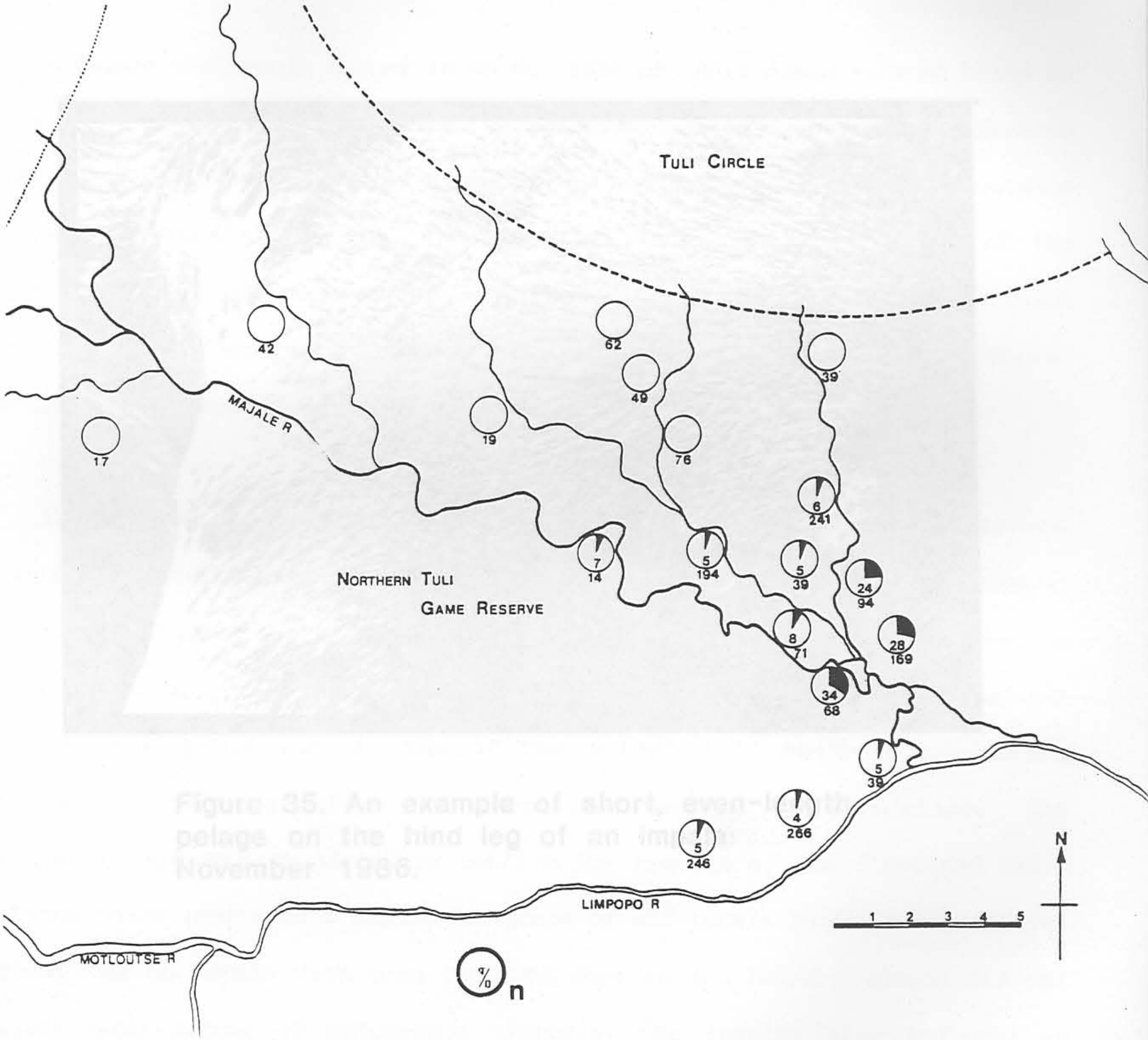

Figure 34. Incidence of autogenous alopecia in adult female impala in the NTGR: hot/dry season, 1986.

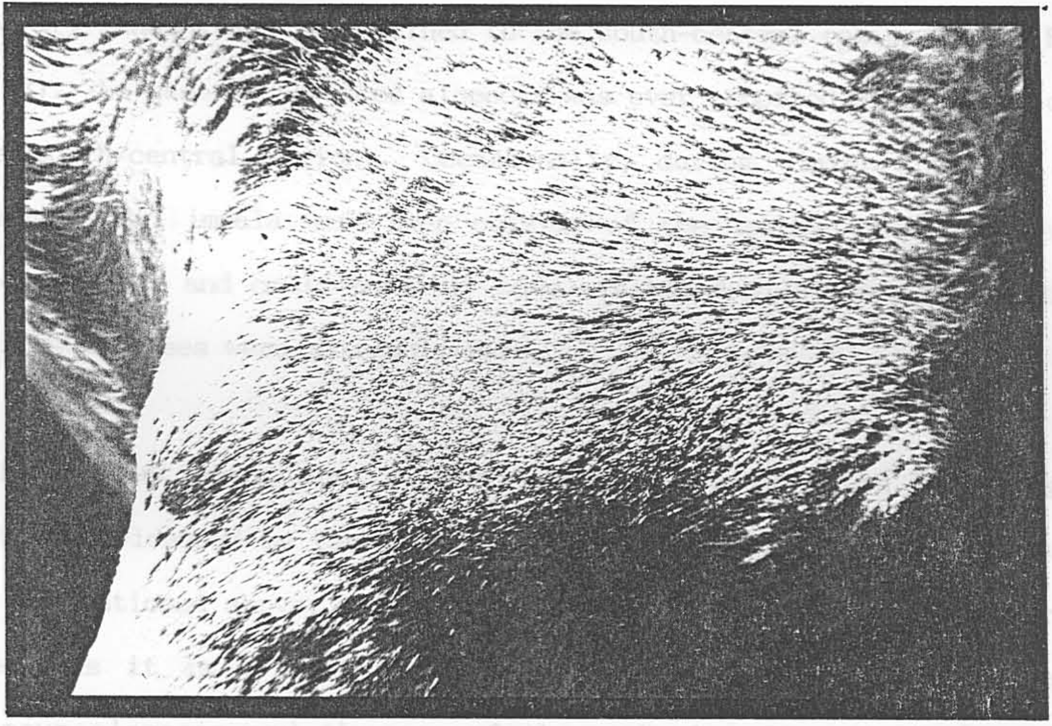

Figure 35. An example of short, even-length pelage on the hind leg of an impala: November 1986.

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.

CHAPTER 5

SPOTTED HYAENAS AND WILD DOGS

SPOTTED HYAENAS

The whooping call of the spotted hyaena is as much part of the African night as is the roar of the lion or the wail of the jackal. While the distinctive vocalizations of the various African predators facilitates the recording of their presence, their absence is not as easily noticed or confirmed. In particular, subtle differences in densities within the same area are subconsciously obscured by an assumption of pristine conditions. This is turn is reinforced by an absence of immediately apparent evidence of active human interference in the ecosystem.

As the jackal study progressed, I naturally began to ponder over what it was that had induced the jackals to become regular predators of adult impala in the south-central region of the NTGR. In considering their immediate environment I began to realise that potential competitors, in the form of spotted hyaenas, brown hyaenas and wild dogs, were conspicuous by their absence. While lions and leopards are subjected to heavy poaching pressure in the NTGR (Patterson 1988), their presence in relatively high numbers created the impression to the casual observer of a natural predator system. Indeed, the lion is so intimately associated with wilderness and wild places that its very presence seems to imply the converse - i.e. that a true wilderness exists wherever the lion walks. In the case of wild dogs and brown hyaenas in the

NTGR the situation is simple and opposite - both species are extinct.

It was only through focussing on the general predator community that I began to realize that there is an uneven distribution of spotted hyaenas in the NTGR. The abundance of spotted hyaenas appears to be far higher in the north, north-west and western areas of the Reserve than it is in the south-central region. In the south it is only in a small valley on the Tuli Lodge property that one can be fairly certain of finding hyaenas. Through living in the north and studying the jackals in the southern areas over a period of two years this observation became re-inforced by daily experience. As this observation then became incorporated into my explanation for the current predator-prey relationships in the NTGR, it became important to quantify this observation in some way.

As mentioned above, absence is a difficult variable to quantify. Relative absence is an even more slippery subject. As any tests applied were to test an hypothesis, objectivity became a real issue in this aspect of the study.

This chapter is a record of the several attempts made to measure in a quantifiable manner the observed paucity of spotted hyaenas in the south-central region of the NTGR. Each aspect is incorporated in a separate section.

SECTION 1 - DIRECTED OBSERVATIONS

Introduction

Having made the general observation that I was encountering less evidence of hyaenas in the south than in the north, I set about making specific observations to confirm or disprove this observation. During this time of directed observation, what was not seen became as important as what was seen.

Methods and Results

Lion Capture

Lions were captured on nine occasions in the south-central region in order to fit or remove radio collars or to remove wire snares (Patterson 1988). In addition, capture of a wounded lioness was unsuccessfully attempted. Impala, kudu and donkey carcases were used as bait on different occasions. The carcase was opened and dragged a variable distance and then chained to a tree. Tape recordings of hyaenas feeding were played through horn speakers via an amplifier on some of the occasions.

Hyaenas were never seen on any of the above occasions, nor were any heard to call.

On six similar occasions in the northern and western regions, hyaenas were heard to call on each occasion, and were seen on two of the occasions.

Jackal trapping

Intensive efforts were made to trap jackals in the south-central region. Trapping took place from November 1986 to February 1987, during April 1987, and in February 1988 (see Chapter 3). Traps used included pit-fall traps, noose traps, foothold traps, drop traps and cage traps, all of which required the use of bait which was derived from antelope shot in the Reserve. In the case of the drop trap a wildebeest carcase was used. Attraction of jackals to within range for darting was attempted using an elephant carcase (see Carcase 4, below), two impala carcases, and a large number of impala remains (skin, bones and viscera) from the impala project.

Despite prolonged activity with attractive (sometimes pungent!) material, only one spotted hyaena was attracted to the jackal trapping activity (see Section 4, below). On no occasion did any hyaena discharge, tamper with or destroy any traps set for jackals in the south-central region of the NTGR.

Elephant carcases

Carnivore activity at six elephant carcases, at the sites shown in Fig. 36, were noted. At carcase 1, three hyaenas were observed. They arrived from a westerly direction. At carcase 2 no hyaenas were observed, although prolonged observations were not undertaken. Carcase 3 was closely observed by Patterson for five nights (Patterson, 1988). No spotted hyaenas were seen or heard in the vicinity of this carcase (Patterson, pers. comm.). Carcase 4 was intensively observed every night for five nights from the time it was deposited at this site, and was sporadically observed for a further ten nights. No spotted hyaenas were seen at this carcase. Carcase 5 was

G.L. Patterson, Tawana Camp, Northern Tuli Game Reserve, Botswana.

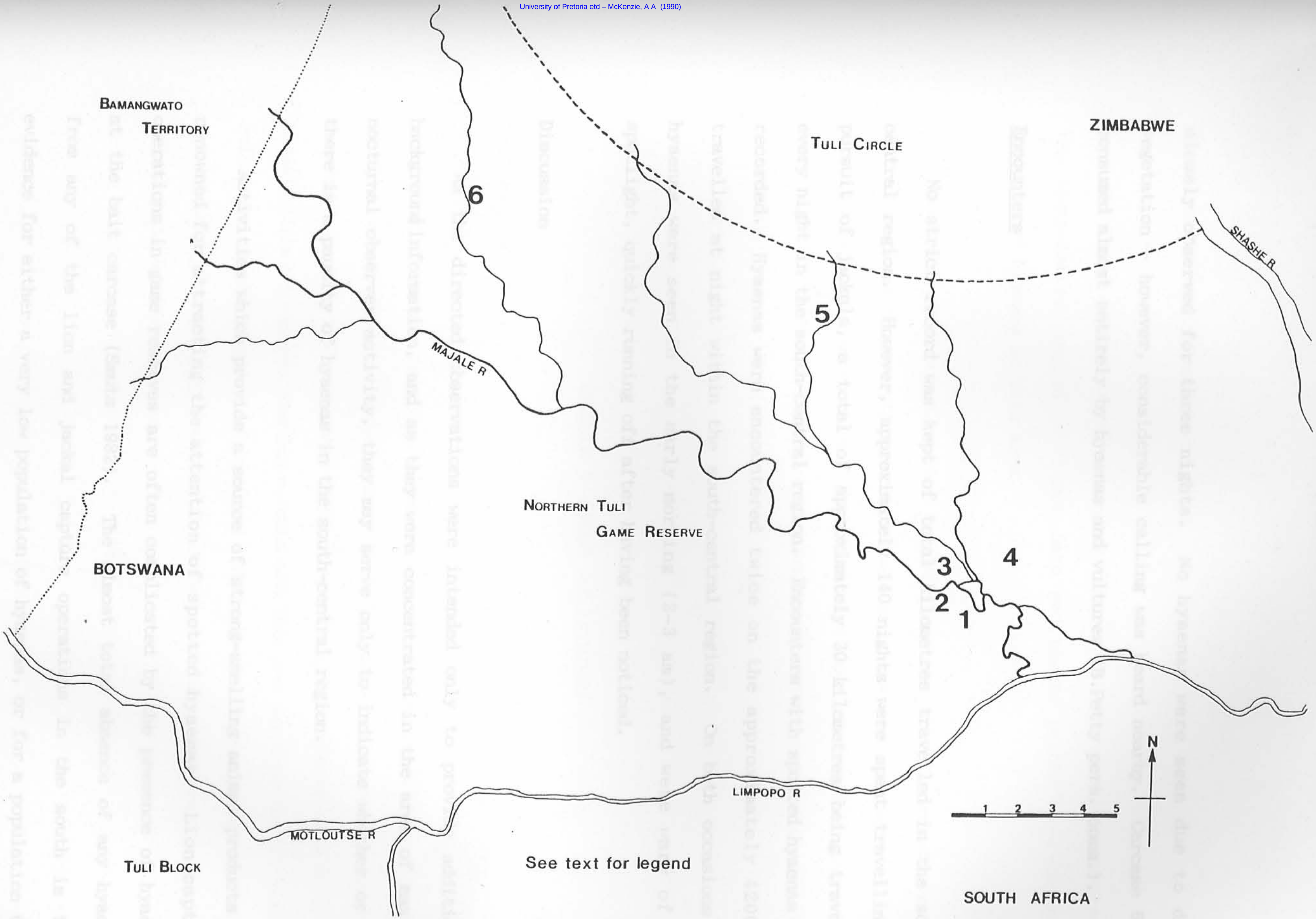

Figure 36. Location of elephant carcases at which spotted hyaena presence was monitored.

closely observed for three nights. No hyaenas were seen due to dense vegetation - however, considerable calling was heard nearby. Carcase 6 was consumed almost entirely by hyaenas and vultures (B.Petty pers. comm.).

Encounters

No strict record was kept of total kilometres travelled in the south-central region. However, approximately 140 nights were spent travelling in pursuit of jackals, a total of approximately 30 kilometres being travelled every night in the south-central region. Encounters with spotted hyaenas were recorded. Hyaenas were encountered twice on the approximately 4200 km travelled at night within the south-central region. On both occasions the hyaenas were seen in the early morning (2-3 am), and were wary of the spotlight, quickly running off after having been noticed.

Discussion

As the directed observations were intended only to provide additional background information, and as they were concentrated in the area of maximum nocturnal observer activity, they may serve only to indicate whether or not there is a paucity of hyaenas in the south-central region.

Activities which provide a source of strong-smelling animal products are renowned for attracting the attention of spotted hyaenas. Lion capture operations in game reserves are often complicated by the presence of hyaenas at the bait carcase (Smuts 1982). The almost total absence of any hyaenas from any of the lion and jackal capture operations in the south is thus evidence for either a very low population of hyaenas, or for a population that

B. Petty, Jwala Lodge, Northern Tuli Game Reserve, Botswana.

is extremely wary of human activity.

The total absence of any hyaenas from two of the elephant carcases in the south-central region over many days and nights points to a remarkable scarcity of hyaenas in this area.

The low encounter rate serves to reinforce the other observations. The fact that those hyaenas that were encountered were encountered only in the early hours of the morning, and that they were wary of the light and vehicle despite relatively heavy and continuous human activity in this region is noteworthy.

SECTION 2 - DENS AND LATRINES

Introduction

Spotted hyaena dens are sites of considerable activity, and their latrines are a highly visible sign of their presence in an area (Kruuk 1972, Bearder & Randall 1978, Henschel 1986). As physical manifestations which are closely linked to hyaena abundance, dens and latrines are thus useful indirect indicators of the presence of hyaenas. These features were thus used in the present study to obtain an index of relative hyaena abundance in the different areas of the Reserve.

Materials and methods

Personal observations, as well as any reliable reports, were used to plot the sites of active hyaena dens on a 1:50 000 map of the Reserve.

Personal observations were made of hyaena latrines, which were also plotted on a 1:50 000 map. An attempt was made to cover as may of the roads in the Reserve as possible.

Results

Recorded den and latrine sites are presented in Fig. 37. The area of greatest observer activity, and thereby greatest chance of observation of dens and latrines, is indicated with a dashed line on the map.

Discussion

Dens

As den sites were points of active discussion between staff in the Reserve, their presence was very likely to be recorded. In addition, the level of game viewing activity, both day and night, in the south-central region is so high that it is impossible that an active den site would remain unnoticed in this area. It is thus highly significant that no den site, active or inactive, was recorded within the south-central NTGR either by myself or by other observers. The dens recorded in the other areas of the Reserve span a period of several years (1985-1988). As hyaenas do not restrict their activity to any one den site, these recorded den sites do not

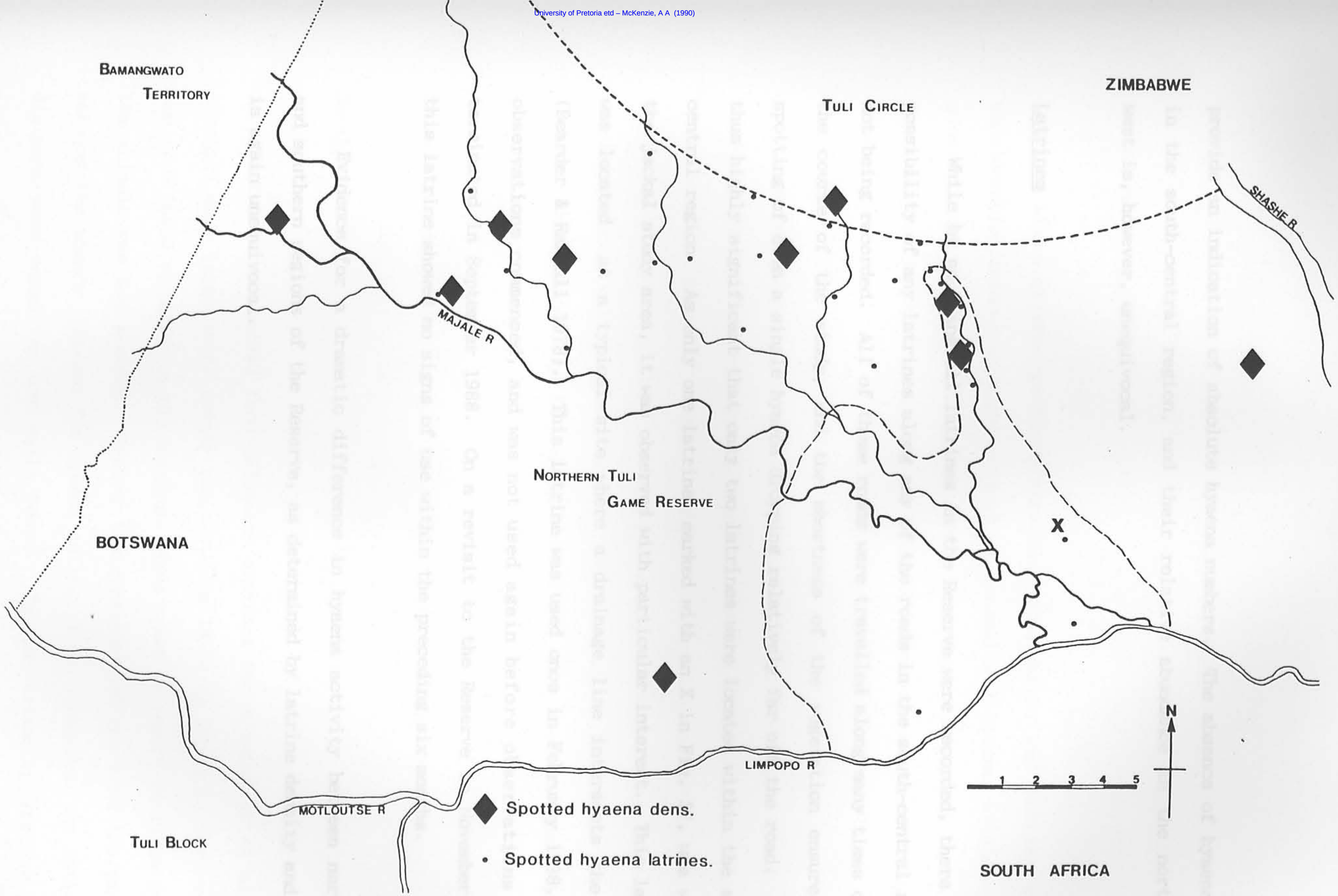

Figure 37. Recorded spotted hyaena dens and latrines: 1985-1988.

provide an indication of absolute hyaena numbers. The absence of hyaena dens in the south-central region, and their relative abundance in the north and west is, however, unequivocal.

Latrines

While by no means all latrines in the Reserve were recorded, there is no possibility of any latrines along any of the roads in the south-central region not being recorded. All of these roads were travelled along many times during the course of the study, and the shortness of the vegetation ensures the spotting of even a single hyaena dropping relatively far off the road. It is thus highly significant that only two latrines were located within the south-central region. As only one latrine, marked with an X in Fig. 37, was within the jackal study area, it was observed with particular interest. This latrine was located at a typical site where a drainage line intersects the road (Bearder & Randall 1978). This latrine was used once in February 1988, when observations commenced, and was not used again before observations were terminated in September 1988. On a revisit to the Reserve in November 1989 this latrine showed no signs of use within the preceding six months.

Evidence for a dramatic difference in hyaena activity between northern and southern regions of the Reserve, as determined by latrine density and use, is again unequivocal.

SECTION 3 - CALL FREQUENCY

Introduction

The whoop of the spotted hyaena is distinctive, and carries over a considerable distance at night. If it is assumed that hyaenas within a small geographical area call at approximately the same frequency, then call frequency can be used to provide an index of relative abundance within that area.

A marked difference in the frequency with which calls were heard in the southern and northern regions was noted on a casual basis. As the obtaining of an accurate index of hyaena abundance was not a priority of the jackal project, precious nights could not be expended on direct personal determination of call frequency both in the north and in the south. For this section, the observations of reliable observers were used to supplement my personal observations.

Materials and methods

South

Jackals were tracked from telemetry stations for a total of 44 nights. Bearings were taken every twenty minutes from 18h00 to 23h00 in the evening and from 06h00 to 08h00 in the morning. Time taken to record bearings of all the animals was 5-8 minutes. During the remainder of the time the persons manning the towers listened for hyaena calls. Time, direction and estimated distance were noted for any calls heard. As the telemetry stations were placed on the highest hills within the jackal study area, and as the observers were sitting in the open, conditions were ideal for hearing any hyaena calls. Observers slept within a low walled enclosure, or in the back of an open vehicle. Under these conditions, small sounds were sufficient to wake the observer. Thus all nearby hyaena whoops were heard and recorded between the evening and morning tracking sessions.

North

The community resident at Fika Futi camp (see Fig. 3) was recruited to note whether or not they heard hyaena calls each night. These observations were then recorded by M.Sekoba. With the human activity associated with this camp, and as the observers slept indoors, only calls of hyaenas close to camp were noted.

Results

Hyaena calls were heard both in the north and in the south. The frequencies with which calls were noted in the two areas are summarized in Table 16. The approximate positions of all calls heard in the south are presented in Fig. 38.

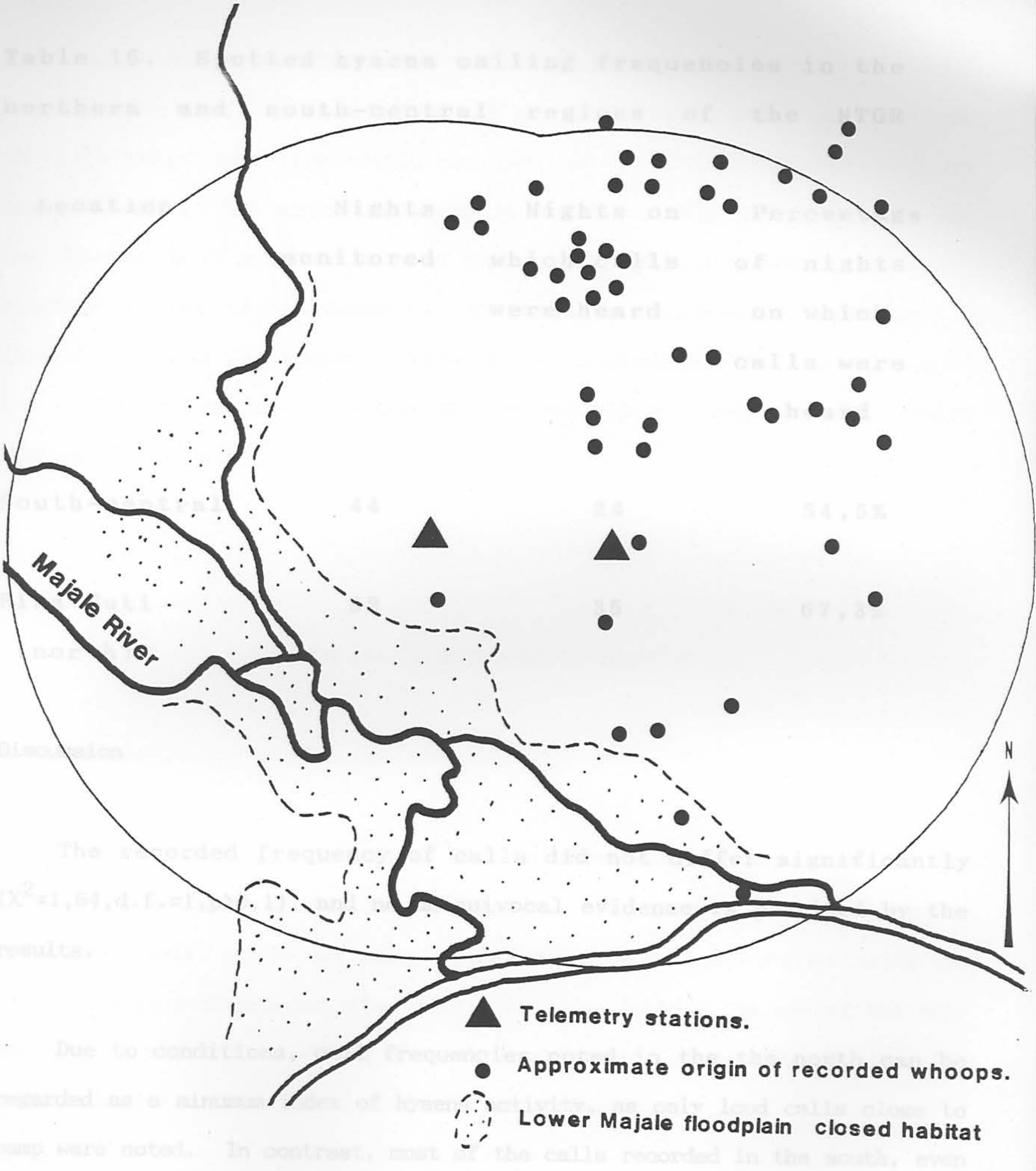

Figure 38. Points of origin of spotted hyaena calls recorded from telemetry stations in the south-central region of the NTGR between 01/03/88 and 15/06/88. Outline represents radius of 3,5 km from telemetry stations, within which 95% of calls were heard.

Table 16. Spotted hyaena calling frequencies in the northern and south-central regions of the NTGR

Location	Nights monitored	Nights on which calls were heard	Percentage of nights on which calls were heard
South-central	44	24	54,5%
Fika-Futi (north)	52	35	67,3%

Discussion

The recorded frequency of calls did not differ significantly (X^2=1,64,d.f.=1,p>0,1), and no unequivocal evidence is provided by the results.

Due to conditions, call frequencies noted in the the north can be regarded as a minumum index of hyaena activity, as only loud calls close to camp were noted. In contrast, most of the calls recorded in the south, even when the observer was woken by the call, were made more than two kilometres away.

The distribution of calls heard in the south is noteworthy (Fig. 38). The joined circles in the figure represent a radius of 6 km from the two stations, within which 95% of the calls were heard. The majority of calls were heard to the north or north-east of the jackal study area - only 6 of the 50 calls heard were from within the part of the study area traversed by vehicle tracks. The marked dichotomy is evident in Fig. 38, and reinforces the observation of a higher level of hyaena activity in northern as opposed to southern sectors of the Reserve. It would be a subjective excercise to separate the data for purposes of statistical comparison. The significance of the scarcity of calls from within the central Majale floodplain will require further investigation.

SECTION 4 - TELEMETRY/RADIO TRACKING

Introduction

Radio collaring of hyaenas did not form part of the jackal study. However, a suitable collar was available. Thus, when the opportunity presented itself, on the one occasion when a hyaena was encountered during the jackal trapping excursions, the radio collar was fitted. As one of the very few hyaenas encountered within the jackal study area, it was intended that its movements within the study area should be determined.

Materials and methods

Capture

The hyaena was darted from a vehicle on 23/11/1987 using a modified Telinject Vario 1V dart pistol (Telinject SA, Randburg, RSA). Drugs administered were 3 mg etorphine hydrochloride (M99, Rickett and Coleman Pharmaceuticals, Pinelands) and 30 mg xylazine hydrochloride (Rompun, Bayer Pharmaceuticals, Johannesburg) (van Jaarsveld, McKenzie & Meltzer 1984).

Radio Collar

The radio collar was constructed from 50 mm wide machine belting. The van Urk (G. van Urk, Potchefstroom University, Potchefstroom, RSA) transmitter with a 25 cm antenna was connected to a size D lithium battery (Israel Electronics Industries, Tel Aviv, Israel), and potted in Araldite potting fluid (Araldite CW 1312 GB & HY 1300 GB, Ciba Geigy Plastics, Cambridge, UK). The collar was affixed around the neck of the hyaena using pop rivets.

Location

The frequency of the radio collar was incorporated in the memory of the Yaesu radios used for tracking the jackals (Chapter 3). Whenever jackals were located from the top of a hill, the hyaena frequency was used to ascertain the presence and position of the hyaena. During the jackal telemetric study the hyaena frequency was searched every 20 min between 18h00 and 23h00 and between 06h00 and 08h00 from both stations for a total of 44 days between 30-03-88 and 15-06-88. The maximum reception range of the towers was 6 km. Reports by other persons who observed the collared hyaena were noted.

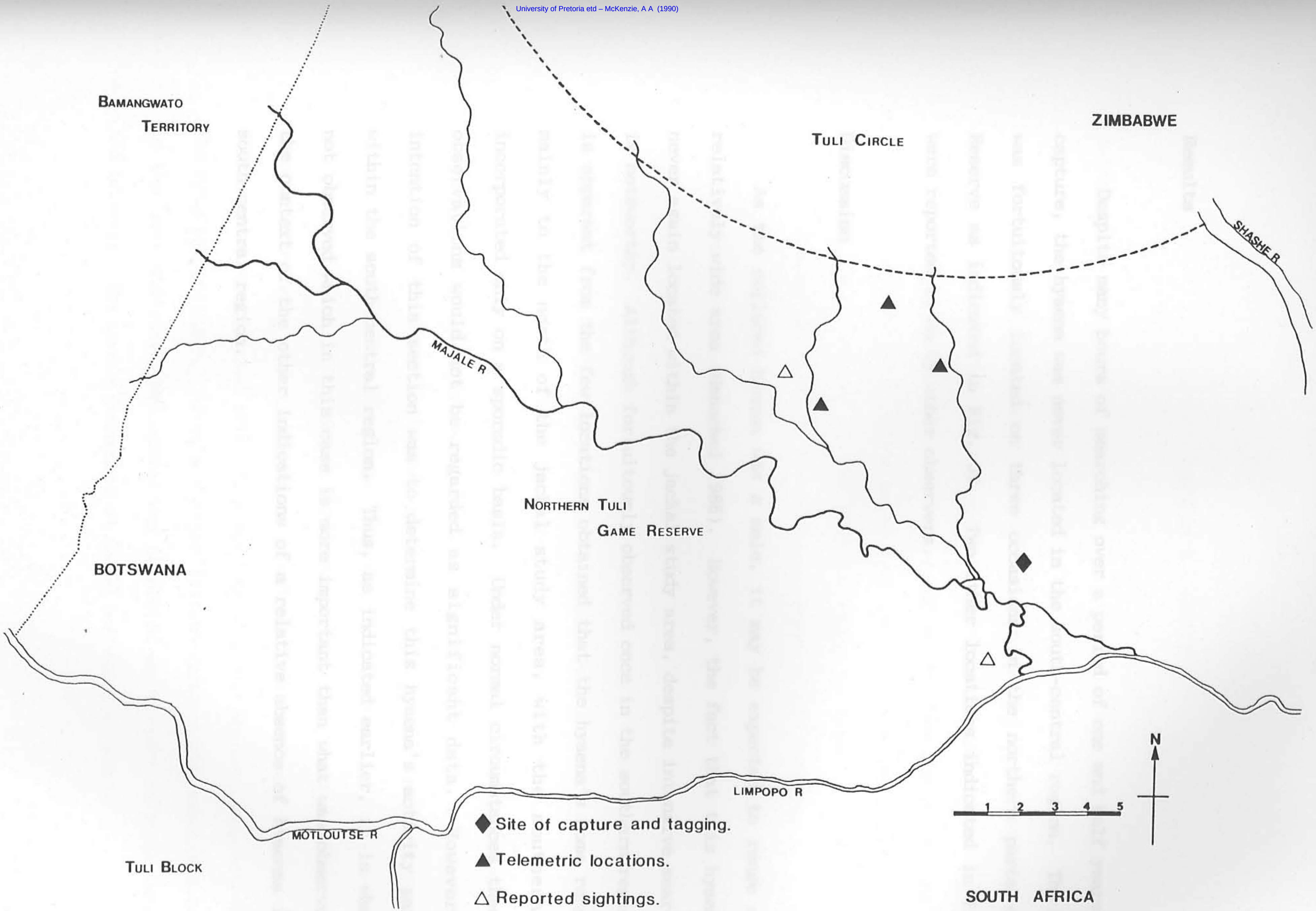

Figure 39. Location records for radio-tagged male spotted hyaena.

Results

Despite many hours of searching over a period of one and half years after capture, the hyaena was never located in the south-central region. The hyaena was fortuitously located on three occasions in the northern parts of the Reserve as indicated in Fig. 39. Two other locations indicated in Fig. 39 were reported to me by other observers.

Discussion

As the collared hyaena was a male, it may be expected to range over a relatively wide area (Henschel 1986). However, the fact that this hyaena was never again located within the jackal study area, despite intensive searching, is noteworthy. Although fortuitously observed once in the southern region, it is apparent from the few locations obtained that the hyaena's home range was mainly to the north of the jackal study area, with the southern area incorporated only on a sporadic basis. Under normal circumstances these few observations would not be regarded as significant data. However, the intention of this section was to determine this hyaena's activity patterns within the south-central region. Thus, as indicated earlier, it is what was not observed which in this case is more important than what was observed, in the context of the other indications of a relative absence of hyaenas in the south-central region.

SECTION 5 - CENSUS

Introduction

As successful scavengers, spotted hyaenas respond to any indication that a meal may be for the taking. Hyaenas can thus be induced to investigate sounds associated with feeding activity, and in this way can be counted (Mills 1985). In the context of other aspects of the present study it was decided to conduct a hyaena census of the NTGR in order to obtain an indication of relative hyaena abundance in the different areas of the Reserve.

Materials and Methods

Two open landcruisers were each equipped with a cassette tape recorder, 12V booster, 45 cm horn speaker, 2 spotlights and 4 observers. Ten sites where hyaenas would be called up in the manner described by Mills (1985) were selected to span the entire NTGR (Fig. 40). At each station tape recorded sounds of feeding hyaenas were played at maximum volume for two minutes with the horn speaker in a horizontal position. With the equipment used this sound was audible to the human ear over a distance of one-and-a-half kilometres on a still night. The speaker was then rotated 180° and the process repeated. Any hyaena calls heard or sightings made were recorded. The process was repeated after five minutes with the speaker perpendicular to the original position. After a further fifteen minutes the vehicle proceeded to the next station. The census was conducted on a night with minimal wind and no moon. The census commenced at 21h00 and ended at 04h00.

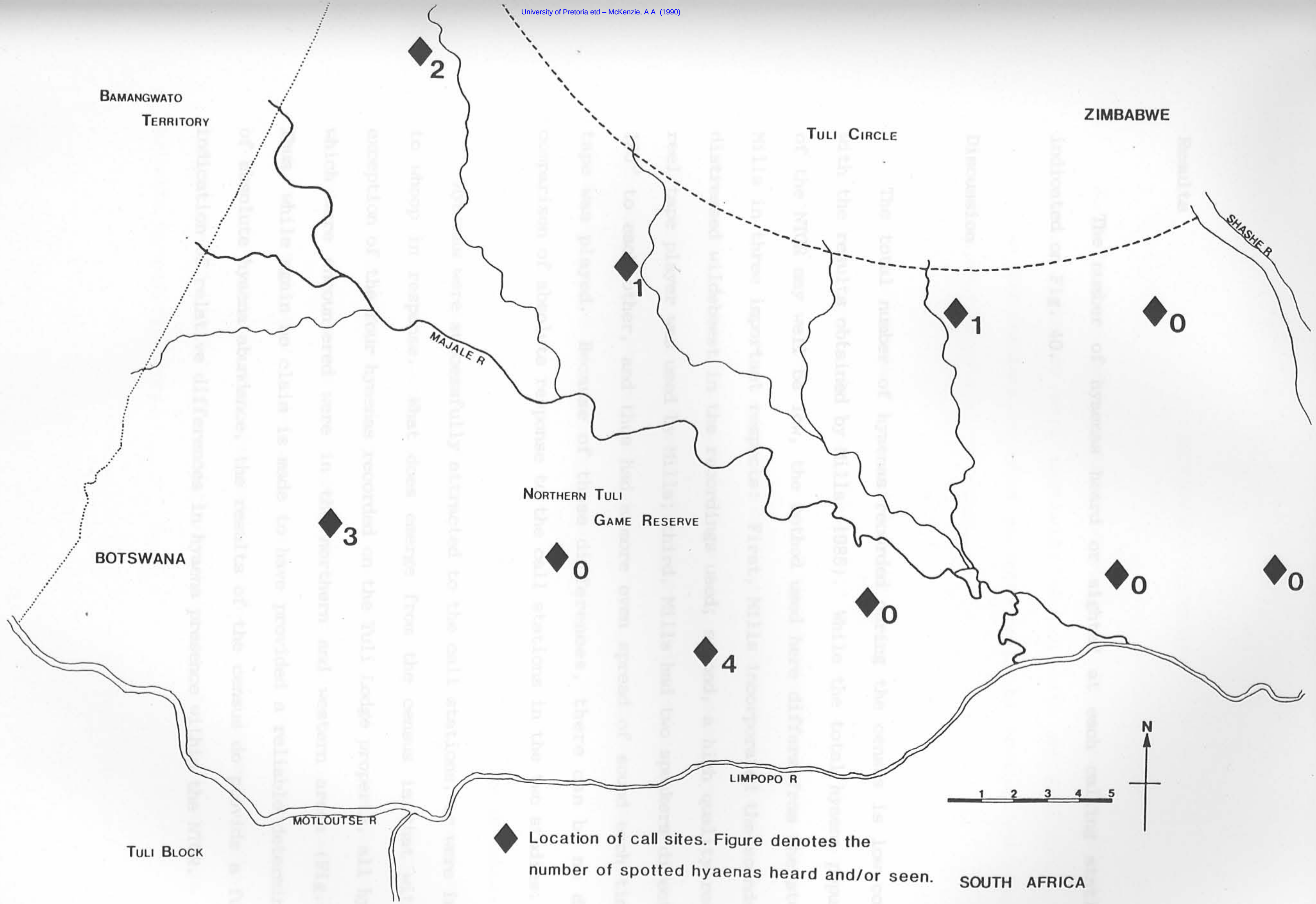

Figure 40. Call-sites and results: spotted hyaena census, 25th May 1986.

Results

The number of hyaenas heard or sighted at each calling station is indicated on Fig. 40.

Discussion

The total number of hyaenas recorded during the census is low compared with the results obtained by Mills (1985). While the total hyaena population of the NTGR may well be low, the method used here differs from the study by Mills in three important respects: First, Mills incorporated the sounds of a distressed wildebeest in the recordings used; second, a high quality reel-to-reel tape player was used by Mills; third, Mills had two speakers directed at 180° to each other, and thus had a more even spread of sound each time the tape was played. Because of these differences, there can be no direct comparison of absolute response to the call stations in the two studies.

Hyaenas were successfully attracted to the call stations, or were induced to whoop in response. What does emerge from the census is that with the exception of the four hyaenas recorded on the Tuli Lodge property, all hyaenas which were encountered were in the northern and western areas (Fig. 40). Thus, while again no claim is made to have provided a reliable determination of absolute hyaena abundance, the results of the census do provide a further indication of relative differences in hyaena presence within the NTGR.

SECTION 6 - INTERVIEWS

As part of the small community of people in the Reserve, my thoughts and developing hypotheses were naturally shared with my fellows. Their interaction and feedback provided an opportunity to develop and change my ideas about many aspects of the study.

An acceptable method of research is to conduct interviews in which people are asked directed questions without any indication of what answer the researcher may be expecting. In view of the abovementioned circumstances, it was not possible, once the importance of hyaena distribution to the study had become apparent, to conduct blind interviews. And, unfortunately, it is only those people who were resident in the Reserve and spent a large proportion of their time in the central and northern areas at night who could provide a reliable assessment of relative hyaena densities.

With the abovementioned limitations in mind, the following people were specifically interviewed on this subject: Fish Maila, Solomon Talana, Johannes Nare, John Modeme, Gareth Patterson, Mark Fraser-Valentine, Geoff Dyer and Kim Wolhuter. Each person was asked where in the Reserve they encountered most hyaenas. They were then asked specifically to recall whether they had seen hyaenas in the south-central region. Each of the people thus interviewed indicated that they rarely, if ever, saw hyaenas in the south-central region, while their sightings of hyaenas in the north were of a moderate to high frequency.

WILD DOGS

Lind (1974) reported that wild dogs were extinct in the NTGR. During the three-and-a-half years of my residence in the Reserve I never personally saw, or heard of, any wild dogs in the Reserve. On one occasion in 1986 there was an unconfirmed report of wild dogs on a nearby farm (Faurie pers. comm.). If these were indeed wild dogs they did not enter the Reserve, nor were they subsequently reported from any other nearby areas.

GENERAL DISCUSSION

While each observation in this section on its own does not constitute irrefutable evidence, the combined result of the various studies discussed above is that the observed paucity of hyaenas in the south-central region has been firmly established. The total absence of wild dogs from the NTGR was also confirmed.

The reason behind the relative absence of hyaenas in the south-central region may indeed be very complex. If one looks for an immediate answer in the present environment, there may be several factors which could play a role. The level of lion activity in the south-central region is the highest in the Reserve (Patterson 1988). As lions and spotted hyaenas are competitors, there may be cause to invoke competitive exclusion as the reason for the inverse relationship. However, there is no evidence from other studies to indicate permanent exclusion of hyaenas by lions or *vice versa* (Kruuk 1972, Schaller 1972, Henschel 1986). If anything, a high level of lion activity results in a higher availability of scavengeable resources, thus resulting in at least a potentially positive effect on hyaena numbers. The distribution of antelope

W. Faurie, Sydney-on-vaal Farms, P.O. Longlands, RSA.

biomass in the Reserve, with far higher numbers of potential prey species in the south-central region than elsewhere (Joubert 1984) also suggests a potentially attractive environment for hyaenas.

As there is no physical barrier between the northern and southern regions of the Reserve there appears to be no immediate factor which would unequivocally explain the discrepancy in spotted hyaena numbers between the adjacent regions.

In looking for an ultimate solution to the enigma, however, the history of the Reserve becomes highly significant (see Chapter 2). Prior to becoming a reserve, the northeastern Tuli Block was a cattle farming area (Lind 1974). It is only its present protected status which allows the existence of the wild fauna in the NTGR. There is, however, no justification for assuming that all species have responded equally to the transition from cattle farm to "wilderness" area. Thus, for example, the white rhinoceros *Ceratotherium simum*, wild dog, roan and sable, previously found in the area, remain extinct to this day (Lind 1974, pers. obs.). Giraffe were re-introduced in 1984 (McKenzie 1985) - otherwise this species would also be extinct in the NTGR. Impala increased rapidly to reach an estimated maximum of 22 000 (Walker 1983). Other species are placed somewhere in the continuum from extinct to over-abundant - each species being subject to different biotic and abiotic influences in the recovering ecosystem.

Farming activities are destined to conflict with nature. There is evidence of intensive human pastoralism in this region of the Limpopo valley since 800 AD (Voight & Plug 1981, Voight 1983). Voight (1983) records that there were large numbers of domestic stock associated with the Mapungubwe settlement at the junction of the Shashe and Limpopo Rivers which, as Voight states (p1) was, from the point of view of human movements, contiguous with the present-day Northern Tuli Game Reserve. The most intensive recorded human activity in the south-central region was between the mid 1800s and 1930 when the lower Majale floodplain was a large Babirwa settlement of several hundred people (Molelu 1985). While these people did not initially possess firearms, their predominantly pastoral activities must have resulted in conflict with the large predators encountered in the area, as evidenced by the ruins of a large number of kraals found in the area (McKenzie 1987, pers. obs.). Kraaling is a defensive means of avoiding the depradations of large carnivores on vulnerable domestic stock. With the arrival of European settlers, firearms became available, shortly to be followed by European occupation of the land and commercial cattle farming.

Without pointing any accusing fingers, it can be assumed that, as in all other farming areas of Africa, large predators were persecuted by pastoralist and farmers alike to the point where their depredations on livestock were of manageable proportions. Furthermore, the intensity of persecution would naturally have varied with the level of human activity, the lower Majale floodplain being the centre of settlement and farming in the region. As an example of the level of human persecution, 150 lions are known to have been shot in the area during the 1950's alone (Lind 1974). Recorded human depradation on wild dogs in the region extends back to 800 AD (Voight 1985:19, 37). This extended to within historical times when a bounty system ensured human persecution of wild dogs in the present-day NTGR (Lind, 1974) and in adjacent areas of Zimbabwe (Skinner pers. comm.).

J.D. Skinner, Mammal Research Institute, University of Pretoria, Pretoria, RSA.

When farming and most of the hunting ceased in the NTGR in the mid-1960s, the fauna of the region were depauperate. Game numbers gradually increased to reach a maximum in 1983 and, with this, predator numbers also increased. Large predators, as judged by sightings, were almost non-existent in 1965, but increased exponentially as conditions improved (Steyn pers. comm.). Naturally enough, lion and leopard sightings were most notable, and an increase in sighting frequency was taken as a sign of general improvement. However, the wild dog remained, as it does to this day, extinct in the NTGR.

There are no records to indicate progress as regards changes in spotted hyaena numbers over the years. As avid predators of domestic stock, hyaenas would not have been immune to persecution. In assuming that the spotted hyaena would mirror the response of the lions and leopards to improving conditions, an important aspect of hyaena biology may be overlooked. As indicated earlier in this chapter, absence is a difficult parameter to quantify. However, both Kruuk (1972) and Henschel (1986) have noted that spotted hyaenas are slow to recolonize areas where they have previously been persecuted by man. However, together with indications that brown hyaenas may have long social memories in relation to territorial boundaries (Skinner & van Aarde pers. comm.), these studies indicate that assumption of an automatic recolonization of an area by hyaenas may be simplistic. In particular, there are no grounds to assume that hyaena populations will "bounce back" following persecution, as asserted by Thomson (1986).

If indeed social memory is operative in the re-colonization by spotted hyaenas of the NTGR (McKenzie 1989c), then this would explain:

1. The relatively low densities of hyaenas in most parts of the NTGR;

E. Steyn, Stillenacht, Steyn ave, Kelvin, Johannesburg, RSA.

2. The flight responses of many hyaenas encountered in the Reserve, despite heavy "friendly" vehicle activity over several years;

3. The observation that hyaenas enter the south-central region when there is unlikely to be any human activity; and

4. The relative paucity of hyaenas in the south-central region and, in particular, the absence of denning activity in this area.

Indeed, as any hunting of hyaenas in the past would almost certainly have taken place at night with the use of a spotlight, the presence of vehicles with spotlights at night in the south-central district may in fact be reinforcing the negative association with this area which has, historically, always been the area of greatest human activity.

It is instructive to consider the area on the Tuli Lodge property where hyaenas are regularly seen. Sightings here are so regular, and the animals are so tame, that the negative influences described above appear not to have affected this clan of hyaenas. However, within recent times hyaenas were encouraged to frequent this area by regular feeding for game viewing purposes (Fuhr pers. comm.). This activity extended over several years, and the remains of the antelope carcases can be found there to this day (pers. obs.). Contrary to refuting the above scenario of negative associations, this observation lends credibility to the hypothesis that hyaenas are highly sensitive to interactive associations. In this case a positive association with man has led to permanent settlement by the hyaenas in this specific area, directly adjacent to an area where hyaenas are almost never encountered.

M. Fuhr, Tuli Lodge, Northern Tuli Game Reserve, Botswana.

GENERAL CONCLUSION

The important outcome of this chapter is the confirmation that there are no resident, and only a very few itinerant spotted hyaenas in the south-central region of the NTGR, and that wild dogs remain extinct in the Reserve. The repercussions which this has had on the processes within the Reserve are discussed in Chapter 7.

This superficial study of the hyaenas of the NTGR does not confirm in any substantive way the role of social memory in spotted hyaena biology. It does, however, add weight to the increasing body of evidence that spotted hyaenas do not simply react to immediate changes in their environment, but are strongly influenced by ultimate factors, including historical associations.

CHAPTER 6

AUTOGENOUS ALOPECIA

Introduction

During the course of the present study a syndrome of partial hairlessness was identified in impala, kudu and steenbok. This syndrome was ascribed to the animals' own grooming efforts, and was thus named "autogenous alopecia". This chapter is comprised of a synthesis of the results of the *post mortem* examination of twelve impala, one kudu and one steenbok in which this condition was diagnosed.

Pathology

Macro-pathology

Integument

General appearance

From a distance the animal appears mottled. In its mildest form this mottling is restricted to the side of the thorax, abdomen and upper hind legs. In the severest cases almost the entire body is affected. This mottled appearance is most apparent in the impala and steenbok which are normally a reddish-brown colour; it is less apparent in the kudu which has a greyish-brown pelage.

On closer inspection it is apparent that the mottling can be ascribed to the exposure of the skin due to the partial or complete lack of hair, the baldness being variable in degree and distribution. The black colour of the skin contrasts strongly with the remaining pelage in the impala and steenbok, and less strongly in the case of the kudu. In severe cases the appearance can best be described as extremely ugly.

Degree of alopecia

The alopecia may be partial or complete. In areas of partial alopecia some of the normal hairs remain, and the skin is visible in proportion to the density of the remaining pelage. The partial alopecia is usually uneven in extent, resulting in considerable variability in the colour and appearance. In areas of complete alopecia the total absence of hair exposes the black colour of the skin. On one impala an area of complete alopecia on the lateral abdomen was interrupted by an area of ± 1 cm^2 of relatively normal pelage which contained one engorged adult female tick (*Boophilus decoloratus*). This area lay caudo-dorsally to a protruding cicatrice of approximately the same size which itself was devoid of hair. Occasional areas of partial alopecia are characterised by the presence of many short hairs of approximately the same length, imparting a velvety appearance to these areas.

Distribution of the alopecia

In the mildest cases alopecia is limited to the sides of the body and in these cases is always partial. In severe cases the alopecia, partial or complete in degree, extends over the entire body, with the constant exception of the head and the neck cranial to the spine of the scapula. In the severest cases the pelage of the neck may be sparse with occasional small bald spots, and there may also be small bare spots on the head. However, even in these cases it is apparent that the pathology is minimal in the head and neck region relative to the rest of the body. Even in the worst cases the tail and metatarsal glands remain well haired, and the lower limbs are less affected than the rest of the body, with the exception of the head and neck area.

Remaining hair

Hair which is present on partially affected areas is usually of normal length and appearance, with the exception of those areas which exhibit evenly short hairs. Remaining long hairs often epilate more easily than would be expected, particularly in the neck region. However, at other times and at other places on the body the hairs appear normally bedded and do not epilate easily. Attempts to obtain an "epilation index" have proved futile because of this variability and also because of the difficulty in exerting a repeatable "epilation force". Nevertheless, the subjective impression is that some of the remaining hairs are more easily epilated than in unaffected animals.

The skin

Completely exposed skin is smooth, clean and supple, and is of an even black colour. No signs of exudation, crusting, thickening, bleeding or fissuring are associated with this syndrome. The skin in partially alopecic areas usually has the same appearance. Occasionally, in the severest cases, exfoliation of the skin is apparent in the partially alopecic areas. The whitish scales are thin and loose, and are easily removed.

Ectoparasites

All affected animals carry large numbers of ticks on those areas where some pelage remains. The abnormally high numbers of adult ticks, particularly of engorged adult female ticks, is particularly conspicuous. In the impala examined in 1986 high levels of louse activity was evident in the long haired areas of the metatarsal glands and the tail. This was characterised by the presence of a large amount of debris, louse exoskeletons, louse eggs and active lice. This exceptionally heavy infestation was not apparent in the animals examined in 1988.

Dentition

In all cases exhibiting alopecia there is some degree of attrition of the incisor-canine complex. There is a strong correlation between the degree of attrition and the severity of the alopecia in animals collected at the same time of the year. The attrition of the teeth is in the vertical plane, affecting the most lateral elements first and progressing to affect the central element - I_1. Horizontal feeding-related attrition is also evident on I_1 if it is not totally worn by the vertical mode of attrition. Attrition is first evident on the tips of the teeth. Later attrition is also evident in the neck region of the teeth in the form of a groove parallel to the plane of the gingiva on the caudal aspect of the teeth.

In the mildest cases moderately advanced vertical attrition of the lateral elements is evident, to the extent that the crowns of these teeth are reduced to approximately half of their original height. The stumps of the teeth are smoothly polished in the vertical plane. In the most advanced cases all of the anterior dental elements are completely worn to below the gumline. In no case were teeth found to be lost; attrition is simply so advanced that nothing remains of the crown. The remaining stumps are smoothly polished and oval to round in shape, and in the fresh specimen the surfaces of all these stumps are below the surface of the surrounding gingiva. In intermediate cases the elements are progressively worn, commencing with the most lateral element - the incisiform canine. Due to the presence of the two apparent points of attrition described above, the remaining teeth of some of the intermediate cases exhibit unusual shapes. The neck-region attrition is evidenced by deep grooves in the neck region of the teeth - in the most advanced cases of this mode of attrition only a small section of the neck remains to connect the root to the remaining crown.

Other findings

Condition

Animals exhibiting autogenous alopecia are in poor condition. In general they are in poorer condition than normal animals, as evidenced by a low Kidney Fat Index and by serous atrophy of fat in late winter. The difference may become obscured at the end of a long winter when all animals may be in extremely poor condition.

Haemopoiesis

A variable degree of haemopoiesis is evident on inspection of the bone marrow. Some animals display a considerable degree of such haemopoietic response while this is less evident or even absent in other animals.

Internal parasites

A subjective assessment of all the cases examined suggests that affected animals carry a greater burden of tape worm cysts in the musculature and in the internal organs, as well as cestodes (*Stilezia sp.*) in the bile duct and liver. Again this feature is highly variable and is difficult to quantify, but is most noticeable in animals that are in extremely poor condition.

Pale musculature

In some of the most advanced cases in extremely poor condition the striated musculature of the entire body displays a pale discolouration and is abnormally friable. In addition, the carcase of these animals has a strange, rancid smell which is evident immediately after slaughter.

Histo-pathology - skin

Histological examination confirms that there is no marked inflammatory process evident in the epidermis of affected animals. There is also no evidence of any mite activity in the skin.

Almost all hair follicles are in the telogen (inactive) phase. Occasional deep follicles are in the anagen phase. Follicles are generally devoid of hair, or the hair shaft is broken off below the surface of the epidermis. (In normal animals collected at the same time of the year (September) most follicles were also in the telogen phase, but the hairs were retained in the follicles). Hair follicles are otherwise normal.

Sub-epidermal blood vessels exhibit thickening of the walls and a moderate to severe perivascular round-cell and eosinophil infiltration. (This is, however, also evident in clinically normal animals).

Pathological anatomical diagnosis

1. A high external parasite infestation associated with variable alopecia of the entire body, with the exception of the head and neck region which is relatively unaffected.

2. Partial or complete absence of anterior dental elements associated with a vertical plane of attrition.

3. Poor body condition and variable degrees of anaemia and internal parasitism.

Aetiological diagnosis

The vertical attrition of the anterior dental elements is due to the prolonged use of these teeth for grooming purposes. Two sources of abrasion operate during the grooming activity. One is active on the tips of the teeth which are rubbed against the surface of the skin during grooming. The other is active on the neck region of the teeth due to the hairs being pulled between the teeth. Individual variation determines which abrasive action is responsible for the final total attrition of the individual teeth. Continued use of the remaining stumps results, through the rubbing mode of abrasion, in attrition of the remaining stumps to below the level of the surface of the gingiva.

Continued use of the partially or totally worn teeth for grooming purposes is no longer effective in removing parasites from the pelage, resulting in a high external parasite burden. The irritation caused by the persistent presence of the parasites coupled with the high parasite numbers results in continued grooming efforts. The persistent grooming efforts result in the epilation or fracture of the hairs, leading to partial and eventual complete alopecia. (Development of patches of alopecia following excessive grooming activity has previously been recorded in mice which are unable to effectively remove parasites due to limb disabilities (Bell, Jellison & Owen 1962, Bell & Clifford 1964), and in moose which experience heavy tick burdens in winter (Glines & Samuel 1984).) The loss of hair may be facilitated by the fact that the hair follicles are in telogen phase in winter. The poor condition of affected animals may exaggerate the looseness of the telogen hairs, further facilitating their epilation. Only those parts of the body which can be reached by the mouth are affected by this process - hence the normal appearance of the pelage cranial to the spine of the scapula.

Tests for possible nutritional causes of alopecia were undertaken on impala exhibiting this syndrome in the Kruger National Park, RSA, by Dr N. Fairall (Fairall *in litt*) during the 1960's. No indication of an alternative cause for the alopecia was identified by these tests, and in fact the cause of the syndrome had remained unidentified until the present study.

The areas of even-length short hairs is suggestive of new, synchronized hair growth. The existence of these hairs may reflect the fact that new, actively growing hairs are not epilated easily or, alternatively, that parasitic irritation has been reduced resulting in a cessation of the repeated grooming efforts that are responsible for the epilation.

Once the pelage is removed, exposed parasites are likely to be removed even by the worn teeth, resulting in the restriction of ticks and lice to those areas which retain some peleage and thus offer some protection. The long haired parts - the tail and the metatarsal glands - remain well covered and retain large numbers of parasites. Exposure of the skin to sunlight is likely to result in UV irritation despite the black colouration, possibly explaining the mild cases of exfoliation recorded.

The ability to remove parasites - and thus the source of irritation - is likely to be correlated to the percentage of dentition remaining. For this reason alopecia is worst in those animals with no teeth, and is less severe in those with only mild to moderate degrees of attrition.

The poor condition is a reflection of the effect of the annual winter dry season on the level of nutrition. The relatively poorer condition of affected animals is likely to be due to: 1. A compromised ability to ingest herbage due to the relative or total absence of the anterior teeth; 2. An increased expenditure of available energy on ineffective grooming efforts; and 3. The general stress syndrome precipitated by the parasaite irritation, loss of condition, and associated derangements in physiology.

Haemopoietic response indicates a responsive anaemia, and is likely to be related to the high but individually variable degrees of external and internal parasitism.

High levels of internal parasitism may reflect compromised immunocompetence due to poor condition and the correlated adrenal hypertrophy (Chapter 4, present study). Alternatively, or in addition, affected animals may somehow be exposed to a greater infestation risk via unidentified processes.

The pale friable musculature of severely affected animals is likely to be a reflection of the advanced state of cachexia as well as the anaemic condition of these animals

The thickening of the sub-epidermal blood vessel walls and the associated round-cell and eosinophil infiltration are suggestive of a chronic exposure to ectoparasite allergens.

CHAPTER 7

EVOLUTIONARY ASPECTS, ECOSYSTEM PROCESSES, AND IMPLICATIONS

INTRODUCTION

Up to this point this thesis has been concerned with the description of the methods and results of various investigations into the community of species co-existing in the northeastern Tuli Block of Botswana. The results have been discussed within the constraints of the particular fields of investigation, and Ockham's Razor has determined that only limited conclusions could be drawn from the results obtained.

What the thesis has thus achieved is a description of a particular pattern, or a particular group of patterns, within a specific temporal and spatial framework. After all, every study refers only to a minute sample of the real world. However, the patterns we see are merely a reflection of the disparate and innumerable processes that underly the fuctioning of every living system. To ignore these processes and to describe only the patterns is to deny the fundamental reality of the biological world. Yet to speculate about processes that have not been specifically studied and identified would be to ignore the constraints of scientific discipline. Yet again, as a Doctorate in Philosophy, this investigation requires a thorough consideration of the philosophical implications of its findings in a manner not permitted by the precise world of published scientific literature.

In order to fulfil the philosophical obligations of this thesis, this chapter is devoted to discussing the implications of the findings of the earlier chapters with unfettered abandon. Once thus recorded, these thoughts may provide the spark for future fires. Unspoken, they would certainly fade, falter and perish with the passage of time. Though I can never pretend to understand the intricacies of the system I have studied, I hope that this holistic discussion will provide some insights into how the different aspects of the study became intertwined to the point where the whole became much greater than the sum of its parts.

EVOLUTIONARY ASPECTS

Jackals and co-operative hunting

Black-backed jackals have been a component of the African ecosystem for over two million years (Wayne, van Valkenburgh, Kat, Fuller, Johnson & o' Brien 1989). The facets of jackal ecology highlighted by the present study are thus a reflection of the evolutionary processes acting on and within the diverse community of African fauna throughout this period.

As a group, the Canidae are particularly well suited to the development of co-operative hunting for the capture of large prey. This can be ascribed to:

1. The absence of morphological adaptations for the efficient killing of large prey by a single animal(such as is commonly evident in the Felidae;

2. Long legs and a cursorial habit facilitating a prolonged chase and eliminat alternative method of close approach - concealment in trees; and

3. A social system wherein strong social bonds exist between the adults and their offspring.

It is the latter trait which facilitates the mutual tolerance between canids at clumped resources and may have facilitated the development of the larger social groups characteristic of the wolf *Canis lupus*, the dhole *Cuon alpinus*, the wild dog *Lycaon pictus* and the bush dog *Speothos venaticus* (Kleiman & Eisenberg 1973). In jackals, the increased family group size and the phenomenon of helping by young from the preceding season are also associated with a well developed social structure (Moehlman 1983).

Wayne *et al.* (1989) have suggested that the similarity in size and morphology between the three sympatric African jackal species, *C. adustus*, *C. aureus* and *C. mesomelas*, is a reflection of the evolutionary processes operating within the rich assemblage of African carnivores. The constraints imposed by the presence of a diverse array of both larger and smaller carnivores in the African environment has resulted in an almost complete absence of morphological divergence between these three species during a period of co-existence spanning over two million years. This is in stark contrast to the marked morphological divergence within less than 250 000 years in South American canids which were not subjected to such restrictions (Wayne *et al.* 1989). If the morphological traits of black-backed jackals reflect these evolutionary constraints, then there can be little doubt that the social and ecological parameters of of this species have been similarly shaped. However, as is typical of the medium-sized canids (Kleiman & Eisenberg 1973), jackals are generalized feeders, and their diet at any particular place and time reflects their adaptibility on an immediate day-to-day time scale.

Furthermore, the ability of the medium-sized canids to adjust their social system within a short time is also reflected in their ability to utilize clumped resources or large prey through increased co-operation (MacDonald 1979, Bekoff & Wells 1980, Bowen 1981).

In considering the results of the present study, the evolutionary background of the jackal is of significance. As demonstrated in Chapter 3, the harassment and killing of impala in the NTGR is undertaken by groups of jackals considerably larger than the average social group. The question that remains is: Why are these aggregations only temporary? Why have the jackals not resorted to living in packs on a permanent basis? Coyotes have been recorded to resort to pack-living when utilizing larger prey (see Chapter 3). Even the golden jackal, under conditions where a reliable source of food is available, has been recorded to resort to pack living (MacDonald 1979). Is the absence of pack living in the presence of an abundant source of food therefore an indication that the jackal differs from other canids in being unable or unwilling to resort to group living?

Lamprecht (1978b) discussed the possibilities of group hunting in jackals. He speculated that the formation of packs by jackals would depend on: 1. The need for two or more individuals to capture and kill the prey; and 2. The absence or scarcity of scavengers stronger than the jackals themselves. The latter was supported by the findings of MacDonald (1979) which were published shortly thereafter wherein golden jackals were recorded to form packs in the absence of any larger carnivores. Pack formation by coyotes is related to the hunting of large ungulates and the defendability of the carcases against other groups of coyotes. This condition is not met under normal conditions in the the African savanna where predators far larger than the jackal abound, which would make defence of a carcase by jackals a dangerous and futile exercise.

Lions and leopards and even occasional hyaenas remain active members of the community of the south-central NTGR. Their presence is thus likely to explain why, even in the presence of a superabundant resource in the form of old, weak impala, the jackals of the Reserve do not display any inclination towards entrenched group living. This deduction is reinforced by the observation, made on many occasions, that the jackals on impala kills were extremely nervous - far more so than when otherwise observed - a reflection, as suggested by Lamprecht (1978a), of their awareness of the potential danger from larger predators. The formation of the packs remains an opportunistic, stochastic event which in this form does not attract undue attention by the larger predators. Jackals in this region have thus escaped the constraints suggested by Lamprecht by a system not previously considered - i.e. the advantages of group living are exploited, while at the same time the disadvantage of attracting attention is avoided by the temporary nature of the group formation.

Competition, therefore, remains a process of considerable importance in the maintenance of the predation pattern recorded during the present study. The presence of the larger predators is likely to be a major factor limiting the emergence of group living in the jackals of the NTGR. However, modification of the large predator community in any way could alter the dynamics of this process, and the observed pattern could, given the potential flexibility of jackal social organization. change substantially from that recorded here.

It is interesting to note that a feature of the well-developed social structure of the wolf is the diverse array of visual, auditory and olfactory communication signals typical of this species; asocial small canids exhibit only a limited communicative ability (Kleiman & Eisenberg 1973). The jackal, while not normally a pack-living canid, utilizes a large number of well developed communication signals (Ferguson 1980, Moehlman 1983). The existence of this entrenched communicative repertoire could represent a pre-adaptation, or exaptation (Gould & Vrba 1982) facilitating the formation of larger co-operative groups under appropriate circumstances while at the same time facilitating a communal response to changing predation pressures, for example the frustratingly ineffective persecution by man. Through this social flexibility the jackal as a predator cannot be classified as a searcher, pursuer or subduer (Griffiths 1980); it is in reality each of these or all of these, depending on the immediate environmental constraints and opportunities. The development of the hunting, harassment, immobilization and killing sequence recorded in the present study is thus no more than a testament to the jackals' ability to respond and adapt on an immediate, rather than on an evolutionary time-scale - an extension of its evolved ability to co-exist in small family groups.

Ungulates and host-parasite coevolution

Janzen (1980:611) has defined coevolution as "an evolutionary change in a trait of the individuals of one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first". In the field of host-parasite relationships selective pressure exerted by the host is often evident in the parasite, but the converse effect on the host is less often demonstrated, particulary in the case of animal parasites (Kim 1985, Timm & Clauson 1985).

Mammalian ectoparasites, such as ticks and lice, exhibit an array of adaptations to their parasitic mode of life. Among these are those adaptations - long, barbed mouthparts, claws, a strong cuticle, and dorsoventrally or laterally flattened bodies - which afford physical protection and facilitate firm attachment to the host. If the primary function of grooming behaviour is accepted as the maintenance of the appearance and integrity of the pelage (Timm & Clauson 1985), then these adaptations can logically be ascribed to the evolutionary pressures eliciting a response to the threat of physical removal during this non-specific activity. If, on the other hand, the grooming behaviour is directed at the removal of parasites from the pelage, then one may expect a coevolutionary response in the host animal to the well-developed holdfast abilities of their respective parasites.

Many mammals possess specialized morphological adaptations which are used for grooming: claws on the hind feet of prosimians and kangaroos (DuBost 1970, Croft 1980) and the tooth-comb of lemurs (Cuvier & St. Hilaire 1825, Rose, Walker & Jacobs 1981). The present study demonstrated that small to medium-sized browsing and mixed-feeding ruminants utilize the lateral components of their incisor-canine complexes for grooming purposes. Does the latter constitute a coevolutionary response to parasitic infestation?

The gene-for-gene concept is used to detect coevolutionary relationships in host-parasite systems (Kim 1985). "A gene-for-gene relationship exists when the presence of a gene in a population is contingent on the continued presence of a gene in another population, and where the interaction between the two genes leads to a single phenotypic expression by which the presence and absence of the relevant gene in either organism may be recognized" (Person, Samborski & Rohringer 1962:562). The present study has provided evidence that the phenotypic absence of the dental comb (in animals with completely worn IC complexes) is accompanied by dramatically increased numbers of ectoparasites on the host, particularly in the well-haired parts of the pelage. The ineffectiveness of the grooming behaviour in the absence of the dental comb thus negates the threat of physical removal to the parasites. If these conditions persisted through true genotypic absence of the dental comb, the frequencies of the genes for the holdfast characteristics of the parasites could conceivably be subject to dimunition.

While the present study thus does not provide robust proof of a coevolutionary origin for the ruminant dental comb, current ecological relationships indicate that, whether by adaptation or exaptation, this structure is intricately involved in the host-ectoparasite relationships of impala and other mixed feeding and browsing ruminants. If not its origin then its persistence, in many diverse species, is suggestive of a strong coevolutionary relationship.

ECOSYSTEM PROCESSES

For the purposes of this discussion, the following are taken as axiomatic:

1. That change is the only constant in the natural world;

2. That patterns observed in ecosystems reflect the underlying processes within those systems, but that identification of a pattern does not imply identification of the responsible process (Cale *et al.* 1989);

3. That a pattern observed in an ecosystem is subject to chaotic forces, and that the development of a particular pattern is highly dependent on the original state of the system (Jensen 1987, May 1989);

4. That the driving force behind all ecosystem processes is the Second Law of Thermodynamics - implying that disruption of any one process within a system has a domino effect on other processes within the system; and

5. That meaningful conservation of any system depends not on the conservation of the components of the system but on the conservation of the processes operating within and upon the system (Ricklefs, Naveh & Turner 1984).

Most of the processes operating within the ecosystem represented by the NTGR are not reflected in the findings of the present study. Others are represented but remain unidentified due to the limitations of the human mind. The following process complexes were identified as playing an important role in the development of the emergent pattern referred to as the Northern Tuli

Game Reserve.

Selective Predation by Jackals

Chapter 3 described and recorded the co-operative, selective predation by jackals on adult impala in the south-central region of the NTGR. As a recorded pattern, these results were very interesting in themselves. But what are the underlying processes which have resulted in the emergence of a pattern not previously recorded in Africa?

As indicated at the end of Chapter 3, one of the possible reasons for this may be the paucity of information on jackal predation derived from direct observation. While this is certainly a factor to be considered, it does not account for everything. The high percentage of old impala in the south-central region, as identified in Chapter 4, and the predominance of these old impala in the jackal prey data suggest that other underlying processes have given rise to a situation peculiar to the NTGR.

Predators have long been accredited with maintaining the health and fleetness of their prey populations by removing the old, the weak and the sick (Errington 1946, Curio 1976) - in effect selectively removing "physiologically" old animals from the system. This was termed the "sanitation effect" by Mech (1970). This "sanitation" effect implies, of course, a process of selective predation. Not all predators are selective all of the time, however, and this broad generalization of the beneficial effect of predators has been the cause of extensive debate and dissension. Temple (1987) has recently suggested that predators are only selective when preying on animals which are relatively difficult to capture, subdue and/or kill. His conclusions were supported by the results of his study on the predatory habits of raptors. Reference to data on large mammalian carnivores from many sources revealed a similar trend (Temple 1987).

In considering the impala as a potential prey animal in relation to the pristine community of the eastern parts of Botswana it is apparent that predation on this species, as a medium sized antelope, was originally of several types. All the large African carnivores, including the jackal, prey on newborn and young impala. Once past the vulnerable early months, the predation threat by the different predators becomes unequal. Lions and leopards cannot hope to outrun a startled adult impala, and their tactics for concealment confirm a need to gain adequate proximity before launching an attack. Under these circumstances it is not surprising that no selectivity for old or weak medium sized antelope by these species has ever been demonstrated. Conversely, spotted hyaenas and wild dogs openly approach and "test" herds of medium sized antelope, and demonstrably select the compromised animals from the population (Pienaar 1969, van Lawick-Goodall 1970b, Kruuk 1972) although this ability seems to depend to some extent on the openness of the habitat (Reich 1981). The cheetah may or may not be selective for vulnerability. Jackals would, under these pristine conditions, be obliged to compete with the wild dogs and spotted hyaenas for the few available old impala and, being a generalist carnivore, would most likely make use of alternative resources - partly accounting for the scarcity of reported predation by jackals on adult antelope.

The pristine complement of predation processes no longer occurs in the south-central parts of the NTGR. The total absence of wild dogs and the relative absence of spotted hyaenas (Chapter 5) means that selective predation definitely does not occur in this area at a rate comparable to the pristine condition. The northern areas, with a higher population of hyaenas, retain at least a component of selective predation by large predators on prey animals of the size of the impala. While the population of cheetahs has noticeably increased in the NTGR in recent years, the population of this species was so low prior to 1984 (Lind 1974, pers. obs.) that its role in the development of the observed pattern is negligible.

Elimination of any ecosystem process imposes a perturbation on the system which induces ecosystem stress (Odum 1985). Such ecosystem stress is responded to first by an alarm reaction and then by the coping reaction (Rapport *et al.* 1985).

In the case of the south-central region of the NTGR the ecosystem stress is represented by the preponderance of old animals in the impala population (Chapter 4, Section 1). A measure of the degree of this ecosystem stress is evidenced by the fact that during the course of the study two kudu and one impala were discovered which had died of old age. In a system which originally provided for removal of weak animals by selective predation, these incidents indicated early on in the study that pristine processes were inoperative or compromised. The coping reaction of the ecosystem in this case is represented by the replacement of the selective predation process by an alternative species not normally a participant - the black-backed jackal. However, total replacement is not achieved as the jackal turns to easier prey - insects - during the wet months of the year (Chapter 3).

Predation by the black-backed jackal does to some extent compensate for the absence of the natural selective predators. The method whereby this replacement is achieved is uncannily reminiscent of the true process - recall the "testing" behaviour during the selection phase and the fact that large groups are formed during predation (Chapter 3)- the norm for wild dogs and hyaenas when hunting such prey. However, despite the established existence of a stereotyped, successful selective predation sequence, a large proportion of the impala in the south-central region remain old, have no incisors, and lose condition severely during winter, confirming that this resource is not utilized to the extent where the pristine age-structure of the prey population is maintained.

The absence of the natural selective predators of impala from the south-central region of the NTGR has therefore resulted in the pattern observed today - a preponderance of old, weak animals in the impala population and the existence of the observed selective predation by the jackals on these same old impala.

The results of the present study could be used to justify even greater efforts to remove jackals from farming areas and even private "conservation" areas. Prejudice against predators is an emotive issue that can easily become inflamed. Yet if the full implications of the highly selective nature of the jackal predation recorded here are considered, it will be realized that jackals may be a most valuable asset in an agricultural system which cannot hope to regain the original predator community. In hunting old antelope, and even in hunting sheep, jackals are expressing a profound instinct to prey upon those animals which are the least well adapted to exist in the environment in which they find themselves. While wanton destruction may seem unacceptable, the final, permanent removal of the jackal from the ecosystem may have even more serious long-term repercussions. Every effort should be made to reduce the conflict between stock-farmer and jackal to the point where persecution is no longer necessary. Surely this is the only long-term solution.

Seasonality in jackal predation

Predation on adult impala was demonstrated to be closely linked to rainfall. When available, following good rains, insects were the major source of food and impala were ignored as a resource - even as scavengeable items. Again this pattern is a reflection of underlying processes. Four processes were perceived to potentially make a contribution to the seasonal pattern:

First, the jackal, as a demonstrably opportunistic predator, is predictably predisposed towards eating whatever is most readily available. The limitations of optimal foraging theory aside, the jackal appears to follow the coyote pattern of foraging for that which can be optimally utilized (MacCracken & Hansen 1987). The superabundance of insects after good rainfall may make these the most profitable resource at that time of the year.

Second, the fact that, at least while the vegetation is green, insects can be found in open areas may be of importance in the selection of insects as prey items. Travelling over large distances and/or penetrating dense vegetation definitely exposes a foraging jackal to a greater predation risk than does foraging over a limited area of open plains.

Third, the risk associated with predation on larger prey, both from exposure to injury by the prey itself and from competitive interaction with larger carnivores is considerably higher than that associated with predation on insects.

Fourth, improved summer grazing conditions may make the older impala more difficult to subdue because they would be in better condition.

The seasonality of the jackal predation is an established fact. Whether it is explained by some, all or none of the above processes is insignificant. It is the seasonality itself, whatever the cause, which is an important component of the dynamics of the observed pattern. The abundance of old impala in the southern areas is demonstrably higher than in the northern areas of the Reserve. A component of this old section of the population will always be more susceptible to predation than the average of the population. If, therefore, predation by jackals on these impala was continuous, a greater proportion would be removed on an annual basis. The fact that the old impala are not reduced to a minimal level is therefore a reflection of the seasonality of the predation pattern. This implies that even though the selective predation by the jackals mimics the pristine process fulfilled by wild dogs and hyaenas, it does not replace it completely. In particular, as shown by the comparison between 1987 and 1988 predation levels, a series of years of good rainfall could mean that this process would be only minimally replaced. The jackals do not, therefore, effectively fill the ecological role vacated by the larger selective predators.

Jackal population regulation

Population density is regulated by a complex array of processes (Caughley 1977). Under conditions where food supply is not limiting, jackals have been recorded to reach a population density of 22 km^{-2} (Hiscocks & Perrin 1987).

The density of 4-6 jackals km^{-2} recorded during the present study is extremely high in relation to other areas which do not have an artificially abundant food supply. However, as demonstrated in Chapters 3 and 4, the impala in the south-central region of the Reserve represent an abundant source of food for the jackals. This source of food is artificially created by the absence other selective predators. Furthermore, the availability of this abundant food supply actually increases (through loss of condition and thereby increased vulnerability) at that time of the year (late/winter spring) when the jackals could conceivably experience a lack of food in the form of insects, rodents and young antelope. Significantly, this time of the year coincides with the period most closely associated with potential recruitment into the population - i.e. the whelping season.

The absence of a process of selective predation by wild dogs and hyaenas (and possibly the absence of more direct competition between these predators and the jackals) is thus responsible for a density of jackals far higher than that which is normally expected in a savanna ecosystem. The root cause of this situation is, of course, the process of predation by man on the wild dogs and hyaenas prior to the formation of the Reserve (Chapter 5).

Man induced process changes may have created the high jackal population in the south-central NTGR via yet another mechanism. Jackals were demonstrated to prefer open habitats both during foraging and during resting (Chapter 3). The extensive *Boscia foetida* savanna of the south central region of the NTGR is a result of intensive human settlement (Chapters 2 and 5). Boscias are not utilized for firewood by the Batswana people but are conserved for use in times of drought (Coates Palgrave 1977), and thus almost all of the remaining trees in this habitat are *Boscia foetida* or *Boscia albitrunca*. The overgrazing and selective wood collection - associated with the settlements fringing the lower Majale River - have yielded the open, pioneer dominated short-grass plains with sparse woody vegetation which is in stark contrast to the adjacent riverine and hilly areas. The artificially increased availability of a preferred habitat type - through the processes of overgrazing and wood collection - is undoubtedly reflected in the sustained high jackal population of the region.

Jackals and other prey

The concept of the regulation of prey populations by predators is the subject of extensive literature. Early consensus was that predators had a major controlling influence on prey population abundance. Studied prey and associated predator populations demonstrated sequential patterns of increase and decline which suited this conclusion very well (Lotka 1925, Volterra 1926 in Chapman 1931). A later paradigm was that the major changes in prey populations were due to other environmental factors - the predators were concluded to only be responsible for removing the excess animals which would otherwise have died of other causes (Errington 1946). This was taken to imply that predators could not exert a controlling influence on prey populations, but could merely modify the changes induced by major cycles in climate and food and habitat availability. More recent work has demonstrated that both may in fact be true (Erlinge, Goransson, Hogstedt, Jansson, Liberg, Loman, Nilsson, von Schantz & Sylven 1984). In situations where a predator depends on a specific prey animal for its survival, its numbers cannot achieve such proportions as to be the major factor in the fluctuations in abundance of the prey. In contrast, however, when a predator has a reliable supply of food from one source it can exert a considerable influence on the dynamics of the populations of other prey species (Erlinge *et al.* 1984, Paine, Wootton &

Boersma 1990, Woodroffe, Lawton & Davidson 1990). In extreme cases, where the predator, supported by an abundant supply of food, is numerically abundant compared to a certain alternative prey species, that species may be said to be in a "predator trap". Under such circumstances the population of the affected species cannot attain a level at which predation is negligible in relation to other processes (Caughley 1981). Predation therefore limits, or may even eliminate, the trapped population. Attainment of a predator trap situation is likely to follow a sudden reduction in numbers due to some other factor to a level at which predation can become a limiting factor (Pearson 1966, 1971, Fitzgerald 1977, Gasaway *et al.* 1983).

Independently to the identification of the impala population as a reliable food resource, anecdotal evidence indicated that a predator trap situation exists in the south-central region of the NTGR with respect to the following species. In all cases healthy populations of these species existed in the area prior to the drought of 1983/84 (Lind 1974, pers.obs.), with a major reduction in all species accompanying this severe drought.

1. Springhaas *Pedetes capensis.* Springhaas were abundant on the short-grass plains of the south-central region - ideal habitat for this species (Smithers 1983). Following the drought of 1984 springhaas were reduced to one colony within the study area. In the following four years no springhaas were seen anywhere else in the south-central region other than at this colony, despite the fact that numbers at this colony are high. Dispersal of these animals across the open plains in the presence of the high jackal population is likely to be almost impossible. Jackals are adept at capturing springhaas, particularly when hunting in groups (Ferguson 1980).

2. Warthog *Phacocoerus aethiopicus.* Warthogs are now extremely rare in the south-central region. Again, this situation was precipitated by the 1984 drought but, despite the subsequent development of dense stands of perennial grasses, no improvement was noted in the subsequent four years. Attempted predation by jackals on a family of warthogs was once observed (Chapter 3). Jackals are capable of capturing and killing warthogs up to a year old (Read pers. comm.). The well developed pack hunting techniques recorded in the present study may or may not increase the susceptibility of adult warthogs to predation. However, the chances of a sow defending a litter of young piglets against a pack of jackals is likely to be negligible - two jackals are 67% successful at killing young antelope despite the defensive behaviour of their mothers (Wyman 1967). In a recent film made in northern Botswana by Derek Joubert (*Journey to a Forgotten River,* Botswana Films (Pty.) Ltd., 1990) a group of four jackals is shown attacking a warthog sow with four young piglets. The sow's attempts at defending her young are nullified by the teamwork of the jackals. Two young are killed while a third is injured during the attack. The inability of the sow to attend to all her piglets and all the jackals at once made the outcome of the encounter inevitable. The influence of group predation on recruitment in this species in the NTGR is likely to be considerable.

Game count data support the observation that warthog numbers have not increased significantly since the drought (le Roux 1988, 1989). This is despite the fecundity of this species which enables it to increase rapidly following a reduction in numbers (Mason 1982).

3. Bat eared foxes (*Otocyon megalotis*). Bat eared foxes were extremely abundant in the central areas of the Reserve prior to 1984 (Lind 1974, pers.

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obs.). Berry (1978) recorded between 2,25 and 9,2 bat-eared foxes km^{-2} in the NTGR. Subsequently none have been seen in the study area despite an abundance of their preferred food - harvester termites *Hodotermes sp.*. One small family group has been reported from the northern parts of the Reserve (Petty pers. comm.). Young bat-eared foxes are susceptible to predation by jackals (Schaller 1972), a fact which may account for the considerable aggression shown by bat-eared foxes towards jackals (Ferguson 1980).

The presence of a generalist predator with a reliable food supply is the classic situation for the development of a predator trap. The anecdotal evidence given above indicates that this is indeed the case, and probably extends to many other species of mammals as well as birds and reptiles which were simply not monitored. The low numbers of the affected species means that the likelihood of finding remains in faeces or of recording predation by direct means is extremely low indeed. In view of the above, the default assumption should be that the populations of at least some of the species - be they insects, reptiles, birds or mammals - in the NTGR are subjected to constraints by the unnaturally high jackal population. While this is likely to be most intense in the south-central region, a spill-over to to other areas is likely in view of the contiguous nature of the different parts of the Reserve.

In the case of the impala population the possibility of a within-species predator-trap is evident in the NTGR. As mentioned above, the high jackal population density can be ascribed to the presence of a high quality, easily available prey - the old impala - at a time of the year when food supply might otherwise be limiting. Jackals are known to be adept at hunting and killing young antelope (Wyman 1967, Pienaar 1969, van Lawick-Goodall 1970a, Lamprecht

1978a, Stander 1987), particularly when huting in groups (Wyman 1967, Lamprecht 1978a). The impact of such predation is cryptic, as the small carcases are rapidly consumed and little remains to tell the tale. In addition, impala give birth within a restricted lambing period during summer (Smithers 1983), and the concentration of predation during this time of greatest vulnerability makes it exceedingly difficult to identify processes responsible for a recruitment lower than the theoretical maximum.

The presence of a high population of a generalist predator with a demonstrated propensity towards co-operative hunting is highly suggestive of a potential dampening effect on the impala population of the NTGR. Inspection of available data supports this hypothesis.

A high impala population in the NTGR (est. 22 000, Walker 1983) declined to approximately 6 600 in 1984 (Joubert 1984), much of the decline being due to the 1983/84 drought, with some of the difference possibly being due to the different census methods used by the two authors. Using the same methods as Joubert (1984), subsequent estimations have been 5 474 (1986), 4 617 (1987), 6 959 (1988) and 5 884 (1989) (le Roux 1988, 1989). The high count in 1988 was ascribed to observer inexperience (le Roux 1988, 1989).

All of the adult female impala shot during the present study between June and November were pregnant - even the oldest individuals with no incisor teeth. Skinner (1969) reported that a single female impala in the northern Transvaal produced lambs every year of her 13 year productive lifespan, and Fairall (1983) recorded a fecundity of 95% in mature impala females in the Kruger National Park, with no indication of reproductive senility even in the oldest animals. Both these authors recorded the fact that drought has little or no influence on the high fecundity of impala.

Taking:

1. A minimum fecundity of 95% in adult impala (Skinner 1969, Fairall 1983, present study);

2. Attainment of female sexual maturity at 18 months - i.e. production of the first lamb at 2 years (Fairall 1983);

3. A potential longevity of 15 years (Skinner 1969);

4. A sex ratio at birth of 1:1 (Fairall 1973);

5. An adult sex ratio in the NTGR of 70% females to 30% males (unpubl. data); and

6. A mortality rate of 36% in the first year under natural circumstances, including predation (Fairall 1983, Kruger National Park data),

and assuming:

1. An even rate of mortality of 4,6% p.a. from the second year (64% of mortality after 1st year (Fairall 1983));

2. That a population of 6 600 was present at the beginning of 1984; and

3. That 25% of the population at the beginning of 1988 consisted of lambs from the 1987/88 lambing season,

then: the impala population could, even under mortality conditions such as those prevailing in the Kruger National Park, including years of drought, have reached a total of 24 200 animals by the beginning of 1989. However, not only has the impala population of the NTGR not increased but, in fact, shows a decline of 11% over this period. Because the animals are being born but are not being recruited into the population it can be deduced that a significant mortality factor is operating within the population. Furthermore, the fact that the population in the south-central region is skewed towards the older age-classes (Chapter 4, Section 1) indicates that it is the younger components of the population which are most affected by this mortality factor. With the ideal theoretical conditions for a predator trap in existence in the NTGR, and the established fact that group-hunting jackals are highly successful predators of young antelope, at least some of this negative growth can be ascribed to jackal predation. The interesting corollary of this situation is that it is the impala population itself - via the high proportion of old animals, which are primary prey for the jackals during winter - which is responsible for its own demise.

Jackals and the epizootiology of rabies

Jackals are accused of being a major vector of rabies in Africa (Meredith 1982). Rabies was not incorporated as a part of the present study, and therefore no substantive discussion on this topic will be attempted. Nevertheless, some recorded observations, combined with the general conclusions of the present study, indicate a possible avenue of future investigation.

Rabies was positively diagnosed in jackals on two occasions during the study, and one further case was suspected but not confirmed. All cases were diagnozed using the Flourescent Antibody Technique by the Veterinary Services Laboratory, Gaborone. In one case distemper was specifically excluded as a differential diagnosis after it was suspected from clinical signs.

What is thus recorded by the present study is two cases of confirmed rabies within an area where the jackal population density was determined to be between 4 and 7 km^{-2}. What is remarkable is not what was recorded but what was not recorded. If indeed the jackal is the ideal vector for rabies as it is claimed to be, then the dense population recorded here combined with the confirmed positive cases could, according to a classical interpretation of the mode of spread of rabies in wild carnivore populations (MacDonald 1980), have led to a large scale rabies epizootic amongst the jackals of the Reserve.

The fact that rabies is relatively scarce in natural ecosystems represented by National Parks has been known for some time (Cumming 1982, de Vos pers. comm.). Cases of rabies in the Kruger National Park, South Africa have been diagnosed in dogs entering the park from neighboring areas, but not in wild carnivores resident in the Park. This situation has been closely monitored by resident veterinarians since 1961. The conclusion drawn from these observations is that the healthy natural system of the KNP does not allow the development of a cycle of rabies (de Vos pers. comm.).

The cases of rabies recorded during the course of the present study may have originated in adjacent areas, as affected animals can move over considerable distances, and rabies in jackals in the adjacent northern Transvaal is commonplace (Meredith 1982). Even if the recorded cases originated from within the Reserve, the present study has demonstrated that even in an artificially high population of jackals the presence of the disease does not manifest itself as an explosive or even a mild epizootic.

V. de Vos, Skukuza, Kruger National Park, RSA.

Springer (1982) suggested that limited aggression within a population of coyotes could be explained by acquaintance with animals in adjacent home ranges. This phenomenon was used to explain the absence of territorial aggression, the high level of tolerance, and the advanced level of co-operation recorded in the present study (Chapter 3).

The spread of rabies within a carnivore population depends on close physical contact (MacDonald 1980). This may be expected to occur as part of the normal social interactions within a group of jackals, or as an aggressive encounter between jackals from different social groups. Under the situation prevailing in the NTGR the former is a possible scenario, but the latter, due to minimal levels of aggression, can be concluded to be of minimal likelihood:An agressive interaction requires motivation from both participants, and the elevated agression of a jackal exhibiting symptoms of "furious rabies" may not be matched by a conspecific which is accustomed to mutual tolerance. A potential mechanism for the spread of rabies through the population is thus reduced by the stable, established social structure of the NTGR jackal population.

In contrast to the above, jackals from farming areas are heavily persecuted. The resultant disruption of the social system is certain to result in a situation with less acquaintance between individuals, less tolerance and elevated aggression, as reported in coyotes by Springer (1982). Under such circumstances, the opportunity for the spread of rabies amongst the few remaining jackals is likely to be enhanced - a consequence of the vacuum effect caused by the removal of established adult animals (MacDonald 1980, 1982).

The fact that the above scenario accords well with observed trends in rabies epizootiology indicates that there may well be reason to suspect that the stable, undisrupted ecosystem is resilient to rabies epizootics. The results of the present study suggest that the key to the enigmatically low incidence of rabies in a normal or even a high jackal population may be the nature and stability of the population. Specific investigations into the processes of spread of rabies epizootics could benefit from further investigations into jackal sociology, particularly the relatedness between individuals within high-risk and low-risk areas.

Grooming and ectoparasite ecology

Grooming has been identified by the present study as an important process for the maintenance of acceptable ectoparasite burdens on impala and possibly many other ruminants (McKenzie 1990). In the context of the results of the present study, grooming is also an important process at the ecosystem level.

As has been shown by the present study, grooming, as a natural bodily function, results in attrition of the incisor-canine complex of antelope. Such attrition, if allowed to proceed for long enough, eventually leads to total absence of any dental elements in the anterior mandible (Chapter 4, Section 1). As indicated in Chapter 6, this condition is characterized by a high parasite load, particularly of engorged adult ticks, poor condition and, through repeated grooming efforts, the baldness here dubbed autogenous alopecia.

As demonstrated in Chapter 4, old impala constitute a high proportion of the adult population of the south-central region of the Reserve. The presence of this high proportion of old animals has profound implications for tick population dynamics. As compromised hosts, the old impala are unable to remove the parasites which infest their bodies. The high numbers of engorged female ticks on these impala means that, per unit time, these animals are producing a significanly greater number of ticks to infest the environment than would normally be the case. Development and engorgement of *Boophilus decoloratus* on the host takes approximately 21-30 days. An adult *B. decoloratus* female lays approximately 2 500 eggs after engorgement (Soulsby 1968). Old, toothless female impala carried a mean of 130 adult ticks (Chapter 4, section 4)). This amounts to the production of approximately 65 engorged female ticks per month per old female. At a density of 15,6 impala km^{-2} there are approximately 700 impala in the south-central region of the Reserve, 5-30% (35 - 200) of which are old animals (Chapter 4, Section 5). This means that the presence of the old animals results in the production of between 5,5 and 32,5 million ticks per annum in the south-central region of the NTGR. These figures are approximate, but as adult tick numbers are at a minimum in winter (Short & Norval 1981), they are likely to represent a minimum value. Even if the true numbers are an order of magnitude less than those calculated the impact of the presence of these old animals remains considerable.

The role of the above scenario in the tick population dynamics of the Reserve is indicated by two related phenomena:

1. Impala generally carry few adult ticks even when larval and nymphal tick burdens exceed 600 (Horak 1982). This is confirmed by the observations on 61 impala shot in the northern parts of the Reserve and by the absence of adult ticks on the two impala from the northern areas processed during the

quantitative study (Chapter 4, Section 4). The presence of relatively high adult tick burdens on the southern control animals (mean = 30±17, n = 6) indicates that some environmental factor has resulted in a higher infestation rate in the south-central parts of the Reserve.

2. Total attrition of incisors naturally represents the oldest age group as can be determined from incisor wear (Roettcher & Hofmann 1970). The oldest age group that can be discerned by attrition of mandibular cheek teeth corresponds to a relative age of 8,5 years (Spinage 1971, Murray 1980), and is distinguished by extreme wear of the first molar tooth (Spinage 1971). Skinner (1969) has recorded a lifespan of 15 years for an impala living under natural conditions in the nearby northern Transvaal. By comparing incisor and molar ages, it can be seen that many of the "old" animals in Tables 11 and 12 and Appendix A8 are not of the oldest age category when molar wear is used as the criterion. Animals with totally worn incisors may be from 6,5 to 8,5 years old as determined by molar attrition, i.e. approximately half the potential lifespan recorded by Skinner (1969). In other words, animals can become "incisor" old before they are "molar" old, implying that incisor attrition, of the type which can be exclusively ascribed to grooming, is proceeding at a relatively rapid rate in this population. No vertical attrition of incisors was recorded by Roettcher & Hoffmann (1970), Spinage (1971) or Murray (1980) even in their oldest age groups. This implies that the animals in the population under consideration in the present study are required to groom themselves at a far greater rate than the populations considered in these three independent studies. And a high rate of grooming supports the above scenario - i.e. the greater rate of infestation by parasites from the old animals necessitates excessive grooming by the younger animals resulting in early incisor attrition. Because of the ecosystem

implications of the grooming process, these animals could be said to become "ecologically" old before they are chronologically old.

A single specimen of an impala mandible exhibiting total vertical attrition has been obtained from Pilanesberg National Park, Boputhatswana. This animal also exhibited the extreme molar attrition described by Spinage (1971). None of the old animals from the NTGR exhibited such extreme molar attrition. In other words, this animal was both ecologically and chronologically old - implying that the above scenario does not exist in the Pilanesberg National Park at the present time, but also confirming that incisor attrition due to grooming is not unique to the NTGR.

The presence of susceptible hosts is known to be a major factor in the build-up of high numbers of ticks in the environment (Patrick & Hair 1978, Lightfoot & Norval 1981, Norval & Lightfoot 1982). What the present study has demonstrated is that susceptibility of antelope to ticks may be strongly linked to grooming ability. This varies not only between species but also between individuals within a species. The presence of animals which are unable to groom, even if only a few individuals, is possibly the single most important factor in the build-up of ticks in the African environment.

The cyclical annual appearance and disappearance of autogenous alopecia is possibly a reflection of tick ecology in mixed habitats. It is known that woodland areas are often the most heavily infested with ticks (Norval 1977, Patrick & Hair 1978, Hair & Bowman 1986). As the open areas of the NTGR are almost totally devoid of vegetation during the winter dry season due to the predominance of annual herbaceous plants (Chapter 2), impala must, of necessity, utilize more densely vegetated habitats in order to obtain sufficient food - those utilizeable trees that are available in the open areas are exceptionally heavily browsed (Joubert 1984, pers. obs.). Following the appearance of fresh shoots of grass and *Tribulis terrestris* following the first summer rains, the impala no longer need to penetrate the dense vegetation in search of food. It appears, therefore, that the sudden disappearance of autogenous alopecia is related to the equally sudden change in habitat following the first substantial summer rains. Certainly both phenomena occur at the same time (Chapter 4). The change to open habitats would result in an immediate decrease in the rate of tick infestation, and thereby a decrease in the necessity to groom. While absolute tick numbers may be higher in summer, risk of exposure to infestation may thus be lower due to changes in habitat choice. Reduced grooming would then allow the pelage to regenerate. The velvety appearance of the old animals at this time (Fig. 35) is evidence of a sudden, synchronised regrowth of the hair, and suggests that this may be the process underlying the cyclical nature of the occurrence of autogenous alopecia. Further investigation may yield interesting results in this regard.

Grooming, autogenous alopecia and disease

Grooming itself is a natural process. Its consequence may be the general maintenance of the appearance and alignment of the pelage, or it may be the more specific process of the control of the number of ectoparasites within the pelage (Snowball 1956, Riek 1962, Bell *et al.* 1962, Bell & Clifford 1964, Bennett 1969, present study).

The consequence of excessive oral grooming in antelope extended by unnatural longevity as recorded in the present study is the attrition and eventual destruction of the organ responsible for this function. Thus the extension of the natural process beyond its natural limitation results in its elimination. The result of the elimination of the process is, in turn, the accumulation of the products (parasites) normally subjected to a degree of homeostasis by this process. These results reflect the usual consequence of the elimination of any natural process. In addition to the loss of homeostasis, the continuation of the process in a non-functional manner results in the syndrome of autogenous alopecia. This pathological syndrome is thus the result of a perfectly natural process - grooming.

The question that arises is "Is autogenous alopecia a disease?". At the level of the individual antelope autogenous alopecia does not constitute a disease. The animals exhibiting this syndrome are merely old - a natural consequence of life. At the level of the population autogenous alopecia also does not constitute a disease. A population must normally be comprised of individuals from each age-class, and the existence of old animals in the population certainly does not constitute a pathological syndrome with respect to the population itself. At the level of the ecosystem, however, autogenous alopecia does indeed constitute a disease. The disease is the consequence of the disruption of the natural process which regulates the number of old animals in the ecosystem. The autogenous alopecia is merely a symptom in the ecosystem indicating that this disruption has occurred. The existence of a positive feedback loop whereby the autogenous alopecia, via the production of excessive numbers of parasites, accelerates its own development is typical of the terminal stages of disease. The transition from a natural to a pathological process following disruption is thus as much a feature of ecosystems as it is of physiological systems.

Selective predation, grooming and man

> "Premeditated control of animals is a prerogative that only man can exercise. If man takes this responsibility lightly, he may alter the natural order and indirectly threaten his own place in the unnatural world thus created" (McCabe & Kozicky 1972: 393,394).

Old animals breed more parasites. Young animals become old when they groom more often than usual. Old animals, in the absence of selective predators, remain active producers of parasites within the system until removed by eventual old age or opportunistic selective predation.

Given a pristine scenario in the African savanna, a certain percentage of impala in any population will belong to the oldest age category within the population. On approaching natural senescence these old animals would become more prone to selective predation than the average members of that population. This susceptibility would, in the normal course of events, be enhanced by factors which would stress the already compromised physiological responses of these animals - eg. starvation, pregancy, lactation, disease, high parasite load etc.. If, however, predation as the final mortality factor is removed, these old animals may persist for many more years in the system.

As a result of the presence of man, wild dogs and hyaenas are absent from most of Africa today. It is possible, therefore, that the scenario which has developed in the south-central region of the NTGR could be the forerunner of similar situations in the many unnatural islands created throughout the continent as nature reserves and game farms where the predator community is no longer intact. The development of the situation described in the NTGR has taken over 25 years to reach current proportions, and may be as a result of processes peculiar to the NTGR itself. The fundamental nature of the processes of grooming and selective predation are, however, likely to result in the development of the same scenario on a large scale in other man-modified ecosystems in Africa in the future. The fact that autogenous alopecia was also recorded in steenbok and kudu in the present study (Chapter 6) highlights the potential of the syndrome described here to involve other components of the ecosystem.

The only other case of a high incidence of autogenous alopecia in Africa known to me at the time of writing was recorded in the north-eastern sector of the Kruger National Park in South Africa in the mid-1960s. Many old impala along the Levubu River in this area exhibited the classic signs of autogenous alopecia as described in the present study (Fairall, *in litt.*) At first the presence of a presumably intact predator population in the KNP appeared to contradict the conclusions of the present study. Significantly, however, Fairall (*in litt.*) who investigated the presence of these "mangy" impala, reports that predators in this area, particularly wild dogs and hyaenas, were attracted over the Reserve boundary, which at that time was unfenced, into neighboring Mocambique where they were destroyed by occupants of an agricultural settlement. The two areas, remarkably similar in other ways, thus are case studies of what may happen to systems when predation processes are removed or compromised. Factors such as dustiness (greater than normal abrasiveness), high impala populations, and the long-standing *status quo* in the two areas may explain why they are the first to exhibit the results of such interference.

Outside of Africa a remarkably similar scenario is evident from Isle

Royale in Canada - coincidentally the site of a long-term study of predation by wolves. Moose on this 544 km^2 island are preyed upon by wolves (Mech 1970, Peterson 1977). Mech (1970) reported that bare areas of skin on the moose were related to tick infestation. This was disputed by Peterson (1977), but later Peterson agreed with this observation (Peterson 1989). Moose first populated this island in the early 1900's. In the absence of any predators moose numbers increased dramatically and crashed several times due to habitat over-utilization (Peterson 1977). Large numbers of old moose in this population were found to carry large numbers of ticks and to have areas of bare skin (Mech 1970) in contrast to Alaskan moose populations (Franzemann in Peterson 1977). Wolves only populated the island in the late 1940's, and subsequent to their establishment were shown to prey selectively on the older component of the moose population. Subsequent to the arrival of the wolves the moose population did not reach such extremely high numbers until the unexplained decline in wolf numbers in the early 1980s. With the increased population and the reduced predation, tick infestation has again become a severe problem (Peterson 1989). The occurrence of alopecia in moose has been found to be correlated to the severity of tick infestation, and has been found to be due to grooming behaviour in response to this infestation (Glines & Samuel 1984). While the parallels between the two studies may be only superficial, the implications from both these areas of the absence of natural processes is readily apparent.

At the time of writing I am aware of increasingly severe tick problems on many small game reserves and game farms throughout southern Africa. Many cases of severe infestation, particularly of the ears of animals (which cannot be groomed!) have been reported in conversation with farmers and conservation officials. Cases of deaths amongst kudu due to tick induced abscesses of the ears represent the most extreme cases. Ferrar & Kerr (1971) reported a crash in a population of reedbuck *Redunca arundinum* ; a high tick population associated with an artificially high ungulate population was considered to have played an important role in this crash. In view of these increasingly severe problems in areas where the natural predator community has vanished, the likelihood that autogenous alopecia and its associated ecosystem ramifications will become of increasing importance is potentially high - time being the factor required for the perturbation to become fully apparent, as is usually the case with disruptions at the ecosystem level (Odum 1985).

IMPLICATIONS

The overall implications of the findings of the present study will be discussed at two levels - first at the academic/heuristic level and second at the management level.

Academic/heuristic implications

Specific implications of the findings of the present study have already been discussed where appropriate. What remains is to briefly discuss the holistic implications of the study from the point of view of its potential contribution to the understanding and conservation of ecosystems in general.

It became apparent to me during the course of the study that I was dealing with a disturbed ecosystem. The disturbance had been created by man, and was manifested in the absence of certain essential processes from the system. My medical background obliged me to conclude that the system was "diseased". Initially this appeared to be a spurious conclusion. Perhaps, however, there may be profound implications to this "clinical" observation.

Strong parallels exist between the functioning, or physiology, of organisms and the functioning of higher-order systems - i.e. ecosystems (Knight & Swaney 1981). At first glance such parallels may appear superficial, and it certainly appears "unscientific" to make too much of this comparison. However, the definition given by Lindeman (1942) of an ecosystem i.e. "The ecosystem [is any] system comprised of physical-chemical-biological processes active within a space-time unit of any magnitude" certainly indicates that the distinction between organisms and ecosystems may not be all that distinct. Indeed, using this definition, the distinction drawn by us between organisms and ecosystems may be said to be entirely artificial.

A holistic understanding of ecosystem or even of bodily function is an almost superhuman feat, and sufficient knowledge of both systems to draw meaningful comparisons is thus a rare accomplishment. Fortunately, however, functional similarities between these different levels of organization are highlighted by dysfunctional similarities. The stress response at the organism and ecosystem levels are uncannily similar (Odum 1985, Rapport *et al.* 1985), drawing us yet closer to considering ecosystems as mega-organisms. At both levels, disruption is followed by a stress reaction, the stress is followed by a coping reaction, and an insufficient coping reaction is followed by system collapse (Rapport *et al.* 1985).

It could be said that the similarities between organisms and ecosystems are simply due to the fact that both systems are cybernetically regulated, and that the feedback loops result in the same sequence of events at both levels - a predictable consequence of the laws of thermodynamics.

Does this parallelism belong in the realms of academia? Or does it have a greater relevance? After all, James Lovelock tried to portray the world as a single organism - Gaia (Lovelock 1982) - yet he failed to convince the public at large - let alone the scientific community - of the relevance of his hypothesis.

I believe that the parallels need to be taken one step further for their significance to become fully apparent. The outcome of stress at the organism level is disease. This disease is manifested in various symptoms, all of which can be traced, via physiological or pathological processes, to the original stressor. I believe that the same principle applies at the ecosystem level, with ecosystem disease and ecosystem pathology being the outcome of unresolved ecosystem stress. With the exception of traumatic events, this disease is a reflection of processes at work within the system. And resolution of all the pathology depends on the reinstatement of the original processes which were disrupted by the original stressor. Failure to do so will result in failure to restore functional status to the ecosystem. Processes, not components, are the key to restoration.

Ecologists know too well the role that processes play in ecosystems. And the burgeoning branch of this science known as "Restoration Ecology" applies this knowledge to restoring disturbed ecosystems. The hiatus that remains is in passing on this knowledge to the general public which is still marching to the tune of species, or occasionally habitat, conservation. I believe that this hiatus is due in no small measure to the fact that nobody can truthfully claim to fully understand the functioning of any ecosystem. How can anyone therefore teach the lay public - who have even greater difficulty grasping the slippery complexities - about ecosystem function. And if we do manage to explain the intricacies of ecosystem funtion, we must now end off by saying that it is all chaos anyway!(May 1989).

Enigmatically, dysfunction is easier to understand than function. Every person on Earth, no matter how "primitive", has an understanding and some personal experience of how their own bodies can, and do, malfunction. Teaching people about disease therefore means teaching them about something which they understand **and can personally relate to.** And using the parallel, as outlined above, between body and ecosystem, an understanding of how ecosystems can go wrong can be almost instantaneously achieved.

The parallel between the body and the ecosystem is not a spurious one. Using this parallel to create increased awareness of the importance of environmental conservation may nevertheless sound simplistic. But if they do not resort to being simplistic when the moment demands it, will ecologists ever transfer their knowledge to where it really matters - the public at large? I believe that the present study illustrates the processes of disease in an ecosystem, and illustrates how this can be ascribed to interference in fundamental processes. The problem, and the solution, illustrate how ecosystems can and should be conserved by conserving the integrity of the ecosystem processes - even if the pristine components (species) have been lost to the system.

Management

The findings of the present study can only be of relevance within a framework of defined management objectives for the NTGR. As I am not aware of any defined objectives for management of the Reserve in existence at the time of writing, the statements made here are made assuming that any such future statement of objectives will include the principle that "The impact of man-induced changes on the functioning of the ecosystem will be minimized".

The following is a brief synopsis of the management implications of the study.

Continued absence of selective predation by wild dogs and hyaenas in the south-central region of the NTGR will mean that numbers of old impala are likely to remain high or even increase in this part of the Reserve. This means that the jackal population will remain high, that parasite numbers will continue to increase, and that small animals will remain in a predator trap situation unless a series of exceptionally wet years allows population recovery despite the heavy predation losses. The spill-over effect of the high jackal population on the rest of the Reserve should continue or increase, with stochastic events making this an unpredictable process.

The components of the ecosystem stress and the coping reaction have been identified. The fact that the stress remains unresolved due to dysfunctional processes means that the next component - ecosystem collapse (Rapport *et al.* 1985) (probably only partial collapse) - is inevitable if the situation is not resolved. As stated by Odum (1985:421) "When stress is detectable at the ecosystem level, there is real cause for alarm, for it may signal a breakdown in homeostasis"

A process-based management approach is essential to permanent resolution of the disruption of the NTGR ecosystem. Essentially this implies the reinstatement of selective predation on impala in the south-central region of the Reserve. In taking a process-based management decision it is essential to realize that it is the process, not the components, which is of paramount importance. The following two management possibilities illustrate the priority assigned to the process.

1. Re-introduction of wild dogs. The findings of the present study provide a strong ecological motivation for the re-introduction of the wild dog into the NTGR. The large numbers of susceptible prey are likely to make the chances of successful re-introduction relatively high, and the exercise would prove instructive for similar undertakings in other areas. A single small pack of wild dogs would be sufficient for the purpose of restoring the pristine selective predation process in the south-central region, and the pack may remain in this region while there is an abundant supply of suitable prey. As the stock of old impala becomes depleted and as the pack increases in size the wild dogs could be expected to move over a wider area. Conflict with stock-farmers in surrounding areas could potentially arise if the Reserve is still not fenced at that time. This problem can be approached in one of two ways. The dogs can be re-introduced under semi-wild conditions wherein they are fed a supplementary diet which would contain them within a restricted area where their predation would be concentrated. Alternatively, the movements of the dogs should be closely monitored using radio-telemetry to determine the site, nature and seriousness of any conflict situations, whereupon appropriate preventative and compensatory action could be taken.

2. Process simulation. If, for some reason, wild-dogs cannot be re-introduced into the Reserve, an alternative would be to simulate the selective predation process. As indicated in Chapter 4, old impala can be reliably identified in winter by the appearance of autogenous alopecia at this time of

the year. These animals could be selectively culled from the population, thus simulating selective predation on the oldest age-class. Ideally, if this could happen over a protracted period, the carcases could be used to encourage the spotted hyaenas from the north to frequent and perhaps eventually settle in the south-central region - a process which could be further encouraged by the provision of suitable, well protected, artificial denning sites. A degree of natural selective predation could thus eventually be established. Practical considerations may, however, dictate that a short intensive culling period be used.

Re-instatement of the selective predation process can be expected to precipitate the following sequence of events:

1. Reduction in the proportion of old impala in the south-central region;

2. Reduction in tick production and infestation. Environmental levels would decline only after several years due to the longevity of ticks;

3. Reduction in the jackal population due to removal of the super-abundant food resource. Initial fluctuations, disruptions and increased predation pressure on scarcer species could be expected;

4. Reduction in recruitment of jackals to areas outside the south-central region, with cessation of spill-over effects;

5. Recovery of scarcer prey species released from the predator trap; and

6. Unforseen consequences.

Because of the possibility of the latter, monitoring of the changes is recommended.

The temptation to short-circuit events by direct reduction of jackal numbers is strongly discouraged. This symptomatic approach would not provide a permanent solution, would aggravate the imbalance in the impala age-structure, and could have severe stochastic consequences - eg. a rabies epizootic.

A process-based management approach will provide the only solution to what I suggest is a serious environmental problem which does require attention. The alternative - a lack of management action - would provide the opportunity to determine at what point ecosystem collapse will occur, and what ramifications this will have. The management decision rests with the landowners of the NTGR. It is hoped that whatever action is taken, or not taken, the opportunity will be used to learn from the experience in order that other conservation areas may benefit in the future.

SUMMARY

Reported predation by black-backed jackals *Canis mesomelas* on adult impala *Aepyceros melampus* in the Northern Tuli Game Reserve, Botswana, was investigated. The study confirmed that jackals in this reserve do prey regularly on adult impala. The predation was found to be seasonal, opportunistic, co-operative and selective.

* Predation on adult impala commenced in late-summer to mid-winter - commencement and incidence of predation apparently being linked to the availability of alternative food resources.

* Predation was undertaken by temporarily co-operating groups of jackals which otherwise resided in individually distinct home-ranges. Group size during hunting and consumption of impala was significantly greater than the average group size.

* Predation was undertaken in well defined phases:

1. One or two jackals rush towards a herd of resting impala. This is followed by close observation of the fleeing animals as well as by excited sniffing at the ground in the vicinity of the herd's original position;

2. A selected impala is cornered and harassed, with the aggregation of a larger group of jackals;

3. The prey is immobilized and possibly silenced by one jackal biting the throat;

4. The prey is killed by severing of the major abdominal arteries, including the aorta, after entrance is gained via a flank wound;

5. The prey is rapidly and completely consumed - only the skeleton and the rumen contents remain after three to four hours. Other jackals arriving after the kill are allowed to feed.

* Predation was highly selective. Eight of the eleven kills recorded were of the oldest impala age-group, all of which were in extremely poor condition. Of the remaining three impala, one had a compound fracture of the right metacarpus.

Insects formed a major part of the diet in summer. This proportion declined during autumn and winter, with a concomitant increase in the utilization of impala.

Male jackal home-ranges were found to increase significantly in size from summer to winter. Involvement in impala kills was usually far from the core-area, suggesting a significance in the excursionary movements of jackals recorded by this and other studies. Strong selection for open habitat types both during activity and during rest periods was recorded.

The population density of jackals was found to be extremely high - estimated at between four and seven per square kilometre.

Extensive use of the lateral anterior dental elements (I_2, I_3 and C) by impala and other browsing/mixed feeding antelope for grooming purposes was identified. Prolonged use of these teeth for this purpose was found to result in total vertical attrition of all the anterior teeth. Impala without these teeth were found to carry significantly higher external parasite burdens than those impala with front teeth from the same area.

Absence of the anterior teeth in antelope was correlated with the partial or complete absence of hair on all parts of the body other than the head and neck. This syndrome was ascribed to repeated ineffective grooming efforts, and was thus dubbed "autogenous alopecia". Autogenous alopecia was found to be strictly seasonal, occurring only during the annual winter drought. The syndrome was found to be limited to the south-central region of the Reserve. Impala exhibiting the syndrome in September 1988 were found to be in significantly poorer condition than impala with unworn teeth from the same area.

External parasite burdens on impala from the northern parts of the reserve were found to be significantly lower than on impala from the south-central region. The age structure of the south-central impala population was found to be significantly skewed towards the oldest age-group.

Wild dogs *Lycaon pictus* were confirmed to be extinct in the Reserve. Spotted hyaenas *Crocuta crocuta* were found to be relatively scarce in the south-central region compared to the nothern and western parts of the Reserve.

It was concluded that the current jackal-impala and impala-ectoparasite relationships in the Northern Tuli Game Reserve are the result of man-induced disruption of the natural large-predator community of the region. Persecution of wild dogs and spotted hyaenas prior to the formation of the Reserve has resulted in the elimination of the natural process of selective predation on old impala. This has resulted in the accumulation of excessive numbers of old animals in the south-central parts of the Reserve which act as a source of food for the jackals at a critical time of the year. This has allowed the increase in jackal population density to present levels, an event which has in turn resulted in increased predation pressure on scarcer prey species. The persistent presence of many old impala in the south-central population due to the generalist nature of jackal predation has resulted in increased infestation of the habitat with external parasites in this region. This in turn necessitates increased grooming activity by all members of the population, leading to early attrition of the anterior teeth, thus further increasing the source of external parasites in the ecosystem.

The ramifications of man-induced disruption of ecosystem processes in the Reserve was concluded to be of considerable heuristic value. It is suggested that the situation evident in the Northern Tuli Game Reserve today is a precursor of similar events in other isolated islands of African environment where natural predation processes have been compromised or destroyed.

The current *status quo* in the Reserve was concluded to be highly undesirable. Rectification was recommended through the re-instatement of the pristine process of selective predation on old impala - either through the re-introduction of selective predators or through the simulation of the natural process. The importance of process-orientated conservation was highlighted by the results and conclusions of this study. Scientific evaluation of the consequences of intervention or non-intervention were recommended, as the results could be of considerable value in the management of ecosystem stress in other areas.

OPSOMMING

Predasie deur rooijakkalse *Canis mesomelas* op volwasse rooibokke *Aepyceros melampus* in die Noordelike Tuli Wildreservaat, Botswana, is ondersoek. Die studie het bevestig dat jakkalse in dié reservaat wel gereeld op volwasse rooibokke prooi. Die predasie is gevind om seisoenaal, opportunisties, koöperatief en selektief te wees.

* Predasie op volwasse rooibokke het in laat somer tot middel winter 'n aanvang geneem - aanvangs en voorkoms van die predasie is waarskynlik aan die beskikbaarheid van alternatiewe voedselbronne gekoppel.

* Predasie is deur tydelik samewerkende groepe jakkalse onderneem wat andersins in individueel aparte tuisgebiede bly. Groepgrootte gedurende jag en verorbering van rooibokke was betekenisvol groter as die gemiddelde groepgrootte.

* Predasie is in duidelik afgebakende fases onderneem:

1. Een of twee jakkalse storm op 'n trop rustende rooibokke af. Dit word gevolg deur noue betragting van die vlugtende diere sowel as deur opgewonde snuiwery van die grond in die omgewing van die trop se oorspronklike posisie;

2. 'n Uitverkose rooibok word in 'n hoek gedryf en gekwel, met die gelyktydige samedromming van 'n groter groep jakkalse;

3. Die prooi word immobiliseer en moontlik stil gemaak deur een jakkals wat die rooibok aan die keel byt;

4. Die prooi word gedood deur die afsnyding van die hoof abdominale slagare, insluitend die aorta, nadat toegang tot die buikholte deur 'n wond aan die sy verkry is;

5. Die prooi word vinnig en in sy geheel verorber - slegs die geraamte en die inhoud van die rumen bly na drie tot vier ure oor. Ander jakkalse wat na die doding aankom word toegelaat om te voed.

* Predasie was hoogs selektief. Agt van die elf opgetekende dodings was van die oudste rooibok-ouderdomsgroep, almal waarvan in 'n uiters swak kondisie was. Van die oorblywende drie rooibokke, het een 'n saamgestelde breuk van die regtervoorbeen gehad.

Insekte het 'n vername deel van die dieet in die somer uitgemaak. Hierdie verhouding het gedurende herfs en winter afgeneem, met 'n ooreenstemmende toename in die verbruik van rooibokke.

Tuisgebiede van jakkals mannetjies is gevind om betekenisvol in grootte van somer to wintertoe te neem. Betrokkenheid by dodings van rooibokke was gewoonlik vêr van die kerngebied wat 'n beduidenheid in die bewegings van jakkalse voorstel wat deur hierdie, en ander, studies aangeteken is. Sterk seleksie vir oop habitattipes, beide gedurende aktiwiteit en rusperiodes, is opgeteken.

Daar is gevind dat die bevolkingsdigtheid van jakkalse besonder hoog is - gereken as tussen vier en sewe per vierkante kilometer.

Uitgebreide gebruik van die laterale voorste tandelemente (I_1, I_2, I_3 en C) deur rooibokke en ander blaarvretende/gemengde-voedende boksoorte vir die doel van lyfversorging is geidentifiseer. Langdurige gebruik van hierdie tande vir diė doel het 'n algehele vertikale wegslyting van al die voorste tande tot gevolg. Rooibokke sonder hierdie tande het betekenisvol meer uitwendige parasietbeladings as normale rooibokke gedra.

Afwesigheid van die voorste tande in boksoorte het met die gedeeltelike afwesigheid van hare op al die dele van die ligaam, uitgesonderd die kop en die nek, verband gehou. Hierdie sindroom is toegeskryf aan herhaaldelike oneffektiewe pogings om parasiete van die vel te verwyder, en is dus "autogenous alopecia" gedoop. Daar is gevind dat hierdie sindroom streng seisoenaal was deur slegs gedurende die jaarlikse winterdroogte voor te kom. Die sindroom was tot die suid-sentrale gedeelte van die Reservaat beperk. Rooibokke wat die sindroom in September 1988 vertoon het, was in 'n beduidende swakker kondisie as rooibokke van dieselfde area met ongeslyte tande.

Uitwendige parasietbeladings op rooibokke van die noordelike dele van die Reservaat is gevind om betekenisvol minder as diė op rooibokke van die suid-sentrale gebied te wees. Die suid-sentrale rooibokbevolking het betekenisvol meer ou diere as die noordelike bevolking bevat.

Wildehonde *Lycaon pictus* is bevestig om binne die Reservaat uitgesterf te wees. Gevlekte hiënas *Crocuta crocuta* was betreklik skaars in die suid-sentrale gebied vergeleke met die noordelike en westelike gedeeltes van die Reservaat.

Daar is tot die gevolgtrekking gekom dat die huidige jakkals-rooibok en rooibok-ektoparasiet verwantskappe in die Noordelike Tuli Wildreservaat die gevolg van mensgemaakte versteuring van die natuurlike groot-roofdier gemeenskap van die streek is. Vervolging van wildehonde en gevlekte hiënas voor die ontstaan van die Reservaat het tot die uitskakeling van die natuurlike proses van selektiewe predasie op ou rooibokke gelei. Dit het tot die versameling van buitensporige getalle ou diere in die suid-sentrale gedeeltes van die Reservaat gelei wat as 'n bron van voedsel vir jakkalse tydens 'n kritieke tyd van die jaar gedien het. Dit het 'n toename in die bevolkingsdigtheid van jakkalse tot huidige vlakke toegelaat, 'n gebeurtenis wat op sy beurt 'n verhoogde predasie-druk op skaarser prooispesies tot gevolg gehad het. Die hardnekkige teenwoordigheid van vele ou rooibokke in die suid-sentrale bevolking, te wyte aan die algemene eienskappe van jakkalspredasie, het tot 'n toenemende besmetting van die habitat met uitwendige parasiete gelei. Dit het op sy beurt verhoogde lyfversorgings-aktiwiteit by al die lede van die bevolking genoodsaak, wat tot vroeë afslyting van die voorste tande gelei het, wat dus verder die bron van uitwendige parasiete in die ekosisteem laat toeneem het.

Daar is tot die slotsom gekom dat die uitvloeisels van 'n mens-geïnduseerde versteuring van ekosisteem-prosesse in die Reservaat van noemenswaardige heuristieke waarde is. Dit word voorgestel dat die klaarblyklike situasies in die Noordelike Tuli Wildreservaat vandag 'n voorloper van soortgelyke gebeurlikhede in ander geïsoleerde eilande van Afrika-omgewings is waar natuurlike prosesse van predasie vernietig is.

Daar is besluit dat die huidige *status quo* in die Reservaat hoogs ongewens is. Regstelling deur die herinstelling van die oorspronklike proses van selektiewe predasie op ou rooibokke - óf deur die inbring van selektiewe roofdiere óf deur die nabootsing van die natuurlike proses. Die belangrikheid van proses-georiënteerde bewaring is deur die resultate en slotsom van hierdie studie beklemtoon. Wetenskaplike opweging van die gevolge van ingryping of nie-ingryping word aanbeveel, aangesien die resultate van aansienlike waarde in die beheer van ekosisteem-spanning in ander gebiede kan wees.

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APPENDICES

APPENDIX A1

Jackal Capture Methods

Darting of jackals was moderately successful, while trapping with foot-hold traps was highly successful, as reported in Chapter 3. The following is an abbreviated account of the demise of the other methods that were tried. If the foot-hold traps had been unsuccessful, the only option remaining was a helicopter with a netgun!

Method 1: Cage Trap.

Cage trap with vertical sliding trapdoor (200x50x40 cm). Baited with remains of impala carcases.

Results: No jackals captured after 40 trap nights. One lioness captured on 41st trap-night.

Shortcomings: The trap was inspected by jackals, but they did not enter the trap despite thorough camouflage with vegetation.

Method 2: Noose trap.

Modification of a noose trap described by Ferguson (1980) as being the most successful method. Instead of a fishing rod, elastic rubber strips were used which were attached to a suitable tree.

Results: Four jackals captured - all juveniles.

Drawbacks: Adults not captured.

Method 3: Pitfall trap.

Holes 1 x 1 x 1,2 m deep were dug in flat alluvial soil. A square metal frame was constructed from 25 x 25 mm square tubing, and placed on the rim of the hole. Four 800 x 800 x 12mm Bison Board boards were placed so as to meet at the centre of the frame and so cover the hole. The boards were attached to the frame and joined with cotton thread at the centre. The boards were covered with a 20 mm layer of soil. All other soil was removed from the site. Bait (meat, rumen contents, blood, jackal urine) was placed at the centre of the covered boards.

Results: No jackals captured. Some of the traps were set off by unidentified animals which were not captured.

Drawbacks: To much activity required. Jackals alerted to human activity by disturbed soil.

Method 4: Drop trap.

A 3 m diameter covered weldmesh drop trap with remote mechanical release was constructed. This was suspended from a central pole over a wildebeest carcase.

Results: No jackals captured. They would not approach the carcase while the trap was in position.

Drawbacks: Too much activity. Too visible. Noisy, movement of the suspended trap in windy weather.

Method 5: Driving into drop net.

Two 4x1,5 m nets of 1 mm dacron with 70x70 mm openings were made by hand. These nets were suspended from poles by clothes pegs. A 70 m funnel constructed of a 400 mm wide strip of woven plastic led to the nets. Jackals were attracted to the mouth of the funnel with an impala carcase. They were then driven towards the funnel with vehicles, with the intention being that they would run into the nets.

Results: No jackals captured.

Drawbacks: Jackals would turn and run past the vehicles, and would not approach the plastic walls or the nets.

Method 6: Driving into boma.

From Method 5 it was apparent that jackals would avoid unnatural objects even at the risk of running towards an approaching vehicle. It was thus surmised that an artificial barrier could be used to direct jackals into a large pen. A 10 m diameter pen with a 400 mm side opening was constructed from weldmesh. A woven-plastic and barrier tape funnel was constructed for Method. Each arm of the funnel was 1 km long. Fourteen helpers drove jackals into mouth of funnel and towards pen.

Results: No jackals captured.

Drawbacks: Too much activity in setting up pen. Jackals ran over or under barrier tape before reaching pen.

Method 7: Drugged bait.

Eight mg of phencyclidine hydrochloride (Syclan, Centaur, Johanesburg, South Africa) were injected into each of two separate small pieces of meat. This dose was based on an approximate dose of 1-2 mg kg^{-2} and the fact that phencyclidine is rapidly absorbed by the oral route (Harthoorn 1975). The pieces of drugged meat were placed on the ground next to the edge of a road in the centre of the study area. Approximately five litres of a mixture of impala blood and rumen contents were spread over an area approximately 10 m in diameter centred on the bait. This was in order to keep jackals at the bait for as long as possible to allow the drug to take effect. Extra meat was not provided as this would have slowed absorbtion of the drug from the stomach. An open, short-grass area with a visibility of 100 m in all directions was chosen to facilitate finding drugged jackals.

Results: No jackals captured. Bait was eaten after one hour and the site abandoned after further fruitless search for more meat.

Drawbacks: Jackals did not remain at bait area long enough for drug to take effect. Use of higher doses was considered unethical due to the prolonged recovery period.

APPENDIX A2

Radio collars

Legend for Figure A2.

A Standard collar

B Activity collar

- a Machine belting collar.
- b Size 'C' Lithium battery.
- c VHF transmitter.
- d Whip antenna.
- e Mercury switch.
- f 2 ohm resistor.
- g Pop rivets.

Construction

Radio collars for jackals were constructed as shown in Fig. A2.

Materials:

1 VHF radio transmitter with 25 cm antenna (G. van Urk, Potchefstroom University for Christian Higher Education, Potchefstroom, South Africa).

1 size C Tadiran (Israel Electronics Industries, Tel Aviv, Israel) lithium battery.

800 x 30 x 1 mm reinforced machine belting (Interbelt, Kramerville, South Africa)

Araldite epoxy casting (CW1312GB & HY1300GB, Ciba Geigy Plastics, Cambridge, UK).

2 mercury switches (Kopp Electronics, Johannesburg, South Africa).

1 2 ohm resistor.

Manufacture:

Standard collars The machine belting was scored and bent to form a hanging compartment of 55 x 38 cm between two layers of belting. The two layers of belting were temporarily joined with cyanoacrylate glue (Bostik, Fernex Industries (Pty) Ltd., Johannesburg, South Africa). One side of the framework was then glued to a smooth cardboard surface using contact adhesive (Genkem, General Chemical Corporation Ltd., Johannesburg, RSA). The radio transmitter was then connected to the battery. The battery and transmitter were placed in the compartment as shown in Fig. A2a, with the antenna between the two layers of belting, and the compartment was filled with epoxy.

Activity collars It was found that if the transmitter was connected for activity detection (ie. rapid pulse rate for active mode), a continuous transmission resulted when the collar was placed on an animal. This was avoided by housing the transmitter in a separate compartment as depicted in Fig. A2b. The battery and mercury switches were housed in the main compartment. Potting procedure was the same as for standard collars.

Ends of the compartments were secured with twin pop rivets. A further two rivets were placed at the most dorsal side of the collar, with the antenna between the two rivets.

Completed collars weighed between 152 and 191 g.

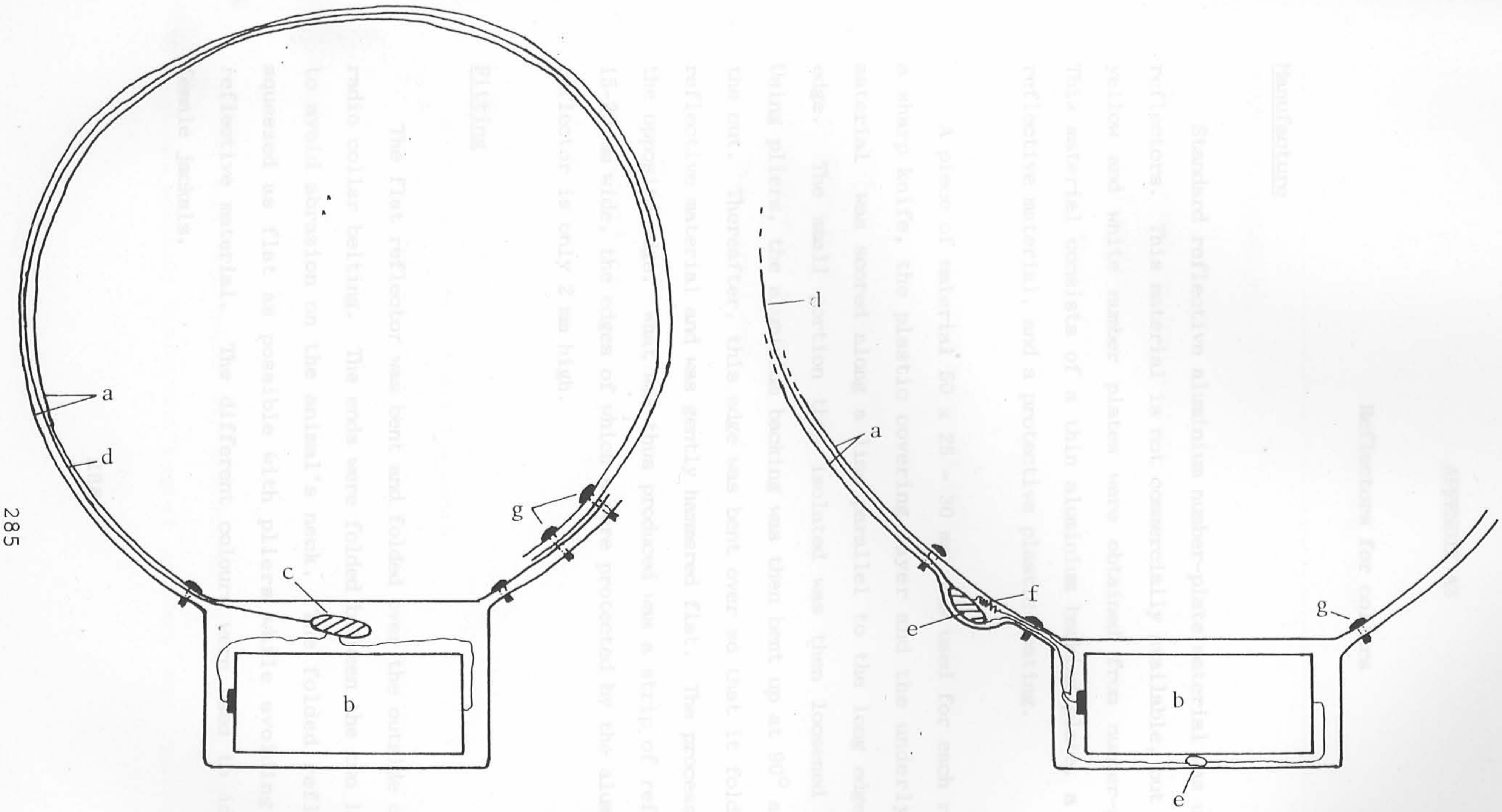

Figure A2. Radio collars. See text for legend.

APPENDIX A3

Reflectors for collars

Manufacture

Standard reflective aluminium number-plate material was used to construct reflectors. This material is not commercially available, but pieces of reject yellow and white number plates were obtained from number-plate suppliers. This material consists of a thin aluminium backing plate, a layer of highly reflective material, and a protective plastic coating.

A piece of material 50 x 25 - 30 mm was used for each reflector. Using a sharp knife, the plastic covering layer and the underlying reflective material was scored along a line parallel to the long edge, 3 mm from the edge. The small portion thus isolated was then loosened and peeled off. Using pliers, the aluminium backing was then bent up at 90° along the line of the cut. Thereafter, this edge was bent over so that it folded on top of the reflective material and was gently hammered flat. The process was repeated on the opposite edge. What was thus produced was a strip of reflective material 15-20 mm wide, the edges of which a were protected by the aluminium fold. The reflector is only 2 mm high.

Fitting

The flat reflector was bent and folded over the outside of the 30 mm wide radio collar belting. The ends were folded between the two layers of belting to avoid abrasion on the animal's neck. The folded reflector was then squeezed as flat as possible with pliers while avoiding damage to the reflective material. The different colours were used to identify male and female jackals.

APPENDIX A4

Yagi Roof Mount

Legend for Figure A4.

A Front-to-back vertical section.
  a Seal retainer.
  b Upper mounting block.
  b' Lower mounting block.
  c Support platform.
  d Support platform retaining bolt and wing nut.
  e Handle.
  f Roof.
  g Nylon bush.
  h Rubber 'O' ring.
  i Yagi support mast

B Support platform.
  a Lateral view.
  b Frontal view.

C Ventral view
  a Recess to receive sliding handle.

Construction

The Yagi roof mount was constructed as shown in Fig. A4. The seal retainer, mounting blocks and support platform were constructed from wood.

The support mast was constructed from 20 mm chromed round tubing, the support bracket from 20 mm cold rolled mild steel angle iron, and the handle from 6 mm mild steel rod.

Operation

In the position shown, the Yagi can be swung in an arc of 250°. If, when in the forward position, the handle is pushed backwards, the slot accepts the handle and stabilizes the antenna in the forward direction. Direction of the animal can then be ascertained by swinging the vehicle through an arc while the Yagi in is this fixed position.

By loosening the butterfly nut and swinging the support platform to the side, the support and handle can be pulled downwards to avoid damage eg. by low branches.

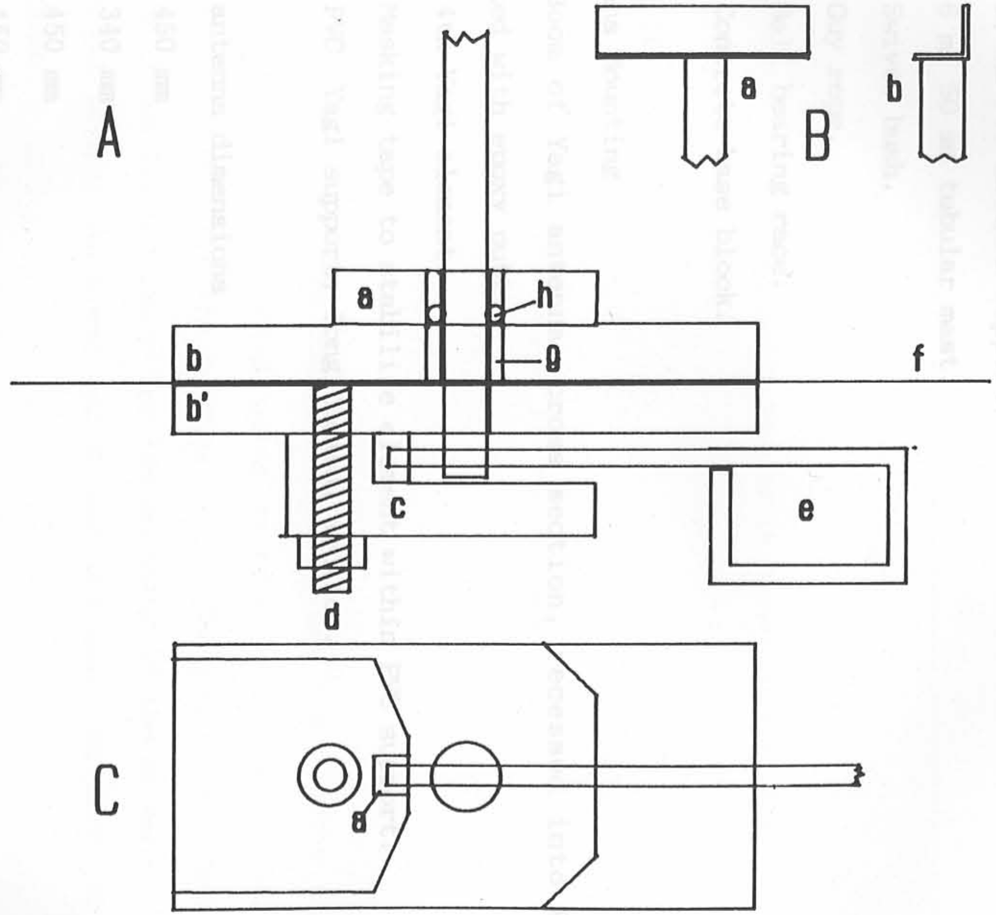

Figure A4. Yagi roof mount. See text for legend.

APPENDIX A5

Telemetry Stations

Legend for Figure A5

A Telemetry Mast

- a 2 m, 5 element Yagi antenna.
- b 30 mm PVC antenna support.
- c 6 m, 50 mm tubular mast.
- d Swivel bush.
- e Guy rope.
- f Ball bearing race.
- g Concrete base block.

B Antenna Mounting

a Boom of Yagi antenna, cross section, recessed into PVC support. Stabilized with epoxy putty.

- b 4th Yagi element.
- c Masking tape to stabilize element within PVC support.
- d PVC Yagi support, longitudinal section.

C Yagi antenna dimensions

a	450 mm
b	340 mm
c	450 mm
d	450 mm
e	1000 mm
f	950 mm
g	870 mm
h	860 mm

Legend for Fig. A5 (cont.): C Yagi antenna dimensions

i 860 mm

j 130 mm (gamma match)

D Wiring diagram

a Yagi antenna.

b VHF Booster, upper component.

c Booster, lower component.

d VHF receiver.

e Earphones.

Construction

The design of the telemetry towers is shown in Fig. A5A.

Co-axial cables

RT58U coaxial cable, length 7,5 m, was used.

Masts

Masts (Fig. A5A) were constructed from two 3 m lengths of 50 mm water pipe. Bases were constructed using reinforced concrete, and incorporated handles and a recess for the bearing race. The top of the mast was extended by 1m with 30 mm PVC waterpipe for the mounting of the antenna. This was done as any metal within the array can affect the gain and directionality of the Yagi antenna.

Compass bearings were marked onto 400x400x4 mm masonite boards such that two halves could be joined to surround the base of the pipe which stood on the bearing race. A pointer was bolted to the base of the mast to facilitate accurate reading of bearings from the compass rose.

Masts were mounted with three guy ropes attached to a swivel bush above the socket connecting the two lengths of water pipe.

Antennas

Two metre, five-element Yagi antennas were constructed from 10 mm aluminium tubing as shown in Fig A5C. This design was obtained from H. de Beer (Omega Communications, Johannesburg, South Africa) (pers. comm.).

Mounting of antenna

A recess was cut into the top of the PVC pipe to accommodate the centre beam of the Yagi antenna (Fig. A5B). Masking tape at the tip of the 4th element ensured a snug fit within the PVC pipe. Pratley's Quickset Putty (Pratley Manufacturing & Engineering Co. (Pty) Ltd., Krugersdorp, RSA) was used to stabilize the antenna in the pipe.

Boosters

12v VHF boosters (Ellies Electronics, Johannesburg, RSA) were connected as shown (Fig. A5D)

Erection and lowering

Once the three anchor points had been established and the tower erected, the tower could be raised and lowered by one person. The compass rose is removed, and the mast is lifted and placed alongside the concrete block. One of the anchors is then loosened. While holding the rope the mast is stabilized and then gradually lowered to the ground, with the bottom of the mast stabilized against the concrete base. The reverse procedure is used to erect the mast again. Single-handed raising and lowering is important in areas where lightning can damage the tower, and where there are not always two people to undertake the procedure.

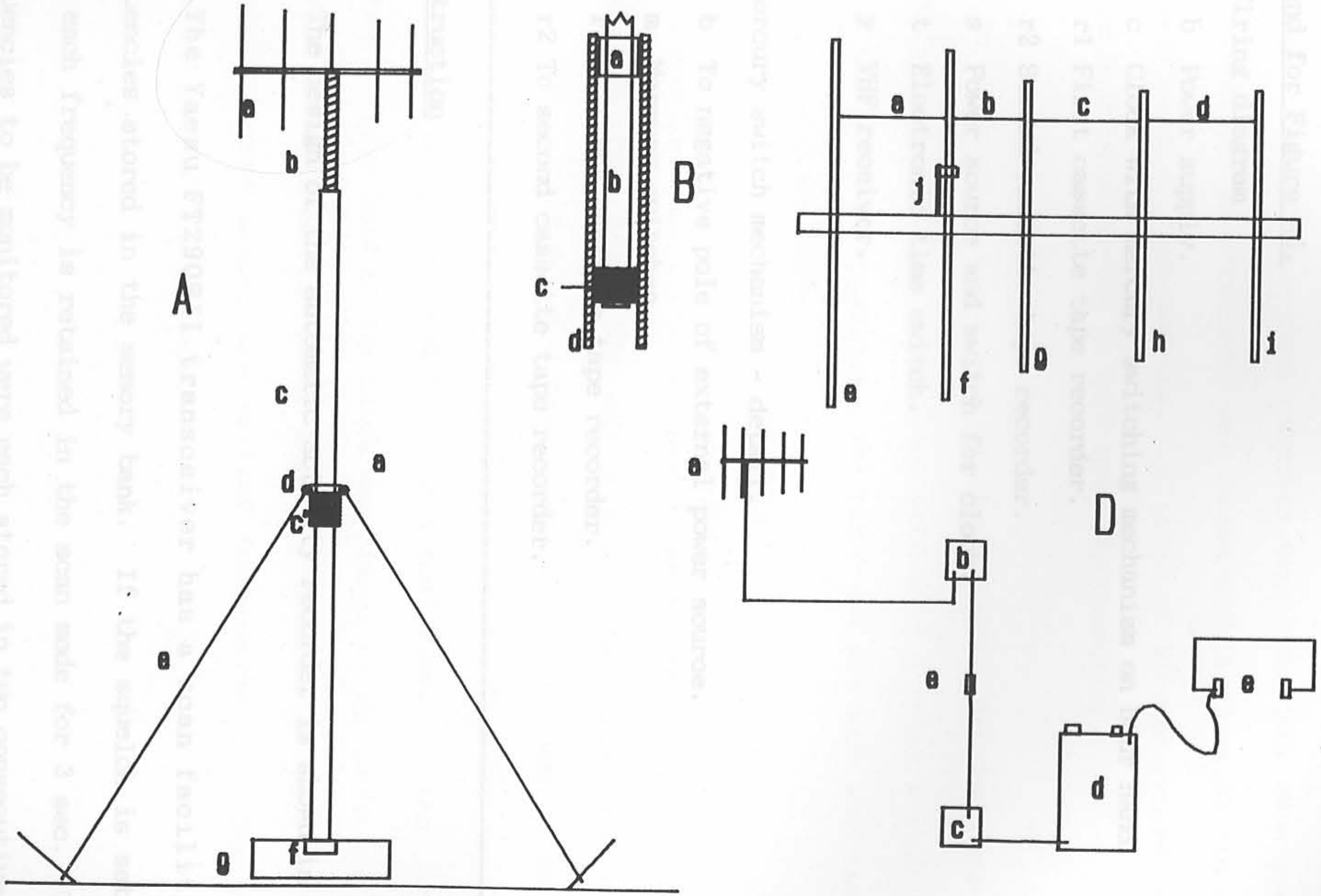

Figure A5. Telemetry station. See text for legend.

APPENDIX A6

Automatic Activity Recorder

Legend for Figure A6.

A Wiring diagram

- b Power supply.
- c Clock with mercury switching mechanism on hour hand.
- r1 First cassette tape recorder.
- r2 Second cassette tape recorder.
- s Power source and switch for clock.
- t Electronic time switch.
- y VHF receiver.

B Mercury switch mechanism - detail.

- b To negative pole of external power source.
- m Mercury switches.
- r1 To first cassette tape recorder.
- r2 To second cassette tape recorder.

Construction

The design of the automatic activity recorder is shown in Fig. A6.

The Yaesu FT290RII transceiver has a scan facility which scans frequencies stored in the memory bank. If the squelch is set to fully off, then each frequency is retained in the scan mode for 3 sec. The four jackal frequencies to be monitored were each stored in two consecutive memory slots - ie. the scan mode remained on each jackal frequency for 6 sec. The ninth memory slot contained an arbitrary FM frequency which resulted in a hissing sound distinctly different from the Upper Side Band mode used for the jackal frequencies. Signal output was conveyed to the input sockets of two cassette tape recorders.

Two Audiodek^R Auto-Stop cassette tape recorders were used to store the activity data. Each recorder was loaded with a clean 90 min cassette tape at the beginning of each session. A total of 90 min recording time was thus available without having to turn over the cassettes.

An electronic timer switch (G van Urk, Potchefstroom University, Potchefstroom, RSA) was used which activated a relay switch between a power source and the tape recorders. The timer was set such that current would flow for 1 min in every 8 min.

A modified wall clock was used to shift power supply from Recorder 1 to Recorder 2 after 5 h. The minute and second hands were removed from the clock. Two mercury switches were glued to the hour hand as shown in Fig. A6B. With this configuration, power supply is shifted from one tape recorder to the other at the 9 'o clock and 3 'o clock positions. At the beginning of each session the hour hand of the clock was placed in the 10 'o clock position i.e. Recorder 1 received the power supply. After 5 h -ie. at the 3 'o clock position - power supply was shifted to Recorder 2. The 90 min of tape therefore stores 12 h of data.

Operation

Each jackal's frequency was stored with a different discrepancy from the true frequency - i.e. the audible tone of each collar was different. Once the scan mode was operating correctly, the lead to the recorders was plugged into the output socket of the transceiver. Record buttons were depressed on both tape recorders, the clock handle was shifted to the 10 'o clock position and the clock was activated. The input lead was removed from Recorder 1. When the timer activated Recorder 1, the date and time of commencement of the session was noted via the condenser microphone onto the tape in Recorder 1. When the timer switched off after one min the lead was re-inserted for commencement of automatic recording.

At the end of each session the clock was switched off, the recorders switched off and the tapes removed.

Data Transcription

After being rewound each tape was transcribed onto a data sheet. As the time of the first recording was known, as well as the spacing of each subsequent recording, the time of each scan could be calculated. In the case of the activity collar, the number of signals/second indicated activity or inactivity. In the case of the normal collars, shifts in signal strength and tone were used to ascertain whether or not the jackal was active. Shifts to a new memory slot is marked by a beep tone. As the sequence of scan was known, position relative to the FM marker slot facilitated the identification of the jackal being monitored. The tone setting differences assisted in identifying the frequency without the need to refer to the marker slot.

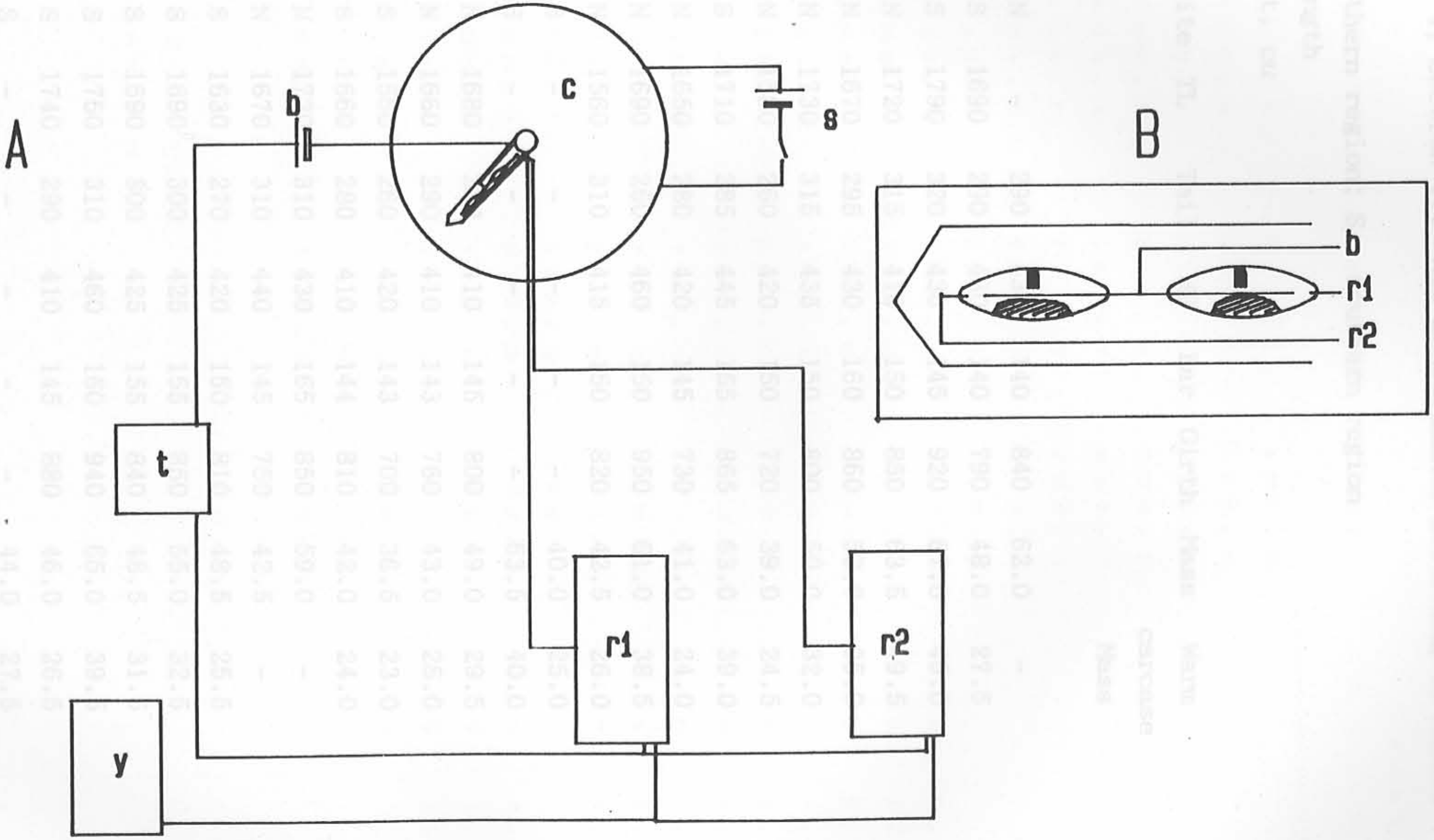

Figure A6. Automatic activity recorder. See text for legend.

APPENDIX A7

Masses and measurements of impala collected for baseline study, (Chapter 4, Section 1). All measurements according to Ansell (1965).

Site: N = northern region; S = southern region
TL = total length
HF = hind foot, *cu*

Date	Sex	Site	TL	Tail	HF	Ear	Girth	Mass	Warm carcase Mass
140486	M	N	–	290	430	140	840	62.0	–
140486	F	S	1690	290	430	140	790	48.0	27.5
140486	M	S	1790	320	430	145	920	67.0	45.0
220486	M	N	1720	315	415	150	850	63.5	49.5
220486	M	N	1670	295	430	160	860	53.0	35.0
220486	F	N	1730	315	435	150	800	50.0	32.0
250486	F	N	1580	260	420	150	720	39.0	24.5
280486	M	S	1710	285	445	155	865	63.0	39.0
290486	F	N	1650	280	420	145	730	41.0	24.0
050586	M	N	1690	260	460	150	950	61.0	38.5
050586	F	N	1560	310	415	150	820	42.5	26.0
120586	F	S	–	–	–	–	–	40.0	25.0
120586	M	S	–	–	–	–	–	63.5	40.0
200586	F	N	1680	280	410	145	800	49.0	29.5
200586	F	N	1660	290	410	143	760	43.0	26.0
270586	F	S	1550	260	420	143	700	36.5	23.0
270586	F	S	1660	280	410	144	810	42.0	24.0
020686	M	N	1730	310	430	165	850	59.0	–
020686	F	N	1670	310	440	145	750	42.5	–
090686	M	S	1630	270	420	150	810	48.5	25.5
230686	M	S	1690	300	425	155	850	55.0	32.5
230686	F	S	1590	300	425	155	840	48.5	31.5
300686	M	S	1750	310	460	160	940	65.0	39.5
300686	F	S	1740	290	410	145	880	46.0	26.5
050886	F	S	–	–	–	–	–	44.0	27.5
140886	F	S	1590	270	425	145	880	40.0	23.5

Appendix A8. Impala Kidney Fat Indices and adrenal masses - Section 1, Baseline Data.

				Adrenals		
Number	Fat	Kidneys	KFI	L	R	Tot
K618	450,4	172,6	261,0			
K625	452,4	177,0	255,6			
K626	716,2	218,5	327,8			
K630	308,6	140,6	219,5			
K631	234,1	165,2	141,7			
K634	184,0	117,0	157,3			
K635	804,5	190,7	421,9			
K638	12,2	147,1	8,3			
K640	222,8	102,6	217,2	1,1	1,2	2,3
K641	600,6	175,5	342,2	1,5	1,7	3,2
K643	83,6	125,8	66,5	1,2	1,0	2,2
K652	321,3	141,1	227,7	1,0	1,2	2,2
K656	271,7	293,0	92,7	1,4	1,8	3,2
K659	160,2	162,5	98,6	1,6	1,7	3,3
K660	85,5	140,6	60,8	1,6	1,4	3,0
K663	237,3	113,3	209,4	1,1	1,1	2,2
K667	41,4	169,6	24,4	1,7	1,7	3,4
K686	729,7	162,8	448,2			
K689	75,3	217,5	34,6	2,1	1,3	3,3
K690	103,5	178,5	58,0	1,7	1,5	3,2
K6113	116,9	162,2	72,1	1,6	1,4	3,0
K6115	615,1	146,3	420,4			
K6119	278,8	160,9	173,3			
K6122	25,7	175,2	14,7			
			181,3 (136,2)			2,9 (0,49)

Mean (std.dev.)

All masses in g.

APPENDIX A9

Ages and dental attrition of impala collected for baseline study
(Chapter 4, Section 1)

Site: N = northern region; S = southern region.

Ageing techniques: M = Murray 1980
S = Spinage 1971
RH = Roettcher & Hoffman 1970

V = vertical attrition of incisor-canine complex elements:
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

G = grooves in the neck region of incisor-canine complex elements:
0 = none
1 = slight indication of groove
2 = well defined groove
3 = deep groove - half or more of diameter of tooth

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

C = canine; 3 = I_3; 2 = I_2; 1 = I_1

No	Sex	Site	M	S	RH	V				G			
						C	3	2	1	C	3	2	1
006	M	N	5.5	D	06	2	1	0	0	0	0	1	0
004	F	N	5.5	D	07	0	0	0	0	0	0	0	0
010	M	N	6.5	D	10	1	0	0	0	0	0	0	0
002	M	N	4.5	D	06	2	1	0	0	0	0	1	0
106	F	N	2.0	3	--	0	0	0	0	0	0	0	0
061	M	N	2.0	3	01	1	0	0	0	0	0	0	0
125	F	N	6.5	D	12	5	5	4	4	3	3	3	3
018	M	N	5.5	D	06	1	0	0	0	0	0	1	0
126	M	N	5.5	D	06	0	0	0	0	0	0	0	0
059	F	N	2.0	A	02	0	0	0	0	0	0	0	0
096	F	N	2.0	3	01	0	0	0	0	0	0	0	0
060	M	N	4.5	B	05	2	2	0	0	0	0	1	0
080	F	N	2.0	3	01	0	0	0	0	0	0	0	0
079	M	N	6.5	D	07	2	2	1	0	2	0	2	0
081	M	N	2.0	A	02	0	0	0	0	0	0	0	0

No	Sex	Site	M	S	RH	V				G			
						C	3	2	1	C	3	2	1
072	F	N	2.0	3	02	1	0	0	0	0	0	0	0
071	M	N	6.5	D	08	1	1	0	0	0	0	1	0
073	M	N	5.5	D	06	1	1	0	0	0	0	0	0
029	M	N	5.5	D	06	1	1	0	0	0	0	1	0
030	M	N	2.5	A	03	1	-	0	0	0	0	0	0
031	F	N	8.5	F	10	1	1	0	0	1	0	0	0
028	M	N	5.5	D	05	1	1	0	0	0	0	0	0
001	M	N	7.5	F	06	3	3	3	1	2	0	2	0
070	F	N	6.5	D	06	1	1	0	0	0	0	1	0
034	F	N	2.0	3	--	0	0	0	0	0	0	0	0
104	M	N	2.5	B	03	1	0	0	0	0	0	0	0
005	M	N	2.0	3	02	0	0	0	0	0	0	0	0
095	F	N	2.5	A	05	0	0	0	0	0	0	0	0
027	M	N	2.5	B	03	1	0	0	0	0	0	0	0
076	M	N	2.5	B	03	1	0	0	0	0	0	0	0
042	F	N	4.5	B	05	2	2	0	0	0	0	1	0
043	F	N	5.5	D	07	0	0	0	0	1	0	1	0
044	M	N	6.5	D	10	2	2	0	0	0	0	1	0
041	M	N	2.5	A	05	0	0	0	0	0	0	0	0
105	F	N	5.5	D	05	2	1	0	0	0	0	1	0
110	M	N	5.5	D	07	1	0	0	0	0	0	0	0
040	F	N	2.0	3	02	0	0	0	0	0	0	0	0
039	F	S	5.5	D	08	4	4	3	2	2	2	2	0
033	F	S	2.5	A	02	1	0	0	0	0	0	0	0
045	F	S	6.5	F	12	5	5	5	4	-	-	-	3
046	M	S	2.5	A	04	1	0	0	0	0	0	0	0
048	M	S	2.5	A	01	0	0	0	0	0	0	0	0
055		S	4.5	D	07	2	2	1	1	0	0	0	0
038	F	S	2.0	3	--	-	-	-	-	-	-	-	-
057	F	S	7.5	F	10	4	4	4	1	2	2	2	2
058	M	S	2.5	A	02	1	1	0	0	0	0	0	0
022	M	S	2.5	A	02	0	0	0	0	0	0	0	0
037	F	S	8.5	F	12	5	5	5	5	-	-	-	-
017	M	S	2.0	3	02	1	1	0	0	0	0	0	0
036	F	S	2.5	3	02	1	0	0	0	0	0	0	0
035	M	S	8.5	F	10	4	4	1	1	1	0	2	0
016	F	S	2.0	3	02	1	0	0	0	0	0	0	0
032	F	S	3.5	A	02	1	0	0	0	0	0	0	0
066	M	S	3.5	B	04	2	2	2	1	1	0	1	0
067	F	S	4.5	D	06	4	3	3	2	2	0	2	2
068	M	S	2.0	A	02	2	1	0	0	0	0	0	0
015	F	S	5.5	B	07	3	3	3	2	1	0	1	1
051	M	S	2.5	A	02	1	0	0	0	0	0	0	0
049	F	S	5.5	D	07	2	2	1	0	2	0	1	0
050	M	S	4.5	B	04	1	1	1	0	0	0	0	0
025	F	S	8.5	F	10	3	3	2	0	3	1	2	0
014	F	S	2.5	B	02	1	0	0	0	0	0	0	0
013	M	S	5.5	D	08	4	4	4	2	2	1	2	2
020	M	S	2.5	A	02	1	0	0	0	0	0	0	0
026	M	S	8.5	F	08	3	3	2	2	2	2	2	1
077	M	S	2.5	A	03	0	0	0	0	0	0	0	0

No	Sex	Site	M	S	RH	V				G			
						C	3	2	1	C	3	2	1
078	M	S	2.5	A	02	1	0	0	0	0	0	0	0
052	M	S	6.5	D	10	3	3	3	1	1	0	2	1
053	M	S	2.5	B	02	1	0	0	0	0	0	0	0
024	F	S	2.5	A	03	2	1	0	0	0	0	0	0
088	F	S	2.0	A	02	0	0	0	0	0	0	0	0
082	F	S	8.5	F	12	5	5	5	4	3	3	3	3
089	M	S	2.5	B	02	1	0	0	0	0	0	0	0
084	M	S	8.5	F	10	2	2	1	1	0	0	2	1
086	F	S	2.0	3	01	0	0	0	0	0	0	0	0
087	F	S	2.0	3	01	0	0	0	0	0	0	0	0
083	F	S	7.5	D	10	0	0	0	0	1	1	2	2
085	F	S	2.0	3	01	0	0	0	0	0	0	0	0
090	F	S	8.5	F	12	5	5	5	4	-	-	-	3
091	F	S	7.5	D	12	5	4	4	4	-	3	3	3
092	M	S	6.5	D	07	3	3	3	2	1	0	2	0
093	F	S	5.5	D	05	1	1	0	0	0	0	1	0
094	F	S	2.0	3	01	0	0	0	0	0	0	0	0
023	F	S	4.5	B	05	3	3	3	2	2	0	1	0
021	F	S	4.5	D	06	1	1	0	0	0	0	1	0
097	F	S	2.0	3	01	0	0	0	0	0	0	0	0
012	F	S	5.5	D	08	3	3	3	2	3	2	3	2
011	F	S	8.5	F	12	4	3	2	1	3	1	2	1
009	M	S	2.0	3	02	1	0	0	0	0	0	0	0
008	M	S	5.5	D	05	3	3	3	1	2	0	1	0
007	M	S	5.5	D	06	3	3	3	1	2	0	1	0
003	M	S	2.0	3	01	1	0	0	0	0	0	0	0
019	F	S	6.5	D	07	2	2	0	0	3	1	3	0
054	M	S	2.5	A	02	0	0	0	0	0	0	0	0
056	M	S	2.5	A	02	0	0	0	0	0	0	0	0
108	M	S	2.0	3	--	-	-	-	-	-	-	-	-
109	F	S	5.5	D	07	2	2	1	0	1	0	2	2
062	F	S	6.5	D	08	4	4	4	3	3	2	3	2
118	F	S	2.5	B	03	1	1	0	0	0	0	0	0
119	F	S	8.5	F	12	3	3	1	1	3	2	3	3
114	M	S	5.5	D	05	2	1	0	0	0	0	0	0
116	F	S	5.5	D	12	5	5	4	3	2	2	2	2
117	M	S	2.5	A	03	1	1	0	0	0	0	0	0
113	M	S	3.5	A	03	1	1	0	0	0	0	0	0
115	F	S	6.5	D	08	4	4	3	2	1	0	2	2
120	M	S	2.5	A	03	1	0	0	0	0	0	0	0
121	F	S	2.5	A	03	0	0	0	0	0	0	0	0
122	F	S	8.5	F	12	5	5	5	4	-	3	3	3
123	F	S	8.5	F	12	5	5	5	5	-	-	-	-
124	M	S	6.5	D	08	0	0	0	0	0	0	0	0
063	F	S	2.0	3	01	0	0	0	0	0	0	0	0
064	M	S	2.5	A	03	1	0	0	0	0	0	0	0
127	M	S	6.5	D	07	1	1	0	0	0	0	0	0
128	F	S	6.5	D	10	4	3	3	2	2	1	2	0
065	M	S	6.5	D	07	2	2	2	1	0	0	1	0

APPENDIX A10

Impala data - Section 3.

Number	Date collected	Mass	Pregnant	Foetal Mass	Sex
M0186	22/10/86	-	Y	-	-
M0286	24/10/86	48,0	Y	2,0	F
M0386	26/10/86	45,0	Y	2,0	M
M0486	26/10/86	46,0	Y	1,5	M
M0586	03/11/86	38,0	Y	-	-
M0686	04/11/86	46,5	Y	2,5	F
M0786	06/11/86	43,5	Y	2,5	M
M0886	06/11/86	45,0	Y	3,5	F
M0986	06/11/86	43,5	Y	4,3	M
M1086	07/11/86	44,0	Y	-	-

All masses in kg.

APPENDIX A11

Impala data - Section 4.

Number	Date collected	Pregnant	Foetal Mass	Sex
M0188	07/09/88	Y	0,31	F
M0288	07/09/88	Y	0,45	F
M0388	08/09/88	Y	0,36	F
M0488	08/09/88	Y	0,41	F
M0588	09/09/88	Y	0,57	M
M0688	09/09/88	Y	0,63	M
M0788	09/09/88	Y	0,55	F
M0888	10/09/88	Y	0,40	F
M1088	10/09/88	Y	0,86	M
M1188	10/09/88	Y	0,36	F
M1288	12/09/88	Y	0,45	F
M1388	14/09/88	Y	0,57	M
M1688	15/09/88	Y	0,56	F
M1788	15/09/88	Y	0,60	M

All masses in kg.
(A11)

APPENDIX A12

Impala external parasites - Chapter 4, Section 4.

	TICKS																									LICE									
	Boophilus decoloratus																				*Riphicephalus zambesiensis*					*Linognathus sp.*					*Damilinia sp.*				
	Adult					Engorged adult female					Nymphae					Larvae					Nymphae														
NO	T	G	L	E	B	T	G	L	E	B	T	G	L	E	B	T	G	L	E	B	T	G	L	E	B	T	G	L	E	B	T	G	L	E	B
M0188	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
M0288	0	0	0	0	0	0	0	0	0	0	2	0	0	3	0	2	0	0	9	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
M0388	0	6	65	7	0	0	0	17	0	0	1	5	36	19	2	3	13	8	8	7	0	0	4	11	0	1	1	6	0	12	2	0	0	1	0
M0488	9	14	44	14	5	0	2	7	0	0	7	28	33	32	11	1	8	26	53	17	0	0	5	0	0	2	0	4	0	203	0	0	0	0	0
M0588	0	8	91	11	0	0	0	1	1	0	0	32	101	60	2	0	14	46	111	0	0	0	5	0	0	0	54	2	0	17	11	0	0	0	13
M0688	1	49	117	20	5	0	7	16	1	0	0	24	101	126	6	0	25	64	220	20	0	0	2	0	0	1	10	47	2	41	19	0	0	0	4
M0788	4	29	85	8	5	0	0	7	0	0	4	12	74	42	5	6	23	109	111	25	0	1	2	0	1	1	93	7	0	41	0	0	0	0	2
M0888	12	46	58	45	4	0	6	7	0	1	11	37	58	98	5	3	22	0	229	14	0	1	19	3	1	10	428	176	6	83	0	0	0	0	2
M1088	1	11	19	18	2	0	0	1	0	0	1	7	37	113	1	0	1	17	278	8	0	1	0	0	0	5	1	19	0	14	3	0	0	0	34
M1188	1	5	51	52	11	0	0	5	2	3	0	2	42	138	5	0	5	47	281	5	0	0	3	0	0	1	1	27	0	2	1	0	0	0	3
M1288	1	6	16	55	2	0	0	0	3	0	1	15	16	153	0	0	1	2	69	2	0	0	0	4	0	0	1	3	0	0	4	0	0	0	9
M1388	0	2	14	63	1	0	0	0	1	0	0	2	27	143	3	0	0	7	214	3	0	0	1	0	1	0	42	12	0	16	3	0	0	0	1
M1688	0	5	17	16	0	0	0	1	0	0	2	3	10	64	0	1	1	4	83	0	0	0	3	0	0	0	0	1	2	0	0	0	0	0	1
M1788	0	4	18	33	3	0	0	1	3	0	0	13	35	130	4	0	5	21	14	4	0	0	1	0	0	0	2	3	2	4	0	1	0	0	15

T = tail; G = Metatarsal glands; L = Legs; E = Ears; B = body.

APPENDIX A12

Histopathologist's report
Chapter 4, Section 4

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DEPT PATHOLOGY

Ons verw U verw Datum

18 January 1990

Dear Dr McKenzie

IMPALA SKIN IN FORMALIN

Herewith the microscopical findings in the skin specimens from Impalas submitted to me.

M3/88 - OUR REF S1115/89

Epidermis normal
There is a conspicuous perivascular infiltration of round cells and eosinophils around superficial dermal blood vessels. The sweat glands are moderately dilated and lined by cuboidal epithelium. Hairfollicles are mostly in a telogen phase and void of hair. A few of the larger deep dermal follicles are in anagen phase and contain normal hair. The walls of the blood vessels seem thickened.

M4/88 - OUR REF S1116/89

This section is identical in all aspects to the above. The section is not cut perfectly perpendicularly and some hair are visible on the surface.

M5/88 - OUR REF S1117/89

Epidermas normal
Sweat glands and cell infiltrate as in M3/88
Hair follicles are dilated, mostly empty while some contain thin hair which are broken off below the level of the epidermis. All hair follicles are in the telogen phase. No hair visible above the level of the epidermis.

M6/88 - OUR REF S1118/89

Very similar to M5/88. A few of the deeper larger hair follicles contain hair and seem to be in anagen phase.

2/.....

M7/88 - OUR REF S1119/89

Epidermis normal
Superficial hair follicles are moderately dilated but most are empty, i.e. does not contain hair remnants or even keratin. The large deep follicles do contain hair. The perivascular cell infiltrate is less intensive than in the previous cases described above.

M8/88 - OUR REF S1120/89

Very similar to M7/88. Some eosinophils present in deeper dermis at the level of the sweat and sebaceous glands. Only club hairs, in telogen phase present.

M9/88 - OUR REF S1121/89

Epidermis normal
Hair follicles are in a better condition showing normal hair growth in some of these a few follicles show superficial dilatation and contain hair in telogen phase. The cell infiltrate is mild with only the odd round cell or eosinophil around sub-epidermal blood vessels. The blood vessel walls seem thickened.

M10/88 - OUR REF S1122/89

This section show features very similar to those of M9/88. Most follicles contain hair but seem to be in the telogen phase.

M11/88 - OUR REF S1123/89

Epidermis normal, sweat glands moderately dilated and lined by flattish epithelium. Moderate number of round cells and eosinophils around sub-epidermal blood vessels. Blood vessel walls seen thickened. Most hair follicles are in telagen phase but contain hair.

COMMENTS: I am not familiar with the normal histology of the Impala skin. In any domesticated ruminant the numbers of eosinophils and round cells found in these sections would be far greater than normal. What bothers me is that these cells were present in your controls as well as the cases showing clinical alopecia - admittedly in lesser numbers though.

My speculation is that the hair are mostly in a telogen phase and not well anchored in the hair follicles. Some form of parasitic allergy is probably present resulting in rubbing and thus resulting in mechanical loss of hair followed by clinical alopecia.

3/....

Examination of the Pilansberg specimens revealed the following:

P01 - OUR REF S1789/89

Epidermis normal, hair follicles mostly in telogen phase but contain hair shafts. Sweat glands moderately dilated lined by cuboidal epithelium. Moderate numbers of round cells and some eosinophils around subepidermal blood vessels. The walls of the latter are not thickened.

P03 - OUR REF S1790/89

Small focal crust on epidermis - unknow cause. Hair follicles telogen phase but contain hair, many round cells and numerous eosinophils around sub-epidermal blood vessels. Sweat glands dilated and epithelium on the flat side (low cuboidal).

P06 - OUR REF S1791/89

Many hairs on surface, most follicles in telogen phase. Epidermis normal. Sebaceous glands prominent. Sweat glands normal. Blood vessel walls moderately thickened. Very few cells present, only a few round cells and a single eosinophil were noticed.

P08 - OUR REF S1792/89

Epidermis normal, sweat glands slightly diated. Most hair follicles in telogen phase. Mild to moderate infiltration of round cells and eosinophils around sub-epidermal blood vessels. Blood vessel walls normal thickness.

I hope that these findings and comments will be of some value and use to you.

Sincerely

Prof IBJ van Rensburg
ACTING HEAD : DEPT PATHOLOGY
VK

Short Communications/Kort Mededelings

Increasing the rate of recovery of projectile syringes and of animals darted at night

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Received 1 November 1988; accepted 16 January 1989

Reflective material applied to commercially available projectile syringes was successfully used to reduce loss of darts and to facilitate following of impala *Aepyceros melampus,* black-backed jackals *Canis mesomelas,* spotted hyaenas *Crocuta crocuta* and lions *Panthera leo* darted at night. Attachment of reflective fabric to darts of several types is illustrated. The modification described is simple and economical, and has the added advantage of reducing littering during darting operations.

Deur weerkaatsende materiaal op verdowingspyle te plak is die verlies van pyle tydens wildvangpogings verminder. Agtervolging van rooibokke *Aepyceros melampus,* rooijakkalse *Canis mesomelas,* gevlekte hiënas *Crocuta crocuta* en leeus *Panthera leo* wat in die nag met pyle verdoof is, is ook hierdeur vergemaklik. Die aanheg van weerkaatsende materiaal op verdowingspyle van verskillende soorte word ge-illustreer. Die modifikasie is eenvoudig en ekonomies, en het die bykomende voordeel dat moontlike omgewingsbesoedeling tydens wildvangoperasies verminder word.

Keywords: Capture, dart, immobilization, projectile syringe, tele-injection.

Capture or innoculation of wild animals through the remote administration of various cataleptic drugs and vaccines has become commonplace in the fields of wildlife research and wildlife management. Such tele-injection or 'darting' is achieved through various applicator and projectile systems which are commercially available. Considerable expense is often incurred through the loss of projectiles, and even greater losses may result if, in the case of immobilization, a darted animal is lost to sight before the drug takes effect.

Richardson (1983) suggested attachment of reflective material to home-made darts. This paper describes the use of a highly reflective material on commercially available projectile syringes used during nocturnal immobilization procedures over a period of three years in Botswana.

Telinject (Telinject SA, Randburg, RSA), Palmer Cap-Chur (Photo Agencies, Johannesburg, RSA) and Fauncap (Fauncap (Pty.) Ltd., Klaserie, RSA) darts were modified for nocturnal use. As most projectile syringes provide minimal surface area for the attachment of reflective material, a highly reflective material — 8910 Silver Scotchlite Reflective Fabric (3M, Johannesburg, RSA) which has a reflectivity of 450 candelas/lux/m^2 — was used. As little as 1 cm^2 of this material is clearly visible at night for over 200 m using a 200 000 c.p. spotlight for illumination.

The material was tailored to suit the dart being modified. As this material is not self-adhesive, a suitable epoxy glue (Pratley Quickset Clear Glue, Pratley Manufacturing & Engineering Co. (Pty.) Ltd., Krugersdorp, RSA) was used to attach the fabric to the darts.

Reflective strips were attached to the flight portion of the dart or as near to the rear end of the dart as possible. Attachment sites for reflective material on several commercially available projectile syringes are shown in Figure 1.

Impala *Aepyceros melampus,* black-backed jackals *Canis mesomelas,* spotted hyaenas *Crocuta crocuta* and lions *Panthera leo* were successfully immobilized at night using reflective darts. Of nine jackals darted, four pulled

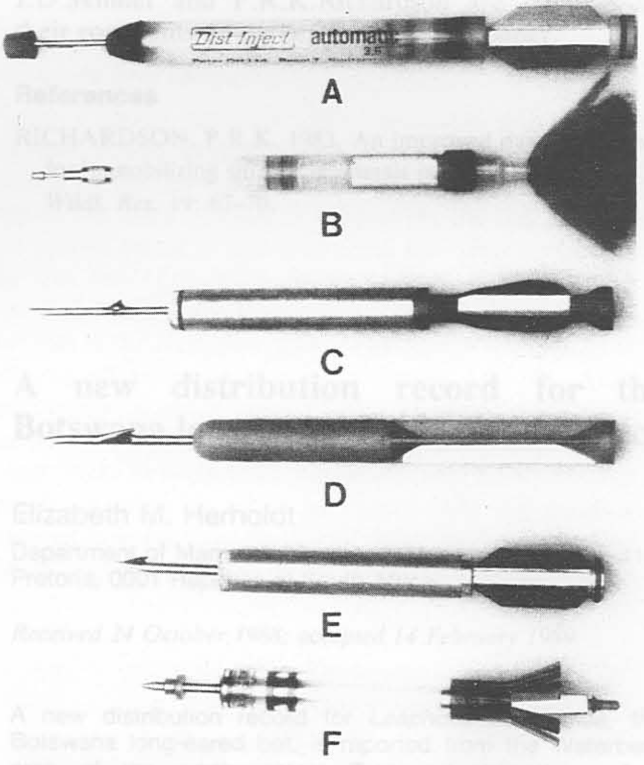

Figure 1 Reflective material (Scotchlite 8910, 3M, Johannesburg) attached to commercially available projectile syringes. Reflective portions show up white on the photograph. (A) Dist-Inject. Peter Ott H E, Postfach CH4007, Basel, Switzerland. (B) Telinject. Telinject GmbH, D6725, Romerberg, W.Germany / Telinject SA, P.O. Box 2377, Randburg, 2125 RSA. (C) Palmer Capchur with plastic tail flight modification. Palmer Capchur Chemical Equipment Co. Inc., Palmer Village, Box 867, Douglasville, Georgia 30133, USA / Photo Agencies, Johannesburg, RSA. (D) Fauncap. Fauncap (Pty.) Ltd., Box 70, Klaserie, 1381 RSA. (E) Palmer Capchur with aluminium and feather tail flight modification. (F) Paxarm. Paxarm Ltd., P.O. Box 317, Timaru, New Zealand. (Photograph: University of Pretoria.)

the darts out, all of which were recovered by searching with a spotlight. In all cases, the reflectivity of the darts facilitated identification and following of darted jackals under conditions (dark, in moderately dense vegetation cover with many other jackals in the vicinity) in which this would otherwise have been extremely difficult. Of particular value was the fact that the darted animals could be followed at a suitable distance (50–80 m), thereby exceeding flight distance and avoiding further panic following the initial trauma of the darting. Two of the jackals which pulled the darts out were lost to sight, while all those retaining their darts were followed until the drugs took effect.

Of four impala immobilized, only one shed its dart, which was later recovered. All the impala were followed until tractable. However, in the instances where the darts remained attached, the reflectivity was invaluable in identifying the animal within the herd. In one case an impala was followed at a distance of 150 m with the dart clearly visible. Impala were noted to take fright at seeing a foreign object (i.e. a dart) attached to the flank, and it is possible that this effect is exacerbated by the reflectivity of the darts. Intermittent illumination alleviated this problem.

Reflective darts facilitated the identification and following of five darted lions and three darted hyaenas until tractable. A fourth hyaena removed and destroyed the dart shortly after darting. The remains of the dart were successfully recovered by torchlight.

Over three years of nocturnal immobilizations numerous darts missed their targets. While few, if any, could have been recovered at night under normal circumstances, the reflective material assisted in the recovery of nearly all darts. Penetration of thick vegetation or sand can render the reflectivity ineffective, and accounted for the few darts that were not found. On several occasions reflective darts were lost during the day despite bright colouration of the flights (Telinject), but were easily recovered by returning to the site at night with a spotlight or torch.

In attaching reflective material to darts care should be taken to ensure that edges are firmly adhered, as loose reflective material can adversely influence the aerodynamic properties of the dart. Epoxy adhesives are preferable to contact adhesives in this regard. In none of the darts so far modified has securely adhered reflective fabric been found to influence the function of the darts in any way. Reflectivity, even from the curved surfaces, is excellent, although there are always angles at which little or no reflection is achieved. The observer must be as close as possible to the source of illumination for optimum results, as the angle between incident and reflected light influences the reflectivity considerably. The brightly coloured self-adhesive reflective fabrics used by Richardson (1983) have a reflectivity only one third that of the silver fabric (i.e. 160 candelas/lux/m^2). These fabrics may, however, serve to increase the visibility of the darts during daylight particularly if the darts are not constructed of brightly coloured materials, and combinations of highly reflective and brightly coloured reflective fabrics could be used to optimize recovery rate of lost darts.

Attachment of reflective material to projectile syringes has two main advantages: First, efficiency and reliability of nocturnal immobilizations is enhanced and second, the recovery rate of darts lost by day or by night is considerably improved, resulting in a saving in time and expense. The incidental advantage of more efficient removal of unsightly and potentially dangerous equipment from the site, often a nature conservation area, also bears mention.

Acknowledgements

I thank Des Anderson and Gregory McKenzie for assistance in obtaining suitable reflective material, and L.P. Colly for the use of some projectile syringes. The technique was developed while conducting research supported by the Foundation for Research Development, The Mammal Research Institute and Mashatu Game Reserve. Research was undertaken with the permission of the Office of the President and the Department of Wildlife and National Parks, Botswana. J.D.Skinner and P.R.K.Richardson are thanked for their comments on earlier drafts of this paper.

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A new distribution record for the Botswana long-eared bat in South Africa

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A new distribution record for *Laephotis botswanae*, the Botswana long-eared bat, is reported from the Waterberg area of the north-western Transvaal, based on four specimens collected over seven months. Some observations on the natural history of this species are made.

'n Nuwe verspreidingsrekord vir *Laephotis botswanae*, die Botswana-langoorvlêrmuis, gebaseer op vier eksemplare versamel oor 'n termyn van sewe maande, word gerapporteer vanaf die Waterberg-distrik van die noordwes-Transvaal. Waarnemings rakende hierdie spesies se algemene biologie word ook genoteer.

Keywords: Bat, mammal distribution, Transvaal mammals, Vespertilionidae

The Botswana long-eared bat, *Laephotis botswanae* Setzer, 1971, has previously been recorded within South

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Humane modification of steel foothold traps

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A modification of a steel foothold trap is described which successfully eliminates direct injury to trapped animals through: (i) reduction of impact force per unit area by increasing surface area of jaws; (ii) cushioning of impact by incorporating pliancy in one of the jaws, and (iii) cushioning of impact and prevention of laceration by padding of the widened jaws. The padding used is easily replaced — an aspect which may encourage the use of this humane modification. Use of the padded trap should reduce mortalities and injuries in non-target species. The successful capture of seven black-backed jackals *Canis mesomelas* using padded traps is reported.

'n Modifikasie van 'n slagyster word beskryf wat direkte besering aan diere uitskakel deur: (i) die slag per oppervlakte-eenheid te verminder deur die vangoppervlak van die slagysterkaak te vergroot; (ii) die slag te versag deur een van die kake buigsaam te maak, en (iii) 'n kussinglaag op die kake aan te bring om sodoende die slag te versag en latere besering te verhoed. Gebruik van die modifikasie word vergemaklik deur die maklike vervangbaarheid van die kussinglaag. Nie-teiken diere wat gevang word, behoort aan minder beserings en vrektes onderworpe te wees. Gemodifiseerde slagysters is suksesvol aangewend vir die vang van sewe rooi-jakkalse *Canis mesomelas*.

Keywords: Carnivore trapping, jackal, problem animal capture, trap design

Introduction

Successful live capture of carnivores often proves to be an obstacle to research or management-orientated projects (van der Merwe 1953; Lynch 1980; Ferguson 1980). One of the most successful techniques for the capture of small canids is the modified foothold trap (Payne, Jenkins & Provost 1966; Gipson & Sealander 1972; Drewek 1980; Rowe-Rowe & Green 1981; Windberg, Anderson & Engeman 1985). The greatest advantage of this technique is that no part of the mechanism is visible when set, thus minimizing, although not eliminating, the problem of trap avoidance. Various modifications can be made to reduce trauma if the animals are to be used for live studies. Traps may be padded with soft material (Drewek 1980; Rowe-Rowe & Green 1981) or rubber-like compounds (e.g. Olsen, Linhart, Holmes, Dasch & Male 1986). However, if the width of the jaws underneath the padding remains narrow, the force per unit area exerted by the closing jaws of the trap remains considerable. This is sometimes alleviated by weakening the springs of the trap (Drewek 1980). However, weakened springs also extend the closing time of the trap, which may result in capture avoidance by the intended subject (pers. obs.; Linhart, Dasch, Male & Engeman 1986), and does not necessarily eliminate trauma to the animal (Drewek 1980; Olsen *et al.* 1986; Olsen, Linscombe, Wright & Holmes 1988).

Padded foothold traps are commercially available in the USA and Canada (Soft Catch™, Woodstream Corporation, Lititz, Pennsylvania 17543, USA). As padded foothold traps are not easily available in southern Africa where foothold traps are commonly used, and as many unpadded traps are currently in use, this paper describes a simple, effective modification of an available trap for the humane capture of jackal-sized carnivores.

Materials and Methods

Figure 1 shows the unmodified foothold trap (Brock Tuchten, Johannesburg, RSA). The width of the impact surface of the jaws is 4 mm. After safely securing the trap in the open position, or removing the coil springs, 5–7 mm of metal is removed from the inner surface of the free jaw (Figure 2). Strips of mild steel plate (28 mm × 1,5 mm) are then cut to size to fit the inner surfaces of the trap jaws, and are brazed or welded to the jaws at all points of contact (Figures 3 & 4). After thoroughly cleaning the trap and filing the edges and corners of the plates, padding material (closed-cell foam, 9 mm thick; Moroak C.C., Johannesburg, RSA) is cut to size (care must be taken to ensure that the padding material is wider than the metal plates by 2–3 mm in all directions) and adhered to the inner plate surfaces using

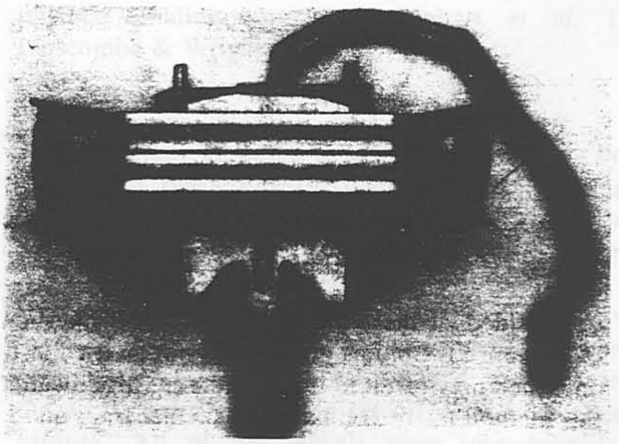


Figure 1 Unmodified steel foothold trap ('Jackal', Brock Tuchten, Johannesburg, RSA). (Photographs: University of Pretoria.)

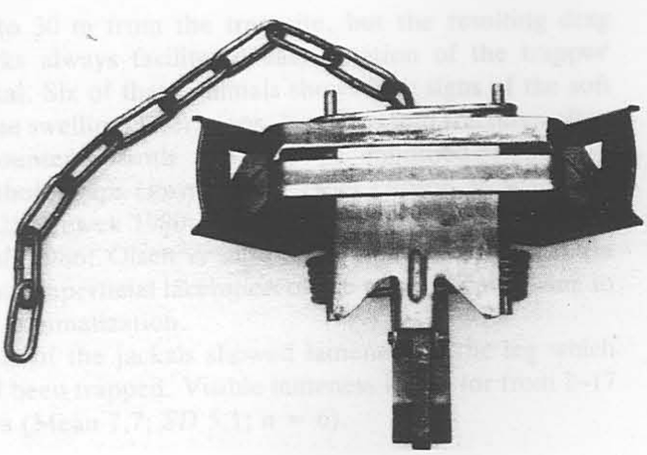
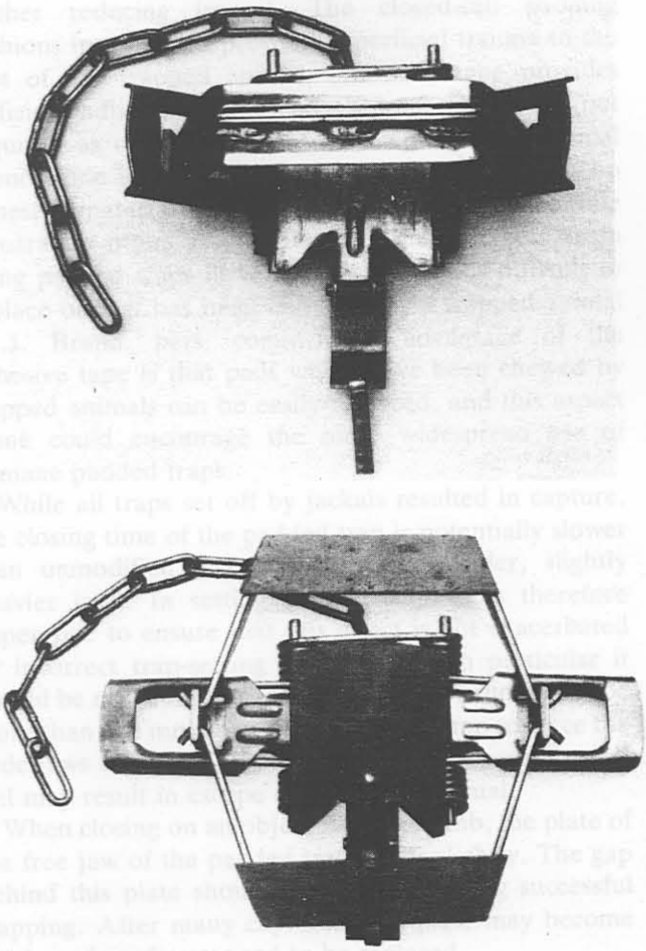


Figure 2 Five to seven millimetres of metal removed from inner surface of free jaw.



Figures 3 & 4 Metal plates welded to inner surfaces of jaws.

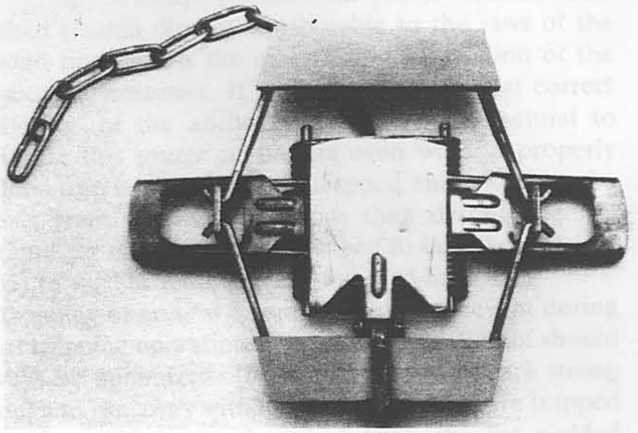


Figure 5 Closed-cell foam pads adhered to inner surfaces of widened jaws.

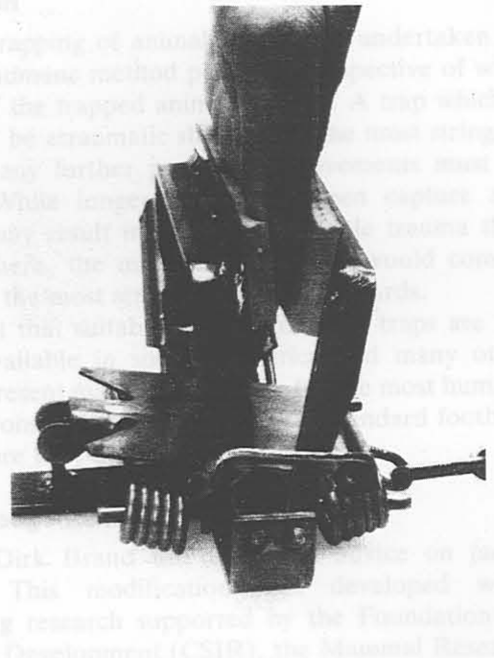


Figure 6 Testing of padded trap.

double sided adhesive tape (3M, Johannesburg, RSA)(Figure 5). Contact glue should not be used as the strong smell may result in trap avoidance. Modifications of this method for use on larger or smaller traps and for traps already being used by farmers and problem animal control units are easily made.

One of the coil springs can be removed to reduce closing impact. This may, however, result in the escape of the subject owing to prolonged closing time and/or reduced holding properties (Linhart *et al.* 1986; Linscombe & Wright 1988).

Results

Foothold traps modified as described can safely be set off against one's fingers (Figure 6). No bruising or lacerations occur. Mild transient erythema may occur following removal of the hand from the trap, but there is no sign of oedematous swelling.

Seven black-backed jackals *Canis mesomelas* were captured in Mashatu Game Reserve, Botswana (22°10′S / 29°10′E) using the padded foothold traps. On no occasion was a trap set off without resulting in capture. All of the jackals were immobilized and released from the traps within 1 h of capture. Traps were attached via a spring to a heavy metal weight (3–4 kg) with irregular projections. The weights were dragged for up to 30 m from the trap site, but the resulting drag marks always facilitated easy location of the trapped jackal. Six of these animals showed no signs of the soft tissue swelling, lacerations, luxations and fractures often encountered with the use of modified ('padded') foothold traps (Payne *et al.* 1966; Gipson & Sealander 1972; Drewek 1980; Rowe-Rowe & Green 1981; Olsen *et al.* 1986; Olsen *et al.* 1988). One jackal suffered a minor superficial laceration of the trapped paw owing to self traumatization.

Six of the jackals showed lameness of the leg which had been trapped. Visible lameness lasted for from 2–17 days (Mean 7,7; *SD* 5,1; $n = 6$).

Discussion

The widening of the jaws from 4 to 28 mm reduces the impact force per unit area by a factor of 7. The gap behind the plate of the free jaw provides 'give', thus further reducing impact. The closed-cell padding cushions impact, and prevents superficial trauma to the foot of the trapped animal. Adhesive tape provides sufficient adhesion of the pads — total adhesion is not required as once the trap is closed the target animal cannot slide its paw out of the trap even if there is no adhesive material between the plates and pads. Time constraints often prevent farmers and trappers from using padded traps in which the padding is difficult to replace once it has been damaged by a trapped animal (D.J. Brand, pers. comm.) An advantage of the adhesive tape is that pads which have been chewed by trapped animals can be easily replaced, and this aspect alone could encourage the more widespread use of humane padded traps.

While all traps set off by jackals resulted in capture, the closing time of the padded trap is potentially slower than unmodified traps owing to the wider, slightly heavier jaws. In setting padded traps it is therefore imperative to ensure that this effect is not exacerbated by incorrect trap-setting procedure — in particular it should be noted that soil covering the jaws should not be more than 5–8 mm deep. Requiring the trap to force the wide jaws through a layer of thick, possibly compacted, soil may result in escape of the target animal.

When closing on an object such as a limb, the plate of the free jaw of the padded trap bends slightly. The gap behind this plate should be re-set following successful trapping. After many captures, this plate may become weakened, and may need to be replaced.

Padded traps should be stored for short periods in the open position to maintain the cushioning properties of the padding material. Pads should be removed for long-term storage of traps in the closed position.

From observations of trapped jackals it is evident that considerable effort is expended in attempting to escape from the trap, particularly when approached for immobilization or release. It is most probable that ligaments, tendons and muscles of the trapped limb are strained during this process. Even muscles and tendons of the free limbs can show signs of trauma resulting from the attempt to escape (Olsen *et al.* 1986). As there is no marked trauma directly attributable to the jaws of the padded trap, this is the most likely explanation of the subsequent lameness. It appears therefore that correct 'buffering' of the anchor via a spring is essential to minimize this source of trauma even when a properly padded trap is being used. If trapped animals are to be left in traps for longer periods than described here, tranquilizer tabs should be attached to the traps (Balser 1965) to further minimize self-inflicted injuries.

Trapping of non-target species is a likely event during most trapping operations, and the effects thereof should always be minimized. If large species which are strong enough to run away with the trap and anchor are trapped with the padded trap described here, the flat padded surface facilitates the withdrawal of the trapped limb from the small trap. Smaller non-target species can be released relatively unharmed from the trap.

Conclusion

Any live-trapping of animals should be undertaken by the most humane method possible, irrespective of what the fate of the trapped animal is to be. A trap which is claimed to be atraumatic should pass the most stringent test, and any further possible improvements must be applied. While longer periods between capture and removal may result in more considerable trauma than reported here, the modified trap itself would comply with even the most stringent ethical standards.

The fact that suitably padded foothold traps are not readily available in southern Africa and many other areas at present makes it necessary for the most humane modifications possible to be made to standard foothold traps before they are used in the field.

Acknowledgements

I thank Dirk Brand for invaluable advice on jackal capture. This modification was developed while conducting research supported by the Foundation for Research Development (CSIR), the Mammal Research Institute and Mashatu Game Reserve. Research was undertaken with the permission of the Office of the President and the Department of Wildlife and National Parks, Botswana. J.D. Skinner and J.W.H. Ferguson are thanked for their comments on earlier drafts of this paper.

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Zoological Journal of the Linnean Society (1990), *99:* 117–128. With 8 figures

The ruminant dental grooming apparatus

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Correlations between dental morphology and dietary preferences in ruminants explain the similarities but not the differences in relative incisor width encountered within the group. Observations on African browsing antelope have revealed extensive use of the lateral anterior dental elements for grooming purposes using a distinctive upward sweeping movement of the head. Inspection of these dental elements (I_2, I_3 and C) reveals a comb-like array remarkably similar to the prosimian tooth-comb. An hypothesis is presented to explain differences in incisor morphology based on the use of the teeth for purposes other than eating. The alternative biological role has implications for the use of dental characteristics in the determination of the feeding ecology of living and extinct ruminants.

KEY WORDS:—Dental morphology – ruminants – grooming – parasites – feeding ecology.

CONTENTS

INTRODUCTION

Mammalian dentition is a key element in the morphological and ecological classification of species and is thus of fundamental importance to taxonomists and ecologists alike. The distinctive patterns of dental morphology associated with different dietary specializations provide us with a valuable insight into the feeding ecology of mammals, whether living or extinct. However, this easily observed and generally well preserved ‘peephole’ has been used so often and for so long that a particular relationship between form and function—that is that feeding habits are the over-riding determinant of dental morphology—is often assumed. Considerable controversy therefore surrounded the suggestion that the comb-like mandibular incisors characteristic of some prosimian primates had evolved specifically as a grooming organ (Cuvier & St. Hilaire, 1825; Stein, 1936; Roberts, 1941; Beuttner-Janusch & Andrew, 1962; Martin, 1972; Gingerich, 1975; Szalay & Seligsohn, 1977; Schwartz, 1979; Eaglen, 1980; Gingerich & Martin, 1981; Rose, Walker & Jacobs, 1981; Rosenberger & Strasser, 1985; Eaglen, 1986). To date the grooming hypothesis appears to have

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gained sufficient support (Roberts, 1941; Beuttner-Janusch & Andrew, 1962; Szalay & Seligsohn, 1977; Eaglen, 1980; Rose *et al.*, 1981; Rosenberger & Strasser, 1985) and, for the moment at least, the case rests. This paper reports the occurrence of a specialized dental grooming apparatus that is widespread amongst ruminant herbivores, and which closely resembles the prosimian tooth-comb.

The incisor teeth of mammals, being the most anterior elements of the dental array, are generally ascribed a 'nipping', 'cutting', 'holding' or 'collecting' function (DeBlase & Martin, 1974). A 'typical' incisor consists of a single relatively deep root and a medium to high spatulate crown—and a row of six such incisors forms a knife edge along the anterior aspect of the jaw which, in occlusion with its counterpart in the other jaw, forms a self-evident food collecting organ. In the case of the ruminants, the lower incisors and the incisiform canine (together here referred to as the incisor-canine (IC) complex) occlude against the fibrous dental pad of the upper jaw. This arrangement, together with the lips, performs the grasping and cutting action required for the ingestion of the vegetable diet.

Extant ruminants are classically referred to as grazers, mixed feeders or browsers according to the composition of their observed diet. Alternatively browsers, which selectively feed on nutritious leaves and shoots, may be classified as concentrate selectors, while grazers may be referred to as bulk feeders (Hofmann & Stewart, 1972). It has been noted that incisor morphology differs

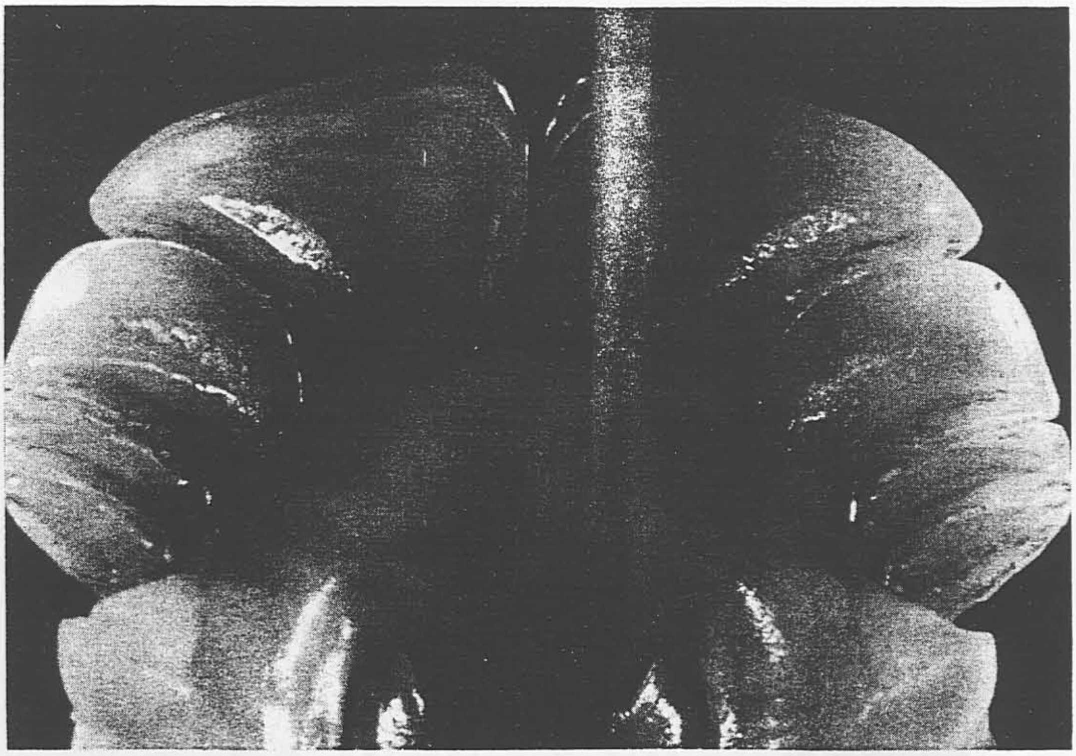

Figure 1. The incisor-canine complex of the lower jaw of an adult impala (*Aepyceros melampus*) showing the considerable percentage of the complex contributed to by I$_1$, and the needle-like structure of the lateral elements (I$_3$ and canine). (Photo: University of Pretoria.)

between these various groups: the incisors of grazers tend to be of an even size, while in browsers and mixed feeders the central incisor is laterally expanded with a concomitant decrease in the width of the lateral elements of the IC complex (Von Lehmann, 1961; Boue, 1970; Janis & Ehrhardt, 1988) (Fig. 1). Being selective feeders, the general narrowing of the muzzle and incisor row observed in the browsers is interpreted as a requirement of this selective feeding habit (Owen-Smith, 1982; Janis & Ehrhardt, 1988). The question of why the narrowing of the incisor row and muzzle is accompanied by expansion of the first incisors and reduction in size but not number of the lateral elements has not previously been addressed.

The expanded central incisors of browsers, sometimes called the pincers (Von Lehmann, 1961; Boue, 1970), comprise up to 60% of the total length of the IC complex (Pockock, 1935; Boue, 1970; Janis & Ehrhardt, 1988) (Fig. 1). While the first two elements (I_1 & I_2) of the IC complex appear well suited to a food collecting function, occlusion of the needle-like third incisor and canine against the dental pad is ineffectual in grasping or cutting food material (Fig. 2). In addition, these teeth are delicate and are relatively loosely embedded in their alveoli. By inference, these lateral teeth are regarded as vestigial by many authors. However, the persistence of these apparently vestigial lateral teeth does require some explanation, and it has been suggested that they perform a scraping, combing action "from the corners of the lips" during browsing (Boue, 1970). It is possible, however, that in seeking a feeding related function for these enigmatic teeth, or in inferring vestigiality, we have overlooked the fact that teeth are not only used for eating.

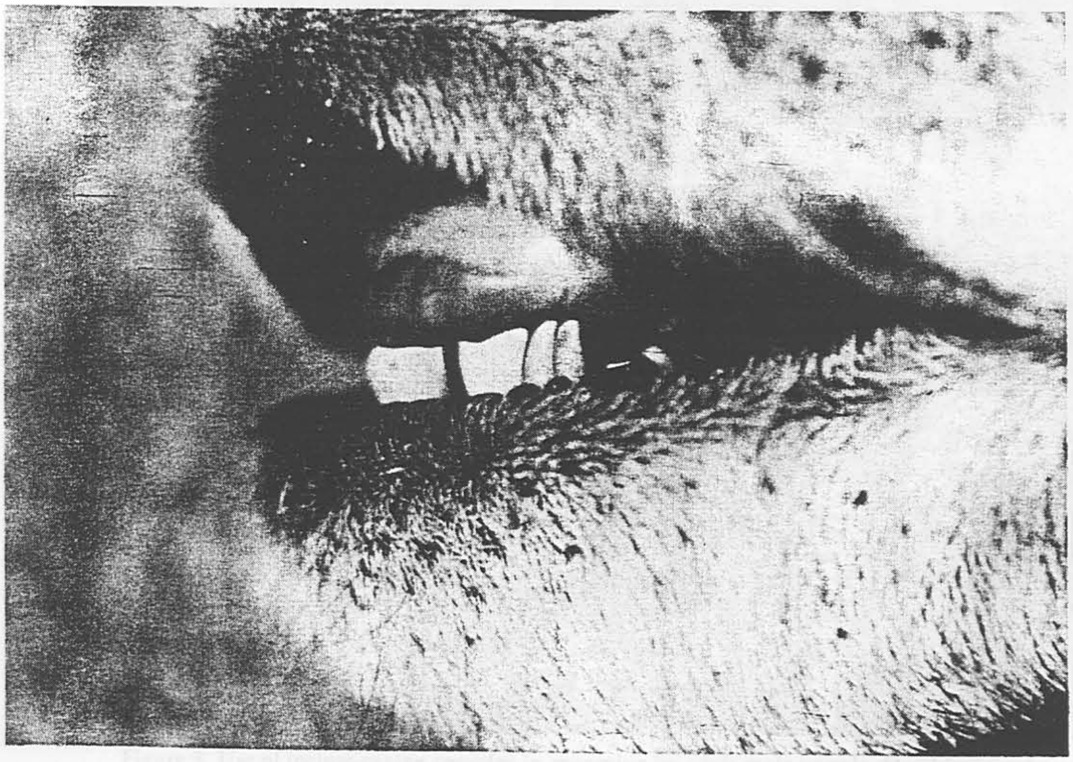

Figure 2. Lateral elements of impala incisor-canine complex *in situ*.

IN MOVING LATERALLY: THE ALTERNATIVE BIOLOGICAL ROLE

Grooming of the pelage forms an important part of the behavioural repertoire of many mammals. The primary function of this behaviour is the maintenance of the skin and associated pelage through the removal of parasites, debris or water, alignment of the hairs of the coat and sometimes the dispersion of odours or secretions through the pelage (Rosenberger & Strasser, 1985). A secondary social function has developed in many group-living species.

To facilitate effective grooming, specialized structures are found associated with the hind feet of many mammals (Dubost, 1970). The comb-like lower incisors of prosimians and tree-shrews are another example of anatomical specialization to facilitate grooming requirements (Cuvier & St. Hilaire, 1825; Roberts, 1941; Beuttner-Janusch & Andrew, 1962; Szalay & Seligsohn, 1977; Eaglen, 1980; Rose *et al.*, 1981; Rosenberger & Strasser, 1985; Eaglen, 1986).

Inspection of the lateral components of the IC complex of browsers and mixed feeders reveals a comb-like structure remarkably similar to the prosimian tooth-comb (Fig. 1). These elements are high-crowned, with a strong median ridge on the lingual surface, and with needle-like tips. The tips are aligned in a neat row directed upwards and outwards (Fig. 2). Observations on three species of African browsing antelope, impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*) and steenbok (*Raphiceros campestris*) have shown that this dental assemblage is used extensively for grooming all accessible parts of the body. A distinct upwards motion of the head is used to comb the teeth through the pelage (Fig. 3). Only close observation reveals that the teeth, not the tongue, are used in this process. Figure 4 shows the alignment of the mandible and teeth relative to the flank with

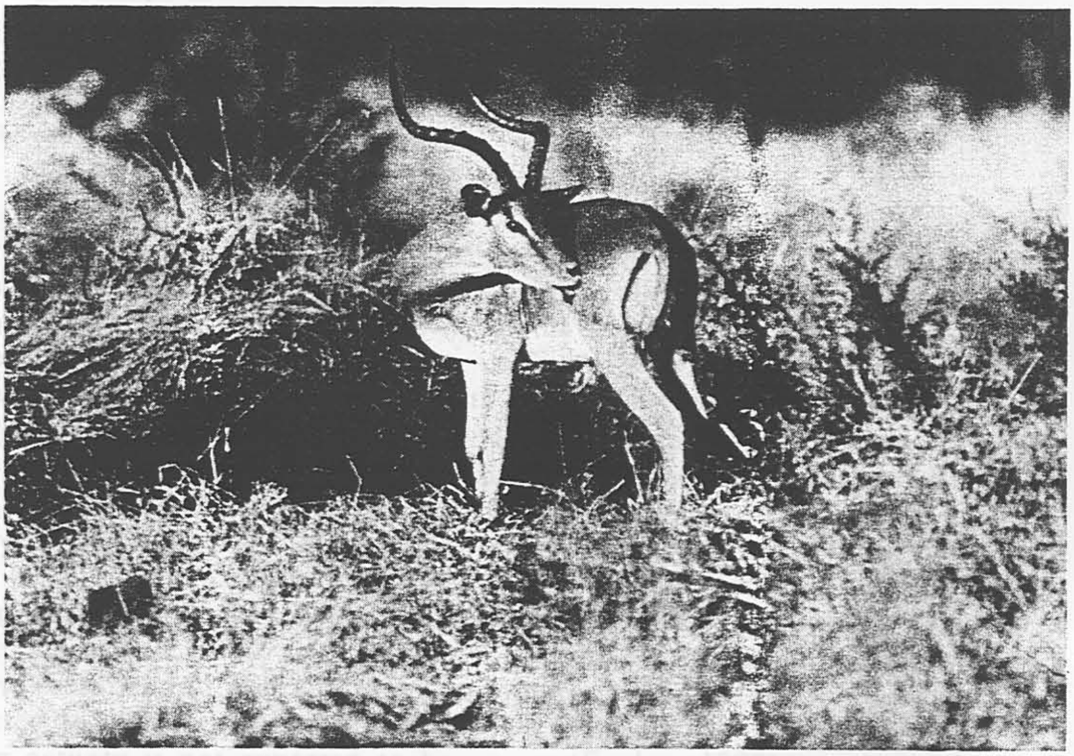

Figure 3. Use of incisor-canine complex in grooming by adult male impala. Head is moved vertically upwards against the body in this position.

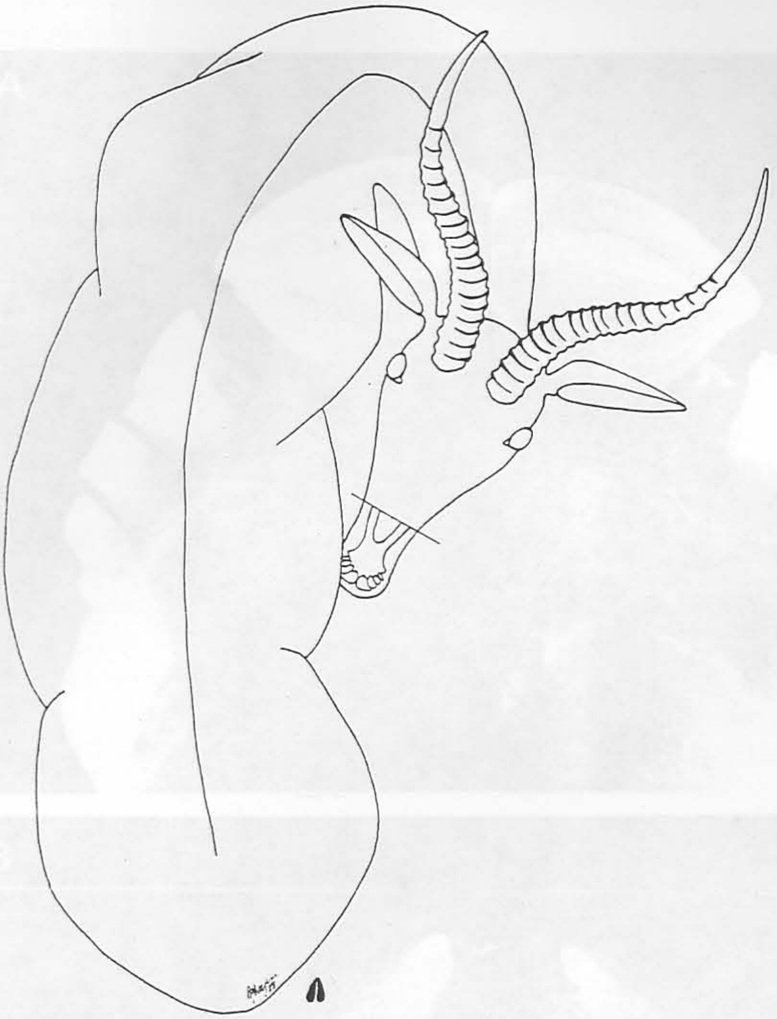

Figure 4. Alignment of components in a typical grooming posture of impala. (Artwork: A. van Rooyen.)

the head in a grooming position. It can be seen that in such a position the toothcomb is so aligned as to rake evenly the selected part of the pelage with a vertical movement of the head. In the narrowing of the muzzle, widening of the first incisor and alignment of the other incisor-canine complex elements, a selective feeding adaptation has been combined with an effective grooming tool.

One limitation of this morphological adaptation is that not all parts of the body are equally accessible. In particular, the head and neck cannot be groomed with the teeth at all. However, behavioural adaptation compensates for this deficiency through ritualized mutual allogrooming, in which individual antelope use their teeth to groom the necks and heads of other herd or family members.

Mammalian grooming behaviour has been shown to control external parasites effectively (Snowball, 1956; Bell, Jellison & Owen, 1962; Riek, 1962; Bennett, 1969), and seasonal and spatial differences in parasite abundance may therefore be expected to influence grooming frequency. While dental attrition through grooming activity is not expected to be severe (Eaglen, 1986), grooming has been shown to result in wear grooves in the anterior teeth of primates (Rose *et*

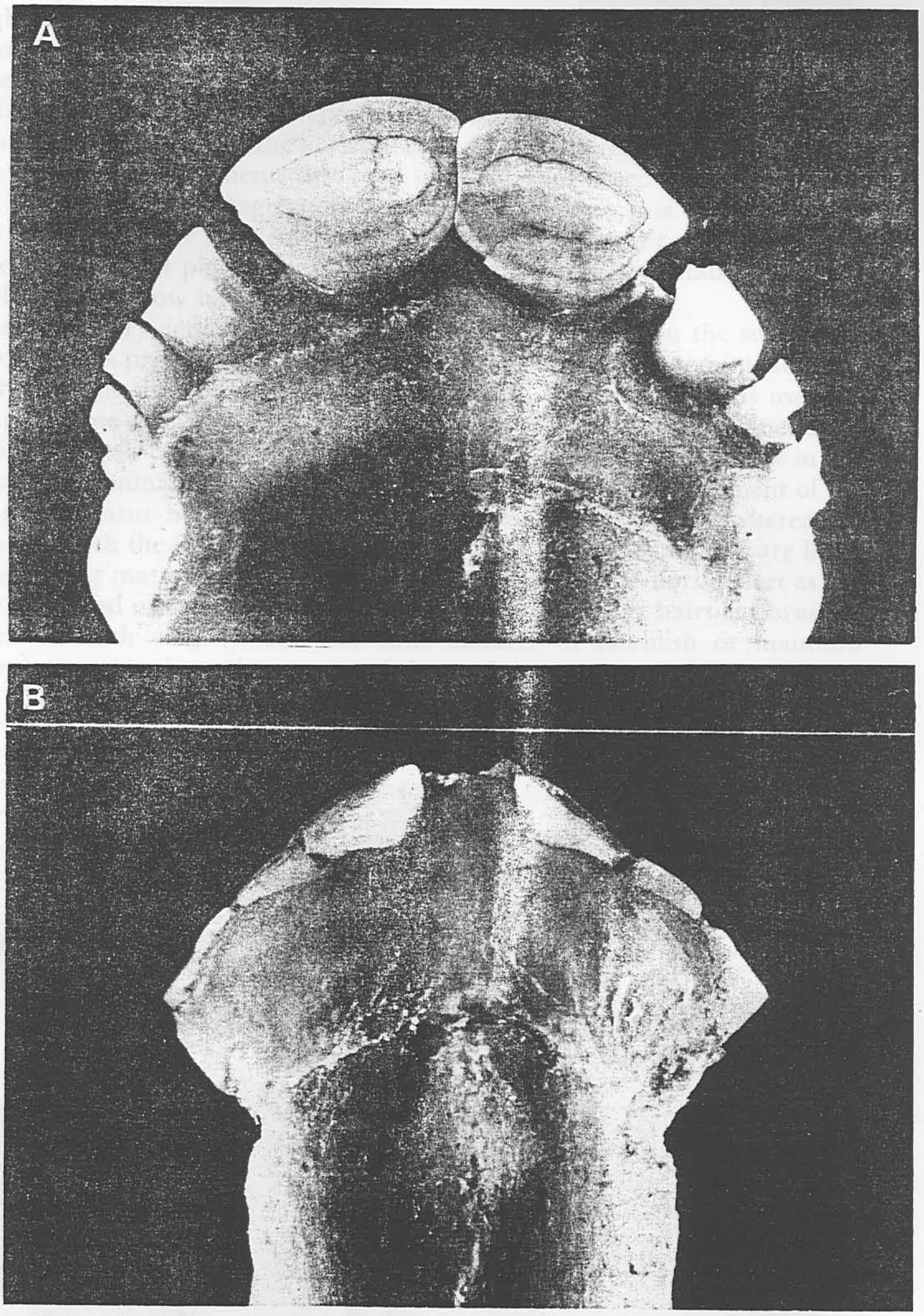

Figure 5. Progressive attrition of incisor-canine complex of impala. A, Horizontal attrition of I_1 due to eating function. Vertical attrition of I_2, I_3 and canine due to grooming activity—tips rubbed against skin. Note notches caused by hair being drawn between teeth. B, Vertical attrition due to grooming progressed to involve all elements of incisor-canine complex. (Photos: University of Pretoria.)

al., 1981). Similarly, prolonged use of the incisor-canine complex for grooming could be responsible for dental attrition in herbivores, particularly in localities with high external parasite abundance, and may indicate the extent to which the dental array is applied to this particular function.

Figure 5 demonstrates progressive wear of the incisor canine complex of adult impala from Mashatu Game Reserve in Botswana (22°10′S; 29°00′E). Feeding-related attrition accounts for the horizontal wear of I_1 and I_2 in Fig. 5A. Vertical attrition of the lateral elements first seen in Fig. 5A is caused by the grooming activity, and eventually progresses to involve all the elements. Eventually, in very old animals, all the IC elements may be worn down to (or even below) the gum line in a vertical plane (Fig. 5B). These old animals are unable to groom effectively, as they now lack the grooming apparatus.

Rose *et al.* (1981) demonstrated clear microscopic grooves on the surfaces of incisors of various prosimian primates which were ascribed to grooming activity. These grooves clearly indicated the extent to which the tooth-comb is used for grooming in those species, and finally ended the controversy over the function of the prosimian tooth-comb. No such clear microscopic grooves are evident in the IC complex of ruminants. This can be ascribed to the fact that movement of the grooming apparatus is against the lie of the hair in ruminants, whereas in primates it is with the lie of the hair. In the latter, the individual hairs are long, and loops of long matted hair therefore would result in a 'rope-burn' effect as the hairs are realigned using the teeth. In the herbivores, the short hairs are brushed aside by the teeth (Fig. 6), and are thus unlikely to establish or maintain microscopic grooves along the crowns of the teeth.

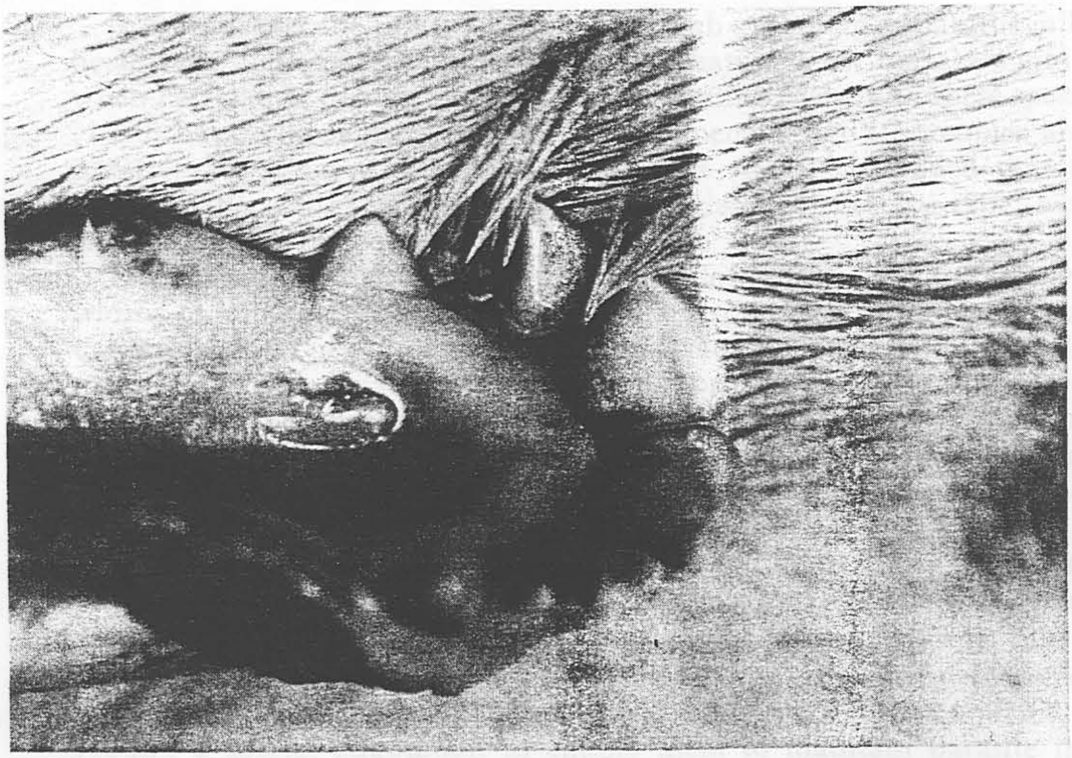

Figure 6. Simulated combing action of incisor-canine complex of impala.

Figure 7. Radiograph indicating macroscopic notches in neck regions of incisors due to grooming activity. (University of Pretoria.)

In ruminants the neck regions of the teeth of the IC complex are, however, subject to a high rate of attrition by the short hairs of the pelage relative to the attrition of the enamel crown. This results in unusual shapes representing macroscopic grooves in old animals which have used their teeth extensively for grooming (Figs 5A, 7).

RE-INTERPRETATION OF STRUCTURE

In considering the utility of the tooth-comb grooming apparatus in browsing herbivores, it becomes apparent that this feature must be taken into account when correlating dental characteristics to feeding ecology in these species. Boue (1970) has declared that the fine lateral elements of the IC complex are used in selective browsing, while Janis & Ehrhardt (1988) concluded that the ratio between the widths of I_1 and I_3 was correlated to dietary type, without an explanation for the correlation.

From Janis & Ehrhardt's impressive collection of data on relative incisor widths of numerous ungulates it is apparent that most of those ruminants with the largest ratio of I_1 to I_3 (i.e. with small lateral elements which could form a tooth-comb) are small to medium-sized browsers or mixed feeders. Other authors have also noted that the inequality of the incisors is most obvious in the small and medium-sized browsers and mixed feeders, is less apparent in the larger browsing species, and is generally minimal in the grazers (Pockock, 1935; Von Lehmann, 1961; Boue, 1970).

Browsers are by nature selective feeders, and come into close contact with vegetation in their quest for selected food items (Dubost, 1979), particularly during the drier months of the year when suitable browse occurs as a clumped resource in moist microhabitats. In so doing, they are potentially exposed to a greater external parasite infestation than the grazers of the open plains, and may require a special adaptation to enable them to maintain parasite infestation within acceptable limits.

In collecting young, nutritious leaves and shoots, browsers experience minimal attrition of their incisors, while grazers of coarse grass experience severe incisor attrition. Spinage (1973) has shown that M1 wear in grazers is generally in unison with incisor wear, while browsers incisor wear proceeds at a relatively slower rate than molar wear. This difference is all the more significant when it is noted that the incisor row of extant grazers is of a far more robust nature than that of the browsers. Thus it is possible that small and medium-sized browsers have been able to set aside their lateral teeth for a purpose unrelated to eating without risking a rapid loss through attrition of the remaining 'collector' incisors—much in the way that the prosimian tooth-comb evolved without affecting feeding ability (Beuttner-Janusch & Andrew, 1962). The parallel between prosimian and ruminant tooth combs is further highlighted by the appearance of the canine in this complex in both groups (assuming that the third element of the prosimian tooth-comb is indeed a canine (Eaglen, 1986)). As in the case of the prosimians (Szalay & Seligsohn, 1977), the inclusion of the canine in the ruminant dental grooming array is highly significant: through inclusion of the canine, an additional long, narrow interdental space is created without, in the case of browsers, a significant addition to the cutting edge created by the incisors. The close similarity in form of the third incisor and the incisiform canine and the persistence of the latter throughout the group indicates the presence of a selective force of not inconsiderable magnitude.

Several variations on the general browser theme serve to place this hypothesis in perspective:

(1) Most very small antelope possess a diastema between the first incisors, as illustrated in Fig. 8. Boue (1970) explained the presence of the diastema as an adaptation for scraping leaves from branches. However, the medial compensation of these teeth in the small browsers (Fig. 8) belies a feeding function of the diastema, and suggests that the teeth are laterally displaced for a reason other than the creation of a gap. Furthermore, it is unlikely that a creature with teeth would resort to scraping branches and thorns against the sensitive gingival mucous membrane at the base of the diastema, and if the branch were of a suitable size for the teeth flanking the diastema to scrape off the leaves and bark, there would be a very real risk of the branch becoming stuck in the diastema. Alternatively, the existence of an effective dental grooming organ in the correct position in these small browsers would necessitate the lateral displacement of the first incisors, there being a limit to the fan-like expansion of I_1 in a lateral direction.

(2) African grazing ruminants classified as fresh grass grazers by Janis & Ehrhardt (1988) without exception exhibit an uneven incisor morphology more similar to the browsers than to the regular grazers. This was not discussed by those authors. These species select green grass in tall stands of vegetation near water, and are thus exposed to considerable vegetation contact, again more similar to the browsers than to the grazers of the open plains. Incisor attrition would also be lower in these selective green grass grazers, thus mirroring the selective pressures working on browser incisor morphology. The lateral elements of the incisor canine complexes of these species form a comb-like array as in the case of the browsers.

(3) It would be unreasonable to expect all ruminants to follow a single simple rule regarding their dental morphology. Thus some authors have noted

Figure 8. Diastema between first incisors of chevrotain (*Tragulus javianicus*). Note medial compensation of I_1 almost closing the diastema. (Photo: University of Pretoria.)

exceptions to the trend towards unequal incisors in browsers and mixed feeders—the camelids (Boue, 1970; Janis & Ehrhardt, 1988) and the musk deer (Boue, 1970) both have more evenly sized incisors than would be expected. Coincidentally, these species also have considerably larger canines than 'average' browsers or mixed feeders. If indeed these species are subject to the same selective pressures as the other browsers/mixed feeders, then these large canines could inhibit the development of a grooming function of the IC complex or, alternatively, could themselves perform an analogous function.

CONCLUSION: SOMETHING TO CHEW ON

Structure and function are the inextricably linked features that occupy the time of evolutionary biologists. It is sometimes taken as axiomatic that "only after the mechanical functions of character complexes are understood can the study of the biological roles of these features proceed based on adequate foundations" (Bock & Von Wahlert, 1965). In considering mammalian teeth, the interpretation of structure has facilitated explanation of feeding function even when the species concerned has been extinct for millions of years. In the case of ruminant dentition, our preoccupation with the functional description along historical lines has obscured the true biological role. When eating is assumed to be the primary function of teeth, explaining all variations we find in structure without question, enigmatic structures and correlations remain. With ruminant incisors, a reversal of the traditional sequence leads to a new interpretation of the biological role, and explains enigmatic structures very well suited to a previously overlooked function.

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