BLACK BACKED JACKAL (CANIS MESOMELAS) PREDATION ON IMPALA (AEPYCEROS MELAMPUS) AT MOKOLODI NATURE RESERVE, BOTSWANA

by

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ABSTRACT

Fieldwork conducted during November 1995 to March 1997 revealed that jackal numbers in Mokolodi Nature Reserve (MNR) fluctuated on a monthly and seasonal basis, with a peak in winter and a nadir in summer. Foraging (28.7%, n=181) was the most common observed behavioural activity pattern, followed by locomotion (23.8%), flight (21.2%), resting (14.4%), and social interactions. Jackals exhibited a bigeminous activity pattern (crepuscular and nocturnal). Peaks of activity suggested that they synchronised their activity with that of their animal prey, and the relative inactivity of their main disturbance factor (man). Mean home-range size was 15.9 km^2 (range = 8.2-20.0 km^2). Home range sizes of individuals differed between seasons with a tendency for range expansion in early winter. Jackal density was estimated at 0.4 animals/km^2. Tree and bush savanna, semi-sweet mixed bushveld and agricultural areas were used much more than expected. Extraterritorial excursions were commonly witnessed, and these were usually directed towards agricultural and human establishments. Jackal foraging ecology involved hunting (76.0%, n=355), scavenging (9.2%), and gathering (14.8%). Jackals fed on ungulate afterbirths, in addition to killing concealed neonates. Jackal predation on impala lambs was extensive, and therefore deemed to depress the impala population in MNR. Overall, jackal foraging behaviour reflected the availability of a wide variety of food items and the differential vulnerability of prey. Jackal social structure comprised solitary residents, transients, and pair/pack members. Groups were uncommon presumably due to persecution by man and a food-base independent of large prey. Territories were maintained directly by aggressive and agonistic interactions, and indirectly by scent marking and vocalisations. Finally, conservation and management options are provided and discussed, their likely impact on jackal behavioural ecology explored, and suggestions for carnivore conservation and management presented.

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Even though only a single name appears on the bottom of this thesis, many people and organisations have contributed to this study. Having completed this piece of work, it is a pleasure to record my indebtedness to these people and organisations who, in a variety of ways, helped me with its conception, its development, and its birth.

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This thesis is dedicated to my daughter Ntwala, born at the time of its execution.

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CHAPTER ONE

GENERAL INTRODUCTION

"Whatever else may be said of predation, it does draw attention..."
Paul L. Errington, 1946

Black-backed jackals *Canis mesomelas* (Schreber, 1778) (Mammalia : Canidae) are members of the family Canidae, the dog and fox family. The Canidae are diverse in their habits and widespread in their geographical range. They occur on every continent with the exception of Antarctica (Kleiman, 1967). Inhabiting the tropics, the deserts, the Arctic, and the temperate regions, they range in weight from a few kilograms to well over 40 kg and eat anything from large game to insects and fruit. This diversity of habits is the result of a lack of specialisation and a built-in ability to adapt to environmental changes. For example, black-backed jackals, coyotes *Canis latrans*, and the red fox *Vulpes vulpes*, have expanded their range and increased in numbers while many other carnivores of a similar size or larger have become rare. Many now live by scavenging on the outskirts of towns and making fruit a regular part of their diet. Their adaptability and non-specialisation has decidedly affected their behavioural repertoire, so that social behaviour and its expression through postures and movements is similar throughout the family despite important ecological differences. Most of the existing behavioural differences are ones of degree rather than kind (Kleiman, 1967; Kleiman & Eisenberg, 1973; Moehlman, 1986).

In southern Africa, the black-backed jackal is both abundant and widespread, particularly in the drier parts. This species also occurs from sea level to the montane parts of the sub-continent. Black-backed jackals are opportunistic feeders with a catholic diet. Jackal diet is reported to range from medium-sized antelopes, hares, rodents, reptiles, birds and birds' eggs, insects, carrion, and even fruits and vegetable matter (Wyman, 1967; Lamprecht, 1978a; Rowe-Rowe, 1983). The relative proportions of the various food items in *C.*

mesomelas diet vary widely with differences in habitat, prey species composition, abundance (and availability), rainfall, and time of year. Hence the black-backed jackal takes whatever vulnerable prey is in greatest abundance or easily captured. Basically, in areas where large predators occur, the jackal scavenges their kills, but when it lives in other areas where there are no large predators, it mainly depends on its hunting abilities, and has even been reported to possess the potential to partially fill a pure predator's vacated niche (Estes, 1967).

Black-backed jackals have been, and will continue to be the subject of considerable controversy. This is because of the popular belief which prevails in much of Africa that jackal predation has contributed to the decline of some medium-sized wild herbivores, and is responsible for much damage to domestic livestock. This perceived damage to small livestock and herbivores was the reason for the development of negative social attitudes towards them. Human-jackal confrontation has impacted negatively on people's perceptions of the conservation of predators in particular, and wildlife in general, but attempts to eradicate black-backed jackals have met with limited success while other predators have succumbed to human pressures such as encroachment and habitat loss. Conservation biology and natural ecosystem functioning on the interface of farmland and nature reserves are becoming increasingly important as human population and economic pressures on reserves increase. Nonetheless, the effect of jackal predation on small livestock and game is a question of substantial theoretical and applied interest.

Black-backed jackals have been reported to occur in large numbers at Mokolodi Nature Reserve (MNR) although this has not been quantitatively established by any study. Circumstantial evidence and reports from game rangers, suggest that these jackals could have a negative impact on the resident impala population, and other small and medium-sized antelopes, presumably by affecting recruitment through lamb mortality, and also by killing adults (D. Reynolds, pers. comm.). It seemed likely that jackals could prey on impala young or even adults at certain times. Moreover, the cooperative hunting behaviour of jackals (McKenzie, 1990) clearly indicates that they are potential predators on certain antelope species. Anecdotal reports were sufficient to justify investigating the nature and effect of jackal predation, primarily on the resident impala population, especially given that *C.*

mesomelas is the **only major mammalian carnivore** in MNR. Brown hyaenas (*Parahyaena brunnea*) and leopards (*Panthera pardus*) are the only large predators that have been sighted within the park, but these predators, most likely represented by single individuals, are quite rare.

Predation

A long standing dispute in community ecology revolves around the question of whether competition or predation is more important in determining the characteristics of organisms (e.g. behaviour, life history), populations (e.g. population size, stability), and communities (e.g. species diversity, total and relative abundance patterns) (Sih, Crowley, McPeek, Petranka, & Strohmeier, 1985). Through the early 1970's the 'competition school' appeared to dominate. However, in recent years a discernible shift has occurred towards the notion that predation often has the greater impact, sometimes by reducing the importance of competition (e.g. Sih, *et al.*, 1985).

Predation has been described as exerting a significant element of control (Keith, 1974), the limiting factor (Bergerud, Wyett, & Snider, 1983), and the regulating factor (Messier & Crete, 1985; Dale, Adams, & Bowyer, 1994). In particular, predation is known to be an important limiting factor of the prey population's rate-of-increase. Frequently, predators have been reported to regulate ungulate populations (Sinclair, 1989; Boutin, 1992; Reynolds & Tapper, 1996). However, the distinction between limitation and regulation is rarely recognised in studies of predators and their ungulate prey and where regulation is implied, the mechanism is seldom demonstrated (Dale, *et al.*, 1994). Predation as a limiting factor simply implies that predation is, at least partially, an additive source of mortality in the prey population. However, a regulating factor keeps prey numbers within a given range (i.e. there is a 'ceiling' and a 'floor'), and therefore requires a density-dependent feed-back mechanism, i.e. the limiting effect must increase when prey numbers increase, and lessen when prey numbers decline. Without this property, predators, let alone jackals, or any other single limiting factor cannot regulate a population. Hence understanding regulating factors is fundamental to understanding predator-prey relationships. Knowledge of regions of prey densities where predators have a regulating influence on prey is important to wildlife managers in determining and maintaining goals for ungulate populations.

Large variations in population abundance and species composition are observed at most temporal and spatial scales in natural populations and communities. Indeed, at some scale of observation all natural systems are variable, and understanding the causes of such variability is a goal of population and community ecology (Chesson, 1978b; Andrewartha & Birch, 1984). Predation has long been demonstrated to be a critical source of variability in many ecosystems, sometimes producing dramatic changes in prey abundance, size distribution, composition, and species diversity (Sih *et al.*, 1985). It has also been implicated as a major selective force in the evolution of several morphological and behavioural characteristics of animals (Lima & Dill, 1990). The importance of predation during evolutionary time is clear, but growing evidence suggests that animals also have the ability to assess and behaviourally influence their risk of being preyed upon in ecological time (i.e. during their lifetime). An animal's ability to 'assess' and behaviourally control one or more of these components strongly influences feeding patterns in animals, as well as when and how to escape predators, and also when and how to be social.

Most information about the effects of predators on prey communities comes from the simple approach of removing predators from a system and monitoring prey response (Sih, *et al.*, 1985). The repetition of predator exclusion experiments has shown that predation intensity varies significantly over space and can in turn account for much of the variation in prey communities (Navarrete, 1996). However, like many physical agents of disturbance, predation not only varies over space, but it also fluctuates over time within a given area and, in many systems, the specific pattern of temporal variation in predation will have distinctive effects on prey populations and communities.

Predation obviously inflicts losses on populations. Its impact is quite difficult to quantify. Among other things, information is needed on: numbers of predators and prey, how the predators select their prey with respect to species, sex, age and condition, and the contribution of mortality factors other than predation (Boutin, 1992; Mills, 1992b). Most studies do not measure changes in population growth but rather, losses due to predation. Predator control continues to be the focus of political, socio-economic, and even scientific controversies, partly because of misinformation (Mech, 1995), and in part because of the need for information about long-term effects of temporary control on predators and the need to evaluate the long-term benefits of predator control to humans.

Although the impact of mammalian predators on their prey is a complex and, at times, controversial aspect of predator ecology, it may have important implications in the management of some species (Schaller, 1972; Mills, 1992b). By extension, as Andrewartha & Birch (1984) rightly stated, controversy, a robust arm of the scientific method, serves to guide theory towards truth and is essential to scientific progress as long as the contestants do not retreat into dogma: "Controversy is most fruitful when the facts have been strictly ascertained and there is agreement about the limitations of scientific knowledge".

Carnivores have received a disproportionate share of the attentions of wildlife scientists and managers (Mills, 1991). This is because of the position they occupy in ecosystems; being at the top of food chains makes them vulnerable to perturbations in an ecosystem at almost any level. They have a disproportionate importance for conservation biology because their extinction can trigger a cascade of unexpected secondary extinctions as a consequence of the disruption of evolved predator-prey relationships (Harris & Saunders, 1993; Palomares, Gaona, Ferreras, & Delibes, 1995; Reynolds & Tapper, 1996). Carnivores are important indicators of ecosystem function and productivity: they are vulnerable to habitat alteration or exploitation; they are thought to provide a protective umbrella for other wildlife species if their conservation needs are ensured; they have a complex historical relationship with humans that continues to be the most influential factor determining their fate; and they pose an enormous conservation policy and management challenge. Since mammalian carnivores frequently compete with man, they are persecuted whenever they are considered to do so. Partly because of this persecution, several species in sub-Saharan Africa are now endangered, with the notable exception of black-backed jackals. Even in protected areas, their role as predators may mean that they affect populations of other animals, which usually causes concern for wildlife managers.

Arguably, no group of organisms offers more challenges to conservation biology and conservation politics than carnivores. Well aware of the socio-political challenges carnivore management entails, Aldo Leopold (1949) considered carnivores as a critical test of society's commitment to conservation. In spite of a great deal of research conducted, knowledge of their role in both protected and unprotected ecosystems is often insufficient and controversial when it comes to making management decisions. Given the dynamic nature of ecosystems, caution should thus be exercised if results are extrapolated from one area to another or even from one time period to another within the same geographical area.

Direct observations have served to confirm that black-backed jackals are efficient and agile hunters (Schaller, 1972; Moehlman, 1979, 1980; Lamprecht, 1978a). Wyman (1967) estimated that jackals are capable of killing about 80% of their prey (food requirements), although this may vary in space and time. Reports of black-backed jackal predation on gazelle lambs and other smaller ungulates elsewhere (Wyman, 1967; Schaller, 1972; Lamprecht, 1978a; Stander, 1987) suggest that jackals could have a significant impact on the survival of impala lambs, and subsequently affect impala recruitment. Moreover, other studies have reported that black-backed jackals are capable of killing adult antelope (Van Lawick-Goodall & Van Lawick, 1970; Schaller, 1972; Sleicher, 1973). Of particular note is McKenzie (1990)'s study in the Mashatu Game Reserve, Botswana, which revealed that, under certain conditions, jackals hunt adult impala on a regular basis. In this instance predation on adult impala was found to be seasonal, opportunistic and selective, and was apparently linked to the availability of alternative food sources.

In agriculture, *C. mesomelas* can legitimately be considered a problem animal on small domestic stock (goats, *Capra hircus* and sheep *Ovies aries*), primarily because of the subsequent loss of income. Sadly though, in much of sub-Saharan Africa, sheep and goats are the poor man's cow. These small ruminants produce vital food and generate income for some of the world's poorest people. Night-raids by jackals on small livestock in the rural countryside at certain times is not an uncommon phenomenon in Botswana (pers. obs.). Mainly neonatal (or relatively small) animals are preyed upon and these events are confined to certain times of the year (Rowe-Rowe, 1976, 1986). Consequently jackals have been declared vermin and eradicated at every opportunity in those areas where predation of small stock is rampant. However, most such attempts have proved futile due to the adaptability and reproductive ability of black-backed jackals (Rowe-Rowe, 1986, 1992). This is a potential source of conflict between the pastoral communities that surround conservation areas and wildlife management authorities. It is in this light that livestock and game farmers adjacent to MNR have thus complained about the effect of jackal predation on their small game and livestock. These farmers view the reserve as a haven for jackals that are allegedly causing a loss of income. On the other hand, a grain farmer may not share the small livestock owner's aversion as the former values any animal that preys on rodent pests - and black-backed jackals are quite efficient at this.

Although the significance of *C. mesomelas* predation on various prey organisms in the savanna ecosystem of Botswana and the southern African region has been widely recognised, scant attention has been focused on the possible impact of such behaviour on specific antelope populations. Most previous studies on jackals have been conducted on Botswana's neighbouring states and on East African populations. Inferences regarding their behavioural ecology and management may not necessarily be relevant to site-specific situations such as that which exists in MNR. Despite the widespread occurrence and abundance of *C. mesomelas* in Botswana, few studies have been undertaken, apart from a report by Smithers (1971) and a study by McKenzie (1990).

There is little doubt that jackal predation may be a limiting factor, but in cases where its magnitude has been measured, its impact on ungulate prey populations is probably not greater than other factors such as disease, malnutrition, drought, and predation by other agents. However the full impact of predation has seldom been measured because researchers have concentrated on measuring losses due to one mortality factor alone presumably because of the difficulty of monitoring mortality in the wild.

Epidemiology

Jackals have also been reported to be susceptible to a large spectrum of canine pathogens commonly found in domestic dogs, including rabies and canine distemper (Van Heerden, 1980; Price & Karstad, 1980; Wandeler, 1992; Bingham & Foggin, 1993). In particular, jackals are one of the main wildlife species that have been implicated in the transmission of rabies in southern Africa (Meredith, 1982; King, Meredith, & Thomson, 1993; Swanepoel, 1994; Von Teichman, Thomson, Meredith & Nel, 1995). For example, 23% of the total confirmed rabies cases in Zimbabwe from 1950 to 1986 involved jackals (Foggin, 1988). In Botswana, confirmed rabies cases of jackal origin during the period 1977-1992 accounted for 66.4% of the total confirmed cases in wildlife species.

As human populations continue to encroach on wildlife habitat in Botswana and much of Africa in general, contact between domestic animals and jackals will increase. This trend could have significant implications as jackals are also frequently in contact with wild carnivores. As such, they could serve as an important link in disease transmission between wild carnivores and human habitations (Alexander, Kat, Wayne, & Fuller, 1994). Juvenile jackals may disperse over 800 km from natal areas (Ferguson, Nel, & De Wet, 1983). This long-range dispersal may have important implications in disease transmission. In addition, since jackals are often the most abundant wild carnivore in many African ecosystems, they could serve as a useful indicator species for monitoring the prevalence of specific canine diseases. Such monitoring could provide important information regarding the potential of disease exposure for rare and endangered canids, such as the African wild dog (*Lycaon pictus*).

Many of the characteristics of rabies epizootics can be interpreted in terms of its vector biology (Macdonald, 1980; Macdonald & Voigt, 1985). Such links make it a priority to study the behaviour of those canids involved in rabies transmission, both in order to understand the behaviour of the disease, and to predict the consequences of attempting to manage it. In Europe, fox-borne rabies has spread at an intriguingly constant speed. Slaughter evidently does not work; and new and exciting ideas in animal behaviour are beginning to suggest that the conventional assaults on what is a subtle problem of biology are at least unadventurous (Bacon & Macdonald, 1980; Skinner, 1982; Fischman, 1984; Ginsberg & Macdonald, 1990). Black-backed jackal social organisation varies dramatically from habitat to habitat, probably in response to ecological factors such as the abundance and dispersion of food, pressure from hunting, rabies, and other exigencies. Territory-size in turn probably influences the contact rate between neighbouring social groups - and the groups also vary in size. Each of these factors is reflected in jackal demography: larger groups result in lowered reproduction per jackal and hunting pressure results in a more youthful age structure in the community. The interplay of all these factors is important to our understanding of rabies, and its control.

Studying the behaviour of wild animals in their natural habitat poses many practical problems. These are especially pronounced among the nocturnal species such as carnivores. Long-term habituation of individual animals (e.g. Mills, 1990) and the use of radio telemetry (Amlaner & Macdonald, 1980) often enables workers to study behaviour. However, observation techniques are subject to suitable habitat, resulting in studies of behaviour, such as the black-backed jackal (e.g. Ferguson, 1978; Moehlman, 1978) and the African lion (*Panthera leo*) (e.g. Schaller, 1972) being restricted to open plains and areas relatively unaltered by anthropogenic activities. Such a limitation may affect for example, the discussions around the evolution of sociality on the one hand, and strategic management decisions in the face of human-wildlife confrontation, on the other.

The objective of the present study was to investigate the role of jackals in the mammalian ecology of Mokolodi Nature Reserve and how this species impacts on small game and domestic livestock, with particular emphasis on predation and movements. In addition, this study also sought to explore the prevalence of jackal rabies in MNR and adjacent agricultural areas. Specific management questions that need to be answered are whether jackals are responsible for excessive predation on impala and other small antelope species resident in MNR, and whether jackals resident in the reserve regularly move into neighbouring farming areas.

Radio telemetry (supplemented by direct observations) was selected as the tool for studying behaviour, movements, social organisation, and also to assist in estimating jackal density in the reserve. Faecal analysis, based on the identification of prey remains in faeces, was chosen as the method to determine diet. It must be emphasised that the present study was more focused on jackal behavioural ecology, than on the ecology of the prey (impala) because of the manpower, time, and budgetary constraints involved, even though an equal assessment of both predator and prey species would have been more meaningful.

Specific Study Objectives

1. To investigate the role of jackal predation on impala recruitment at Mokolodi Nature Reserve, Botswana

Aims: a) Determine jackal diet with respect to changes in season

b) Determine the nature and extent of jackal predation on impala at MNR

2. To investigate jackal and impala population parameters at Mokolodi Nature Reserve:

Aims: a) Determine jackal density, home-range size, social organisation, and activity, with changes in season

b) Determine the resident impala population size and age-class structure.

CHAPTER TWO

STUDY AREA DESCRIPTION

Geographical Location

Mokolodi Nature Reserve is situated in the South East District of Botswana, approximately 15 km south-west of the capital city, Gaborone (Fig.1.). The reserve lies in the middle of hills to the west of the main Gaborone-Lobatse road, an area falling within latitudes, 24° 42' and 24° 47' south, and longitude 25° 45' and 25° 50' east.

The reserve encompasses an actual land area of 30 km^2 bounded on the east and the south by freehold land in the form of farms and small holdings, and by the Bamalete tribal lands and a small block of freehold land in the form of small holdings on the north, and on the western side by the Bakwena tribal lands. The 'flat map' area (i.e. the area exclusive of slopes and hills which is suitable for most grazing and browsing ungulates) of MNR is 2.58 km^2 (M.R. Greig, pers. comm.).

Past and Present Land Use

Mokolodi Nature Reserve was first established as a conservation area on 1st November 1991 when the Mokolodi Wildlife Foundation entered into the formal lease of the property. The Government of Botswana Statutory Instrument No. 7 of 1992 legally declared it a private game reserve on 20th January 1992.

The reserve was established to (MNR Management Plan, 1993; D. Reynolds, pers. comm.):

1) Preserve a portion of the hill country of southeastern Botswana where the conservation and wise use of natural resources would be undertaken,

2) Establish an area for the re-establishment and propagation of rare and/or endangered species indigenous to the South East District and/or other areas of Botswana, particularly the white rhino (*Ceratotherium simum*),

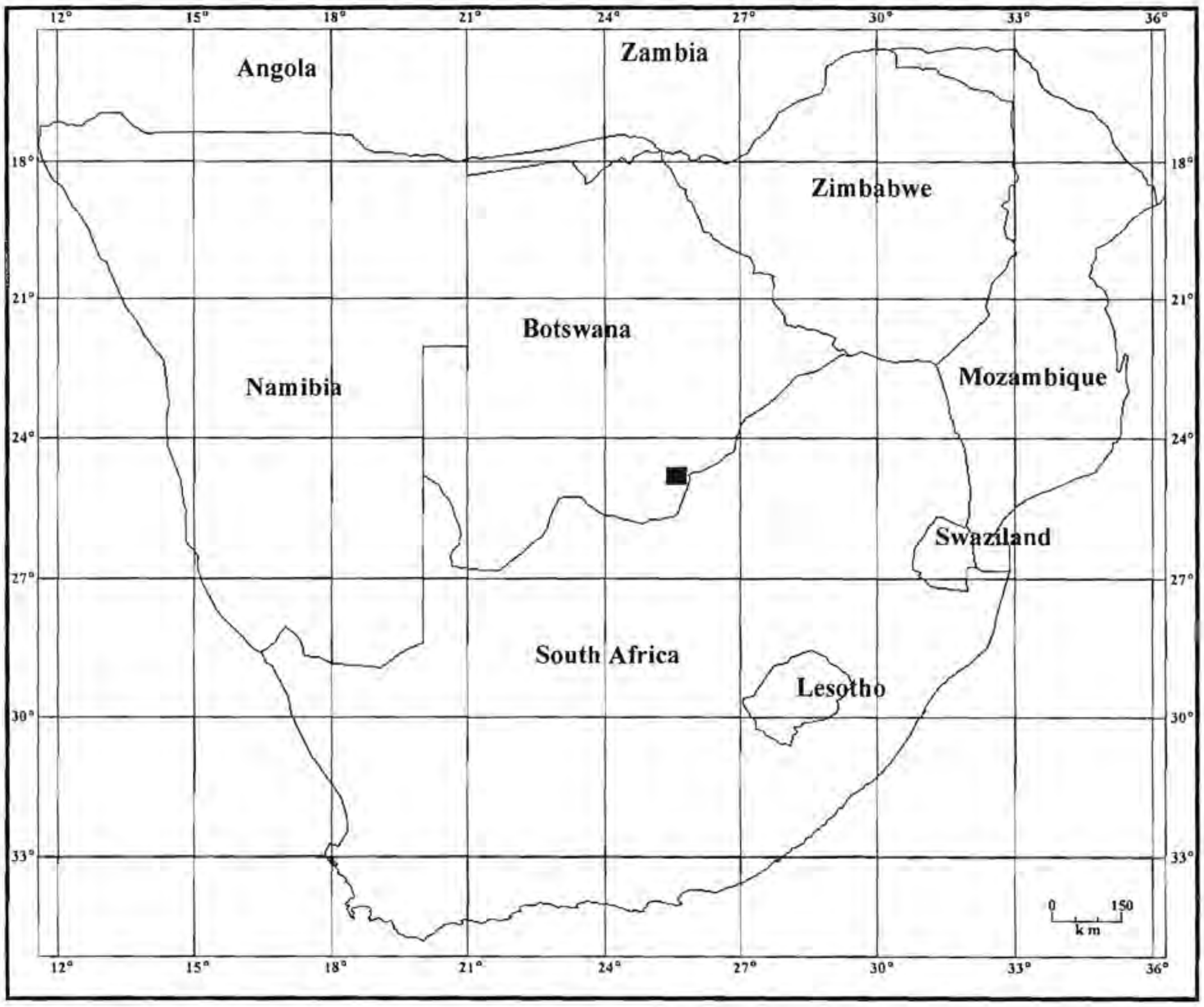

Fig. 1. Geographical location of Mokolodi Nature Reserve in Botswana, Southern Africa.

3) Establish an area where environmental education courses can be conducted in reasonable proximity to the human population concentration of south-eastern Botswana, and also

4) Conduct limited and controlled ecotourism to supplement the financial income of the reserve.

The reserve was finally opened to the public in 1994.

Prior to the proclamation and fencing of the reserve and some other farms adjacent to the present MNR, the area had widespread land use practices over the preceding hundred and fifty years and much of the vegetation was more open and showed signs of disturbance.

The hardveld areas generally suffered more intense land use than sandveld areas, as the majority of the human population was found here (Timberlake, 1980). Much of the area was grazed at different intensities by livestock, particularly cattle *Bos indicus*, but goats *C. hircus*, sheep *O. aries*, and donkeys *Equus* sp. were also reared. This land-use practice persists to date in farming communities around the nature reserve, and is also relevant to the state of affairs in the area before the present MNR was cordoned off from communal use. Much of the hardveld, especially the areas of deeper and loamier soil, was cultivated on a subsistence level using traditional methods. Crops grown here included sorghum *Sorghum vulgare*, maize *Zea mays*, squashes and melons (Family: Cucurbitaceae), and occasionally millet (*Pennisetum* spp.) and sunflower *Helianthus annuus*. The rest of the area was mostly grazed as it supported more nutritious grasses than the sandveld. Grazing pressure was high and many areas became overgrazed. There was a certain amount of localised burning, but fire was uncommon in these vegetation types because of lack of sufficient fuel loads. Land use was minimal on rocky hills and rocky outcrops in most cases, the hills being used for grazing livestock and, near settlements, for the felling of building materials and firewood, and also for 'fencing' agricultural fields. Both dry and recently dropped wood was utilised for such purposes. Some grasses, e.g. *Eragrostis pallens* were collected for thatching purposes. Many settlements are presently found at the base of hills, possibly due in part to the perennial springs which are, or used to be, found there when the vegetation was still pristine (Timberlake, 1980).

Outside MNR and some adjoining private farms, there was little wildlife apart from the occasional kudu *Tragelaphus strepsiceros*, duiker *Sylvicapra grimmia* and other small antelopes.

Climate

Temperatures for the area are generally relatively high with mean maximums of 22.2°C to 32.6°C. Average minimum temperatures range from 3.6°C to 19.7°C. The extreme range is from -6.5°C to 43.5°C. Frost occurs frequently especially within the valley bottoms and watercourses during the winter season (May to July). November to February are the hottest months of the year and June to August the coldest.

The area experiences a unimodal subtropical savanna climate with a single rainy season in the summer (November to April), followed by a single dry season from autumn through winter to spring (May to October). Mid-summer dry spells or droughts commonly interrupt the rain sequence. The mean annual rainfall for the area is 450-600 mm, with the valleys receiving slightly less and the hills and interfluves, receiving more. About 90% of the annual rainfall is precipitated during the hot summer season. Rainfall patterns in the entire country are highly variable and unpredictable in both space and time, with a reliability level of 50% in southeastern Botswana. The rainfall periods 1995/96 and 1996/97 had exceptionally high rainfall for the area, the latter period having three rain gauge stations within the reserve recording an average annual rainfall of 702 mm (Bushy Farm = 706 mm, Hundred Kraal = 668.4 mm, and Gate Entrance = 732.5 mm). This period also coincided with the duration of the present study (November 1995 to March 1997).

Topography, Geology, and Soils

The Mokolodi landscape is composed of moderately dissected, steeply to gently rounded hilly terrain, which rises from 1000 m above sea level at the northern end where the Tlhwane river drains from the area. The topography rises to the southwestern corner of the reserve to reach a maximum altitude of 1342 m on the crest of the Phiriyabokwete Hill.

The general fall of the land is from the range of hills along the western boundary of the park to the east, in which direction the two major catchments within the park drain. The Tlhwane River drains the northern portion of the park whilst tributaries of the Metsimaswaane River drain the southern portion of the reserve. A line between the Mmatshidikwe Hill in the west and the Taukobong Hill to the east forms a watershed between these two catchments. As can be seen from the topographic map of the area (Appendix 1), the reserve is basically situated between two series of hills on the western and eastern boundaries, extending from north to south.

The reserve is situated on the transition between the basement rock structures (metamorphic and igneous), and the Waterberg, Transvaal and Ventersdorp Supergroups (sedimentary and igneous rocks) (Key & Wright, 1982). The major portion of the property is developed on granite-gneiss which is an acid intrusive volcanic rock (The Gaborone Granites) (Wright, 1958; Key, 1983). Chestnut brown sands derived from weathered granite cap most of the hills and interfluves.

The present Mokolodi landscape has been derived from a reasonably undulating series of hills and intermediate drainage lines, where the rate of erosion has been accelerated by relatively recent past land-use practices such as high density cattle grazing (Timberlake, 1980). The reserve lies in the hardveld area and the soils consist of the shallow well-drained brownish, rocky soils of the hills and eroded areas, and the moderately deep and moderately well drained reddish loamy soils on the flats of the Basement complex.

All the drainage lines on the complex are seasonal, with only the dam on the Tlhwane River holding water throughout the dry season in most years. This dam allows a substantial amount of seepage water to pass through the wall and this forms a reasonable flow in this drainage as long as the dam levels remain relatively high.

Vegetation (or vegetation types)

The woody vegetation of Mokolodi Nature Reserve is primarily composed of the following major species:

Species Name	**Common Name**
Acacia erubescens	Blue thorn
Acacia mellifera	Black thorn
Acacia nilotica	Scented-pod acacia
Acacia tortilis	Umbrella thorn
Boscia albitrunca	Shepherd's tree
Combretum apiculatum	Red bushwillow
Dichrostachys cinerea	Sickle bush
Euclea undulata	Common guarri
Grewia bicolor	False brandybush or bastard brandybush
Grewia flava	Brandybush
Peltophorum africanum	African (weeping) wattle
Sclerocarya birrea	Marula
Spirostachys africana	Tamboti
Terminalia sericea	Silver terminalia
Ziziphus mucronata	Buffalo thorn

At a spatial resolution of hundreds of metres, vegetation at MNR can broadly be divided into sandveld and hardveld vegetation. Sandveld vegetation comprises relatively open woodland savanna of *Acacia* spp. and broad-leaved species (e.g. *Terminalia sericea*, *Spirostachys africana*, *Sclerocarya birrea*), with a well-developed grass layer. The hardveld vegetation in MNR encompasses a considerable proportion of the reserve and is generally a denser tree and shrub savanna or woodland of *Acacia* spp. and *Combretum* spp., also with a good grass layer. Hence the vegetation cover is usually dense woodland with a wide variety of woody species and forbs, many of which are only found on hills. The relative intensity and duration of frost seems to have an influence on their distribution.

The vegetation of the area in general has thus been classified as being intermediate between the *Peltophorum africanum*, *Acacia tortilis/Terminalia sericea* association and the *Combretum apiculatum*, *Acacia nilotica*, *Acacia tortilis* association and can thus be classified as an *Acacia erubescens*, *A. tortilis*, *Boscia albitrunca* association (Timberlake, 1980; Bekker & De Wet, 1991). Most plant species in MNR are drought and temperature deciduous.

The growing season for most species is from September to April, and during this season, water availability is probably the major constraint to growth. The main grass species found here include; *Digitaria eriantha*, *Eragrostis lehmanniana*, *E. rigidior*, and *Schmidtia bulbosa*. Grass cover is usually less than 10% but can reach 30% after good rainfall as was evident in the reserve for the duration of the present study. The status of the forage was consequently in good condition.

The major vegetation types or plant communities in Mokolodi Nature Reserve include the following (MNR Management Plan, 1993; D. Reynolds, pers. comm.):

Aquatic Communities

Seasonal still waters (pools, pans, and dams)
Seasonal acid seepline bogs and seepage streams

Grass Communities

Seasonal floodplain (hygrophilous grasslands)
Contour seeplines (hygrophilous grasslands)
Termitaria
Valley floor areas
Old man-made fields and clearings

Savanna communities

Tree and bush savanna (*Combretum apiculatum*)
Semi-sweet mixed bushveld (*Acacia/Combretum*)
Tree savanna of the rocky hill slopes (*Croton/Combretum*)
Tambutigroves on clay soils (*Sprirostachys africana*)
Short thorn savanna in valleys (*Acacia erubescens*, *Acacia tortilis*, and *Acacia mellifera*)

Thicket Communities

Riparian (water courses)
Calc-brak
Termitaria
Tree-base
Rocky outcrop

Due to their better soil moisture balance, the most important pastures are the contour seepline grasslands, which provide green forage well into the dry season. These bands of contour seepline grassland provide surface water and a diversity of other habitat features, which greatly enhance their ecological significance. These include (MNR Management Plan, 1993; D. Reynolds, pers. comm.): (a) surface water for drinking and wallowing, (b) green forage which is available well into the dry season, (c) abrupt openings in otherwise dense and heavily wooded terrain, and (d) mosaics of tall, short, sour and sweetveld herbage, due to the juxtaposition of an acid duplex sand groundwater podzol along the upper margin, merging into a calc-brak clay on the lower margin.

Another important habitat feature that provides browse as well as sweetveld conditions into the driest part of the year are the common guarri thicket (Euclea undulata) - savanna mosaic on the calc-brak clays (Sodic sites). The sand/clay savanna and rocky outcrop cover, which jointly constitutes a major proportion of the reserve area, are the most deciduous habitats.

Mammals of Mokolodi Nature Reserve (adapted and updated by the author from MNR Management Plan, 1993). Nomenclatural usage follows that of Skinner & Smithers (1990).

ORDER : INSECTIVORA

Family : Soricidae (The Shrews)

Crocidura bicolor	Tiny muskshrew
C. cyanea	Reddish-grey musk shrew
C. gracilipes	Peter's musk shrew
C. hirta	Lesser red musk shrew

Family : Erinaceidae (Hedgehogs)

Atelerix frontalis	South African hedgehog

ORDER : MACROSCELIDEA (Elephant shrews)

Family : Macroscelididae

Elephantulus brachyrhynchus	Short-nosed elephant shrew
E. intufi	Bushveld elephant shrew
E. myurus	Rock elephant shrew

ORDER : CHIROPTERA (Bats)

Family : Pteropodidae

Eidolon helvum	Straw-coloured fruit bat (migratory range)

Family : Emballonuridae

Taphozous mauritanus	Tom bat

Family : Molossidae

Tadarida aegyptiaca	Egyptian free-tailed bat

Family : Vespertilionidae

Miniopterus schreibersii	Schreibers long-fingered bat
Eptisicus capensis	Cape serotine bat
Scotophilus dinganii	Yellow house bat

Family : Nycteridae

Nycteris thebiaca	Split-faced bat

ORDER : PRIMATES

Family : Galagonidae

Galago senegalensis	Lesser bushbaby

Family : Cercopithecidae

Papio hamadryas	Chacma baboon
Cercopithecus pygerythus	Vervet monkey

ORDER : PHOLIDOTA

Family : Manidae

Manis temminckii	Pangolin

ORDER : LAGOMORPHA

Family : Leporidae

Lepus capensis	Cape hare
Lepus saxatilis	Scrub hare
Pronolagus randensis	Jameson's red rock hare

ORDER : RODENTIA (The rodents)

Family : Bathyergidae

Cryptomys hottentotus	Common molerat

Family : Hystricidae

Hystrix africaeaustralis	Porcupine

Family : Pedetidae

Pedetes capensis	Springhaas

Family : Myoxidae

Graphiurus murinus	Woodland dormouse

Family : Sciuridae

Paraxerus cepapi	Tree Squirrel

Family : Muridae

Otomys angoniensis	Angoni vlei rat
Acomys spinosissimus	Spiny mouse
Rhabdomys pumilio	Striped mouse
Mus musculus	House mouse
M. indutus	Desert pygmy mouse
Praomys natalensis	Multimammate mouse
Thallomys paedulcus	Tree mouse
Aethomys namaquensis	Namaqua rock mouse
A. chryophilus	Red veld rat
Rattus rattus	House rat
Desmodillus auricularis	Short tailed gerbil
Tatera leucogaster	Bushveld gerbil
T. brantsii	Highveld gerbil
Saccostomus campestris	Pouched mouse
Dendromus melanotis	Grey climbing mouse

ORDER : CARNIVORA

Family : Hyaenidae

Parahyaena brunnea	Brown hyaena

Family : Protelidae

Proteles cristatus	Aardwolf

Family : Felidae

Panthera pardus	Leopard
Caracal caracal	Caracal
Felis silvestris	Wild cat

Family : Canidae

Canis mesomelas	Black-backed jackal
Vulpes chama	Cape fox
Otocyon megalotis	Bat-eared fox

Family : Mustelidae

Mellivora capensis	Honey badger
Ictonyx striatus	Striped polecat

Family : Viverridae

Civettictis civetta	African civet
Genetta genetta	Small spotted genet
G. tigrina	Large spotted genet

Family : Herpestidae

Suricata suricatta	Suricate
Galerella sanguinea	Slender mongoose
Cynictis penicillata	Yellow mongoose
Mungos mungo	Banded mongoose
Helogale parvula	Dwarf mongoose

ORDER : TUBULIDENTATA	
Family : Orycteropodidae	
Orycteropus afer	Aardvark (antbear)
ORDER : PROBOSCIDEA	
Family : Elephantidae	
Loxodonta africana	African elephant
ORDER : HYRACOIDEA	
Family : Procaviidae	
Procavia capensis	Rock hyrax or dassie
ORDER : PERISSODACTYLA (Odd-toed ungulates)	
Family : Rhinocerotidae	
Ceratotherium simum	White rhino
Family : Equidae	
Equus burchellii	Burchell's zebra

ORDER : ARTIODACTYLA (Even-toed ungulates)

Family : Suidae

Phacochoerus africanus	Warthog

Family : Hippopotamidae

Hippopotamus amphibius	Hippopotamus

Family : Giraffidae

Giraffa camelopardalis	Giraffe

Family : Bovidae

Connochaetes taurinus	Blue wildebeest
Alcelaphus buselaphus	Red hartebeest
Damaliscus lunatus	Tsessebe
Sylvicarpra grimmia	Grey duiker
Oreotragus oreotragus	Klipspringer
Rhaphicerus campestris	Steenbok
Aepyceros melampus	Impala
Oryx gazella	Gemsbok
Tragelaphus strepsiceros	Kudu
T. scriptus	Bushbuck
Taurotragus oryx	Eland
Redunca arundinum	Reedbuck
R. fulvorufula	Mountain reedbuck
Kobus ellipsiprymus	Waterbuck

Mammalian species actually sighted by the investigator at Mokolodi Nature Reserve during the study period include:

Carnivores

Banded mongoose
Black-backed jackal
Brown hyena
Caracal
Dwarf mongoose
Leopard
Pangolin
Slender mongoose
Spotted genet

Herbivores

Blue wildebeest
Burchell's zebra
Common reed buck
Eland
Elephant
Gemsbok
Giraffe
Greater kudu
Grey duiker
Ground squirrel
Hippopotamus
Hyrax (rock rabbit)
Impala
Klipspringer
Mountain reedbuck
Porcupine
Red hartebeest
Rodents (various species)
Scrub hare
Steenbok
Tree squirrel
Vervet monkey
Warthog
White rhinoceros

CHAPTER THREE

GENERAL MATERIALS AND METHODS

Introduction

Biologists use animal radio tags for two main purposes: to locate study animals in the field, and to transmit information about the physiology or behaviour of wild or captive animals (Kenward, 1987). These uses are called "radio tracking" and "radio telemetry", respectively. By stalking a radio-tagged animal a biologist can greatly increase his chances of watching its behaviour and so discovering not only where it is, but what it is doing, and with whom it is interacting (Ables, 1969; Macdonald & Amlaner, 1980). Since the time of Cochran & Lord (1963), radio tracking has revolutionised studies of elusive species such as black-backed jackals in many ways, and has also become one of the most powerful tools for the wildlife biologist because of its potential for providing unbiased data on an animal's use of time and space (Aebischer, Robertson, & Kenward, 1993).

Radio tracking provides a useful technique for studying the mechanics of wildlife populations. Movements provide information on how animals use the environment, migration patterns, dispersal, and activity patterns. Home range estimates quantify the area used by the animal. Habitat use studies provide information on habitat preferences and, if properly defined, can provide information on the need for various habitat types. Survival studies provide estimates of mortality rates, and population estimation studies estimate the number of animals in a population (White & Garrott, 1990). However, whether radio tracking should be used in a study depends on the objectives of the study, the type of data to be collected, and the constraints put on the investigator regarding funding, field conditions, equipment limitations, and the general biology of the species under study.

Capture

Jackals were captured in rubber-padded, steel-jawed, foot-hold traps (Victor® "Soft-Catch®" No.3 for foxes; Woodstream Corp., Lititz, Pennsylvania, USA) which were baited with commercially prepared canid lure (Pete Rickard, Inc. Cobleskill, New York, USA). Traps were placed according to visual assessments of the study area based on jackal activity and previous sightings. Traps and equipment were treated in plant extract prepared from plants occurring within the study area. The treated equipment was handled and set as described by Rowe-Rowe & Green (1981) and Mckenzie (1990). Traps were set at each station for a maximum period of 14 days, and thereafter moved to another site. Each trap had a 0.5 metre-long heavy-duty chain attached to a 30 cm steel rod. A coil spring with elasticity potential capable of withstanding a force of 150 N was attached to cushion the struggle of captured animals. A 10-15 cm diameter hole was dug and the rod driven into the ground to anchor the trap. The chains were secured to small trees during the rainy season because trapped animals could easily pull the rod loose in wet soil. The set trap was then placed over the anchored rod and chain. A 150 X 150 mm cotton mutton cloth was placed over the trigger plate (to prevent soil from getting under it). The trap, chain, and protruding portion of the peg were then buried, whereupon fine soil and ground vegetation debris were sprinkled on the whole set to remove signs of disturbance and avoid visual detection by jackals. During rainy days trap sets were sprinkled with water from rainwater puddles or ponds. Bait was placed approximately 20-25 cm behind the trap. Branches or stones were used to block three sides of the set and force the animal to approach the bait from only one direction. Recorded sounds of a distressed scrub hare were sometimes played at maximum volume from a portable cassette tape recorder (Phillips "AQ 5150", Hong Kong, Far East) for 15-20 seconds while turning the recorder to cover all directions. Baits such as dead guinea fowl, scrub hare, and animal offal were also used to lure jackals to traps (Norton & Lawson, 1985) with limited success.

In some of the adjacent farms, jackals killed during problem animal control operations were collected for various procedures. Brain tissue specimens, stomachs, and morphometric data were however taken from such jackals for laboratory analyses, whenever possible

(Tables 1, 2, & 3). In addition, data were also amassed from dead jackals (and other selected species) resulting from road traffic mortality along the Gaborone - Lobatse road, which passes on the eastern boundary of the Mokolodi Nature Reserve. Each animal was assigned a code consisting of three letters and a number (Table 1), whereby the first letter denoted relative age class (Y = 'young' or individuals less than one year with playful behaviour, J = 'juvenile' or individuals between 1 and 2 years old, and A = 'adult' or individuals older than 2 years), the second letter indicated the sex (M=male or F=female), while the third letter represented the species (J=jackal, D=dog, and M=mongoose), in that particular order, e.g. JFJ5. The number denoted a particular individual and its partner, e.g. JFJ5 is the partner of JMJ5.

During the present study three jackals were captured using leg-hold traps. Animal (cattle) offal was the preferred bait item, but any food used in a trap set attracted a jackal if it came near. Several adult jackals consistently avoided traps, but escaped with the baits nonetheless. Jackal behaviour after capture ranged from much high anxiety with much tagging on the chain in an attempt to escape, to initial excitement followed by lying next to the trap. When the veterinarian approached trapped animals to administer immobilisation drugs, individuals exhibited attack postures and advanced with displayed teeth and growling, and readily lunged towards the veterinarian.

Capture efforts using leg-hold traps in the present study resulted in 3 captures in 204 nights (68 trap nights per capture). None of the captured jackals was subsequently recaptured. Fuller *et al.* (1989) reported capture success of jackals in foot-hold traps which averaged 16 captures/100 trap nights (6 traps per capture) versus 10/100 trap-nights for cage traps. Using padded foot-hold traps similar to mine, Rowe-Rowe & Green (1981) had 3 *C. mesomelas* captures/100 trap-nights (31 trap-nights/capture) in Giant's Castle Game Reserve, South Africa, where the density was about 0.4 jackals km^{-2} (Rowe-Rowe, 1982). Non-target species were either immediately released when found unhurt or sacrificed when injuries were so serious as to make their survival impossible, as was the case with small birds and scrubhares (*L. saxatilis*).

Table 1. Morphometric measurements and other details of captured and incidentally collected jackals in and around Mokolodi Nature Reserve between November 1995 and February 1997

Jackal ID #.	Date of collection	Locality	Mode of Capture or kill	Dose[1]	Ataxia	Tract. time[2]	Move[3]	Walk[4]	Mass	Total length	Ear length	Hind foot (c.u.)	Tail length	Girth	Neck	Cond.
AFJ1	13-11-95	MNR	Leg-hold	50 mg	2	5	65	109	5.8	926	87	138	270	390	210	Fair
AMJ7	02-06-96	Lion Park	Leg-hold	50 mg	4	6	75	135	7.3	964	92	144	290	415	225	Good
AMJ13	25-10-96	MNR	Leg-hold	50 mg	4	7	85	140	8.0	1060	100	165	360	450	280	Good
AMJ2	11-12-95	Mok. Farms	Shot	-	-	-	-	-	6.7	930	90	140	280	410	225	Good
AFJ3	27-03-96	MNR	Shot	-	-	-	-	-	6.0	920	94	136	255	385	200	Rabid
AFJ4	12-05-96	Boatle Farms	Road traffic	-	-	-	-	-	7.5	1020	104	155	315	377	240	Fair
JFJ5	18-05-96	Brink Estates	Cage trap	Killed	-	-	-	-	4.8	796	75	117	226	335	189	Good
AMJ6	18-05-96	Brink Estates	Cage trap	Killed	-	-	-	-	8.9	1067	110	163	327	429	227	Good
AMJ8	14-06-96	Lion Park	Shot	-	-	-	-	-	9.2	1055	105	170	348	440	233	Good
JFJ9	06-07-96	Mok. Farms	Shot	-	-	-	-	-	5.0	867	74	130	213	365	172	Poor
JMJ10	13-07-96	Gabane Farms	Shot	-	-	-	-	-	4.5	750	69	106	215	319	175	Fair
AMJ11	22-07-96	Boatle Farms	Road traffic	-	-	-	-	-	6.8	960	88	140	264	405	200	Poor
JFJ12	10-08-96	Mok. Farms	Shot	-	-	-	-	-	5.4	799	70	100	215	323	180	Poor
AFJ14	27-11-96	Gabane Farms	Shot	-	-	-	-	-	8.7	1035	120	171	320	460	230	Good

Animal condition was assessed visually by looking for signs of general state of health (good, fair, poor) and/or debilitation (e.g. rabid).

Note: Time (in minutes), Measurements (in millimetres), Mass (in kilograms)

[1] Zoletil: total dose

[2] Time till sufficiently anaesthetised for safe handling without physical restraint (after McKenzie, 1990)

[3] Time till first purposeful movements

[4] Time till successfully rises and walks

Immobilisation

A private veterinarian administered immobilisation drugs. Captured jackals were immobilised with an intramuscular injection of Zoletil (50 mg) based on the mean of 5.6 mg/kg for Canidae (Boever *et al.*, 1977, in McKenzie, 1990). Zoletil (CI-744: Anchorpharm (Pty) Ltd, Bramley) is a 1:1 combination of zolazepam hydrochloride (CI-716) and tiletamine hydrochloride (CI-634). Tranquilliser darts propelled from a distance using Telinject equipment (Telinject SA, Randburg) were used to immobilise jackals caught in foot-hold traps to minimise trauma and injury caused by attempts to escape when the veterinarian approached the jackal. Zoletil achieves smooth immobilisation, rapid recovery, wide ranges of ages and physiological condition, and lack of mortality. It has got a relatively wide safety margin and is widely used in canids and is especially useful for immobilising wild animals that can be lost before they become recumbent (Van Jaarsveld, 1988). Following immobilisation, any captured jackal was treated according to the clinical procedures described in McKenzie (1993). After immobilisation the jackal was then weighed, its sex determined, and standard body measurements taken (Ansell, 1966) taken (Table 1). The age-class of the jackal was determined from tooth eruption and attrition according to Lombard (1971) and Ferguson, *et al.* (1983)'s methods. Age classes were divided into three categories: young, sub-adult (juvenile), and adult.

All jackals recovered following immobilisation and were left to wander off into dense bush to rejoin their mates. Recovery time included the period from complete immobilisation of the animal, until the time when the jackal was able to walk away from the capture site. The recovery process in jackals followed a similar pattern among individuals. The recovery events of the female captured on 13th November 1995 (AFJ1) illustrate an example. The animal was injected with 50 mg of Zoletil at 05h55. Two minutes after injection the animal began showing signs of the drug taking effect, with wobbly movements and swinging its head from side to side. About five minutes after injection, the animal was completely immobilised, whereupon a radio collar was fitted, and measurements and blood samples taken. At 06h37 the animal began licking its lips. At 07h00 there was a slight head movement; 07h22 the hind legs moved slowly in a stretching motion and the head was lifted slightly; 07h25 the jackal tried to sit but struggled; 07h27 it managed to roll over but still had trouble holding its head erect; 07h33 the animal sprang up, attempted to run then fell over on its side several times. It then lay down in typical resting posture with head erect while panting heavily. At 07h40 the jackal moved about 13 m into some nearby shrubs and dropped; finally, at 07h44 it walked off into some dense bushes near complete recovery.

Radio Collars

After being weighed and measured (Ansell, 1965), the study animals were fitted with collars to which a radio transmitter and battery pack were attached. Estimated battery life was 12 months. Radio collars were privately constructed in the laboratory using the method of McKenzie (1990) and M. Haupt (pers. comm.). Only adult animals of both sexes were collared, due to the potential detrimental effects of relatively large collars on young jackals. Collars comprised less than 10% body mass (Harrison, 1992). Collars had a 35 cm inside circumference and the mass ranged from 180g to 200g depending on the transmitter. One adult female jackal (AFJ1) and two adult males (AMJ7 and AMJ13) were fitted with radio-collars (Table 1).

Radio Tracking

The basic operation of a radio tracking system involves a battery-powered transmitter that emits low powered pulsed signals via a transmitting antenna. These signals are received by another, directionally sensitive antenna which connects to the receiver. Ideally, the directional properties of the receiving antenna allow bearings to be taken on the animal's position from two places and the point at which these bearings intersect marks the animal's location (Ables, 1969; Macdonald & Amlaner, 1980; Kenward, 1987; White & Garrott, 1990).

Ultra-high frequency (UHF) telemetry equipment operating on transmitter frequency within the range of 146-152 MHz was used. This consisted of a Yaesu FT290R Mark II 2m transceiver (Yaesu-Musen Co. Ltd., Tokyo, Japan), an RT58U co-axial cable, and a 4-element hand-held Yagi antenna (Telonics, Arizona, USA). Numbered reflective ear-tags, colour-coded for sex were also attached to aid identification and following of focal animals at night. The collared jackals were then left to recover, while observing them all the time from a distance. Time to recovery was then recorded (Table 1). The collared jackal was then observed until it disappeared out of sight. No following was conducted immediately thereafter for at least 24 hours to minimise disturbance and enable full recovery.

Collared jackals were radio-tracked from various high points in the reserve, which were reached by a 4X4 vehicle (Toyota Hilux, Japan) and on foot. A system of easily identifiable locations such as fence corners, waterholes, and marked road junctions were plotted and numbered on detailed field maps. Locations of radio-collared jackals were obtained by triangulation, based on two bearings close enough to be fairly sure of the occupied habitat. When possible three or more bearings from different tracking stations were collected for each jackal. For most of the time only one observer was available for radio tracking at any time, so simultaneous bearings could not be obtained. Instead the technique used was to take bearings from one point, the vehicle quickly driven to another point where the second bearing was taken, and the position plotted on a 1:50 000 map subdivided into smaller blocks. Radio-collared jackals were located using the 4-element hand-held Yagi antenna and receiver. The 2- to 5- minute intervals between fixes did not produce large errors if the animals were slowly moving or stationary; but if an animal was moving rapidly, unacceptable errors resulted. Approximately 17% of the moving fixes were discarded because of this limitation. For the purposes of home range calculations, it is assumed that fixes represent the true locations of animals.

Observations were conducted throughout the day using 10 x 50 'Minolta' binoculars, but were mostly obtained during periods of activity using both the focal animal and *ad lib* sampling techniques (Altmann, 1974). For late night observations, once a clear signal was received, a hand-held 'million candle-power' halogen spotlight (Coleman Co. Inc. US Patent No. D-300, 470, China) was used to search for the jackal until visual location was achieved. In cases where collared jackals could be located visually, the exact positions of such jackals were recorded after the animal had moved off, using a GPS (Global Positioning System, Garmin GPS-75, Garmin Corp. Lenexa, Kansas, USA). When possible, sequential coordinates of the radio-collared jackal were obtained by carefully following the animal from a distance so as not to influence its behaviour, while monitoring its trajectory. Full technical details for position-finding and data acquisition are discussed by Argos (1987) and Fancy, Park, Douglas, Curby, Garner, Amstrup, & Regelin (1988). In most instances, rough topography and large differences in elevation prevented me from using standard triangulation methods. Instead locations were normally obtained by walking in to the animals whenever possible, and then recording their positions using the GPS. Full details of the estimation of home-range size are presented in Chapter Four.

Prevalence of Jackal Rabies

Fluorescent Antibody Test

The brain samples selected for the assessment of rabies infection included nine free-ranging jackals killed during problem animal control operations by commercial and subsistence farmers in the area surrounding MNR. In addition, two more jackals which were hit by road traffic (but remained intact to allow for laboratory diagnosis) along the Gaborone-Lobatse road, two mongooses from MNR, and two dogs which died of road traffic mortality were also collected for rabies inspection. The above species were selected as they are commonly infected with the rabies virus in southern Africa (Meredith, 1982).

In most cases, the brain samples of jackal specimens were collected and taken to the National Veterinary Laboratory, Gaborone, Botswana for analysis. Whenever this was not possible, whole jackal heads or animals were delivered to the veterinary laboratory for analysis. Fixed brain material was stored in formalin for subsequent analysis. Brain tissue received in formalin was tested for the presence of rabies antigen by the fluorescent antibody test (FAT). The brain tissue was pre-treated with trypsin before FAT could be conducted.

Trypsin solution was put in a water bath at 37°C, while approximately 0.5 g of brain tissue, preferably the hippocampus, was ground up in Tris buffer. If the hippocampus could not be found, samples of the cerebrum at the junction of the brown and white brain were used. The suspension was centrifuged and the supernatant liquid was eventually discarded. The pellet was then re-suspended in trypsin solution and put in a 37°C water bath for an hour, after which it was centrifuged again and the supernatant discarded. The pellet was then re-suspended in 2 ml Tris buffer. Two drops of the suspension were then put onto a microscopic slide, spread out and allowed to dry. These smears were then fixed in acetone at -20° C for a period of 25-30 minutes after which FAT was performed as described below (National Veterinary Laboratory, Gaborone, 1992).

Slides were removed from the acetone and the excess acetone wiped off and left to dry at 37°C. Using a grease pencil, a ring was marked close to the smear without touching it. Four drops of conjugate were then put on the smear and the stain spread out to the pencil ring with a fresh piece of applicator stick. The slides were then placed on pieces of sponge in a petri dish, wherein distilled water was added at the bottom. These were then incubated at 37°C for 25-35 minutes, after which slides were placed on a staining rack over a sink. Phosphate buffered saline (PBS) was then slowly added from one end of each slide until all the conjugate had poured off at the other end. The slides were then left flooded with PBS for a minute, whereupon it was tipped off and replaced with fresh PBS. This was also tipped off and the slides washed with distilled water and left at 37°C to dry. Two drops of glycerol PBS mountant were placed onto each smear, and the coverslip then carefully lowered onto the mountant. The smear was finally examined under ultra-violet light for fluorescence

Fifteen individual animals of different species were tested for the rabies virus using the Fluorescent Antibody Test, 11 of which were black-backed jackal specimens (Table 2).

Overall the FAT revealed positive results for 6 out of the 15 brain samples (40.0 %), four of which were black-backed jackal specimens. Positive FAT results for black-backed jackal specimens represented 36.4% (4/11) of all black-backed jackals diagnosed,, while one slender mongoose (*Galerella sanguinea*) and one domestic dog (*C. familiaris*) also revealed positive results for the rabies virus.

Table 2. Flourescent Antibody Test (FAT) results for animals collected in Mokolodi Nature Reserve and the surrounding farming areas between November 1995 and February 1997

Specimen ID	Species Name	FAT Results
AMJ2	*C. mesomelas*	Negative
AFJ3	*C. mesomelas*	Positive
AFJ4	,,	Negative
JFJ5	,,	Negative
AMJ6	,,	Negative
AMJ8	,,	Positive
JFJ9	,,	Negative
JMJ10	,,	Positive
AMJ11	,,	Positive
JFJ12	,,	Negative
AFJ14	,,	Negative
AMM1	*Mungos mungo*	Negative
AMM2	*Galerella sanguinea*	Positive
AMD1	*C. familiaris*	Positive
AMD2	*C. familiaris*	Negative

In the case of the radio-collared jackals, blood samples were collected from the lateral saphenous vein or the jugular vein, and serum samples were stored at -20°C until tested. Serologic tests were performed within 10 months of collection. Sera were evaluated for the presence of antibodies against the rabies virus. Neutralising antibodies to rabies virus were detected using a modified rapid fluorescent focus inhibition test (Smith, Yager & Baer, 1973; Alexander, *et al.*, 1994). Titres were expressed in International Units (IU)/ml determined by comparison with standard serum, and ≥ 0.5 IU was considered sero-positive based on the WHO standard for human vaccination. Rabies antibodies were detected in two of four jackal serum samples (Table 3).

Table 3. Seroprevalence of neutralising antibodies to rabies virus in three radio-collared jackals using a modified rapid fluorescent focus inhibition test (Smith, *et al.*, 1973). Specimen AFJ3 belonged to the jackal which was subsequently killed.

Specimen ID	Species Name	Test Results
AFJ1	*C. mesomelas*	Sero-negative
AFJ3	*C. mesomelas*	Sero-positive
AMJ7	*C. mesomelas*	Sero-positive
AMJ13	*C. mesomelas*	Sero-negative

Seroprevalence and FAT results for jackal AFJ3 were both positive, lending support to the abnormal behaviour observed in the field for this particular individual. Jackal AFJ3 was observed gnawing at tree trunks, and ran at vehicles, sometimes even threatening to bite at wheels of mobile vehicles. These symptoms are typical of acute or 'furious' rabies infection (Foggin, 1988). This clearly rabid animal was subsequently shot as a directive from the Department of Wildlife and National Parks, Gaborone. Seropositive jackal AMJ7 did not show any signs of acute rabies infection.

When the results of the two methods are combined, the rabies virus was detected in 7/18 (39.9%) animal specimens, five (27.8%) of which were black-backed jackal specimens. Overall, 45.5% (5/11) of the jackals were detected to be harbouring the rabies virus.

CHAPTER FOUR

SPATIAL UTILISATION AND ACTIVITY PATTERNS

Introduction

Proximate factors such as social organisation, food availability, and environmental conditions influence various aspects of the activity patterns of black-backed jackals (Ferguson, *et al.*, 1988) and may also be the ultimate sources of inborn activity patterns, based on the endogenous circadian rhythm of animals. The size and utilisation of the home range, their foraging strategies, and activity budgeting are apparently determined by environmental conditions that may directly influence prey availability and thermoregulation (Lourens & Nel, 1990). For example, prey animal activity in conjunction with the risk of 'predation' by man, may be some of the causes of a predominantly crepuscular/nocturnal activity pattern of black-backed jackals. Thus, animals frequently limit their activity to a particular area within which they find the resources necessary for growth, maintenance and reproduction. Such an area is defined as a home range (Bowen, 1982).

The concept of a home range has been defined and refined by several authors (Mohr, 1947; Ables, 1969; White & Garrott, 1990; Harris, Cresswell, Forde, Trewhella, Woollard, & Wray, 1990; Gautestad & Mysterud, 1995). A home range consists of a more or less restricted area within which an animal moves when performing its normal activities (Bowen, 1982; Harris *et al.*, 1990), exclusive of dispersal or unusual erratic wanderings (Brown & Orians, 1970). Home range is defined and estimated without reference to the presence or absence of particular types of behaviour (e.g. defence or advertisement) or of other individuals (e.g. exclusive areas); only the presence of the animal is needed (Brown & Orians, 1970). Stating the time period over which a home range is measured, and the status (e.g. sex, age, or class) of the individuals involved, should be fundamental to the definition of a home range.

There can be value in recording an average home range *size* of secretive or highly mobile species, e.g. when planning the dimensions of nature reserves. However, many studies are also interested in home range *shape*, e.g. to define the habitat available to an animal, or to identify other individuals with which it may interact. Home range *structure* or *pattern* may sometimes be necessary, for example, in defining whether dens coincide with foraging centres, and whether there are one or many such centres, or to separate excursive areas which may overlap between individuals, from cores which may be defended (Harris *et al.*, 1990; Kenward, 1992). Measuring an animal's home range size, shape, and pattern of utilisation can be important in most ecological and/or behavioural studies, particularly those concerned with, e.g. population density, foraging behaviour, habitat selection and distribution of resources, spacing of individuals and their interactions.

Species differ in the degree to which home-ranges overlap intraspecifically. In some there is no overlap, while in others overlap is nearly complete. The causative factor of non-overlap of home ranges is typically behaviour (Brown & Orians, 1970). In most cases this behaviour can be classified as territoriality. However, it is important to note that exclusive occupancy of an area and territoriality are not synonymous (Brown & Orians, 1970). Non-overlap of home ranges might also be caused by mutual avoidance, by preference for an unexploited food supply, by physical barriers, or by different habitat preferences.

Many factors determine the size of an animal's home range; among these, some, such as age, sex, and physiological status of the animals are related to individual features, whilst others depend on the availability of food resources, competitive interactions, energetic requirements and population density (Clutton-Brock & Harvey, 1978; Massei, Genov, Staines & Gorman, 1997). In hunted or exploited species such as black-backed jackals, human interference (predation risk) can also be an important factor. Most studies of black-backed jackals have been conducted in relatively undisturbed areas such as national parks, primarily due to the difficulty of studying this species where hunting or persecution has resulted in acute wariness. However, inferences derived from these relatively undisturbed populations are unlikely to be relevant to jackals that have been subjected to persecution or harvest. It is likely that where jackals are subjected to hunting pressure, home-range sizes and general social organisation may differ considerably from those of unexploited populations.

Knowledge of seasonal and yearly home ranges is important for effectively managing jackals, whether for agricultural, epidemiological or conservation purposes. In areas where jackals occur at high densities, they have the potential to exert levels of predation that are unparalleled under more pristine conditions. Knowledge of habitat use is important to identify areas that may be adversely affected by high jackal densities. Where black-backed jackals cause damage to small livestock and important wildlife conservation areas, information on home-range size and movements may determine over what area management is necessary. Also, an understanding of home range size and possible dispersive behaviour will help with the planning of areas to be quarantined during disease outbreaks.

There remains a lack of information about individual differences in habitat use, particularly with respect to short-term and long-term movement patterns. A variety of analytical techniques exist to evaluate home-range size and to determine home range utilisation, based on sampling an animal's position along a time-base. Radio tracking is a technique that is frequently used to provide data on location, movement and behaviour of members of a species, from which home-range size and patterns of utilisation can be determined. (Harris *et al.*, 1990). Since radio tracking is a study of the behaviour of individual animals, it is ideally suited to the study of differences between individuals. Individual differences in performance have often been neglected by ecologists, and radio tracking offers one of the best means of studying them. In addition to limitations of an adequate sample size to look at population parameters, the present study also seeks to investigate individual differences.

The main reason for the paucity of observations using radio-telemetry are that jackals usually live at low densities, are trap-shy, often nocturnal, and occupy extensive home-ranges. By skilful study of the behavioural activity patterns and habitat requirements of the jackals within a particular area, it is possible to define some enlightened strategies directed at the management of jackals as problem animals in nature reserves and agricultural areas. Such a study does provide a biological basis for management efforts such as through population reduction. As a result, predator reduction through translocation or culling can achieve considerable measure of success.

Methods

Behavioural Activity Patterns

A 25 km standard circuit route was chosen to be representative of the study area. From November 1995 to February 1997 observations were conducted *ad libitum* (Altmann, 1974) using a slow moving (10-20 km/h), open-back vehicle. At night, both sides of the road were lit with a portable "million candle-power" spotlight, whose beams regularly swept the countryside. Observations were conducted using 10 x 50 binoculars, and activity recorded on a portable tape recorder to be transcribed at a later date. The sampling occurred every month, four days (1 day = 1 session) in succession, according to the following protocol;

i. First Day (A): from 16h00 to 22h00

ii. Second Day (B): from 22h00 to 04h00

iii. Third Day (C): from 04h00 to 10h00

iv. Fourth Day (D): from 10h00 to 16h00

Since weather conditions (mainly due to precipitation) sometimes fluctuated during these sampling periods, the days not conducive for observations were skipped and sampling postponed to the following favourable days. In addition every behavioural activity of black-backed jackals sighted was systematically recorded. This supplemented observations from focal animal sampling and opportunistic observations. Five categories of activity were observed and documented:

i. Hunting and foraging

ii. Locomotion: direct travel without foraging or obvious flight

iii. Flight

iv. Resting

v. Interactions: intra- and interspecific contacts

Observed foraging behaviour was further subdivided into "Feeding" "Scavenging", and 'Gathering' (refer to Chapter Five). Social interactions were further subdivided into "Amicable", "Agonistic", and "Aggressive" categories (see Chapter Seven).

Home Range and Movements

Study animals were observed from a vehicle at variable distances or when possible, followed on foot. Observations on the behaviour of radio-collared jackals was recorded using the focal animal sampling technique (Altmann, 1974). Focal animals were selected on a first seen - first followed basis. Direct contact was maintained for up to three hours. The first two jackals captured were initially sequentially located at hourly intervals over 24-hour periods (seven periods for the female and three for the male), and also sporadically at different times of day and night. Tracking periods were later modified to 12-hour sessions coinciding with jackal nocturnal activity in MNR. Positions from triangulation were plotted on a 1:50 000 topographic map and later recorded as X-Y coordinates on the Universal Transverse Mercator grid. Patterns of activity were estimated from rates of movement (Palomares & Delibes, 1991), i.e. distances covered in one-hour intervals at different times during the activity period. Daily movements were estimated by summing straight-line distances between consecutively plotted locations (Laundre, Reynolds, Knick, & Ball. 1987; Fuller & Kat, 1990). Sightings of any other jackals encountered were recorded. A total of 786 hours of observation was made during 16 months of fieldwork. Some 317 jackal radio-locations were accumulated during this period. Radiolocations of jackals were obtained both within the reserve and in the surrounding agricultural areas, whenever possible.

Jackals were tracked from 3 to 10 days each over periods ranging from 3 to 25 days in length. The number of fixes per 12-hour tracking period ranged from 0 to 15, and during 23% of the 12-hour tracking periods, 10 or more fixes were taken on each animal. Sixty-seven percent (67%) of the fixes were taken between 18h00 and 06h00 with the tracking effort evenly distributed throughout the tracking periods. The three radio-collared jackals were studied for various periods as indicated in Table 4 primarily because of differences in capture dates, differential success in radio locations of particular individuals, and differences in the battery lives of the radio collars of individual jackals. No replacement of radio-collars was undertaken thereafter.

Locational data collected from radio-collared jackals was used to plot home ranges. Home range analysis was also based on locating by radio tracking, the daytime resting spots of jackals and where they chased and/or killed prey. Such positions were recorded using Global Positioning System (GPS). A hundred and twenty-two (38%) of 317 radiolocations used to estimate seasonal home-range sizes were observations of jackals or locations determined using GPS. All other locations were determined by triangulation, with a mean of 2.3 bearings /location made 5 minutes apart within a distance of 1.1 km (Fuller *et al.*, 1989). Since it is important to test the radio tracking regime before launching into the detailed study (Harris *et al.*, 1990; Kenward, 1987; White & Garrott, 1990), accuracy of triangulation was estimated from 13 tests with transmitters located at positions unknown to the investigator determining telemetry bearings. Mean error of bearings was 6 degrees (Range = 1-15 degrees), resulting in a calculated error of approx. 115 m at a distance of 1.1 km. Seasonal home range sizes were calculated using all locations, however when a jackal rested in one place for several fixes, only the first fix was used. Excursions, especially those directed towards farmland were frequent and accounted for 21.1% (66) of all relocations.

Table 4. Radio-tracking details of black-backed jackals captured in Mokolodi Nature Reserve and surrounding farms

Jackal ID.	**Social Status**	**Period monitored**	**Number of relocations per season**						**Remarks**
			Su	**Au**	**Wi**	**Sp**	**Su**	**All**	
AFJ1	Mated resident	15/11/95-05/12/96	30	43	38	26	22	**155**	Radio-collar malfunction
AMJ7	Mated resident	05/06/96-13/02/97	-	-	34	40	24	**98**	Weak radio signal
AMJ13	Lone resident	25/10/96- 26/03/97	-	-	-	35	29	**64**	Terminated - end of study

The frequency of recording coordinate locations for each individual was mostly opportunistic, regularly depending on weather conditions, topography, and vegetation cover. In some cases I determined a location by closing on a radio signal until I saw the collared jackal. However, I did not monitor all collared jackals continuously throughout the study period because of variable radio-attachment dates and malfunction. For these reasons, and because radio signals from some collared animals could not be received at all times, all home range analyses were conducted using jackals that were monitored for the longest period of time. Of the 98 nights that jackals were followed, they were irrevocably lost on 52 occasions (53%). Whenever possible, I kept as far away from the animals as I could without risking losing information and this was usually much farther than the distance at which jackals showed any reaction to the vehicle.

Movements

In order to establish whether jackals (and other animals) resident in the reserve regularly moved into neighbouring agricultural areas, the boundary fence was also examined for points of exit. These were subsequently monitored by direct observation of animal traffic through the passage-ways (usually hollows excavated under the reserve fence mainly by warthogs *Phacochoerus africanus*, aardvark *Orycteropus afer*, and jackals *C. mesomelas*). Observations were usually conducted during periods of peak jackal activity (06h00-08h00 and 18h00-20h00). Furthermore, the grounds on and around the 'conduit holes' were brushed with branches to record animal tracks passing through, when possible. Animal spoors were identified using reference field guides (Skinner & Smithers, 1990; Walker, 1996).

Systematic counts of jackal scrapes and tracks were made along the standard 25 km path circuit during the four sample periods. These track censuses were used to complement the radio tracking data, and were also used to detect jackal relative density and areas of activity. The ground was cleaned of old tracks a day before each census and again cleaned each day after the track counts until the census ended.

Calendar years were divided into seasons corresponding to the different phases of jackal breeding behaviour:

Summer: November - January (weaning)
Autumn: February - April (dispersal)
Winter: May - July (pair formation, breeding, and pregnancy)
Spring: August - October (whelping, lactation, and weaning)

Home-range Size Estimates

A computer programme for the analysis of animal home ranges, CALHOME (Kie, Baldwin, & Evans, 1994) was used to carry out analyses on aggregate and seasonal home ranges. CALHOME allows the user to choose from four different methods of analysis: adaptive kernel (Worton, 1989), harmonic mean (Dixon & Chapman, 1980), bivariate normal (Jeinrich & Turner, 1969), and minimum convex polygon (Mohr, 1947). Radio fixes more than 5 km from the established territory were interpreted as excursions and were excluded from the analysis. It was evident that jackals were engaged in excursions of less than 5 km, but I could not discard these excursions objectively because the circumscription of a territory was, to some extent, arbitrary (i.e. determined by the computational procedure). This consideration justified the use of 95% convex polygon method. For the present analysis, only one algorithm, the minimum convex polygon (MCP) was chosen. Comparative estimates of home-range size using the other methods will be reported elsewhere.

The MCP method has several disadvantages in that calculated range size is strongly influenced by peripheral fixes, and the range area can include areas that are never visited (Macdonald , Ball, & Hough, 1980; Harris *et al.*, 1990). It also does not show the intensity of range use. However, the MCP method was used as it enables comparisons with other studies of jackal home-range sizes, it is robust compared with other techniques with a low number of fixes (Harris *et al.*, 1990), and it is not invalidated by the inclusion of autocorrelated fixes.

Aggregate home ranges were calculated for jackals whose home-range size and cumulative number of fixes (including trap locations) appeared visually to be reaching an asymptote. In reality, this asymptote is probably never reached, and the aggregate home ranges reported can best be interpreted as the home range utilised by jackals during the period they were radio tracked (approx. 12 months). Likewise seasonal home ranges reported should be interpreted as the home ranges utilised by jackals over a 10-day period during each season.

Density Estimates

I estimated the density of jackals in MNR basically in two ways. Estimations of jackal density was primarily based on (i) home-range size and social organisation (Rowe-Rowe,

1982) assuming exclusive home ranges, and (ii) the number of animals sighted during routine monthly surveillance of the study area (Meia & Weber, 1992, 1996).

The mean of the minimum seasonal home-range sizes derived from the home range calculations was 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 large area, based on the results of Rowe-Rowe (1982), yields a minimum of four jackals active within the home range of an adult jackal pair. This method was also used by McKenzie (1990) to estimate jackal density in Mashatu Game Reserve, Botswana.

I also estimated the density of jackals in MNR from routine monthly surveys. First, I counted the individuals observed during nightlighting sessions (see Methods section). Since the number of jackals seen fluctuated, I have chosen to use seasonal data. The possible changes in the density was estimated using the higher number of jackals observed per session in each season: I divided this number by the surface of the study area to obtain a minimal estimate, and by the surface lit up with a 'one million candle power' spotlight to obtain a maximal estimate (Meia & Weber, 1992, 1996).

Habitat Use

I assessed habitat preference relative to various habitat components within the home range area. The habitat type was recorded at each jackal location. I used visual confirmation in addition to triangulation to determine jackal locations. Habitat preference was evaluated using the method of Neu, Byers, & Peek (1974), clarified by Byers, Steinhorst, & Krausman (1984). This method involves two steps employing Bonferroni *z*-statistics and confidence intervals (Caley, 1997). First, the differences in the proportions of available habitat were compared with the proportion of used habitat using a chi-square test. Secondly, if the chi-square test showed significant differences, Bonferroni confidence intervals of the difference in proportions were calculated for each habitat type to test for habitat preference. For the second-order habitat preference assessment, the available habitat at each site was determined by mapping habitat types from aerial photographs using topographic maps. Habitat use was estimated by the proportion of each habitat type in the home range. Habitat type for triangulated radiolocations was recorded as the most abundant type within 100 m.

The vegetation of the study area was subsequently classified according to the following general categories: (i) Tree and bush savanna, (ii) Open savanna grassland, (iii) Semi-sweet mixed bushveld, (iv) Riparian woodland, (v) Croton/Combretum tree savanna (vi) Agricultural land, and (vii) Seasonal floodplains.

Results

Behavioural Activity Patterns

The number of black-backed jackals fluctuated on a monthly and seasonal basis (χ^2 = 33.9, *d.f.* = 6, $p<0.01$; Fig. 1). Generally it increased throughout winter and reached a nadir in summer. Fewer jackals were seen between October and February. Sixty-four sessions were made (Table 1). This represented a total of 181 jackal observations that were not evenly distributed between the four sampling periods. More jackals were seen during winter (29.3%, n = 181) than in summer (12.7%) during the present study as is also evident from other observations of jackal behavioural activities e.g. vocalisations (Chapter Seven). However, caution should be exercised in invoking activity levels because visibility levels in a summer rainfall area such as MNR increase in winter when most plants shed their leaves, and decrease in summer when leaves sprout. This may consequently lead to spurious results on the relative activity levels of jackals among seasons.

Table 5. Number of jackal sightings in Mokolodi Nature Reserve during the monthly standard circuit census. The letters A, B, C, D correspond to the part of the day the observation was made (see text for explanation).

	Sampling Period				**Mean no. of jackals per session**
Month/Year	**A**	**B**	**C**	**D**	
Nov. 1995	2	3	1	0	*1.50*
Dec. 1995	2	3	4	1	*2.50*
Jan. 1996	3	0	3	1	*1.75*
Sum. 95/96					
Feb. 1996	0	4	6	2	*3.00*
Mar. 1996	7	1	2	1	*2.75*
Apr. 1996	6	3	5	1	*3.75*
Aut. 1996					
May 1996	7	1	3	2	*3.25*
Jun. 1996	9	3	4	5	*5.25*
Jul. 1996	9	2	1	7	*4.75*
Win. 1996					
Aug. 1996	5	5	3	1	*3.50*
Sep. 1996	2	4	4	0	*2.50*
Oct. 1996	5	6	2	0	*3.25*
Spr. 1996					
Nov. 1996	4	3	2	0	*2.25*
Dec. 1996	0	3	1	1	*1.25*
Jan. 1997	3	2	0	3	*2.00*
Sum 96/97					
Feb. 1997	6	0	0	2	*2.00*
Total # of sightings	**70**	**43**	**41**	**27**	
Aggregate mean	4.38	2.69	2.56	1.69	
SD	2.85	1.66	1.75	1.92	

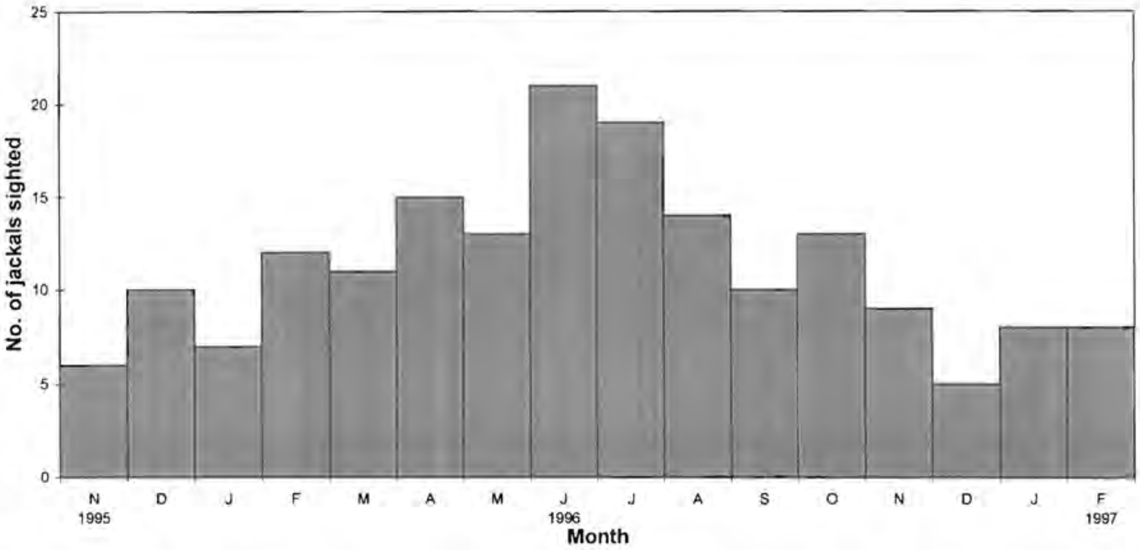

Fig. 2. Monthly sightings of black-backed jackals in Mokolodi Nature Reserve during standard circuit censuses

The behavioural activity types of 181 jackals were recorded and are presented in Table 6. Data amassed from the standard circuit censuses revealed that "hunting/foraging" (28.7%, n = 181) was observed significantly more often than any other behavioural activity, followed by "locomotion" (23.8%), "flight" (21.2%), “resting” (14.4%), and “interactions”, in that order (Table 6). Thirty-eight percent of all standard circuit observations of jackal activity occurred during the period 16h00-22h00, while observations between 22h00-04h00 and 04h00-10h00 occurred in similar proportions (23.8% and 22.7%, respectively), and purely diurnal activity was the least observed (14.9%).

Table 6. Activity types of jackals when first located (instantaneous sample), that were recorded during the 4 sampling periods (A, B, C, D)

	Sampling Period					
Type of activity	**A**	**B**	**C**	**D**	**Total**	**Percent Occurrence**
Hunting/ Foraging	23	15	10	4	**52**	28.7
Locomotion	16	11	13	3	**43**	23.8
Resting	10	2	7	7	**26**	14.4
Flight	14	5	8	11	**38**	21.0
Interactions	7	10	3	2	**22**	12.2
Total	**70**	**43**	**41**	**27**	**181**	

The frequencies of occurrence (%) of different activity types during the four sampling periods are presented in Fig. 3. Overall, the frequency of occurrence of activity types were pronounced for Period A, thus accentuating the predominantly crepuscular/nocturnal activity of black-backed jackals in MNR. Reduced activity during daylight hours was probably a response to environmental conditions such as ambient temperature or insolation, and cloud cover. In addition, the need to elude disturbance by human activities also probably influenced activity patterns in MNR during daylight hours. Behavioural activity types during the period 16h00-10h00 occurred in similar proportions. However, there were some noteworthy variations in the frequency of occurrence of activity types for the periods B, C, and D. The frequency of occurrence of social interactions were particularly pronounced at night, and less so during daylight hours. Hunting/foraging activity was also prevalent during the late afternoon and in the early evening, but reached a nadir during the day. Black-backed jackal diurnal activity was principally characterised by flight behaviour and resting, while locomotion or trotting was primarily a crepuscular/nocturnal activity pattern, and the latter was usually interspersed with foraging and territorial maintenance behaviour (see Chapter 7). In general, the frequency of occurrence of each activity type differed according to the part of day (24-h period) it was recorded ($\chi^2 = 4.32$, *d.f.* = 8, $p<0.05$; Fig.3, Table 6).

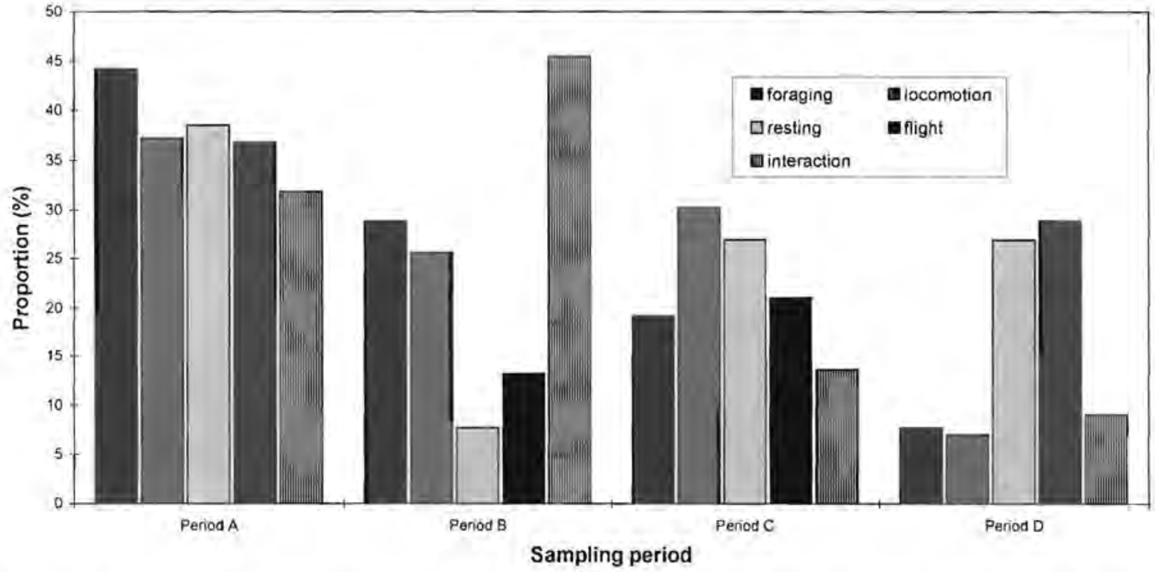

Fig. 3. Frequency of occurrence (%) of different activity types during the four sampling periods (A: 16h00-22h00; B: 22h00-04h00; C: 04h00-10h00; D: 10h00-16h00).

When results of the standard circuit, focal animal sampling, and opportunistic observation were pooled together, a similar general pattern to the standard circuit results appeared with hunting/foraging activity (35.4%, n = 1306) predominating over locomotor activity (23.5%), human avoidance (flight) behaviour (23.2%), social interactions (13.9%), and the resting (5.0%) activity types (Table 7). However, 'Interactions' ($\chi^2 = 37.6$, *d.f.* = 4, $p<0.0001$) and 'Flight' ($\chi^2 = 17.5$, *d.f.* = 4, $p<0.05$) activity types, differed significantly with season, whilst there were no significant changes in the occurrence of other activity patterns (Foraging: $\chi^2 = 3.5$. *d.f.* = 4, $p>0.05$; Locomotion: $\chi^2 = 3.2$, *d.f.* = 4, $p>0.05$; Resting: $\chi^2 = 6.3$, *d.f.* = 4, $p>0.05$) between seasons.

Table 7. A summary of seasonal activity patterns of black-backed jackals recorded in Mokolodi Nature Reserve between November 1995 to February 1997 (pooled data for 'standard circuit', 'focal animal sampling', and 'opportunistic observations').

Activity Type	**Summer 1995-96**	**Autumn 1996**	**Winter 1996**	**Spring 1996**	**Summer 1996-97**	**All Seasons**	**Percentage occurrence**
Foraging	84	90	131	87	70	**462**	35.4
Locomotion	50	77	86	53	41	**307**	23.5
Rest	19	8	10	13	15	**65**	5.0
Flight	25	55	68	94	48	**290**	22.2
Interactions	18	42	60	37	25	**182**	13.9
Total	**196**	**272**	**355**	**284**	**199**	**1306**	

Black-backed jackals in MNR exhibited a bigeminous activity pattern (crepuscular and nocturnal periods). Periods of activity were found to occur from 17h00 to 22h00, and also from 05h00 to 08h00, with peaks around 18h00 and 06h00. The initiation of activity in summer was from 17h00 to 22h00, and also from 04h00 to 08h00. In winter, initiation of activity shifted about one hour earlier, while cessation of activity became about an hour later than in summer. Peaks of activity were found to occur at about 18h00 and 06h00 for both summer and winter activity periods, and did not differ for the various activity types. Peaks of activity suggested that jackals synchronised their activity with the activity of their animal prey and that of the jackals' major 'predator' (man) as field observations revealed. The apparent persecution by farmers in the surrounding areas could account for this enhanced vigilance behaviour. There was a seasonal change in the general activity periods of jackals at MNR. Total activity was more pronounced for winter (27.2%), followed by spring (21.7%) and autumn (20.8%). The two summers (1995-96 and 1996-97) revealed similar proportions of total jackal activity (Table 7).

Jackals encountered outside the reserve always bolted for cover upon detecting the investigator irrespective of the time of day (n=24). However, jackals inside the reserve could be approached much more closely to within 50 m at times, especially at night. This suggests that jackals could have been responding to some perceived disturbance factor (i.e. hunting pressure) outside the reserve, which was apparently not prevalent within the confines of the reserve. The high hunting pressure occurring in the region probably induced a predominantly nocturnal pattern of activity. In areas where cover was scarce, some jackals (eg. AFJ1 and AMJ13) spent the day in dens and were strictly nocturnal most probably for safety reasons. For other jackals, diurnal activity was usually limited to movements between resting sites. Foraging activity was uncommon during daylight hours.

Home Range and Movements

Relocations of the three radio-collared animals both within and outside the (fenced) nature reserve, have served to confirm that jackals go on foraging excursions outside MNR into the surrounding agricultural areas. Direct and indirect monitoring of exit holes has revealed that there is extensive jackal (and other animals) utilisation of these hollowed-out areas to enter and exit the reserve. This complemented radio (re)locations of the radio-collared jackals outside the reserve. It was clear that jackal home ranges transcended the geographical confines of MNR to include areas in surrounding farming properties. The relative degree by which each of these outlying areas comprised MNR jackal home ranges was quite difficult to ascertain due to limited access to such areas, even though radio telemetry revealed such usage.

Home-range Size Estimates

Mean seasonal home-range size was greatest for jackal AMJ7 (17.2 km^2, n = 98 radio fixes), while the resident male AMJ13 revealed a range size of 16.8 km^2 (n = 64 radiolocations) (Table 8). The only jackal radio-tracked for all five consecutive seasons

(AFJ1), had the smallest home-range size (13.7 km^2, n = 155 locations). The mean aggregate home-range size for the 3 radio-collared animals was 15.9 km^2. Mean home-range sizes varied between seasons with a tendency for range expansion during the dry winter months but did not differ significantly (Kruskal-Wallis one-way ANOVA, $p >$ 0.05). Mean seasonal home-range size was also highest for the winter period (20.0 km^2) than for other seasons.

Table 8. Seasonal home-range size estimates (based on 95% MCP) of 3 radio-collared black-backed jackals at Mokolodi Nature Reserve and surrounding agricultural farms from November 1995 to February 1997, based on a total of 317 radio fixes.

Jackal ID.	**Social Status**	**Period monitored**	**Seasonal home-range sizes (km^2)**					
			Summer 1995-96	Autumn 1996	Winter 1996	Spring 1996	Summer 1996-97	Mean range size
AFJ1	Mated resident	15/11/95-05/12/96	8.2	13.9	18.5	10.7	17.0	13.7
AMJ7	Mated resident	05/06/96-13/02/97	-	-	21.9	15.2	14.6	17.2
AMJ13	Lone resident	25/10/96- 26/03/97	-	-	-	10.2	23.4	16.8
Mean seasonal home-range size			8.2	13.9	20.2	12.0	18.3	15.9

Movements

Collared jackals (AFJ1 and AMJ7) had similar movement activity patterns (p=0.88) (Fig. 4). Differences between time-periods of activity, however, were highly significant (p=0.03). Based on these results, the activity data in each time period for both male and female were pooled. To enhance the main trends in the daily cycle, a running average smoothing procedure was performed before plotting the data (Fig. 4). In agreement with other studies where persecution of jackals was a major factor, (Bothma, 1971; Rowe-Rowe, 1976, 1982; McKenzie, 1990), both animals seemed to prefer sunset and dawn hours to get on the move (Fig. 5). Their mean travelled distances per 24-hour period were 15.3 km for the male and 13.8 km for the female. The 24-hour period comprised intervening periods of about eight hours of inactivity during the daylight hours. Even for the collared jackals, peaks of foraging activity suggested that they synchronise their activity with that of their animal prey (e.g. rodents *Aethomys namaquensis*, *Saccostomus campestris*, *Otomys angoniensis* etc.) above the ground.

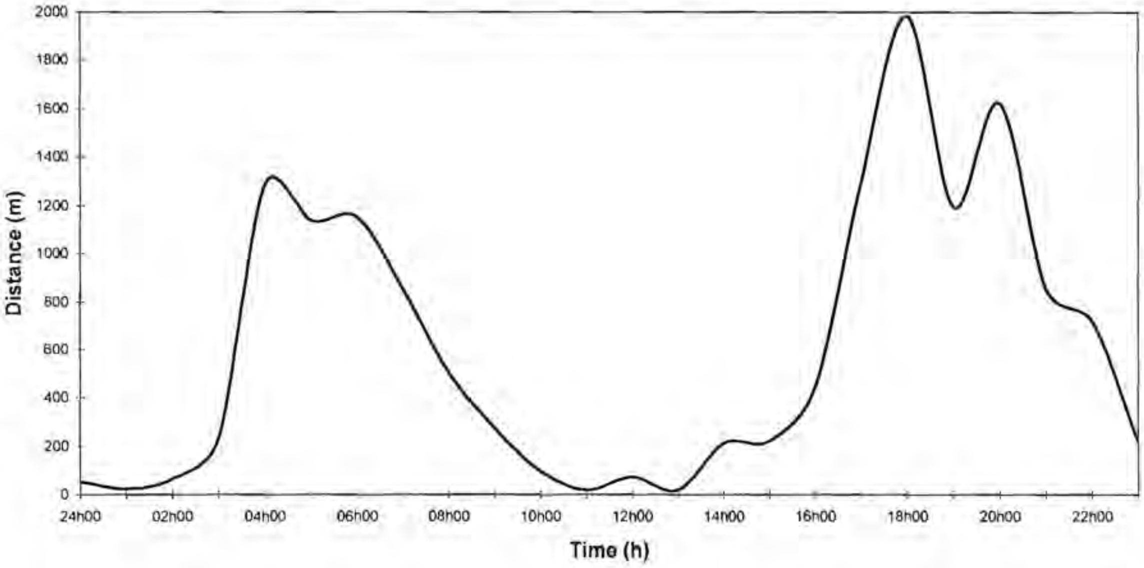

Fig. 4. Combined average activity patterns of two radio-collared black-backed jackals in MNR, estimated as the mean distance (m) travelled by hour, as a function of time of day (n = 10, 24-h tracking periods).

The overall mean distance moved between hourly re-locations for AFJ1 and AMJ7 was 1400 m (range 2- 2964 m). Average distances moved between hourly relocations differed between individuals, being highest for jackal AMJ7 (mean = 1772 m, range = 15-2964 m) and lowest in jackal AFJ1 (mean = 922 m, range = 2-1405 m). Time of day influenced movements considerably, with greater distances being moved during the late afternoon, evening and in the morning than during the day (Fig. 5).

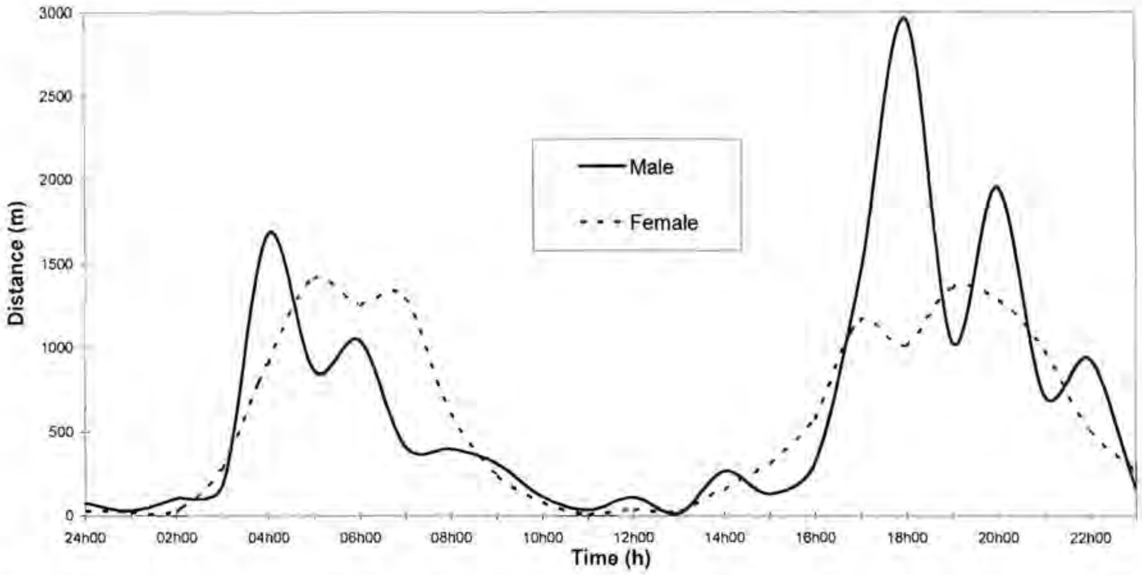

Fig. 5. Diurnal and nocturnal activity patterns of two radio-collared jackals at Mokolodi Nature Reserve

The presence of carcasses influenced the movement of resident jackals since when jackals used a carcass (n=5), resulting either from predation or other natural mortality, they tended to stay in its vicinity for up to three weeks. The relatively low group sizes and an absence of the larger social carnivores in the study area permitted prolonged consumption of carcasses. These typical movements, or lack thereof, created a clumped distribution of location taken when carcasses were available. Mated pairs left their territories to drink from waterholes and scavenge from carcasses. Three different resident pairs were sighted in MNR. When leaving its territory for water resident jackal AFJ1 trotted steadily in a fairly direct line. Jackals were also sensitive and responded to the flight patterns of vultures, eagles and raptors. If a jackal observed avian predators or scavengers making a rapid descent and landing, it would swiftly run to the spot to investigate any potential food source, and as a result trespassed other jackals' territories. Whenever there were a food source, residents would initially threaten and drive away intruders, but if individuals from several territories converged on that food source (e.g. a carcass), then it became impossible to drive them all away, and this led to fairly large aggregations. Thus it is quite likely that a shortage of food (or availability of it) clearly brings about increased trespassing into neighbouring home ranges and territories, particularly those in which desired food items can be found, e.g. at carcasses and on refuse sites next to human settlements. Caution should be exercised when delineating home ranges in such situations because it may lead to wrongly invoking cases of home range overlap between solitary individuals and also between specific pairs.

Two types of home sites used by black-backed jackals in MNR were identified: the den site, occupied during the early life of the pups, and the rendezvous site occupied after the pups were about 6 months old. Eleven rendezvous sites were subsequently examined during the present study. Rendezvous sites were characterised by a system of trails, beds, and activity areas. In the latter, some areas of vegetation, usually grasses and forbs, had been levelled presumably as a result of playing by the pups or of feeding activity by pups or adults. Radio collared jackals appeared to follow the same general trail as was depicted by jackal AFJ1 and its family. Radio collared jackals were also located by members of the public outside the nature reserve. Consequently, such human activity or disturbance greatly affected jackals' daily movement patterns.

Nine holes were found under the MNR boundary fence during the study period. Evidence in the form of hair and spoor confirmed that the mammals responsible for using or digging the holes were warthog, porcupine, aardvark, black-backed jackals and some birds (e.g. guineafowl, francolins, etc.). Unfortunately, such evidence was only recorded at less than 25% of holes because of multiple animal use (especially of birds and small mammals such as mongooses) and poor soil conditions for identification spoors. Subjective assessments however suggested that holes dug by warthog and porcupine were most common. In 25.9% of the cases, holes were dug from the reserve side through to the farms, 28.0% were dug from the farms, while 45.6% of the holes showed evidence of two-way usage. It was not possible to determine the direction of movement in 0.5% of the holes.

Density Estimates

The density estimate used here is crude and conservative as it in turn depends on other estimates. However, on the basis of social organisation and the mean of the minimum seasonal home-range estimate of 8.2 km^2 it is suggested that MNR with an estimated area of 30 km^2 supports a jackal population of at least 13 individuals - a density of 0.4 jackals/km^2. These comprise; 3 mated adult pairs (6 individuals), 3 current offspring (one per pair), 3 subadults (offspring of the previous year) covering a larger area and, perhaps, an unmated adult solitary jackal. In the present study, two of the mated pairs belonged to radiocollared jackals AFJ1 and AMJ7, which maintained exclusive home ranges.

The number of jackals per session (monthly means) sighted during nightlighting ranged from 1.25 to (summer) and 5.25. There were some fewer observations in summer than in other seasons presumably due to the difficulty of locating animals in dense vegetation associated with high precipitation during this season. Maximum and minimum seasonal density estimates are presented under Table 9. Relatively high jackal densities were recorded during the winter season. The overall seasonal density estimates (based on nightlighting sessions) lay between 0.1 (minimum estimate) and 1.8 (maximum estimate) individuals per km^2. These estimates were calculated assuming roadside visibility levels of 100 m per side, which yielded a 25 km long lit area of approximately 5 km^2.

Table 9. Maximum and minimum seasonal density estimates of black-backed jackals at Mokolodi Nature Reserve as determined from nightlighting sessions during 25 km long standard circuit surveys.

Density Estimates	**Summer** 1995-96 (4)	**Autumn 1996** (7)	**Winter 1996** (9)	**Spring 1996** (6)	**Summer 1996-97** (4)	**All seasons (Means)**
Minimum	0.1	0.2	0.3	0.2	0.1	0.1
Maximum	0.8	1.4	1.8	1.2	0.8	1.2

Note: Numbers in parentheses ( ) indicate the highest number of jackals observed per session in each season

Habitat Use

Black-backed jackals in MNR utilised wooded cover for denning, predator avoidance, and foraging purposes. They did not use habitats according to their proportional availability in any season ($G = 28.6$, *d.f.* = 12, $p=0.05$). In all seasons jackals used open savanna grassland, Croton /Combretum tree savanna, and seasonal floodplains less than expected from their availability, and used tree and bush savanna, semisweet mixed bushveld and agricultural areas much more than expected (Table 10), the latter increasingly so during the spring and summer months. Agricultural areas were used more than expected ($G= 19.8$, *d.f.* =6, $p= 0.03$; also see Table 10) during both the 1995/96 and 1996/97 summer seasons, and less than expected during the intervening autumn, winter and spring seasons.

Jackals were found to utilise the low-elevational and relatively open woodland areas in the middle of the nature reserve, sandwiched between the series of hills along the western and eastern boundaries of the nature reserve. However, this utilisation varied on a daily and seasonal basis. In winter, jackals tended to select areas of relatively high insolation ($G = 14.2$, *d.f.* $= 6$, $p<0.027$), whereas in the hot summer months, these were avoided and jackals instead utilised the fairly wooded and shady terrain during surface activity. Most jackal sightings 67%, n= 232 and signs (58%, n= 332) (associated with their activity such as tracks, droppings, and urine-deposits, were located along or next to roads traversing these areas (see Chapter Seven).

Table 10. Habitat preferences of black-backed jackals in Mokolodi Nature Reserve from November 1995 to February 1997

Vegetation	**Seasons**				
	Summer 1995-96	**Autumn 1996**	**Winter 1996**	**Spring 1996**	**Summer 1996-97**
Tree and bush savanna	16.2+	16.0+	21.5+	16.3+	10.6+
Open savanna grassland	0.8-	0.9-	0.7-	0.8-	0.9-
Semi-sweet mixed bushveld	21.5+	13.5+	2.5+	30.0+	12.3+
Riparian woodland	0.1-	0.2-	0.2-	0.2-	0.3-
Croton/Combretum tree savanna	0.2-	0.0-	0.2-	0.0-	0.1-
Agricultural land	5.4+	0.7 ns	0.0-	0.4-	3.0+
Seasonal flood plains	0.2-	0.0-	0.1-	0.2-	0.4-

Note: Numbers represent the ratio of observed to the expected number of locations in each vegetation type, based on the hypothesis that habitat used is proportional to habitat area. Significant positive preferences are marked with a plus (+) sign and significant negative preferences are marked with a minus (-) sign based on 95 % confidence intervals; n.s. not significant

It must also be noted here that the method presented here to evaluate habitat selection assumes that the location of the animal is without error. When animals are preferentially using habitats that occur in small patches, radio tracking location error can cause the extent of this preference to be underestimated (White & Garrott, 1986; also see 'Practical Considerations' below).

Discussion

Behavioural Activity Patterns

The circadian activity pattern of black-backed jackals has been reported to coincide with those of its prey animals (Ferguson *et al.*, 1988; Hiscocks & Perrin, 1988). When summer is compared with winter, the initiation and cessation of activity may be related to the shift in the times of sunrise and sunset (Ferguson *et al.*, 1988). The increased locomotor activity during winter could be explained on energetic grounds. This could be a behavioural adaptation whereby some animals maintain body temperature during cold nights by increased activity. Extreme cold weather conditions during the night could contribute to an increase in nocturnal activity. Since it appears that cold weather induces jackals to keep moving, such movement in turn increases their energy requirements, and consequently they get hungry. This in turn sharpens their hunting instincts and, naturally, their predisposition to kill. The shorter diurnal activity in summer may also be due to higher temperature and insolation. Subtle effects of study site topography and habitat structure on insolation, is likely to induce some variations in the activity patterns of resident jackals since areas of utilisation fluctuated on a diurnal basis as well as seasonally. In winter, jackals may move to areas of relatively high insolation whereas in summer, when temperatures are relatively high, low insolation areas are more preferred and utilised. However, the relative influence of other factors such as accessibility, the distribution of prey, and the incidence of human disturbance on jackal behaviour, does militate against the preponderance of insolation effects *per se*.

The human factor is also considered to be important. The high hunting pressure occurring in the region probably induced a predominantly nocturnal pattern of activity. Although low-intensity hunting of jackals may not appear to cause large shifts in home ranges, it is quite plausible that constant harassment can cause jackals to vacate their previously occupied home range. Hunting pressure may also determine the incidence of 'flight' and 'resting' behavioural patterns, although the latter is much more likey to be influenced by environmental conditions such as ambient temperature and cloud cover. In areas where cover was sparse, some jackals (e.g. AFM1) spent the day under rock crevices or in termitaria thickets and were strictly nocturnal. Activity cycles of black-backed jackals has survival value in that it allows them to forage during those periods when their prey populations are active, and also when their primary enemies (humans) are relatively inactive - a behavioural trait which may partly explain their relative success in many environments.

Ferguson, Galpin & de Wet (1988) suggested that differences in activity levels of adult and immature jackals probably reflect the difference in social role between the two age-groups. Since adults perform activities such as territorial advertisements, pair-bonding behaviour and breeding (see Chapter Seven), they may be placed under different energetic constraints when compared with immatures which do not perform these activities (Ferguson, 1988). An increase in the incidence of social interactions in winter is expected since jackals mate in winter. Often jackals do not engage in behaviour that is exclusively classed as hunting or foraging behaviour. Various other behavioural activities are performed during hunting such as, territory marking, agonistic behaviour, and sexual behaviour while trotting around within their home ranges (Ferguson, 1978). The main function of trotting behaviour, which differs from "flight" , could be to search for prey.

Suffice to note here that nightlighting is a useful and reliable technique for giving relative population estimates. Although it does not give any absolute density, it allows comparison between populations in different areas or to follow the evolution of a population in the same area: seasonal and long-term fluctuations are obviously revealed (Weber *et al.*, 1991) as long as the sampling is rigorous: standard route, low speed, same observer(s), monthly counts and `favourable' weather conditions. Besides, this technique also allows the collection of valuable behavioural information. Thus it is necessary to use it in tandem with other field techniques (i.e. animal tagging and radio tracking). However, many factors such as habitat type, weather conditions, time of day, and prey availability (abundance) and dispersion can influence the counts. As nightlighting is also frequently used in the reserve for game viewing, it is possible that animals gradually become accustomed to it, aiding in the collection of behavioural data without disturbing the animals. Jackals at MNR seemed to associate areas outside the park with high levels of disturbance and were consequently more wary when foraging outside the park, but less so within. This allowed behavioural activity patterns to be documented reasonably well within the park than outside.

Home Ranges and Movement Patterns

A structurally complex home range containing areas of unsuitable habitat that must be avoided, would require increased travel time from one section to another compared with a less complex home range (Harrison, 1997). In a developed area like MNR, roads, roadsides, cleared fields, subdivisions, or other anthropogenically modified areas will be encompassed within a typical jackal home range. Roads and fences may influence dispersal direction and movements or correspond to home range boundaries.

More jackals were killed by trapping and hunting outside of their home ranges than along the periphery. No residents were reportedly killed within their respective home ranges. This suggests that young dispersing jackals may be more susceptible to hunting than resident jackals because they are away from familiar terrain. However, avoidance of roads and hunters during daylight hours are learned responses, and younger jackals may be more susceptible to hunting primarily in early autumn. Vulnerability may be more a function of lack of experience rather than unfamiliarity with the surrounding territory (Roy & Dorrance, 1985).

Extra-territorial excursions were commonly witnessed in this study area particularly those directed towards the surrounding farming areas and human settlements. Food stress upon groups entailed hazardous extraterritorial movements and may have caused some human-related deaths (i.e. concealed natural mortality). Possibly, human-caused mortality altered group dynamics of some families but not sufficiently to invalidate the description of jackal social organisation discussed in Chapter Seven.

In the present study, estimates of real movements were calculated by summing straight-line distances between successive hourly relocations of radio-collared animals. Relocation intervals sometimes ranged from approximately 1 to 3 hours. However, some studies have used perceived distances determined by measuring the distance between the first and last locations of each 24-hour monitoring session, usually from successive mornings. But to validly use perceived movements for making comparisons among subsets of a population, there would have to be a consistent and directional correlation between perceived and real movements. Most animals have a few select resting sites, and typically move from these sites at about the same time each day, travel to various areas within their home-range boundaries, and later return to rest near these same sites. Because we cannot assume that small perceived movements indicate small, real movements or that large perceived movements represent large, real movements, perceived movements apparently have little value as a measure of normal diurnal movement (Laundre, 1987).

Home-range Size Estimates

In the family pairs of jackals observed in the present study, the home ranges of individuals did not overlap totally, but corresponded more closely to the situations observed by Ferguson *et al.*, (1983) who noted that subordinate individuals only use a small part of the group range. There was no overlap between the ranges of adjacent pairs, but it appeared that jackals entered the range of adjacent groups to access some rich feeding patches such as anthropogenic food sources and carcasses as observed elsewhere (Moehlman, 1983; Ferguson *et al.*, 1983).

Range sizes of radio-collared *C. mesomelas* located more than twenty times elsewhere in southern Africa approximated 10-40 km^2 per individual for adults, about 30-35 km^2 per individual for subadults (1-2 years) and $<$ 10 km^2 per individual for juveniles though young animals dispersing from natal areas used areas of up to 842 km^2 per individual (Rowe-Rowe, 1982; Ferguson *et al.*, 1983). Range sizes varied with prey abundance and fixed ranges disappeared in the presence of clumped resources e.g. water points (Ferguson *et al.*, 1983). In northern Tanzania, Wyman (1967) estimated *C. mesomelas* ranges to be about 8 km^2 per individual, and suggested that some *C. mesomelas* might have been nomadic and followed migrating wildebeest (*Connochaetes taurinus*) herds (van Lawick & van Lawick-Goodall, 1971). Territories of *C. mesomelas* in the Serengeti were about 1.7-4.5 km^2 per individual (Moehlman, 1983, 1986), and sometimes changed substantially in size. These jackals left their territories for water and to scavenge carcasses for short periods (Moehlman, 1983), and thus had ranges somewhat larger than territories.

The home-range sizes of canids tend to be inversely correlated to population density (Andelt, 1985). McNab (1963,1989) established a relationship between metabolic rate, body weight and size of home range in mammals, with home range increasing as a power of the body weight. For carnivores the home-range area has been related empirically to body weight by the equation, $\textit{home range} = 0.11 \times \textit{body weight}^{1.36}$ (Harestad & Bunnell, 1979; in Sillero-Zubiri & Gotelli, 1995). For black-backed jackals with an average mass of 8.0 kg, this equation predicts a home range of 1.8 km^2. The predicted home-range size is not consistent with the average home range size (15.9 km^2) of jackals found in the present study. The interplay between group size and territory size was not investigated in the present study due to small sample sizes. However, no correlation has been found between group size and territory size among other group living, solitary foraging carnivores (e.g. badgers, *Meles meles*, red foxes *Vulpes vulpes*) (Sillero-Zubiri & Gotelli, 1995).

If home range size in carnivores increases with metabolic needs (Gittleman & Harvey, 1982; Gittleman, 1989), any food limitation expressed in this way should appear during spring and summer when females are first lactating, and then gathering food for both themselves and their pups. However home range size may be reduced to minimise the time spent taking food back to the natal den (Saunders *et al.*, 1993). Greater mobility coupled with an abundance of dead livestock enhanced agricultural areas as jackal habitat in winter. In the case of the rural farming communities surrounding MNR, this is a time when there is also minimal husbandry for small livestock, a practice that is otherwise mainly directed to curb the crop-raiding activities of livestock.

Territories being specific defended areas, are often considered as spatially consistent throughout the lifespan of an individual (e.g. Brown & Orians, 1970). However, in some circumstances territory size and configuration may be adjusted to incorporate changes in the occupancy of neighbouring territories or changes in the distribution of certain limiting resources (Kruuk & Macdonald, 1985; Doncaster & Macdonald, 1991). Relative values of mortality for dominant animals rather than overall values are likely to be of greatest significance for territory stability since these are the individuals which spend most of their time in active territory maintenance and defence (White, 1996). Hence any mortality of dominant animals will act to destabilise existing social hierarchies, and consequently, surviving animals may make opportunistic adaptations to their behavioural patterns to exploit resources in neighbouring territories made available by the death of a dominant animal. In cases where mortality rates of dominant animals are high, such destabilisation will be more frequent, and spatial organisation will be more unstable as a result (also see Chapter Eight).

Density

There is considerable agreement between the density estimates from home range and social organisation on the one hand, and those from the standard circuit nightlighting sessions, on the other. Density estimates from the former method fell within the range revealed by the latter. However, it is difficult at this stage to state whether jackals occur at high or low population densities in MNR because there are a few figures with which to compare this density estimate. Hence the population may be said to be viable and stable, with recruitment through birth and immigration being approximately equal to mortality and emigration.

Habitat Use

Habitat use by black-backed jackals was concentrated on tree and bush savanna and semi-sweet mixed bushveld that provided the jackals' essential requirements for shelter and food. Conversely, jackals may avoid open savanna grassland and seasonal floodplain habitats because of a lack of security, food, or both. However, given their ready use of agricultural areas, jackals are probably not using these habitats because of comparatively low availability of food, even though agricultural areas were mostly utilised during periods of minimal human activity (e.g. in the evenings).

Agricultural areas within foraging distance were also used extensively when available. There was also a positive relationship between jackals in the densely wooded confines of MNR and the adjacent agricultural areas. Agricultural edge represents a highly productive situation for jackals. Within MNR where they were not persecuted, jackals obtained den sites and protective cover. At the habitat boundary, jackals foraged on the increased density and diversity of prey items. On the non-wooded agricultural side, jackals made use of small livestock and agricultural grain crops (see Chapter Five). As an indigenous species in relatively undisturbed areas, jackals are rarely considered overabundant. However, when an indigenous species undergoes a population increase as a result of anthropogenic food sources, it can have the same negative effects on indigenous flora and fauna (including agricultural resources).

CHAPTER FIVE

JACKAL FORAGING ECOLOGY

Introduction

Jackals (*Canis* spp.) are possibly the most common of the larger carnivores in Africa and some parts of Asia, yet they have not attracted the attention of biologists as much as the rare social carnivores, i.e. lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*) and wolves (*Canis* spp.) (Lamprecht, 1981). Since the use of food items by jackals varies with location and time in response to spatial and temporal variation in food availability (Bothma, 1971; Rowe-Rowe, 1983; Hiscocks & Perrin 1987), site- and time-specific investigations are necessary to accurately describe local jackal foraging patterns. Very few investigations of jackal diets have been conducted in Botswana (Smithers, 1971; McKenzie, 1990) and none were specific to southern Botswana, let alone Mokolodi Nature Reserve where they occur as the **only major mammalian carnivore**.

Black-backed jackals are typically described as opportunistic predators, capable of exploiting a wide range of prey depending on local availability (Wyman, 1967; Lamprecht, 1978a; Moehlman, 1978; Rowe-Rowe, 1986). Optimal foraging theory predicts that as the availability of a particular resource (in this case food) decreases, niche breadth (utilisation of that resource) should increase (Krebs & Davies, 1984). This would imply that a species would include more prey species in its diet in areas of lower productivity or if food becomes progressively scarcer in a given area.

Studies on the interactions between social carnivores and their prey species have resulted in useful insights into the evolution of group formation, cooperative hunting, and optimal foraging (Packer & Ruttan, 1988). Such studies often involve an examination of correlations between grouping patterns and hunting success. The type and dispersion of food eaten by members of a species exert an important influence on the social organisation of African ungulates (Jarman, 1974; Underwood, 1982), primates (Clutton-Brock & Harvey, 1978), and carnivores (Kruuk, 1972; Kleiman & Eisenberg, 1973; Mills, 1978). There are, however, far too few scientific data on the impact of the jackals on prey populations. Fundamental research needs to be initiated to obtain a better understanding of the functional role that jackals play in ecosystems.

A number of methods, both direct and indirect, can be used to investigate the diet of a carnivore (Korschgen, 1971; Mills & Mills, 1978). The most effective one depends on several factors such as the habits and size of the animal, the nature of the study area and the funds at the disposal of the researcher. A study area such as MNR makes it very difficult and laborious to collect direct observational data on foraging habits of black-backed jackals. Satisfactory results are difficult to obtain, especially on smaller food items. This is more so given that black-backed jackals become quite wary and secretive whenever humans persecute them. Hence analysis of black-backed jackal faeces might show the extent to which livestock and small game species are represented in jackal diets. Scat analysis therefore provides a valuable back up as a means of identifying certain food items that were not identifiable from direct observations, and also as a means by which comparisons can be made.

This chapter reports on the foraging/feeding ecology of black-backed jackals at Mokolodi Nature Reserve, Botswana.

Methods

Black-backed jackal foraging ecology was investigated using two main methods: 1) Direct observations; 2) Indirect observations; i) analysis of faecal material, and ii) analysis of stomach contents of jackals killed during problem animal control operations in farms surrounding MNR.

Direct Observations

Direct observations of jackal behaviour were hampered to a large extent by the pronounced human avoidance behaviour of the jackals, probably precipitated by apparent persecution by man as was evident in the areas surrounding the reserve. Throughout much of the present study, flight distance of jackals exceeded 50 m although closer approach could be achieved within MNR at night. In addition, the rugged terrain coupled with dense vegetation did not allow off-road navigation by vehicle, whilst it was also extremely difficult to follow the jackals on foot due to the dense Acacia thickets. Hence it was difficult to employ the focal animal technique exclusively.

Black-backed jackal foraging behaviour was studied during 786 hours of focal animal observations (Altmann, 1974) and also opportunistically. Individual jackals bearing radio collars and ear tags were observed from distances of 50-450 m using 10 x 50 binoculars. Foraging behaviours of other jackals encountered during focal animal sampling or during routine censuses were also recorded. Prey types and sex of prey organisms (wherever applicable) were recorded whenever possible. Observations lasted 1-230 min before the animal was lost to sight. All hunting and feeding attempts, both successful and unsuccessful were recorded. Signs of jackal predation within the park were found by combing through areas where female antelopes had been located with lambs, and also opportunistically during other data-gathering activities.

Reports of jackal predation on livestock from herdsmen and farmers necessitated that observations also be conducted outside the park. Alleged jackal attacks on livestock were investigated at kraals whenever they were reported.

Scat Analysis

Jackals' feeding habits were determined through the analysis of 237 scats collected in MNR from November 1995 to February 1997. Seasons were defined according to jackal breeding biology (see Chapter Four). Faecal analysis is a useful technique for a basic description of a carnivore's diet, particularly where other types of observations are impossible or where time does not permit detailed observations (Korschgen, 1971; Bowland & Perrin, 1993). It is also quite useful in dietary studies of secretive nocturnal animals like black-backed jackals. Furthermore, this technique does not require the sacrifice of the study animal. Faecal analysis may thus be used as a primary or supplemental source of information on animal feeding habits.

Collection

Fresh scats were collected within MNR along paths, roads and opportunistically in other areas. Old scats that appeared to have been defecated in a previous season were not used as samples for the subsequent analysis. All scats around settlements where domestic dogs were common were omitted from analysis. During the study it was notable that jackal pups regularly defecated around the dens although adults were not observed to do so. Faecal pellets at dens were also much smaller in size than faecal material collected elsewhere. I therefore assumed that all faeces collected at dens belonged to pups and that faeces collected elsewhere belonged to adults. Scats were stored in numbered paper bags with the date and position of collection determined by GPS. Each scat was dried at 60°C to constant mass for storage. Since it is possible for seasonal and temporal factors to influence the diet of a predator, the number of scats of the recommended sample size should ideally be collected within a season and in a particular area to enable the accurate determination of the carnivore's diet.

Despite the voluminous information available on the diets of predators, the minimum number of scats required for analysis has not been determined for most carnivore species (Mukherjee, Goyal & Chellam, 1994). Hence, 50 scats were randomly chosen, individually washed over a sieve to remove soil, and oven-dried at 60°C to facilitate handling. This was done to thoroughly mix all the hair and other indigestible remains in the scat. Since it is impossible to analyse every hair in the scat, from the 50 scats, 20 scats were randomly chosen to estimate the minimum number of hairs required for detecting all prey species represented in each scat. As a conservative estimate, Mukherjee, et al. (1994) recommended a minimum of 20 hairs per scat of the Asiatic lion. Henschel & Skinner (1990) also found that 25 scats per month were found to be adequate for analysing hyaena scats. In the present study, percentage occurrence of prey species in the scats of jackals was constant above 30 scats. Therefore a minimum of 30 scats per season was deemed sufficient for estimating diet.

In the laboratory faeces were sterilised at 110°C for 2 to 4 hours to kill the ova of microorganisms. During analysis, dry scats were weighed, soaked in water and 4% formalin for 12-24 hours with occasional stirring and then rinsed with water over a series of sieves (mesh openings of 3.36, 2.0, 0.6 and 0.25 mm) and then air-dried. This was done to thoroughly mix all the hair and other indigestible remains in the scat. Constituents of each scat sample were then examined under magnifying glasses and a binocular dissecting microscope (2-12.5 X). Food items were then sorted out and identified to the lowest possible taxon. Hair remains were compared with known hair samples.

In addition, detection of mammalian food was based on identification of hairs. Diet was quantified using presence or absence of prey such that equal weight was given to hairs ingested in small amounts. Hairs recovered from scats were identified using published keys (Keogh, 1979, 1983; Buys & Keogh, 1984) and a specially prepared reference collection. Data was recorded as the presence or absence of each prey species in a scat using reference material (mounted hair sections and photographic material of hair sections and the actual mammalian hair collections), housed at the Mammal Research Institute, University of Pretoria. This reference collection contains material of most South African mammals (Bothma & le Riche, 1994.) Some material was sent to specialists particularly at the Transvaal Museum for further analyses.

Hairs were cleaned in absolute alcohol then rinsed in water and air-dried. Scale patterns were obtained from impressions of hairs placed on a slide in a film of coloured 5% gelatin solution. Slides were allowed to cool at room temperature before removal of the hairs. Cross sections were made by placing cleaned hairs in a short, 4 mm internal diameter plastic tube, sealed at one end (Douglas, 1989). Tube and hair were then placed in a test tube containing molten wax (75% paraffin wax and 25% commercial depilatory wax) and returned to an oven heated to about 90°C for 24 hours. Thereafter the tubes were cooled at room temperature. Sections were cut with a sharp scalpel on a sectioning stand (Douglas, 1989) and then glued onto a microscope slide. Macroscopic examinations of prey remains were conducted on hair width and medulla width, texture, colour and banding patterns. In microscopic examination a combination of hair characteristics such as medullary pattern, other than cuticular characteristics alone was employed in the analysis.

Percentage occurrences of nine broad categories of food were recorded: mammals, birds, reptiles, invertebrates, fruits, vegetable matter, scavenged items, unidentified items, and soil. Small mammalian, and other small vertebrate remains in scats were identified from teeth, jaw fragments, skulls and other bone fragments, and hairs. Avian remains were identified by claws, beaks, and feathers (Bowland & Perrin, 1993). Seeds of fleshy fruits were identified by comparison with known specimens (Rowe-Rowe, 1983; Lindstrom, 1994). Vegetable materials other than fruits were classified as 'Vegetation'. Anthropogenic food items were identified from the presence of curiosities (bone chips, plastic, paper, and string) and undifferentiated matrix (Doncaster *et al.*, 1990). This category was underestimated if processed foods (off-the-bone meats, pure fat, and potato chips) were eaten. Other food items possibly missed by faecal analysis included apples (*Malus* spp.) from which the seeds were left uneaten.

Stomach contents

Stomach contents from 7 jackals killed during problem animal control operations in various farms adjacent to MNR were examined and identified based on the relative frequency of occurrence. Notes on the general condition of the animals were taken where possible.

Animals were examined post-mortem either fresh or after storage in a deep freeze. The jackals were weighed, the gut discarded, and the stomach was stored in 70 % alcohol prior to examination. Obviously, most jackals were killed when some stomach contents had been digested. It was therefore impossible to record volumes or weights of individual food items.

For examination, each stomach was opened and the contents emptied into a white enamel dish. The stomach contents were then washed through a 710 micron wire sieve and immersed in water. Species identification was initially possible in a few cases when the remains of a whole 'small' prey item were present. Otherwise identification of other prey items followed that described under 'Scat analysis'.

Results

Direct Observations

Jackal foraging behaviour was categorised into gathering, hunting and scavenging (Lamprecht, 1978a). Gathering is defined as a type of foraging behaviour, in which food items located by random or non-random search need only be consumed. Food normally obtained in this way consists of relatively small items that cannot escape or evade being eaten by a predator, e.g. fruits.

For the purposes of the present analysis, 'hunting' is defined as a means of acquiring food items, which are either able to escape or to fight back when intercepted by the predator. Hunting thus involves pursuing, catching, and subduing the prey organism concerned. 'Scavenging' here is distinguished from its colloquial use of searching for refuse near human habitations, even though it cannot really be distinguished from gathering small food items in other areas. Typical scavenging in the present context refers to eating from a sizeable prey which had been killed by disease, another predator, an accident, or any other mortality agent, other than the particular jackal under observation. The crux of this rather vague term for the present purposes is that a scavenger eats prey, which would otherwise have required a considerable hunting or searching effort (Lamprecht, 1978a).

Jackals were observed foraging during 37.1% of 786 hours of focal animal observations (including 62.9% of those in which the jackal was foraging when the observation began) and opportunistically in many other instances. It is quite evident that jackals strayed from their territories to devour fresh kills or carrion elsewhere. Hunting accounted for 76.0% (n = 355) of all foraging observations. Scavenging was observed 43 (9.2%) times, while gathering accounted for 14.8% (n = 69) of all feeding observations. Jackals were observed attempting to kill prey on 355 occasions (Table 11), successfully killing and eating prey on 101 (28.5%) occasions. Of all feeding instances, 21.1 % were kills of rodents. Catches of rodents accounted for 36.6% (n = 45) of all successful hunting attempts.

Table 11. Food items eaten by black-backed jackals during direct observations at MNR for the period November 1995 to February 1997

	Hunting		**Scavenging**	**Gathering**	**Total Feeding**	**% of all feeding observations**
Prey Type	Not Successful	Successful				
Impala	9	3	3		6	2.8
Steenbok	2	-	-	-	-	-
Ungulate afterbirth	5	3	-	3	6	2.8
Cape hare	1	-	1	-	1	0.5
Scrub hare	13	5	1	-	6	2.8
Mongoose	3	1	4	-	5	2.3
Rodents	102	37	8	-	45	21.1
Donkey	-	-	12	-	12	5.6
Sheep	1	1	2	-	3	1.4
Goat	3	2	2	-	4	1.9
Game birds	15	2	3	-	5	2.3
Poultry	1	1	3	-	4	1.9
Invertebrates	66	41	-	-	41	19.2
Wild fruits	-	-	-	29	29	13.6
Cultivated crops	-	-	-	7	7	3.3
Anthropogenic scraps	-	-	-	19	19	8.9
Unidentified prey items	33	5	4	11	20	9.4
TOTAL	**254**	**101**	**43**	**69**	**213**	

During patrols along roads and tracks, jackals made some incursions into nearby shrubs and long grass searching for potential prey. It was during such explorations when jackals sometimes flushed their prey, (e.g. rodents, scrub hares, and concealed lambs), which immediately fled. Jackals attempted to catch scrub hares in 13 of 18 instances where hares were flushed. In only 5 of the 18 observed hunts were the hares killed and devoured.

Potential animal and plant food available to jackals varied throughout the year because of its seasonal character. I did not measure prey abundance systematically, but in general, it was apparent in the field that invertebrates at MNR conformed to the general tropical seasonal pattern, with arthropod numbers and biomass peaking in response to vegetative productivity during wet conditions, whilst rodents peaked during the dry season. The two exceptionally good rainy seasons experienced during the study period resulted in huge numbers of both arthropod and rodent prey during the two respective seasons. Most ungulates dropped their young between November and January at MNR. Estimates of ungulate numbers in jackal territories were difficult to determine especially in summer, as was jackal group size because of the difficulty of viewing jackals for extended periods during this season. However, an assessment of the early 1997 stocking rates for mammalian herbivores in MNR are presented in Table 12 (M.R. Greig, unpubl. data).

Jackals at MNR foraged in pairs for most of the time, normally spread out over several hundred metres and covering considerable portions of their range either walking or trotting. Jackals foraging in this manner usually maintained contact by calling or howling. Patches with abundant prey such as rodents and insects were carefully investigated by each of the pair. On several occasions jackals at MNR were observed to walk amongst herds of large wild ungulates and livestock in open grasslands with high rodent densities, moving in zigzag formation presumably foraging for afterbirths or to ambush rodents out of their holes, probably using the herd as a mobile shield (Sillero-Zubiri & Gotelli, 1995) against their prey and their human enemies.

Table 12. Population estimates of large herbivores in Mokolodi Nature Reserve, April 1997

Herbivore Species	**Numbers in MNR**
Selective grazers	
Impala, *Aepyceros melampus*	35-40
Eland, *Taurotragus oryx*	30-35
Hartebeest (Red), *Alcelaphus buselaphus*	35
Hippo, *Hippopotamus amphibius*	2
Warthog, *Phacochoerus africanus*	50-60
Mountain reedbuck, *Redunca arundinum*	10-15
Ostrich, *Strutheo camelus*	16
Bulk grazers	
Gemsbok, *Oryx gazella*	20
White Rhino, *Ceratotherium simum*	6
Waterbuck, *Kobus ellipsiprymus*	15
Zebra (Burchell's), *Equus burchelli*	25
Elephants, *Loxodonta africana*	4 (subadults)
Browsers	
Bushbuck, *Tragelaphus strepsiceros*	4
Giraffe, *Giraffa camelopardalis*	14
Steenbok, *Raphicerus campestris*	ECC
Klipspringer, *Oreotragus oreotragus*	ECC
Grey duiker, *Sylvicarpra grimmia*	ECC

NB: ECC denotes those species that have been left to attain 'ecological carrying capacity' in MNR.

Stalking, followed by pouncing on unsuspecting prey on all fours was also displayed as an aspect of foraging behaviour. The extent to which different hunting methods were employed varied according to the size of the prey and the individual hunter (or pair's) skills. Apart from feeding incidents on large carcasses and other clumped food resources (e.g. refuse dumping sites), jackals were located as a group of four individuals on one occasion at the '100' waterhole drinking together. Whether they were or had been foraging as a group at that time was not clear, although they could have been searching for refuse at the chalets next to the waterhole. However, the group disbanded within 15 min.

Pairs of *C. mesomelas* usually approached herds of female impala presumably searching for concealed lambs. Jackals then inspected such areas, sniffing at high grass and shrubs. When nothing could be found, the jackals trotted away to another area where searching was continued. During antelope lambing periods, pairs of jackals moved among female herds presumably inspecting them for signs of lambing. Mostly, the jackals waited until the female had given birth and then worked as a team; one of the pair distracting the female, while the other attacked the young (see Chapter Six). On the one occasion when a pair of jackals encountered a lamb within the herd, the adult impala rescued the lamb by charging the jackal. Both jackals gave way and trotted off. Of the three observed occasions when lambs were flushed out of seclusion in the absence of the mothers, two were successfully killed by a pair of jackals and subsequently disembowelled. Feeding then ensued at a fast rate until they were satiated, whereupon the remains were, in both cases, carried into the nearby bushes presumably to be cached. The other incident was unsuccessful because the single jackal had difficulty in subduing the lamb, whereupon its mother, who was feeding nearby successfully defended it within seconds of the attack.

I also had the opportunity of observing some fascinating jackal predatory behaviour on both domestic and wild ungulates. These interactions were between black-backed jackals and females of parturient impala and livestock (cows *Bos indicus*, and goats *Capra hircus*). As jackals moved among female herds, presumably inspecting the latter for signs of lambing, they also fed on both domestic and wild ungulate afterbirths almost immediately after expulsion. In fact, in two instances involving impala and a single case involving a nanny goat, the jackals attacked when these ungulates were lying down calving, particularly during contractions in the recumbent position (see Chapter Six). In such instances the partly born calf is eaten and the vulva of the mother may also be chewed, with the result that the injured animal ends up being killed by the farm owner. Goats and sheep were the most targeted animals in this case, but circumstantial evidence indicates that cows (*B. indicus*) and other larger wild ungulates were also likely targets.

In addition, informal reports from farmers indicated that injuries inflicted on domestic stock in this manner were a common occurrence in the area during calving periods. Mostly, parturient females were targeted, but even females not in labour were sometimes attacked in a similar manner as evidenced by vulva injuries to those animals that managed to escape and return to kraals.

Jackals were reported to kill stray adult sheep and goats on farmland outside the park boundary, although such predation on adult animals was rarely successful. Herdsmen in the tribal grazing lands reported two sheep and three goats that had been attacked by jackals. Inspection of wounds inflicted on animals which survived attacks revealed typical jackal attack behaviour (Rowe-Rowe, 1986) for the two sheep and one juvenile goat. However, feral dogs could well have savaged the other two goats, although the evidence was not conclusive. Three attacks by jackals on kids were recorded. Location of these was made possible with the assistance of herdsmen. Typically there were neck bites on the carcass (Rowe-Rowe, 1986). Only on one occasion was a jackal observed attacking and subduing a young sheep. The lamb was partially disembowelled during feeding. Thereafter the jackals then tore off chunks of meat, which were carried away into the reserve. Jackals were twice observed feeding on donkey carrion. Such large carcasses were visited many times by several (1-4) jackals, which sometimes also carried lumps of carrion away, presumably to feed pups at dens.

Jackals carried chunks of livestock carrion from the surrounding farming areas into the reserve where it was devoured at leisure. A single male goat carcass was found within MNR. Judging from the large size of the goat carcass, it was probably killed by a leopard (or died of other causes) which dragged it into the reserve where it was fed upon. In another incident, a mangled goatskin was also found at a deserted jackal den. It was impossible to conclude whether the skin was scavenged or a result of predation. Six remains of poultry in the form of feather clusters were also found at various sites within the park, albeit it was not possible to determine whether they had been killed after straying into the reserve, or were predated upon outside.

There are few observations from which useful generalisations can be drawn on the subject of jackals preying on small livestock (goats, sheep, etc.) and small game (e.g. steenbok *Raphicerus campestris*, impala, etc.). To begin with, jackal kills are often indistinguishable from those of other wild predators and domestic dogs. Moreover, it has been noted that most healthy ungulates living in the same locale as jackals are able to defend themselves against single jackals, so that instances of such predation are rare and hence difficult to observe. The few data that do exist indicate that two or more jackals are usually required to take down, say, a healthy impala adult. In most cases jackals appear to kill either young ungulates or weak ones, typically by attacking the head, lower neck, belly, and rump.

Non-target species such as birds, especially francolins (*Francolinus* sp.) and helmeted guinea fowls (*Numida meleagris*), scrub hares (*Lepus saxatilis*), and mongooses (Family: Herpestidae) caught in traps were most often found to have been retrieved either by jackals, brown hyaenas (*P. brunnea*), leopards (*P. pardus*) and even banded mongooses (*M. mungo*), as was indicated by examination of spoor. Black-backed jackals were also observed caching freshly caught prey on five occasions and retrieving caches on two occasions. Two rodents were cached whole, whereas only remains of one impala lamb, one scrub hare, and a chunk of ungulate carrion were cached. Prey was cached some distance away from the kill. Caching involved digging a shallow hole in a concealed place, usually under some shrubs, and covering the food with soil and/or vegetation. All caches that were observed took place after a jackal had eaten at a kill, usually within 10 min.

Male jackals regurgitated food to respective lactating female partners and young at the den on three occasions. Only one instance of a subordinate jackal regurgitating food at the den was recorded. This behaviour pattern usually occurred after successful foraging. In the pair with no helpers, both members of a pair left the den unguarded to forage on two occasions, but most of the time they alternated, one of the parents (usually the female AFJ1) remaining at the den with the pups. Regurgitating food is an efficient way for adults to transport and share food. It enables the lactating mother to stay with her pups during their most vulnerable period. This is also beneficial in cases where the level of intra- and interspecific kleptoparasitism is high. Food is much safer within than carried conspicuously outside where it can be misappropriated by other predators or scavengers. Typically, jackals fed on a kill first, and then made off with chunks of meat in their mouths.

The main drawback of the direct observation method was that I was unable to identify many small food items from a distance where normal jackal foraging behaviour could not be disrupted.

Scat analysis

A total of 237 scats, representing 518 items were selected and analysed. Seasonal relative frequencies of occurrence of prey remains in jackal faeces are presented in Table 13 and Table 14. Smaller animal prey species (e.g. rodents and invertebrates) were virtually eaten complete, for fragmented crania, mandibles, teeth, feet, tails, as well as hairs and scales were all found in scats. At least 26 mammal species, 5 bird species, 8 fruit species, and several invertebrate species were recorded as food items of jackals at MNR.

Across all seasons, mammals were the most common food resource (32.4%, n = 518; Table 13), followed by anthropogenic items (14.8%), fruits (12.9%), invertebrates (10.8%), birds (8.5%), unidentified items (3.5%), and reptiles (1.4%). Vegetation (8.8%) and soil (6.9%) represented potentially non-food remains. Small mammals (mostly rodents) comprised 39.9 % (n = 168) of all mammalian prey remains, wild ungulates accounted for 18.5%, while domestic mammals and medium-sized mammals comprised 15.5% each. Unidentified mammalian prey represented 10.7% of all mammalian prey remains.

Table 13. A summary of the seasonal relative frequency of occurrence of prey remains (%) in 237 black-backed jackal scat samples collected in the Mokolodi Nature Reserve from November 1995 to February 1997. n = number of scats; N = number of specific prey items

	All Seasons (n = 237)		**Summer 1995-96** (n = 38)		**Autumn 1996** (n = 53)		**Winter 1996** (n = 58)		**Spring 1996** (n = 54)		**Summer 1996-97** (n = 34)	
Prey category	N	%	N	%	N	%	N	%	N	%	N	%
Mammals	168	32.4	42	31.3	23	25.8	38	41.8	29	30.9	36	32.7
Birds	44	8.5	10	7.5	4	4.5	6	6.6	13	13.8	11	10.0
Reptiles	7	1.4	1	0.7	1	1.1	3	3.3	1	1.1	1	0.9
Invertebrates	56	10.8	21	15.7	8	9.0	5	5.5	10	10.6	12	10.9
Fruits	67	12.9	31	23.1	13	14.6	2	2.3	4	4.3	17	15.5
Vegetation	46	8.8	10	7.5	8	9.0	7	7.7	14	14.9	7	6.4
Anthropogenic items	76	14.8	8	6.0	19	21.3	24	26.4	12	12.8	13	11.8
Unidentified items	18	3.5	4	3.0	3	3.4	3	3.3	6	6.4	2	1.8
Soil	36	6.9	7	5.2	10	11.2	3	3.3	5	5.3	11	10.0
Total # of prey items (ΣN)	**518**		**134**		**89**		**91**		**94**		**110**	

Overall, animal prey remains accounted for at least 53.1% of all prey items found in scats, while fruit remains represented 12.9% of all prey items. This relationship was also found in all seasons. Seasonality of prey occurrence in scats was pronounced for small mammals, miscellaneous fruits and invertebrates: Small mammals (mostly rodents) were more frequently eaten in the dry season ($\chi^2 = 48.22$, *d.f.* = 1, $p<0.01$) and fruits during the wet season ($\chi^2 = 98.09$, *d.f.* =1, $p<0.001$; Table 14).). All other prey remains occurred in similar proportions regardless of season (Tables 13 & 14).

Table 14. A detailed presentation of the seasonal occurrence of prey items in 237 black-backed jackal scats collected in Mokolodi Nature Reserve for the period November 1995 to February 1997. N = number of specific prey items.

MAMMALIA (N= 168)

Prey remains	**Summer 1995-96**	**Autumn 1996**	**Winter 1996**	**Spring 1996**	**Summer 1996-97**	**All seasons**
	N	N	N	N	N	ΣN
Ungulates	**10**	**3**	**3**	**8**	**7**	**31**
Taurotragus oryx	1	0	0	1	0	2
A. melampus	4	0	1	3	2	10
Tragelaphus strepsiceros	2	1	1	1	0	5
Equus burchelli	1	0	0	0	1	2
Phacochoerus aethiopicus	1	1	0	1	3	6
Raphiceros campestris	0	1	1	2	0	4
Unidentified	1	0	0	0	1	2
Medium-sized Game Mammals	**3**	**6**	**5**	**3**	**9**	**26**
Lepus capensis	0	1	2	0	1	4
L. saxatilis	1	2	2	2	4	11
C. mesomelas	1	0	0	0	3	4
Genetta genetta	0	2	0	1	1	4
Unidentified	1	1	1	0	0	3
Small Mammals	**19**	**9**	**22**	**10**	**7**	**67**
Mungos mungo	2	1	1	0	1	5
Saccostomus campestris	3	2	2	0	0	7
Rattus rattus	2	0	3	3	1	9
Rhabdomys pumilio	4	1	4	2	1	12
Aethomys namaquensis	1	2	2	1	1	7

Tatera sp.	0	1	2	1	0	4
Galerella sp.	1	0	1	1	0	3
Otomys angoniensis	1	1	3	0	0	5
Unidentified	5	1	4	2	3	15
Domestic Mammals	**4**	**2**	**3**	**5**	**12**	**26**
Capra hircus	2	1	0	3	6	12
Ovis aries	1	1	2	1	3	8
Equus sp.	1	0	1	0	3	4
Bos indicus	0	0	0	1	1	2
Unidentified mammals	**6**	**3**	**5**	**3**	**1**	**18**
N =	**42**	**23**	**38**	**29**	**36**	**168**

AVES (N = 44)

Pterocles bicinctus	1	0	1	1	0	3
Strutheo camelus	2	1	0	2	1	6
Francolinus sp.	3	0	2	1	1	7
Numida meleagris	1	3	2	3	1	10
Egg shells	0	0	0	2	3	5
Unidentified	3	0	1	4	5	13
N =	**10**	**4**	**6**	**13**	**11**	**44**

REPTILIA (7)

Lacertidae	1	1	1	1	0	4
Unidentified	0	0	2	0	1	3
N =	**1**	**1**	**3**	**1**	**1**	**7**

INVERTEBRATA (N = 56)

Coleoptera	1	1	1	2	2	7
Orthoptera	10	3	0	1	4	18

Myriapoda	2	0	0	0	1	3
Scorpionida	0	1	0	0	1	1
Hymenoptera	2	1	0	1	0	4
Isoptera	4	2	3	5	2	16
Unidentified	2	0	1	1	3	7
N =	21	8	5	10	12	56

FRUITS (N = 67)

Grewia spp.	11	7	1	1	6	26
Ximenia caffra	4	0	0	1	3	8
Ziziphus mucronata	3	0	0	0	1	4
Sclerocarya birrea	2	2	0	2	1	7
Zea mays	6	1	0	0	3	10
Malus spp	3	2	1	0	2	8
Unidentified	2	1	0	0	1	4
N =	31	13	2	4	17	67

VEGETATION (N = 46)

Twigs	3	2	1	3	1	10
Dicot Leaves	3	4	2	6	1	16
Monocot Leaves	4	2	4	5	5	20
N =	10	8	7	14	7	46

ANTHROPOGENIC ITEMS (N = 76)

Bone chips	2	4	7	1	1	15
Plastic	0	2	3	2	0	7
Paper	0	1	1	1	0	3
String	0	0	1	0	0	1
Bottle tops	1	2	1	0	0	4
Fish remains (bones & scales)	2	1	3	1	3	10
Poultry remains	1	4	2	3	5	15

Cultivated fruit seeds	0	1	0	0	1	2
Cloth	0	0	2	0	0	2
Leather	1	0	0	1	0	2
Rubber	0	2	1	2	0	5
Unidentified	1	2	3	1	3	10
N =	**8**	**19**	**24**	**12**	**13**	**76**

UNIDENTIFIED ITEMS (N = 18)

N =	**4**	**3**	**3**	**6**	**2**	**18**

SOIL (N = 36)

N =	**7**	**10**	**3**	**5**	**11**	**36**
ΣN	**134**	**89**	**91**	**94**	**110**	**518**

On an aggregate level, the seasonal pattern of use of mammalian prey was rather constant, with a moderate decrease during autumn (Table 13), but these differences were not statistically significant (T-test: $t = 5.7$, $p = 0.055$). Impala (*A. melampus*) comprised the bulk (32.3%, n = 31) of ungulate scat remains, followed by warthogs (*Phacochoerus africanus*) (19.4%), and kudu (*Tragelaphus strepsiceros*). Remains of impala and other medium-sized ungulates were probably a consequence of lamb mortality partially precipitated by jackal predation as is suggested by results from direct observations. Neonatal ungulates are vulnerable to mortality agents at or shortly after birth, but they quickly outgrow this vulnerability. It is most likely that large ungulate remains were scavenged as carrion or fresh kills of other carnivores such as leopards (*Panthera pardus*). Medium sized prey accounted for 15.5% of all mammalian prey, and these were mostly represented by scrub hares (*Lepus saxatilis*) (42.3%, n = 26), followed by Cape hares (*Lepus capensis*) and small spotted genets (*Genetta genetta*) in similar proportions of 15.3% each. Jackal hair remains (15.3% of medium-size mammals) were probably a result of (allo)grooming, although intraspecific predation on young (and feeding on jackal carrion) is not a remote possibility (Moehlman, 1983). Domestic mammal remains were represented by sheep (*Capra hircus*) (66.7%, n =

18), goats (*Ovis aries*) (44.4%), donkeys (*Equus* sp.), and cattle (*Bos indicus*) (4.5%) remains. Most small mammalian preys were terrestrial, crepuscular and nocturnal, and inhabitants of Acacia savanna woodland and grassland, whereas few species (e.g. *Otomys angoniensis*) were predominantly diurnal. Other animal preys were largely diurnal. As previously noted in Chapter Four, jackal activity periods in MNR closely coincided with that of its prey, in addition to the relative activity of humans.

The crested guinea fowl (*Numida meleagris*) represented 22.7 % (n = 44) of all avian remains, whereas ostrich (*Struthio camelus*) and francolins (*Francolinus* sp.) accounted for 13.6% and 15.9%, respectively. Invertebrate remains were represented by the exoskeletons of ants (order: Hymenoptera), dung beetles (order; Coleoptera), grasshoppers (order; Orthoptera), termites (order; Isoptera), millipedes (order; Myriapoda), and scorpions (order; Scorpionida). The Isoptera were mostly represented by harvester termites *Hodotermes mossambicus* (which were the most abundant and more often consumed prey item during the dry season), *Trinervitermes* sp., and the mound-building termite *Macrotermes* sp.

Two types of anthropogenic food items were identified in the scats. First, remains from domestic animals typified by white chalky faeces containing abundant poultry claws, feathers and bone chips, and fish remains (e.g. fish scales and bones) resulting from the activities of anglers who operated in the nearby rivers and dams. The second type, derived from feeding on exploitable scraps from refuse disposal sites or garbage bins, typified by dark brittle faeces containing plastic bags, bottle tops and fragments of glass, together with some commercial fruit pips (e.g. apples *Malus* sp. and oranges *Citrus* sp.). Remains of domestic mammals were however classified under the general 'Mammals' food item category, while remains of locally cultivated crops (e.g. maize *Z. mays*, melons and squashes) were included under 'Fruits'.

'Fruits' included seeds of *Grewia* spp., large sourplum (*Ximenia caffra*), buffalo thorn (*Ziziphus mucronata*), melons and squashes (Family: Cucurbitaceae). Single seeds of marula trees (*Sclerocarya birrea*) were also retrieved from scats. Jackals usually rested under the shade of marula trees and fed on the fruits which had fallen to the ground. Usually the pulp was ingested whilst the hard seed was spat out, but these were sometimes swallowed. Exosperm remains of maize (*Z. mays*) were also found in jackal scats. It is unclear whether these fruits were eaten for their energetic content or moisture content, but individuals were observed to eat, and then drink at waterholes. The fruits of *Grewia* spp. were eaten throughout the year by jackals except when the parent plants were in flower.

Stomach contents

The sample for stomach contents was unevenly distributed throughout the year since animals used were obtained from problem animal control operations which were naturally biased to the winter season when jackals were most often intercepted by hunters and trappers.

Table 15. Percentage occurrences of food items found in stomachs of black-backed jackals in Mokolodi Nature Reserve and surrounding areas

Food Item	**No. of Stomachs**	**Percent occurrence (%)**	**Relative percent occurrence (%)**
Game carrion	2	28.6	4.3
Livestock carrion	3	42.9	6.4
Other carrion	3	42.9	6.4
Artiodactyla	2	28.6	4.3
Sheep	2	28.6	4.3
Goats	1	14.3	2.1
Rodentia	3	42.9	6.4
Aves	1	14.3	2.1
Invertebrates	5	71.4	10.6
Cultivated crops	1	14.3	2.1
Unidentified mammals	4	57.1	8.5
Vegetation	4	57.1	8.5
Anthropogenic items	3	42.1	6.4
Soil	6	85.7	12.8
Unidentified items	7	100.0	14.9

Analysis of 7 jackal stomachs revealed an array of prey organisms (Table 15). Dipteran larvae were found in some stomachs, thus indicating that jackals also fed on carrion in addition to live prey. Carrion (game and livestock) accounted for 17.0% of all prey items in stomachs. Invertebrates were the most common single prey item occurring in 71.4% (n = 7) of all jackal stomachs, and this represented 10.6% of all prey items found in stomachs.

Discussion

Direct Observations

Jackal predatory behaviour on ungulates observed in the present study is of particular note because although jackals may be small relative to most wild and domestic ungulates, they have nonetheless perfected their predatory behaviour to be capable of causing substantial losses to ungulate herds through natal mortality. The injuries inflicted on the vulva of parturient females is also important, particularly in domestic stock where the injured animal usually ended up being killed, sometimes in addition to the loss of its young to jackal predation. Such behaviour clearly underlines opportunistic predation by jackals, usually depicted in the variety of prey items taken, but also in the modes of food acquisition under varying ecological circumstances. Jackals have also been reported to scavenge on wildebeest (*Connochaetes taurinus*) afterbirths in the Serengeti plains (Jarman, 1976) and have been implicated in causing similar injuries to cows (*B. indicus*) in labour (Skead, 1973). The killing method used in the subjugation of ungulate young is typical black-backed jackal killing behaviour; neck and head bites aimed at severing the trachea and suffocating the prey (Rowe-Rowe, 1986). Of special note is the apparent selection of neonatal impala by jackals, since these were some of the least common age group of the population. However, this could also be due to the inability to detect neonatal impala by the investigator, relative to jackals.

Jackals changed their diets when prey species became vulnerable to predation. For example, impala lambs were most vulnerable when less than two weeks old. Jackals took advantage of this vulnerability, as field observations suggested. When jackals were feeding mostly on small prey, group size was smallest consisting of single individuals. Jackals do not need to hunt together when preying on rodents, fruits, reptiles, or insects, and one jackal does not benefit from the small prey that another has caught. When large prey were intercepted, pairs and sometimes groups of three individuals cooperated in bringing the animal down. Larger jackal groups were both evident in summer and winter, but these were seldom observed to hunt cooperatively. Possible mechanisms driving the increase in jackal group size and subsequent change in foraging ecology may be increased sociality among pack members during the breeding season and delayed juvenile dispersal (Gese, Rongstad, & Mytton, 1988; Moehlman, 1986). The interplay between group size and prey size is presented and discussed in Chapter Seven.

In black-backed jackals, pair-hunting may be an adaptation to overcome hunting problems: lambs are often defended by their mothers, and a pair of jackals can more easily cope with the double task of catching the lamb and warding off its mother (Eaton, 1969; Lamprecht, 1978a). Pair hunting may also considerably offset the competitive pressure, as two jackals can eat a lamb much faster than one, thus lessening the risk of kleptoparasitism. In MNR however, such a situation may not predominate presumably because potential large carnivore competitors do not exist apart from the rare brown hyaena and the occasional leopard. However, intra- and interspecific kleptoparasitism cannot be completely ruled out since observations revealed that trapped non-target species were retrieved by predators other than jackals, in addition to observations of caching behaviour which suggests the presence of competition. A jackal family in possession of a carcass (either killed or scavenged) can exploit it more fully than a single individual. I have observed single jackals at carcasses spending most of the time threatening vultures rather than feeding, and occasionally being driven away by vultures. Thus the feeding ecology of black-backed jackals involves not only availability, distribution, and size of food items, but also intra- and interspecific competition to retain and consume food. In addition, the high level of hunting pressure around the MNR area would select for rapid feeding on kills outside the reserve to avoid detection by humans. Under such circumstances it would also benefit jackals if kills outside the park were brought within where they could be consumed in a relatively safer environment. The fact that remains of a number of domestic species were found in the reserve partly serves to support the jackal foraging behaviour described here. However, transportation of food into the park would also involve the risk of being detected or being dispossessed of the kill by other kleptoparasites. We would therefore expect the animal to 'trade-off' between feeding on the site of the kill and transporting to an area of safe feeding, according to the local ecological setting.

Although cooperative hunting has previously been invoked to account for large group size in most social predators, its general application is somewhat misplaced. It is often thought, mistakenly, that the terms 'hunting group' and 'social hunting' imply the wholesale adaptation of all such units to cope with big and/or fast prey animals, i.e. that they are invariably adapted to the requirements of the hunt. But in the case of black-backed jackals in MNR, this only rarely seems to be the case. Where it does apply, hunting groups tend to consist of only two or three individuals. Bigger groups more often seem to be adapted to problems arising only after a successful hunt, e.g. competition with kleptoparasites for the kill. In fact, sometimes the groups seem to be adapted to problems quite unconnected with hunting and feeding, such as protection from intraguild predators, kleptogamy, and even competing for territories, but which nonetheless compel animals to live together (Lamprecht, 1978b; 1981). Besides, some overlap of group home ranges, especially at crucial areas such as watering holes or in the vicinity of carcasses, has been observed for this species in which the groups are normally mutually exclusive (Rowe-Rowe, 1982; Ferguson, Nel & De Wet, 1983; Moehlman, 1983, 1986).

Scavenging may also be seen as an added dimension that gives those carnivores that practice it the potential to increase far beyond the bounds imposed on pure predators. However, not every scavenging carnivore succeeds equally. A classic example in African savannas is that epitomised by the rare striped hyaena (*Hyaena hyaena*) and the relatively common spotted hyaena (*Crocuta crocuta*). Success demands on exactly the right combination of attributes; a species with antisocial, retiring habits, which is largely restricted to habitats with limited food resources, obviously will not be as successful as a gregarious one utilising a variety of habitats. Hence it must be their ability to exploit scavenging to the limit, added to their abilities as predators, that accounts to the numerical ascendancy of black-backed jackals and spotted hyaenas in much of sub-Saharan Africa.

The senses of black-backed jackals in MNR that facilitate the location of prey are most probably the following (in decreasing order): olfactory, visual, and auditory, but this may vary according to the nature of the habitat and prey being sought. In MNR where visibility is limited by dense woodland vegetation, olfactory cues may definitely predominate over sight, whereas sight would be more important in open grasslands. This is of particular adaptive importance for hunting cryptic prey such as impala lambs, which are usually hidden by their mothers for the first few days after parturition (see Chapter Six). Furthermore, olfactory cues are quite important in woodland habitat for avoiding humans where hunting pressure is high. This was clearly manifest in the difficulty of trapping jackals during the present study. When prey are visible, pursuit based on visual cues is most likely to start before olfactory or auditory cues can come into play, but when prey are well-hidden, jackals probably rely on some combination of olfactory and auditory cues. The exact combination probably depends on the aeolian conditions and the amount of noise made by prey. Jackals are efficient predators and can always switch back and forth between these various hunting modes in order to take maximum advantage of whatever the environmental conditions are at the time.

It must be noted that the risk of predation is an integral part of the foraging behaviour of animals. For example, an animal that has been observed to locate and consume several prey items may be said to be exhibiting foraging behaviour. Surely the animal may have ingested some food, but was it just 'foraging'? Surely this animal must have been 'considering' not only its options as they relate to efficient food intake, but also how those options influence its risk of being preyed upon. To the extent that the term 'foraging behaviour' is associated strictly with the act of food intake, its use in describing behaviour is misleading because it detracts attention from important determinants of behaviour that are unrelated to energy. The same can be said of any behaviour, not only foraging. Furthermore, it is also important to note that the risk of predation does not 'constrain' behaviour. Although it is often stated that the risk of predation acts as a constraint on foraging behaviour (e.g. Krebs & Davies, 1984; Milinski, 1986), one could just as easily argue that foraging is a major constraint on predator avoidance (Lima & Dill 1990). The fact is that neither foraging nor predation act as constraints. The behavioural options open to a feeding animal lie on a continuum between energy maximisation (at the complete expense of predator avoidance) and minimisation of risk (at the complete expense of feeding). Clearly, neither extreme option is desirable and optimal behaviour will lie somewhere in-between. Lima & Dill (1990) suggested that the term, 'constraint' be reserved for factors such as gut size, day length, which are not under the individual's control and therefore actually constrain the animal to a particular set of behavioural options.

Stomach contents

Although the sample size of stomachs used for the analysis of jackal feeding habits is small (n = 7), indications are that the jackals in MNR also scavenge, thus playing an important role by eating garbage and animal carrion in and around towns and villages. The diet is dependent upon the availability of food items and ranges from vegetable matter to ungulate prey. This is not surprising since in Bangladesh, golden jackals (*Canis aureus*) have even been reported to feed on sugarcane and rice stems (Poche, Evans, Sultana, Hague, Sterner & Siddique, 1987).

The consumption of grass is known to be both voluntary and involuntary, possibly aiding in food digestion and to satisfy their vitamin (C) requirements. Smithers (1971) found that green grass occurred in 14 out of 59 stomach contents. In seven of these cases the stomach containing the green grass was empty or nearly empty. Domestic dogs (*C. familiaris*) and cats (*Felis catus*) frequently eat green grass, and this is usually taken when the stomach is empty (pers. obs.). Unlike green grass, dry grass occurred along with other detritus but it is likely that the latter was ingested fortuitously or along with Isoptera or other invertebrates. Grass could also appear in remains or stomach contents if ingested with the alimentary canal of the prey species. Rowe-Rowe (1976) also reported on a jackal stomach that entirely contained grass.

The presence of fly larvae in stomach contents would depend on how long after death the jackal found and fed on the carcass, the time of year that the antelope died, and the portions eaten by the jackal. (Dipteran larvae that were found with mammal remains were not recorded separately as insects). Some of the other antelopes were also eaten as carrion as fly larvae occurred in some stomach contents. Carrion might have been the remains of animals killed by a jackal, but which were too large to be entirely consumed on the day of the kill - or the animal might have died of other causes (Rowe-Rowe, 1976, 1983) Similarly, fresh meat found in the stomach might have been from an animal killed by the jackal, or from an animal that had died of other causes and had been scavenged by jackals shortly afterwards. Jackals can legitimately be considered as problem animals on sheep farms and other small livestock since they are responsible for the loss of potential income (Rowe-Rowe, 1976; Fair, 1994).

Scat Analysis

Prey occurrences found here are similar to those found in previous studies (e.g. Bothma, 1971; Rowe-Rowe, 1976,1983). As previously stated, jackals changed their diets when prey species became vulnerable to predation. Selection of the neonatal antelopes (e.g. steenbok, *Raphicerus campestris*, and impala, *Aepyceros melampus*) could account for the preponderance of ungulate prey in the wet season scat samples. Impala lambs are most vulnerable when less than two weeks old, and during the present study, jackals took advantage of this vulnerability. Small mammals and murids constituted a major part of jackal diet, particularly during the dry season (winter-spring). In the case of small mammals, while there is no evidence to prove this, it is assumed that the jackal had killed them itself. Remains of springhaas (*Pedetes capensis*) and scrub hares (*Lepus* spp.) were found in scats, but murids constituted a major proportion of the diet. These included *Tatera* sp., *Aethomys namaquensis*, *Saccostomus campestris*, *Rattus rattus*, and the diurnal species *Rhabdomys pumilio* and *Otomys angoniensis*.

The presence of poultry remains (e.g. feathers, beaks, and claws) in scats reveals their importance in the diet of jackals and the tendency of jackals to frequent human settlements in search of food. The dietary habits of black-backed jackals in the present study at MNR reveals that, in order to obtain sufficient food, they extended their range from their woodland refuges within the MNR to include human settlements where livestock damage was observed. Refuse dumping sites near human habitation were frequently utilised at night as sites of reliable food sources. It was apparent that rodents (particularly *Rattus rattus*) also occurred at high densities at refuse dumping sites, underscoring the jackals' preference for such rich patches of food. Although wild animals played a considerable part in jackal diet, jackals probably incorporated domestic species into their diets due to reduced availability of their usual wild prey.

Based on faecal analysis jackals undergo seasonal changes in the relative frequencies of animal and plant matter ingested. The seasonal increase in remains of fruits in the faeces of jackals should not necessarily be interpreted as a decrease in consumption or importance of animal matter (Ball & Golightly, 1992). For example, if jackals in the wet season ingested the same number of rodents as in the dry season, and incorporated fruits into their diet, the remains of rodents would be a smaller percentage of all the food remains. It might appear as though fewer rodents had been eaten, and that jackals had changed from a diet of predominantly animal prey to fruit. However, in a study on grey foxes (*Urocyon cinereoargenteus*), Ball & Golightly (1992) found that berries contributed little to protein balance; other sources of protein (animal matter) must be ingested, even if the foxes could consume adequate amounts of berries to meet their energetic requirements. They found that even if a fox ate about 1,6 kg of berries, the small amount of protein in that diet would be inadequate for maintenance and the fox would still have to forage for animal prey. Furthermore, percent digestible and metabolizable energy of a mice diet was significantly greater than that of berries. Digestible crude fat and crude protein were also found to be significantly greater for diets composed of mice than of berries. By extension, an exclusively frugivorous diet can impose a premium on the energetic and nutrient demands of jackals at MNR. Hence, jackals may switch to animal diets in response to increased demands for protein, energy and other nutrients probably as a result of their reproductive activities. In particular, on an aggregate level, in MNR the importance of animal diet for jackals is manisfested in the similarity of the frequency of occurrence of mammalian prey remains across all seasons (Table 13), albeit noteworthy differences are revealed at finer levels of resolution (Table 14).

Seed dispersal by jackals probably benefits host species. Fruits, when they are abundant, provide an easily obtainable source of carbohydrates for jackals. Further, fruits are a sessile food resource and grow in patches. Their yearly presence within the home range of a black-backed jackal, given climate-induced fluctuations, is relatively predictable in time and space. Encounters with fruit patches by jackals could occur while searching for animal prey. When a patch is encountered, a volume of berries could be exploited from the plants with relatively little expenditure of energy and/or time, while yielding some energy to the jackal. In areas of restricted fresh water, jackals that consume fleshy fruits may reduce the amount of time they spend travelling to other water sources. Hence jackals may ingest fleshy fruits more for water content of the fruit than for energy content, especially under moisture limited environments.

Whether the jackals were acting as predators or dispersers of seeds cannot be determined from a study of this type. In order to define the role of jackals in plant reproduction in the area, studies which examine the viability of seeds after passing through the jackals' digestive tract and selection of foods in relation to availability would be required. If seeds were viable after consumption by jackals, some aspects of their behaviour such as the extensive use of roads for travelling and defecating, might enhance its importance as a seed disperser, helping plants to recolonize abandoned roads, old fields, and other clearings due to human extractive activities in the area. On the other hand, these same habits could result in ineffective seed dispersal when faeces are deposited in areas of perpetually high disturbance where seeds have little chance of germinating, such as along the maintained roads, on rocky outcrops, and in the gravel pits. The role of the jackals in plant reproduction in the area merits further investigation due to the relatively high numbers of jackals and their high consumption of fruits.

A striking observation on the potential of jackals in seed dispersal in MNR was noted in the dispersion of *Grewia* spp. plants, whose seeds occurred most frequently in jackal faeces throughout the year. There was a marked difference in the abundance and distribution of *Grewia* spp. within the reserve and in the tribal grazing areas. *Grewia* spp. occurred widely and were well-established within the park, while they were almost non-existent in the surrounding farming areas, save for a few tufts of stems almost browsed to ground level. Repeated browsing by domestic livestock (especially goats) outside the park is likely to account for this difference but I suggest that defecation activities of jackals while marking territory is also likely to have an effect through seed dispersal and subsequent (re)establishment in various localities. This is more likely to be the case since defecation activities were confined to areas of low disturbance such as inside the reserve. This clearly indicates the potential of jackals to contribute to plant reproduction, but still, this merits further investigation.

Birds were a relatively minor part of the diet throughout most of the study. Birds are generally difficult to catch, and jackals have many failures between catches. The peak in bird remains in faeces occurred in spring and summer when ground-nesting game birds were brooding and the population was swollen by chicks, presumably easier prey than adult birds. Their higher mortality also would have made them more commonly available as carrion. Birds also featured strongly in the scat remains in the dry season when their access to vegetative cover possibly was limited. However the interpretation of jackal diet based on game bird (or poultry) plumage remains must be treated with caution, especially when assessing the impact of jackal predation on avian prey. In the red fox, *Vulpes vulpes* it has been found that feathers stay longer in the stomach than smaller plumage and other parts of prey (Reynolds & Aebischer, 1991; Lovari & Parigi, 1995). Therefore it has been suggested that a scat analysis based on micro-fragments should be used to assess the real contribution of birds, which otherwise may be underestimated, to the diet (Reynolds & Aebischer, 1991). On the other hand, after undergoing prolonged digestion in the stomach, feather fragments are presumably passed on through the pyloric sphincter. Thus, smaller plumage and fragmented feathers of the same bird are likely to show up in separate scats, and this would result in an overestimate of the importance of birds in scat analysis (Lovari & Parigi, 1995).

Based on my field observations, I suspect that during the wet season, jackals ingest higher quantities of arthropods than are detected in faeces. Several times I observed jackals feeding on areas heavily infested with caterpillars. These observations suggest that the jackals were primarily eating the larvae and adults, and may have helped reduce damage to grassland and crops inflicted by caterpillars. However, detection of larval remains would be limited by digestion of all soft body parts. In winter the activities of harvester termites (*Hodotermes* spp.) could impact heavily on the relative availability of graze to ungulates and livestock, especially during prolonged drought periods (Kaunda, 1994; J.M. Dangerfield, pers. comm.). Thus the predatory activities of jackals on Isoptera could help reduce 'overgrazing' by termites on pasture and also decrease damage to crops during the harvesting season. Like jackals, aardvarks (*O. afer*) and bat-eared foxes (*O. megalotis*) have also been implicated as allies in the fight against termites and other insect pests (Van Heerden, 1988).

Given the addition of anthropogenic food resources and altered habitats in human settlements, black-backed jackals' diet at MNR was more diverse and differed from that reported in relatively undeveloped areas (Wyman, 1967; Hall-Martin & Botha, 1980; Smithers, 1971; Lamprecht, 1978a; Rowe-Rowe, 1983). Results of observational data and scat analysis reported here indicate that jackals are opportunistic feeders, that eat carrion as well as practically any animal they can easily overpower - a behavioural trait which led Estes (1967) to designate them as 'predator scavengers' as compared to the pure predators ('scavenger predators'). Jackals are highly adaptable animals being able to exist as predators on small game and livestock, scavengers, eat insects or rodents, and as indicated in the present study, also feed on anthropogenic food sources, wild fruits, and agricultural crops. The relative importance of scavenging and predation in the lives of jackals varies according to both time and place. Where large social carnivores and their prey are plentiful, they may live largely as scavengers if they themselves are not too numerous (Estes, 1967). Where pure predators are scarce, as is the case in MNR, they may be very active hunters; in fact they have been implicated to even partially fill a pure predator's vacated niche. Like other predators, jackals behave so as to maximise their fitness, which is often done by maximising their net energy intake. In fact, a predator's prey choice is not only a consequence of prey energy content, but it also depends on the predator's success in finding, handling, and consuming its prey. Other studies on jackals' diet have revealed similar feeding behaviour (e.g. Wyman, 1967; Bothma, 1971; Smithers, 1971; Rowe-Rowe, 1976), albeit with some deviations from the findings of the present study.

There are a number of difficulties inherent in the interpretation of carnivore diets based on scat analysis. Only indigestible material can be recorded so that the consumption of soft tissue from large carcasses without the ingestion of hair would be difficult to detect. It is also impossible to differentiate with certainty between prey that have been killed by the predator and those that have been scavenged. Conversion of items from frequency of occurrence to contribution to the diet of biomass is also liable to severe bias. Large prey cannot be consumed totally at one meal and the remainder could either be eaten at subsequent meals or alternatively by other predators and scavengers. Small items may be consumed totally but the presence of their remains in scats cannot be used to determine how many individuals were represented. Furthermore, small prey containing a relatively higher proportion of indigestible matter (hair, bones, and teeth) and their remains are over-represented in scats. This makes analysis of diet data involving percentage volume or percentage weight of prey remains in scats biased towards smaller prey. Scats also cannot be identified to individual predators, so that specialist and generalist foragers cannot be distinguished. Interpretation of data based on scat analysis must, therefore, be done cautiously within the constraints of the methodology (Oli, Taylor, & Rogers, 1993; Weaver, 1993). Even with an adequate faecal sample, there are problems with the analysis of the data (Mills, 1992a). The identification of hair is often difficult particularly in species with a diverse diet. Finally, for most prey species it is impossible to differentiate between the hair of adults and juveniles.

The percent occurrence of prey in the diet also gives no measure of the proportion of encounters in which a prey type is ignored. It could be argued that a reduction in the percent occurrence of an item in the predator's diet reflects a reduction in the proportion eaten of that item. This would only be true if densities of each prey item were to remain constant. Otherwise, changes in percent occurrence of an item in the diet could be caused by changes in the density or proportion of other prey eaten. Without relative measures of prey density it is impossible to determine the cause of the change and thus make predictions to test prey choice models. Interpretations of prey choice models are further complicated when prey types differ considerably in size. Changes in the number of large items consumed will have a relatively greater influence on the dry matter ingested than similar changes in the number of small prey consumed. Percent occurrence in the diet must be converted to some index of the actual number of prey consumed to be able to test prey choice models (Boutin & Cluff, 1989).

Finally it is impossible to determine whether food was scavenged or killed by the predator, which is an important consideration, particularly for the jackals (Bowland & Bowland, 1991; Bowland & Perrin, 1993). Although a more realistic measure could be obtained from intestine/stomach contents when digestion of items is not yet completed, faecal analysis is a non-intrusive method of estimating diet, and also provided sample sizes sufficiently large to measure relative changes in composition from season to season without disturbing the population under study (Doncaster *et al.*, 1990).

CHAPTER SIX

JACKAL PREDATION ON IMPALA

Introduction

The impala (*A. melampus*) is an abundant antelope species inhabiting the woodlands and savannas of eastern, central and southern Africa. They are typically found in riverine habitat in the dry season, moving into surrounding deciduous woodland or savanna in the wet season (Jarman & Jarman, 1973; Murray, 1982). Locally, their dispersion may be clumped or irregular, but groups are known to have open membership and no social units other than that of mother and young (Schenkel, 1966; Jarman & Jarman; 1973). A gradual disintegration of the mother-young bond is usually evident in the declining proximity between dam and lamb and the increasing proportion of observations in which lambs associate with peers (Jarman, 1976; Mooring & Rubin, 1991). The formation of peer groups has been seen as one indication of the start of a weakening mother-infant relationship (Lent, 1974; in Mooring & Rubin, 1991). Near the equator, reproduction is not seasonal and births occur throughout the year (Jarman & Jarman, 1974). However, breeding activity in southern Africa takes place during a 'rut' of 3-5 weeks in May-June (Fairall, 1972; Murray, 1982; J.D. Skinner, pers. comm.). Thus breeding is short and synchronised. During the remainder of the year, male impala are found in loose coalitions with other males (bachelor herds) or in herds of mixed sex. Lambs are no longer isolated from the herd with the dam after about the first week (Schenkel 1966; Jarman, 1976; Mooring & Rubin, 1991).

Predation has been offered as a cause of synchronised breeding in ungulates (Estes, 1966; Kruuk, 1972), the advantages being increased predator detection, predator confusion and satiation of predators (Ims, 1990). However, Skinner & Van Jaarsveld (1987) argued that predator swamping must have been preceded by seasonal reproduction, the former just acting to tighten-up the breeding season. Intermittent breeders (Dott, 1987) react to environmental cues (e.g. lunar cycle, Murray, 1982) but predation reduces the breeding period, as young born during the fringes of the calving season have a higher mortality rate (Estes, 1966). Impala react to a shortening day-length and mate in May in order to lamb after the spring rains, probably to ensure optimal milk production for the young when there is a high quality food source during summer (Skinner, 1989). Rainfall regimes in habitats such as the Kalahari strongly affect vegetative productivity (Van Rooyen, Bredenkamp, & Theron, 1991). In environments in which seasonal climatic changes significantly alter resource availability, reproductive success often depends on the timing of breeding: offspring born late in the breeding season have a lower probability of survival and grow at a slower rate than those born earlier. Synchrony of reproduction with environmental factors ensures that females have access to good food supplies during energetically demanding periods, which for mammals occur during late gestation and lactation.

Predation risk is an important element of the environment influencing animal behaviour, reproduction, and distribution. An individual's risk of predation varies over time and from place to place depending on such factors as the amount of cover, the type of predator, and visibility (Lima & Dill, 1990). In addition, foraging benefits also vary and frequently conflict with anti-predator behaviour, so individuals are forced to 'trade-off' the benefits of foraging against the need to reduce the risk of predation. The ability for prey animals to select their 'enemy-free space' (Jeffries & Lawton, 1984) has evolved as an adaptation under different circumstances of time, habitat, and predator type.

In some mammals, the predation risk level depends on the amount of activity leading to increased visibility, audibility, or smell (Norrdahl & Korpimaki, 1995). A considerable body of evidence suggesting that reproductive activity places animals under increased risk of predation (or fatal parasitism) exists (Lima & Dill, 1990). For example, the risk experienced by males may be increased in several ways, especially by calling and display behaviours conspicuous to both females and predators (reviewed in Lima & Dill, 1990). Although most such cases reported to date deal with insects, the effect is undoubtedly more general. In the case of females, pregnancy may increase predation risk by increasing visibility to predators or decreasing speed and manoeuvrability. One or both sexes may also pay a cost in terms of increased vulnerability to predation often associated with parental duties. Furthermore, as breeding increases activity, noise, and smell, and as olfactory cues are important in breeding, but may be used by predators as cues in hunting, a non-breeding mammal probably has lower predation risk than a breeding one.

For all these reasons, the reproductive period is often a time of greatly increased predation; this is part of the 'cost of reproduction' which influences the evolution of life-history patterns (Stearns, 1976). Given that reproductive activities increase the risk of predation and that animals have made mortality-reproduction trade-offs in evolutionary time, it would be surprising if they did not do so in ecological time as well, i.e. base reproductive decisions on estimates of the prevailing risk of predation. For example, animals may delay reproduction under temporarily high predation risk. If temporarily high predation risk has a suppressive effect on prey reproduction on a large scale, we expect a negative association between predation risk level and the proportion of breeding individuals in prey populations. But animals cannot delay breeding forever, as dying without breeding means a fitness of zero. So, delayed breeding is expensive and should only happen under temporarily high predation risk i.e. there has to be a high probability that predation risk will decrease in future (Korpimaki, Norrdahl, & Valkama, 1994; Norrdahl & Korpimaki, 1995). Thus if mating and reproduction increase the risk of being preyed upon, trade-offs between current reproduction and future survival might result in a temporary reduction in reproductive investment when predation risk is high.

In most studies of jackal predation it has been found that the animals killed by jackals are not a random sample of the available prey population with respect to age, sex, and body condition (e.g. Rowe-Rowe, 1983, 1986; Stander, 1987; McKenzie, 1990). However, the selectivity shown by jackals varies between areas and different prey types, as a result of the inherent vulnerabilities of prey types, environmental conditions, or the spatial distribution of prey (Wyman, 1967; Smithers, 1971; Lamprecht, 1978a; Moehlman, 1978). Selective predation occurs when the relative frequencies of prey types in a predator's diet differ from the relative frequencies in the environment (Chesson, 1978a,b). Selectivity for prey types within the principal prey species influences how jackals affect population dynamics of their prey. Although impala are killed by a large range of predators (all the larger felids, canids, and hyaena, as well as baboons (*Papio hamadryas*), bateleur eagles *Terathopius caudatus*, pythons *Python sebae natalensis*, and crocodiles), black-backed jackals are particularly adept at killing impala, especially where the larger social carnivores are absent. Reduced mobility and alertness of the female during parturition increases her vulnerability to predation at this time and new-born impala become easy prey for black-backed jackals (Schenkel, 1966).

Predation can confound interpretation of vegetation-ungulate relationships because low survival of young can be viewed as an indication of food limitations when actually the population is being limited by predation. However, the general effects of predation on ungulate populations such as impala, are difficult to assess without intensive studies. Furthermore, detailed studies of maternal behaviour in species with precocial young are more difficult to carry out on wild animals than those involving altricial young. This is because close observation is generally impossible without causing disturbance. Detailed behavioural observations are difficult to make from a distance since parturition frequently takes place in an area concealed by vegetation or within a group of conspecifics. However, information concerning the development and survival of newborn lambs is critical to proper management. Since dead neonates are virtually impossible to locate, it has not been practical to appraise directly the extent of these losses. But because this information is needed for sound management, the subject could hardly be ignored however difficult to document. This chapter reports on observations of jackal predation on impala at MNR.

Methods

Observations of jackal predation on impala were conducted through focal animal sampling of jackals during their foraging activities, opportunistic observations, and from routine track censuses. Evidence that an animal was killed by jackals included an obvious chase sequence in sandy areas, signs of a struggle, haemorrhage associated with bite and claw marks, blood splattered on nearby vegetation, distance between canine bites and site of bite (Rowe-Rowe, 1986; Thurber & Peterson, 1993).

Population Size and Composition

Counts of impala in the study area indicated the proportion of lambs, subadults, adult males, and adult females. Counts were conducted along the extensive road network in the reserve especially on rarely driven roads for 2-4 days preferably after rainfall events. The sizes of impala herds and their composition by sex and age class (lamb, adult female, adult male) were determined from all herds seen incidentally during fieldwork. Each recognisable herd was recorded only once per day. Mandibles of impala carcasses were collected for relative age determination from tooth wear, replacement, eruption, or growth (Fuller & Kat, 1990).

During some 40 000 km of driving and walking within the nature reserve, so few animals were seen that it would have been meaningless to attempt a quantitative analysis of road strip counts and other sightings as only small numbers of impala herds were seen within the study area. No attempt was also made to capture and mark impala lambs due to the risk of parental desertion associated with handling by humans. Capturing impala lambs may cause abandonment and subsequent starvation especially given that conspicuous collars, ear markers, and other tags may make marked lambs more vulnerable to predation than unmarked ones. This is much more likely to happen when lambs are only a few hours old and/or when the mother is primiparous.

Habitat Overlap of Impala and Jackals

Ground locations (including telemetry locations for jackals) of impala and jackals were recorded. The vegetation type at each location was recorded to determine habitat use. The locations were assigned to one of seven broad habitat types on the basis of habitat classification of the park (see Chapter Four). Habitat overlap of jackals with the different classes of impala was assessed with the percent overlap measure (Krebs, 1989). Since no lambs were radio-collared, habitat use by lambs and dams was assumed to be the same.

Results

Although circumstantial evidence indicated the prevalence of jackal predation on impala at MNR, direct observations of such predation were quite difficult to document. Dense or closed vegetation structure and the rugged topography did not allow for observations of study animals for extended periods. The secretive nature of the jackal population at MNR also exacerbated this shortcoming. In addition, locating impala proved to be a particularly daunting task since their positions at any particular time could not be readily determined to enable direct observations. This was primarily because they were not radio-tagged in addition to the fact that their areas of utilisation were sometimes inaccessible. Besides, since impala hide their young during the first few days after birth, data on birth behaviour and subsequent neonate mortality could not be documented satisfactorily.

Notwithstanding these limitations, opportunistic observations resulted in the documentation of two noteworthy jackal attacks on parturient impala dams. Jackals probably decoded some behavioural peculiarities of impala in parturition since they were observed to frequent female impala herds during the lambing period. Pre-birth cues such as the unusual position of the tail which was held away from the body and obvious contractions thereafter, while assuming the straining posture similar to the urinating posture, were probably used by jackals to single out females about to give birth. Parturient females that isolated themselves from the herd in preparation for labour were then followed from a distance. Both attacks on impala occurred during labour, the first while the female was in the recumbent position. On the afternoon of 21st November 1996, a pair of jackals attacked a parturient impala dam that had isolated itself from the herd to give birth lying down. The two jackals grabbed the half-expelled foetus, pulled it from the vulva, and killed it instantly by puncturing the head region. The two jackals then speedily consumed the dead foetus by tearing it into two chunks. The mother, which had trouble getting up presumably due to exhaustion, finally managed to stand up and disappeared into some nearby bushes and was lost to sight.

The second interaction occurred during the same summer (16th December 1996), while radio-tracking the family of jackal AFJ1. This altercation involved three jackals and another parturient female impala that had some foetal legs protruding from the vulva but clearly had trouble isolating from the main herd for seclusion preparatory to imminent delivery. The jackal group in this instance somehow managed to spot the 'unusual' behaviour of the impala. The male of the jackal pair approached the parturient impala, by first sniffing at drops of birth fluids while searching the immediate vicinity. The male jackal was then quickly joined by its female partner AFJ1 and what I judged to be a subadult jackal (presumably the pair's offspring of the previous year). Upon ascertaining the source of the scent the three jackals converged on the parturient impala and attacked it from the rear, the sides, and head region of the impala dam. The other members of the impala herd disappeared into the bushes oblivious to the struggles of the impala under attack. No attempt to mob the marauding predators was attempted. The adult male and subadult jackals grabbed the protruding legs and head region of the foetus from the vulva, while the adult female delivered some bites to the neck and head region. There were some futile attempts to disgorge the foetus from the vulva, and this ended in two of the jackals tearing at the vulva, while the third jackal delivered a suffocating grip on the lower neck of the impala dam. Eventually the clearly exhausted impala dam was overpowered and died on the spot. The whole interaction from attack to eventual subjugation lasted for 27 min. Within a further 20 min of this kill some vultures and one lone jackal had congregated on the kill, which was devoured frantically, in what appeared to be a clear case of intra- and interspecific competition. It is quite plausible that the impala dam was an inexperienced primiparous female, judging from its inability to identify and select a concealed spot for giving birth prior to the appearance of the foetus from the vulva. Except for signs of the kill, no remains of the impala carcass were located on the site the following morning. The carcass or what remained of it, was probably misappropriated by kleptoparasites (leopards or brown hyaenas) as revealed by spoor remains.

Impala breeding at MNR was restricted to less than six weeks in November/December, 1996. No breeding out of season was observed. Although two births were observed, it was not possible to obtain enough accurate data to present a complete description of the development of the mother-young bond. It appears that parturient impala dams give birth in isolation presumably under cover of some bush thickets since very small lambs were mostly observed in dense undergrowth. Young impala do not follow their mothers within a few hours (as in wildebeest) or days (as in hartebeest *Alcelaphus* spp. or gazelles *Gazella* spp.) after parturition (Schenkel, 1966; Jarman, 1976). For quite a number of days and during many hours each day the young is hidden in undergrowth, while the mother remains vigilant in the vicinity. Later, the lamb moves more and more frequently around its mother, but during this period the synchronisation of movement, which appears between mother and young in many ungulates of the open savanna grasslands, was not observed in impala.

Two more impala females showed evidence of similar past jackal attacks as evident from vulva scars during the 1996-97 lambing season. Older concealed lambs were killed by pairs of jackals searching through impala lambing grounds, probably using olfactory cues (see Chapter Five). Whenever the lamb was with its mother, one jackal attempted to distract the mother while the other member of the pair attacked the lamb. In MNR this was observed on three occasions, two of which were successful (Chapter Five), but indications are that such phenomena are more common than appears from these observations for reasons already alluded to previously. Jackals could be found among impala herds (n = 7) during the late afternoons and at night during the lambing periods. Although up to three jackals could be observed to take part in a hunt, in general jackals hunted impala lambs in pairs, as described in Chapter Five. Impala lambs were captured due to total exhaustion after persistent attacks, by being bitten under the neck, and then persisting with the pressure. In some instances, impala dams and sometimes the whole herd, tried vigorously to protect their young from jackal attacks through predator harassment with varying degrees of success.

Jackals were observed hunting adult impala other than females in labour and lambs on four occasions. However, none of these were successful, even though in one case, a pair of jackals could not bring down a clearly emaciated adult male impala, even after repeated mock-attacks. I documented adult impala in MNR charge and chase jackals on five occasions. Four of these cases involved impala dams while one involved members of a bachelor herd. Three of the chases by impala dams involved individual lone females while the other involved the whole herd with lambs among them. No lone males were observed to be involved in predator harassment, presumably due to the risk involved in singularly intercepting a potential predator.

Despite the paucity of direct observations of jackal attacks on large mammalian prey, it is plausible that the presence of fresh lamb remains (e.g. portions of legs or hooves) found scattered at certain sites within MNR could have signified jackal predation or other mortality factors although such evidence remains inconclusive (also refer to the discussion under Chapter Six). This was apparent during late November and early December 1996. In total, nine signs of impala lamb kills at different sites were identified from remains of body parts within the reserve, six of which were associated with jackal modes of killing. These remains were found scattered over what appeared to be impala lambing grounds or areas where lambs may have been concealed. In particular, observations from some of the farming properties next to MNR (Lion Park and Brink Estates) where there were relatively larger resident populations of impala, the situation was so severe that numerous leg-portion remains could be found literally strewn over known impala lambing grounds. However, it was not possible to undertake a direct quantitative appraisal of jackal predation in these areas, although this may had shed some more light on the nature and extent of jackal predation in such environments.

Most causes of lamb mortality were difficult to determine in MNR because remains of lambs (when there were any) were located a long time after the lamb's death and were badly mangled and had begun to decompose. Frequently, only lamb remains in the form of uneaten portions of legs were found. Either these were also eaten as part of the kill or immediately scavenged by other predators or scavengers e.g. brown hyaenas (*P. brunnea*), mongooses (Family: Herpestidae), bateleur eagles (*Terathopius caudatus*) and Cape vultures (*Gyps coprotheres*). Hence complete information was not obtained on every specimen. No lamb carcasses were found intact apart from those few instances when jackals were directly observed feeding on freshly killed lambs. Remains of impala lambs were mostly found within jackal home ranges, which closely corresponded with those of female herds. Impala dams had greater habitat overlap with jackals than did males (Table 16).

Table 16. Habitat use by impala in Mokolodi Nature Reserve and habitat overlap with radio collared jackals.

	Proportional use of habitat by:		
Habitat type	**Male Impala**	**Female Impala**	**Black-backed Jackals**
Short thorn savanna	0.39	0.26	0.21
Tree and bush savanna	0.21	0.36	0.42
Open savanna grassland	0.01	0.02	0.03
Seasonal floodplain	0.07	0.10	0.10
Semi-sweet mixed bushveld	0.18	0.15	0.13
Riparian woodland	0.14	0.11	0.09
Croton/Combretum tree savanna	0.00	0.00	0.01
% Overlap with jackals	70.3	88.8	

The number of herds incidentally seen during fieldwork and the average size are presented in Table 17. Most impala encountered were members of bachelor herds, while female herds, usually accompanied by a single male harem-holder, were encountered less often. Lambs and herds of mixed composition were particularly rarely encountered.

Three juvenile male impala were injured by predators (presumably by leopards or feral dogs), but nevertheless survived the attacks as shown from bite marks over their bodies. Fresh carcasses of two more yearling male impala, one adult male, and an adult female, were located in MNR during the present study. None of the carcasses could be connected to any particular mortality factor, apart from the yearling male impala that had a fractured limb which could partially be attributed to jackal predation as indicated by signs associated with jackal killing methods. This yearling impala carcass was later found on two occasions being devoured by groups of 2-4 jackals and some vultures.

Table 17. Composition of the impala population, the relative numbers of herds of each class, and their average size

Sex-age class	**Number of times herds were seen**	**Mean Size of herd**	**Proportion**
Males > 1yr	19	5 (range = 4 to 7)	0.48
Females > 1yr	11	16 (range = 10 to 22)	0.29
All Lambs	4	6 (range = 3 to 9)	0.10
Mixed herds	5	12 (range = 7 to 19)	0.13

Most carcasses were so old that collection of femur for the analysis of the Bone Marrow Fat Index (Depperschmidt, Torbit, Alldredge, & Deblinger, 1987; Shackleton & Granger, 1989; McKenzie, 1990) would have been impractical. However, whenever possible, skulls were collected for relative age determination. While it would have been desirable to augment these data by shooting some proportion of the impala population in MNR, this was not done because of likely disfavour from reserve management especially given their concern for the dwindling impala population.

On an individual basis, lambs and male yearling impala appear to be slightly selected for, while adult females are strongly underrepresented. Because males show less habitat overlap with jackals, they are encountered proportionately less often, and the observed kills probably represent a slightly higher selectivity for males upon encounter. On a herd basis, however, both adult classes are underrepresented and lambs are strongly over-represented. There are fewer males than females in the population, but because females are in larger herds, numbers of male and female herds are almost equal. Lambs occur in far fewer herd equivalents, because they make up a small proportion of the dam-lamb herds in which they are found. This results in fewer expected encounters with herds containing lambs, and the number of lamb kills represent strong selectivity for lambs upon encounters with herds.

Discussion

Although evidence of black-backed jackal predation on impala was difficult to obtain, information garnered from the present study was quite indicative. The fact that jackals were found to predate on neonatal impala as well as on yearlings and emaciated or senile adults indicates jackal potential to limit impala population increase in MNR, particularly through natal recruitment. The impala population in MNR has been estimated at 35-45 individuals, and at least 22 of these were females (pers. obs.). The findings of the present study indicate that two impala lambs were directly observed being killed and devoured by jackals, while another two died at foetal stage before expulsion from the parturient dams' vulvae. In addition, six lamb remains found in MNR during the 1996-97 lambing period alone, were attributed to jackal predation, yielding a total of at least 10 impala lambs killed that season. Given that each female impala gives birth to a single lamb per breeding season, and assuming that half of the impala dams had successfully conceived, it becomes evident that jackals in MNR may be limiting the population growth of resident impala. At a conservative estimate, overall, at least half of the annual calf crop (approx. 25% of the total impala population) fell prey to jackals during that season alone. The number of impala lambs that succumbed to jackal predation therefore constitutes a significant proportion of the impala population, and in conjunction with other natal and adult mortality factors, can considerably limit, or rather depress population levels.

A number of studies of predation on ungulates have demonstrated selection for lambs and calves (e.g. Mitchell *et al.*, 1965; Lipetz & Bekoff, 1980; Stander, 1987; the present study), while in other studies calves were taken in proportion to their abundance, or selectivity changed seasonally (Rowe-Rowe, 1975, 1976; Fuller & Keith, 1980; Lipetz & Bekoff, 1980). Similar selectivity for young and old animals has been found in studies of predation on white-tailed deer, though selectivity for calves was not always apparent (Huggard, 1992). Selectivity for calves may also be stronger when the prey species is more abundant (Huggard, 1992). Local fluctuations in lamb survival rates may also be attributed to changes in predator density, abundance of alternate prey, and vegetation production and its impact on female impala nutritional status (Huegel, Dahlgren, & Gladfelter, 1985)

During the breeding season, adult impala seem to be in little danger of predation by jackals since impala lambs present during the lambing period are more susceptible to predation than adults. However, jackals may prey on adult impala at other times, e.g. during the dry season. Selectivity for calves when they are available is expected, as they are generally slower, less dangerous, and inexperienced with predators. In a study of predation by a switch of predators on large mammalian prey in Kafue National Park, Zambia, Mitchell, Shenton, & Uys (1965) found that predation was heavy on the juvenile group, reduced on yearlings, whilst the sub-adult groups were hardly taken at all, undoubtedly due to the vigour and alertness of the subadult age-group. Mitchell *et al.*, (1965) reported that predation (by lions *Panthera leo*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus*, and wilddog *Lycaon pictus*) on antelope lambs and calves on average accounted for 27.9% of large mammal deaths. The sex ratio of large mammalian prey was male biased (1: 0.85, n=470)). Impala prey sex ratio was also particularly skewed with a ratio of 1 male: 0.5 females (n=18). In moose, adult males were selected over adult females in some systems (Fuller & Keith, 1980), while females were selected in others (Ballard *et al.*, 1981, in Huggard 1992). In other areas either no selectivity is found or the selected sex may change seasonally (Messier & Crete, 1985).

Neonate Concealment

The main antipredator behaviour used by the young of many bovids and cervids is to hide (FitzGibbon, 1993). The mother and infant are only in contact for short periods and infants rely on cryptic coloration and minimal activity to avoid detection by predators. The success of the hiding behaviour depends on the mother minimising the transmission of information concerning the lamb's presence (Byers & Byers, 1983). Otherwise, predators searching for hidden lambs could use this information to increase their chances of success. As most predators hunt visually, isolation from the herd and concealment would act to reduce possible predation on mother and young. While a mother can merge, behaviourally and physically, with other herd members, the anti-predator benefits of herding apply. However, as soon as she differs from them she is relatively more at risk from predators (the 'oddity effect' - Lima & Dill, 1990) and concealment becomes a more profitable strategy (Jarman, 1976). The importance of this behaviour is indicated by the very strong urge to isolate even when harassed persistently by a territorial male attempting to keep parturient females within the herd. It appears that impala lambs fall between a pure-hider and a pure-follower strategy, while the mother-young bond is weak and ephemeral. Observations of wild impala have shown that offspring do not preferentially associate with the mother after weaning at 4-6 months, but instead associate most with age-mates (Murray, 1981). New-born impala have been reported to show a strong and initially unspecific following response (Jarman, 1976): In fact, new-born impala which happen to be near other impala frequently attempted to follow individuals (or any moving object) other than their mothers and tried to suckle from strange females and even males.

The time available for the formation of the mother-young bond may be limited. It is well known that domestic goats will reject their newborn young as early as one hour after birth (pers. obs.). Similar behaviour has been observed in sheep (Jarman, 1976). Basic behavioural similarities between impala, sheep (*Ovis aries*), and goats (*Capra hircus*) suggest that such cognate behavioural patterns also exist in impala. The development of mobility by the young impala in the first half hour after birth adds to the danger that if the mother-young bond is not well-established soon after birth, the young may either be rejected by the mother, or if it is temporarily separated from its mother, it may not be recognised when relocated. Impala females are known to only suckle their own offspring; orphans still dependent on milk are rejected by other lactating females and die of starvation (Jarman, 1976). Lack of isolation from conspecifics could easily delay the formation of the mother-young bond. As most impala females stand up from time to time while giving birth, the preferred bush clumps were considerably more effective as shields than the long grass or shrubs used by other females. Too thick bush areas or too long grass could be detrimental as mother and young need to maintain visual contact in the first hour, particularly while the following response is unspecific. It was apparent that most females were unsuccessful in isolating and concealing themselves and reliance on this alone as an anti-predator device would be precarious. Newborn impala are particularly vulnerable to predators in the first hour after birth (Jarman, 1976); the following response is not yet specific to the mother and they tend to scamper away from her as soon as they are mobile. Consequently, giving birth in the middle hours of the day presumably allows several hours for the development of the mother-young bond before predators become active at dusk.

Placentophagia

Jackals are known to feed on ungulate afterbirths, but the extent to which this behaviour pattern occurred in MNR was quite noteworthy. The fact that impala dams usually eat their own placenta immediately after the expulsion of young at birth could predispose them to jackal attacks as soon as signs of imminent birth appear. Although the motive (from the jackals' perspective) may primarily be to feed on the placenta, the fact that the incidence of placentophagia is immediate for impala may necessitate early attacks by jackals, which could eventually lead to the death of the partially-born foetus, and injury or even certain death to the mother too. It has been reported that in some cases, impala in labour even start consuming their birth membranes and cleaning birth fluids even before the foetus is completely delivered (Jarman, 1976). Thus a jackal foraging for impala afterbirth would benefit from attacking the parturient female before the latter feeds on the after-births or placenta itself.

Placentophagia and the consumption of all birth fluids in impala may act to reduce predation by removal of attractants for predators such as jackals that have acute olfactory senses. Wildebeest also exhibit placentophagia but whereas the time from birth to expulsion is variable for impala, in wildebeest expulsion is delayed for at least three hours (Estes, 1966; Jarman, 1976). This has an obvious advantage for wildebeest, as it allows the calf more time to gain co-ordination before the expulsion of a placenta, which in many instances was eaten by jackals or vultures who homed in on it almost immediately. Presumably, the anti-predator behaviour of concealment in impala, which is a reasonable possibility in their relatively more wooded habitats, reduces the advantage gained by delaying expulsion (but not for long), and this behaviour in wildebeest is part of a complex of adaptations to existence in open country. However, as evidenced by jackal attacks on parturient impala in the present study, it appears that the hiding strategy and the promptitude of the onset of plancentophagia seldom pays dividends for impala since black-backed jackals have apparently perfected a versatile 'counter-strategy' to circumvent such a situation.

Although most senses of the black-backed jackal are acute, their sense of smell is exceptionally well-developed (Skinner & Smithers, 1990). In particular, Skinner & Smithers (1990) reported an instance of a single jackal seen following up the downwind scent of a dead springbok in the open plains of Botswana from a distance of well over a kilometre! Such sensory acuity does not bode well for impala reproduction in dense habitats such as in MNR because although impala mothers can hide their lambs, the well-developed sense of smell of jackals probably enables the latter to eventually locate and kill hidden lambs. Hence, even with relatively dense vegetative cover, predation by jackals may be intense during the hiding phase of impala lambs. Besides, although lambs may be relatively safe from predation during the early 'hiding' phase, the onset of flushing age at about 2 weeks heralds another episode of enhanced vulnerability of lambs. Predation could be severe during this transition period when there is vulnerability and lambs are more active and detectable but still catchable (Nelson & Woolf, 1987; Kunkel & Mech, 1994). Hence in areas of relatively elevated jackal densities, neonate mortality may considerably limit population increase. In the present study, sample sizes for lamb mortality were however too small to make strong inferences from such data. Further research is needed to determine whether neonate mortality is compensatory or additive and how this affects impala population dynamics. It is however plausible that wherever jackals and impala are sympatric it is likely that some level of predation whether on lambs or adults is bound to occur; however the extent and nature of predation may vary among areas and among years within an area.

The individuality of behaviour of impala females during parturition was very striking, particularly in the reaction to and early care of the newborn. The behaviour of the females which may have been primiparous indicates that some mother-young behaviour may be learned, and an experienced mother may improve the young's chances of survival by helping it to suckle and by cleaning up the birth fluids and membranes more quickly and efficiently than primiparae do (Jarman, 1976). There are strong selection pressures operating at this time for the accomplishment of isolation, concealment, and parturition in a minimum of time at the right time of day. Any variation in behaviour may influence the survival of both the mother and young.

Discussions of predator-prey relationships have often focused on the direct effects of reduction in prey abundance due to predation. However, other less direct effects of predation pressure have also been recognised. These include behavioural modifications that result in shifts in habitat usage and changes in foraging activity (Kennedy, Shave, & Spencer, 1994). In the presence of a predator, foragers must choose between a loss in foraging time through engaging in avoidance and escape behaviours or a potential loss in resource availability through a shift to a predator-free habitat. Optimal foraging models have been used as a way of examining how the presence of a predator affects the behaviour of prey species (Krebs & Davies, 1984; Lima & Dill, 1990). Any change in the ability to discriminate among the relative profitabilities of sites can affect the forager's distribution among those sites (Dukas & Ellner, 1993). The poorer the information available to the foragers the more likely they are to choose randomly among the sites and consequently become vulnerable to predation. As the change in behaviour coincides with the addition of a predator into the foraging environment, it is reasonable to assume that the predator's presence causes the change in the forager's behaviour. Animals may, therefore, alter their behaviour as a trade-off between perceived danger and food intake rate (Krebs & Kacelnik, 1991).

For example, most African antelopes avoid cover which might obscure and/or harbour predators; for these animals cover is not only a refuge, but also a source of risk (Underwood, 1982). In particular, impala generally occur in bush and mixed habitat which led Fuller & Kat (1993) to surmise that this made them relatively easier to fall prey to predators such as wild dogs in dense habitat. Vegetation density may also affect the survival of neonatal impala because increased cover may reduce predation for predators that rely primarily on visual cues to locate prey, e.g. aerial predators (Moreno, Villafuerte, & Delibes, 1996), especially during the first few days when lambs are most sedentary. The reduced size of exposed areas tends to reduce the chance for foraging predators to detect their prey. But carnivorous mammals such as black-backed jackals are primarily stalkers, relying on auditory and olfactory, in addition to visual cues, to detect and capture their prey in shrubs and bushes. By extension, dense vegetation, which characterised much of impala habitat utilisation in MNR, may also be a high-risk habitat for impala. Hence, habitat structure can determine prey availability as well as prey vulnerability (Corley, Fernandez, Capurro, Novaro, Funes, & Travaini, 1995).

In the case of impala at MNR familiarity with the area was tantamount to breeding success especially with respect to the selection of calving grounds free from core jackal activity or even outside the predators' home ranges. Interestingly in the present study, female impala habitat utilisation overlapped that of jackals to a greater extent, and it was apparent that most impala lambing areas were effectively within jackal home ranges. Since the recognition of mammalian predators by their prey could be based on olfactory cues, we would expect prey to be able to 'decode' the carnivore scents used for territory marking, individual and intersexual recognition (Jedrzejewski, Rychlik, & Jedrzejewska, 1993) to avoid core predator activity centres for improved prey breeding success. However, this may not be the case in MNR because selection of sites relatively free of predators may be difficult in such a relatively small, physically circumscribed area.

The Effect of Herds

The spatial distribution of male and female impala may also be proposed as a factor generating increased predation on yearling males, which tend to be found on the periphery of preferred areas, where they are more likely to be encountered by predators, especially at the height of the rut (Skinner & Smithers, 1990). A similar effect may explain the bias towards young males in predator kills. Male juvenile impala remain with their mothers until the rut in autumn of their second (yearling) year, at which time the harem-holding male chases the yearling males to the fringes of his territory, while female yearlings remain in the breeding herd. Yearling males in this study were often observed at the edges of larger herds in autumn. Peripheral individuals are the first to be encountered when predators attack an impala herd, and naive male yearlings are likely to be particularly vulnerable during these encounters.

During the lambing season (late spring/early summer) impala usually occur in small bull herds and larger dam/lamb herds (Estes, 1995). Animals in herds can see and hear others in the herd and all react to danger together. Increased wariness by impala after an attack probably makes them less vulnerable to subsequent attacks by jackals. Charnov *et al.* (1976)

have termed this effect 'behavioural depression'. The detected presence of a predator may increase alertness of the prey and temporarily depress prey availability. An increased alertness of impala following an attack by jackals causes the jackals to move to another area. In the present study, jackals moved throughout their territory and did not remain in individual areas of high (impala) prey density, and the kills were distributed more uniformly than the prey. Such patterns indicate that kills cannot be made repeatedly from one herd. Females may be underrepresented compared with males because females usually occur in herds with young that are preferred by jackals. When jackals encounter a female herd, they are more likely to attack the young, and the alerted females become less vulnerable to predation. Males generally do not have the benefit of lambs to divert such predation. From this herd-based point of view, males are not necessarily more vulnerable or preferred than females. They are encountered proportionately more by jackals because they occur in small, and therefore relatively numerous herds, and do not benefit by associating with calves. Lambs, though preferred by jackals, are not highly selected for overall because they occur in fewer herds.

Because little to no detailed information is available on the interrelationships between jackals and prey prior to the increase in modern man's influence on wildlife and habitats, the character of that relationship under pristine conditions remains to a large degree speculatory. As human encroachment and agriculture continue to reduce wildlife habitat in Botswana and other parts of the world, management decisions must be founded on a precise understanding of wildlife ecology and population dynamics. In particular, one important aspect of ungulate ecology is the extent and causes of lamb mortality. Although it is usually impractical to eliminate or even reduce the major factors in lamb mortality, an understanding of these factors is necessary to further our understanding of herd dynamics and improve the predictive capabilities of wildlife managers (Kunkel & Mech, 1994). Although the general effects of predation on ungulate populations are difficult to assess without intensive studies, monitoring prey with radio telemetry is a more direct method of measuring losses to predation. Collaring dams and lambs for prompt relocations of dead and live animals as indicated by radio signals (mortality sensors) can provide better tally of losses to predation or other mortality factors, thus improving diagnostic opportunities.

CHAPTER SEVEN

SOCIAL BEHAVIOUR AND ORGANISATION

Introduction

A social system has been defined as the manner in which individuals position themselves in space and time in relation to other conspecifics and some features of the environment (Ferreras, Beltran, Aldama & Delibes, 1997). Social organisation refers to the number of individuals in a social group, their behavioural and genetic relationships, and the way in which reproduction is partitioned among them. Social organisation comprises the most fundamental defining features of animal societies, forged by ecological and social selection acting over the history of a population, and creating social and genetic environments that govern the course of subsequent social evolution (Creel & Macdonald, 1995; Ross & Keller, 1995). Some of these powerful evolutionary forces acting on animals are those imposed by group living, the interaction between, and competition among members of the same species. The study of social behaviour, called behavioural ecology or socio-biology seeks to understand how relationships between individuals shape the social systems and mould the evolution of individual form and behaviour (Mills, 1978; Ross & Keller, 1995; Frank & Glickman, 1996). For example, a species' social system can act as a natural regulatory mechanism, limiting the proportion of the population reproducing and, consequently, the rate at which the population can increase (Ferreras *et al.*, 1997). Therefore understanding the social organisation of predator species and the factors that influence their social behaviour is of fundamental importance for their management and conservation.

Most anatomical, physiological, and behavioural adaptations have evolved through the interaction between heredity and the environment, having been fixed genetically, and are passed from parent to offspring. The key to evolutionary success is very simple: leave more offspring than other members of your species. Genetic changes that increase the number of one's descendants (or the descendants of one's close relatives) will spread through the species (Hamilton, 1964; Dawkins, 1989). The fitness of each individual organism in a biological community may be affected by the adaptations of all other individuals. That creates the essential elements of a 'game' among the individuals (Vincent, Van, & Goh, 1996). It is an evolutionary game where the individual organisms (players) inherit their phenotypic characteristics from continuous play of the game from generation to generation. Any dynamic process where the 'fitness' of a given individual in a population is determined by the adaptations used by all individuals has the potential to evolve with time.

Biologists measure an organism's relative genetic potential with a theoretical construct termed fitness. An individual with greater fitness is more likely to leave descendants than one with less. All aspects of an organism's biology - for instance, longevity, tolerance of environmental extremes, and the abilities to feed itself, escape predators, find mates, and raise offspring - contribute to its fitness. One of the most important components of fitness is reproductive success, which can also be measured in various ways: number of mates, number of offspring born, number of offspring that survive infancy, or number of offspring that survive to reproduce. Each of the four aforementioned measurements gives a better tally of descendants than the preceding one, but each is successively more difficult to measure in practical terms. Only through long-term studies of known individuals (e.g. Schaller, 1972; Kruuk, 1972; Moehlman, 1978, 1979, 1980) can one gain good measures of reproductive success and understand the behavioural characteristics that contribute to it and, hence, to fitness.

Since a great many aspects of a species' social behaviour ultimately affect individual survival and reproductive success, social forces have profound implications for the evolution of most animals, including humans. Selection has favoured the capacity for social animals to adjust group size in response to a suite of ecological factors, primarily those affecting temporal and spatial patterns of resource availability (Caraco & Wolf, 1975; Emlen 1982a, b). These patterns influence foraging efficiencies, mating probabilities, and reproductive success (Moehlman, 1983). Predation pressure also often constitutes another important factor determining social tendencies. Group size may then be optimised in response to the most important environmental characteristics, in an attempt to maximise the total benefit-to-cost ratio for individual group members. Among social animals, stable groups are almost always characterised by dominance hierarchies such that certain individuals have priority of access to food, mates, or other limited resources. In the absence of stable relations among individuals, life would be an endless squabble over resources. Dominance relations impose order and stability, albeit often to the detriment of low-ranking individuals (Mech, 1970, in Meia & Weber, 1996; Macdonald, 1980) and sometimes even to dominant individuals themselves (Creel & Creel, 1996; Morell, 1996)!

An individual's social behaviour can be represented by analogy as the solution to a cost-benefit analysis of the interacting consequences of its actions (Macdonald & Moehlman, 1983). The choice between different rules for action is dynamic in the sense that the magnitude of the costs and benefits of a given behaviour vary continually with each individual's circumstances. So, as animals can adapt their social behaviour to prevailing circumstances, we should expect not only that different individuals will behave differently, but also that each individual's behaviour will vary as the social and ecological circumstances change (Kruuk & Macdonald, 1985). However, real costs and benefits are so notoriously hard to measure that one too easily ends up in speculation (Macdonald & Moehlman, 1983).

Social organisms exhibit conspicuous intraspecific variation in all facets of their social organisation. It has become evident that social organisation varies not only among species but also within species or even populations. Striking variation in group composition and in the partitioning of reproduction among group members is proving to be the rule rather than the exception in a wide array of vertebrate and insect species. Variation in social organisation is the product of diverse extrinsic selection pressures generated by the local ecology that interact with intrinsic selection pressures related to competitive and cooperative interaction among group members. Thus studies of variation in social organisation may shed light on how ecological and social factors jointly influence the course of social behaviour (Ross & Keller, 1995). Within the Carnivora, there is much variation in social organisation between species, with some participating in cohesive, intricately structured groups whereas others live alone (Kruuk & Macdonald, 1985). Moreover within several species, different populations show marked variation in social organisation, for example with respect to group size and range size (Macdonald, 1983). The question arises as to what environmental factors underlie this variation. Understanding intraspecific variation is fundamental to understanding the evolution of carnivore communities and, furthermore, it is important for predicting the consequences of management of these species and their habitats (Kruuk & Macdonald, 1985; Creel & Macdonald, 1995).

In Africa, few animals are as unfairly maligned and as intrinsically fascinating as black-backed jackals. Commonly reviled as lowly scavengers, they are, in fact, highly successful predators and the most abundant of the larger carnivores in Africa. It has been shown that jackal diets vary markedly within and between habitats (Wyman, 1967; Lamprecht, 1978a,b; Du Bothma, 1971; Rowe-Rowe, 1976, 1983; Hiscocks & Perrin, 1987). A conspicuous feature of this variation, in addition to the diversity of the diet, which is made up of different-sized prey (see Chapter on Foraging Ecology), is the proportions in which the different-sized prey are taken. In addition to variation in diet, there is evidence that jackal social organisation varies from one area to another (Ferguson, 1978; Moehlman, 1978; Fuller, Bikneviscius, Kat, Van Valkenburgh, & Wayne, 1989). Given this variation in diet, it seems likely that the social organisation of jackals could also vary in relation to other factors such as hunting pressure and habitat type.

Territoriality and the nature of the mating system (e.g. monogamy, kleptogamy, etc.) are arguably some of the most important behavioural traits affecting the spatial organisation of animal populations and, therefore, population dynamics. The existence of territories, under one definition or another, is integral to many models relating the availability of resources such as food, mates, and shelter, to social behaviour and density dependent regulation (Brown & Orians, 1970; Macdonald, 1983; Carr & Macdonald, 1986; Doncaster & Macdonald, 1991; 1992). In practice, the acts recognised as defence of an area include two categories (Brown & Orians, 1970), namely: 1) actual defence, such as attacking, chasing, and threatening rival intruders, and 2) identifying acts that designate the defender and that make his presence conspicuous to his rivals; these include certain vocalisations, displays, and scent-markings. When such acts typically fail to keep out rivals, the area should not be designated a territory.

Thus the essential characteristics of a territory (Brown & Orians, 1970) are: 1) a fixed area, which may change slightly over a period of time (otherwise known as 'drifting territoriality', Doncaster & Macdonald, 1991), 2) acts of territorial defence by the possessor which evoke escape and avoidance in rivals, so that, 3) the area becomes an exclusive area with respect to rivals. These conditions must be satisfied for an area to be recognised as a territory. However, although in many species the entire home range is defended, in others defence may be limited to a mating spot, a nest, a feeding area, or a roost. It should also be noted that territoriality is intraspecific.

Monogamy, as defined by Kleiman (1977) is a rare mating system which is common only among birds (roughly 90%) (Moehlman, 1986), but is among the more highly evolved forms of social organisation in mammals. Among canids, the basic mating system is long-term monogamy, a system that is taxonomically scattered among mammals (< 3%, Kleiman, 1977; 3-5%, Mock & Fujioka, 1990). However, an examination of the social organisation in the continuum of small to large canids reveals major trends in adult sex ratio, dispersal, mating systems, and neonate rearing systems (Moehlman, 1986; 1989). Small canids (< 6.0 kg) tend to have an adult sex ratio skewed towards females, dispersal biased towards males, female helpers, and they exhibit a tendency toward polygyny. Medium-sized canids (6.0-13.0 kg) have equal sex ratios, equivalent sexual emigration, both sexes as helpers, and observations at present indicate that they are strictly monogamous. Large sized canids, with the exception of the maned wolf (*Chrysocyon brachyurus*), have sex-ratios skewed towards males, primarily female emigration, male helpers, and indications of polyandry (Moehlman, 1986). Medium-sized canids may have the most flexibility in terms of altering their social behaviour and organisation (Moehlman, 1986).

Black-backed jackals are one of the species that do maintain enduring pair bonds in animal societies (Moehlman, 1986, 1989; Rowe-Rowe, 1986), some of which may remain intact for up to six or eight years, which effectively means that the animals can pair for life. Moehlman (1979, 1983,) asserted that some jackal offspring (called 'helpers') of both sexes remain in their natal territory where, although not breeding themselves, they help provision and guard subsequent litters and also feed the nursing mother. All offspring that remained in their natal range past age 12 months did so for only one year. Since jackals can be reproductively mature at 11 months old, those that stayed with parents were perhaps delaying their own reproduction (Moehlman, 1983; Macdonald & Moehlman, 1983; Rowe-Rowe, 1986; Creel & Macdonald, 1995). Mated pairs hunted cooperatively but helpers were rarely involved in collaborative hunting. In some respects, the social organisation of black-backed jackals is similar to that of baboons and other terrestrial primates that have long served as models for understanding human social behaviour. In any event, jackals present a rare opportunity to observe and perhaps to understand how and why family bonds develop among hunting-and-gathering mammals. They give us ideas about the evolution of monogamy and helping behaviour (Moehlman, 1980). As social carnivores who share their food and care for dependent young, they contend with conditions similar to those experienced by early man, and provide insight into our own behaviour.

Methods

General Observations

Quantitative data were collected through systematic counts, incidental observations, and through radio tracking of known individuals. Some individual jackals could be identified from natural markings such as ear notches, scars, and colour differences. Observations were made by following individuals as they foraged and also at dens. Every sighting of jackals during the study period was registered and behavioural attributes as stipulated in Chapter Four recorded, with further notes on date, time, position, group size and composition according to age and sex, where possible. During the day, the area was searched for tracks and signs, such as faeces, regular paths and resting sites.

In addition to the three radio-collared jackals, eleven jackal corpses were incidentally collected (run over by vehicles or shot during problem animal control operations). Approximate ages of all jackals were determined from tooth eruption sequences or wear on the incisors (Lombard, 1971). According to size and behaviour, the sighted jackals could be classified according to three broad age categories: adults, juveniles (sub-adults), and young (see Chapter Three). The difference in size between sub-adults and adults was usually discernible when the two classes were together; seen alone, subadults might have been mistaken for adults. But in spite of the difficulty differentiation facilitated the recognition of family units.

During incidental observations, determination of sex and identification of individuals could not be carried out since sexual organs were often difficult to see, as long hair and the bushy tail obscured them. Additional sexual characteristics used were the teats of lactating females and the positions adopted during urination, which is typical of most canids (Kleiman, 1967).

Categories of Social Interactions

Social interactions among black-backed jackals were divided into three categories (Kleiman, 1967; Ferguson, 1978):

(a) Aggressive interactions, in which the confident animal physically attacks the subordinate jackal, and the apparent aim of the confident jackal is to harm its subordinate counterpart physically.

(b) Agonistic interactions, in which the confident animal asserts its superior social status over the subordinate jackal. Actions are mostly exaggerated or ritualised. Although physical contact may occur as in aggressive interactions, it is not with the apparent intention of inflicting any bodily harm on the subordinate.

(c) Amicable interactions, in which confident or subordinate jackals cannot be clearly recognised and no clear elements of aggression or agonism can be seen.

Agonistic and aggressive interactions are characterised by distinct elements of threat and submission, and amicable interactions by the lack of these elements. During aggressive interactions, threat and submission are intense, and a fight/flight type of interaction is the result. In agonistic encounters, there are no signs of attack or flight by either of the interacting jackals, although threat and submission still characterise these interactions (Ferguson, 1978). Functionally, amicable interactions serve to strengthen social ties, i.e. the equality of social status among animals, whereas agonistic and aggressive interactions reinforce the difference in social status among animals (Fox, 1971; in Ferguson, 1978), and thus effectively separate them socially.

Vocalisation

Data collection involved opportunistically recording the incidence of jackal calls in the study area. Records were made of whether the calls were made by an individual or group (two or more animals). It was not possible to be more specific about the number of jackals calling in a group because more than two animals could not be distinguished with confidence.

Two types of vocalisations were noted; single and group. During a bout of howling, a single jackal usually called about once every 30 sec. Thus a single session was considered terminated if more than one minute of silence followed a single howl. Group sessions were generally started by one or two single calls, with other animals joining immediately.

Denning

The study area was searched for dens occupied by jackal litters. Footprints of jackal pups, prey remnants and smell of jackal scent and putrefying prey remnants at the den openings were signs of jackal litters. In addition, at weaning the pups begin to play around the den and this flattens the vegetation around the den. These signs together made it possible to determine whether a jackal litter occupied a den or not.

Results

Group Size and Composition

During the present study, 226 sightings of black-backed jackals were recorded representing 377 animals. Most sightings (48.2%) were of single animals, 39.3% were of two, 9.7% were of three, and six groups of four animals were seen (Table 18). Mean group size was 1.7. Mean group sizes were smallest during autumn (1.4) and greatest from winter (1.7) through spring (1.8) and summer (1.8). The greatest number of jackals that I observed at any one time was 5, but this probably represented under half of the total number living within the reserve. These jackals indulge, several times a night, in howling and in so doing provided me with a means of estimating their numbers. While it was extremely difficult to distinguish individual voices from the chorus, I estimated the vocal population of the area to be in excess of five individuals (at least two pairs with some transient, solitary, or satellite individuals) (also see Chapter Four).

Only one case of group hunting (> two individuals) was observed in this study (Chapter Six). I found little evidence of jackal groups in MNR (28 out of 226 sightings) and as such they could be classified as transients, solitary residents, and members of pairs or packs (adult pair with offspring). Resident pairs defended well-defined territories (with sizes lesser than home ranges) which were maintained by scent marking, vocalizations and dyadic interactions. Superimposed on this territorial mosaic were the nomadic movements of transient or dispersing individuals.

Seasonal variation was also observed in the number of single animals, two's, and groups of 3 to 4 individuals (Figure 6). Seasonal differences were pronounced for single animals and groups of two, and followed a pattern that was related to reproduction and social behaviour (Chapter Four). Family groups usually consisted of two parents and from 1 to 3 young - an average of 1.2 (n = 7) young. This effectively means that jackal pairs in MNR were able to successfully raise only a single offspring on average, and observed offspring were obviously those that had survived neonatal mortality.

Table 18. Seasonal occurrence of black-backed jackal group sizes in Mokolodi Nature Reserve from November 1995 to February 1997

	SEASONS							
GROUP SIZE	**Summer 1995-96**	**Autumn 1996**	**Winter 1996**	**Spring 1996**	**Summer 1996-97**	**All Seasons**	**Relative percentage**	**Total no. of jackals sighted**
1	19 (48.7)	31 (64.6)	25 (37.3)	16 (47.1)	18 (47.4)	109	48.2	109
2	10 (25.6)	16 (33.3)	37 (55.2)	11 (32.4)	15 (39.5)	89	39.3	178
3	8 (20.5)	1 (3.2)	4 (6.0)	6 (17.6)	3 (7.9)	22	9.7	66
4	2 (5.1)	0 (0.0)	1 (1.5)	1 (2.9)	2 (5.3)	6	2.7	24
Total	**39**	**48**	**67**	**34**	**38**	**226**		**377**
Mean group size	1.8	1.4	1.7	1.8	1.7	1.7		

Note: Figures in parentheses represent the seasonal frequency of occurrence (%) of each group size

Although no clear seasonal pattern was evident in the relative frequency of solitary animals ($\chi^2 = 6.45$, $d.f. = 4$, $p > 0.05$) most sightings (31) of single animals were recorded during autumn. Pairs were most numerous in winter ($\chi^2 = 17.5$, $d.f. = 4$, $p < 0.05$; Fig. 6) and this was probably the pairing-mating season, as the first cubs were seen during August to September. However, it is likely that seasonal differences in visibility levels could also have influenced the number of sightings. Groups of more than two were most numerous around summer (December and January) but no significant differences between seasons were revealed. ($\chi^2 = 3.5$, $d.f. = 4$, $p > 0.05$). As no sub-adults were seen after March, the animals are presumably fully grown at 5-6 months, and groups of three to four animals are predominantly families with grown-up offspring. These groupings seemed to split up when the next breeding season approached

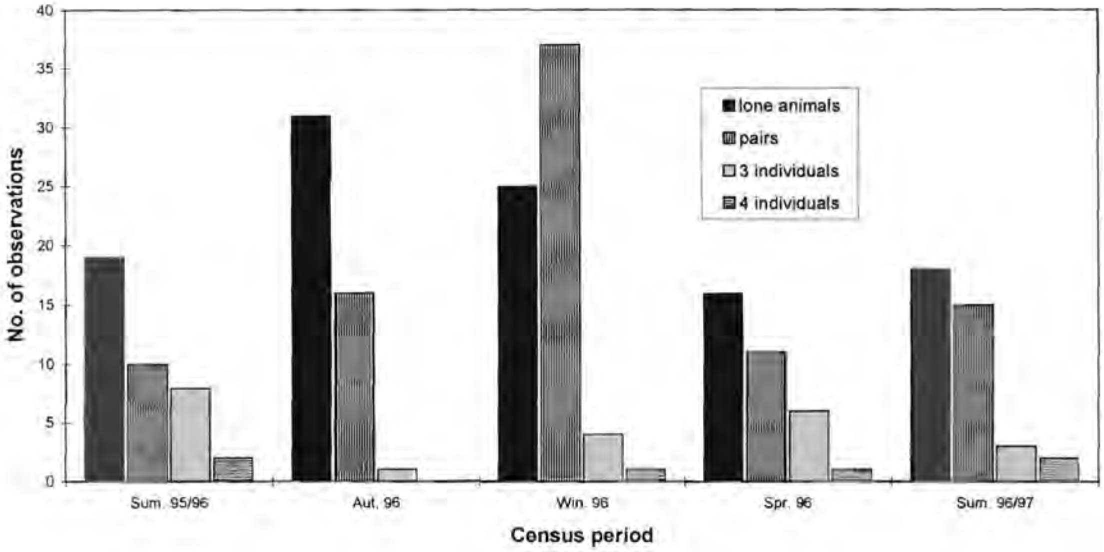

Fig. 6. Seasonal occurrence of black-backed jackal group sizes in Mokolodi Nature Reserve from November 1995 to February 1997

Sex Ratio and Age-group Structure

Direct counts of jackal pups could not be conducted in the present study due to the wary nature of the jackals within predominantly stock-farming areas (such as the area around MNR) and as such, cannot be readily observed in most free-ranging situations. Wherever age and sex could be determined, pairs were found to consist of an adult male and female. Adults could be identified within groups of all sizes, usually in pairs, and larger groups often together with young (Fig. 6). In 117 recorded groups (i.e. pairs included), pairs with young were only seen on seven occasions, usually at the den accompanied by non-breeding yearlings.

The live-trapped and radio collared animals consisted of two males and a single female, while the eleven incidentally collected jackals comprised five males and six females, yielding an overall sex-ratio of unity, despite the small sample sizes. Morphometric measurements and relative age-groups of all 14 jackals are presented in Table 1. Adult male mass averaged 7.8 kg (range, 6.9-9.2 kg, n= 6), while the average adult female mass was 7.0 kg (range, 5.8-8.7, n=4). Juvenile jackals comprised two males and two females of the sample population available for analysis. No young were available for morphometric measurements.

Rowe-Rowe (1978) reported that jackal males are significantly larger than females and possibly kill larger prey than do females, as has been found in some predators exhibiting sexual dimorphism. Moehlman (1983) reported that an adult jackal hunts and kills for his mate who remains with her pups in the den for the first few weeks after whelping. In some cases, samples may consequently be biased in favour of males who may be encountered too often during their foraging excursions.

Categories of Social Interactions

In all social interactions between pair members in which food was not involved, the behaviour of both animals towards each other was classed as amicable or friendly (n. Grooming between and behind the ears, and on the back was recorded. Allogrooming was usually accompanied by self-grooming as reported by Ferguson (1978) and Moehlman (1983). When members of a pair had been separated for some time, a short greeting ceremony took place. No sign of dominance was observed in pairs, except when with subordinate offspring.

Agonistic postures and signals are well-developed in black-backed jackals (Ferguson, 1978). Of the 182 observed social interactions, 44 (38%) belonged to this type. During aggressive interactions, there was a definite dominant animal and an extremely submissive jackal, but the dominant animal either physically attacked the intruder, or otherwise tried to attack an intruder if one came near. Aggressive interactions occurred on 38 occasions (19.8%) and were not observed between members of a pair. Most of the aggressive interactions occurred around food (23 out of 38 occasions) and on known territorial boundaries (on 9 occasions).

Of the 13 recorded group contacts, 10 occurred during March-July 1996, the time of year when family groups seemed to break up, and the animals were typically seen in pairs. Of these 10 contacts, seven included biting and chasing, and in only one case, two jackals merely watched one animal, which trotted past some 100 m away. Six more group encounters were noted in August at a time when gravid females and families with pups had been recorded. The rest of the encounters could be described as indifferent. In four of these encounters the animals were resident neighbours. The increase in territorial activity coincided with the breeding season and an increase in mobility of the resident and non-resident jackals. This suggests that mating activities and increased territoriality of jackals initiated a late summer/early autumn dispersal peak by non-resident jackals (Chapter Four).

Social encounters within pairs or family groups (n= 86) included social grooming (24%), play fighting (45%), and running play (31%). Intra-group aggression was in connection with incidents involving ano-genital sniffing of females by males, and sometimes some attempts at mounting. Occasionally, the female jackal responded by snapping, whereupon the male withdrew. On one occasion the female held still and allowed the male to sniff, without defending herself. Nevertheless, no copulation was observed. Seventy-eight percent (78%, n = 15) of ano-genital sniffing was recorded from May to July. Encounters between heterosexual individuals of different groups never ended in biting and/or chasing, whereas this seemed to be the rule in encounters between two strange females (n=3), and between two strange males (n=5). Encounters between neighbours (n= 11) were less aggressive than between apparently strange groups (n=13).

Sexual behaviour was not observed among helpers, and male helpers had small testes when visually compared with their sires. The social status of helpers was always submissive with respect to the parents (n=19). Black-backed jackal parents rarely regurgitated to helpers (n=2) but did share food with the older offspring and engage in such affiliative behaviour as allogrooming (n=8). Subordinates or helpers did assist their same-sex parents in territorial defence against same-sex conspecific intruders (n=8). However, these subordinates did not engage in scent marking. Unlike their parents, helpers trespassed on adjoining territories and foraged for rodents and fruit (n= 17), sometimes until they encountered a resident and were driven back to their natal area. This type of trespassing may provide important information to young jackals on the availability of unoccupied or suitable habitats. Mated pairs only left their territories to drink water and scavenge from carcasses (22%, n= 191). When leaving their respective territories for water, residents trotted steadily in fairly direct routes (following paths to waterholes) and did not scent-mark.

Little to no overlap existed between territories of adjacent pairs, and boundaries between adjacent pairs were often distinct, although it is likely that over long periods they may shift somewhat. In several areas in which resident groups or pairs were encountered, only one pair of these jackals was found a year later. However, only once was another pair observed for a considerable amount of time, but these were certainly not any of the animals seen the previous year. It therefore appears safe to assume that black-backed jackals at MNR did not use the same territory or breeding range year after year, although in relatively undisturbed environments, territories may tend to remain stable in size and location over some period of time.

Territorial Marking

Boundaries and the internal area of the territory were actively defended. All observed territorial conflicts involved aggression between animals of the same sex. Territories were maintained indirectly by scent marking and vocalisation.

Adult males usually raised and extended a hind-leg side-ways when urinating, while the back was held straight, and the tail held straight out behind in the typical adult male dog (*C. familiaris*) urination posture. The urine was ejected side ways, aimed at a grass tuft or small shrub (height usually <30 cm) while balancing on three legs. However, there were a few instances when male jackals urinated with both hind-feet on the ground and stretched backwards, while the urine was ejected downwards just behind the forefeet (n=3). Individuals that assumed this posture were taken to be immature or subordinate males that had not yet perfected the typical raised leg urination posture.

Female jackals urinated while flexing forward a lifted hind leg, but also in some intermediary positions between squatting and leg-lifting while the urine was jetted backwards onto the ground. After urinating, both sexes executed some mild scratching movements with all four legs next to the site of micturition. The most frequent sequence was sniffing, micturition, and scraping/scratching for both sexes.

A total of 112 urinations of adult paired males and 72 of females were recorded. Males directed urine 67 times onto sites where the female had first urinated, mostly within 30 seconds of each other. In all instances the male first sniffed at the female's urine or faeces before depositing his onto it, and sometimes repeated this behaviour. The remaining 45 urination events of males were often directed at small tufts of vegetation, and on the base of tree trunks, typical of male *C. familiaris* urination. In 17 of 28 cases where notes were made, the male first sniffed at the site. Sniffing preceded urination in males 88.2% of the time. This indicates a frequent deposition of sites by males, which is typical of territorial marking behaviour. In 13 of the 72 urinations of female jackals, urine was directed onto the spot where the male had urinated, each after preliminary sniffing. In the remaining 59 episodes, urine was directed onto flat ground, six times with preliminary sniffing and 42 times without. This suggests that females too were also involved in territorial marking, albeit to a lesser extent.

During defecation both males and females assumed similar postures, closely resembling the 'squatting' of the females during urinations. The only difference was that defecation took longer than urination. Of the 17 observed and documented defecations, 11 were on or closer to older black-backed jackal faeces. Two pairs defecated in succession 5 - 10 m apart. Lone faecal depositions on sites other than on older scat deposits were observed on nine occasions. Black-backed jackals at MNR used 'latrines' and these were probably visited by the same pair as indicated by radio tracking. In most cases, faeces were lodged on small tufts of vegetation (grass and shrubs of height <30 cm) shorter than the hindquarters of the animals. No faecal material was found deposited on flat ground. The animals were never observed sniffing at faecal deposits before or after defecating. Adults were not documented defecating in the vicinity of denning sites, while only one instance of a juvenile was observed defecating next to the den within a radius of approximately 10 m. However, direct observations and the presence of small-sized faecal pellets around dens suggested that pups utilised the den vicinity for defecation.

Studies of hyaenas (Kruuk, 1972), golden jackals *Canis aureus* (Macdonald, 1979), and others suggest that the positioning and distribution of faeces can have an important intraspecific communicative function for carnivores. While collecting jackal faeces for scat analysis some were found singly, while others were found in piles or middens. Faeces constituting a pile were defined as those within a circle of 1m diameter (Macdonald, 1979). At each of the 132 defecation sites, I estimated the minimum number of separate faeces, judged on the basis of similarities of colour, age, and shape; the biggest pile contained an estimated 14 separate faeces. The positions of all these sites were recorded using GPS and are plotted in Fig.7. In the field, it was apparent that some piles were linearly arranged, usually following an obvious jackal path, road or some topographic discontinuity. Most of the latter cases were on rocky outcrops and so it remains probable that they too followed a well-trodden jackal route even if the hard ground obscured the tracks. In contrast the single faeces were scattered more randomly across the study area. Following the lines of piles gave the impression that they bordered an area, which was otherwise devoid of middens, but through which were scattered many singles as reported by Macdonald (1979) for golden jackals in Israel.

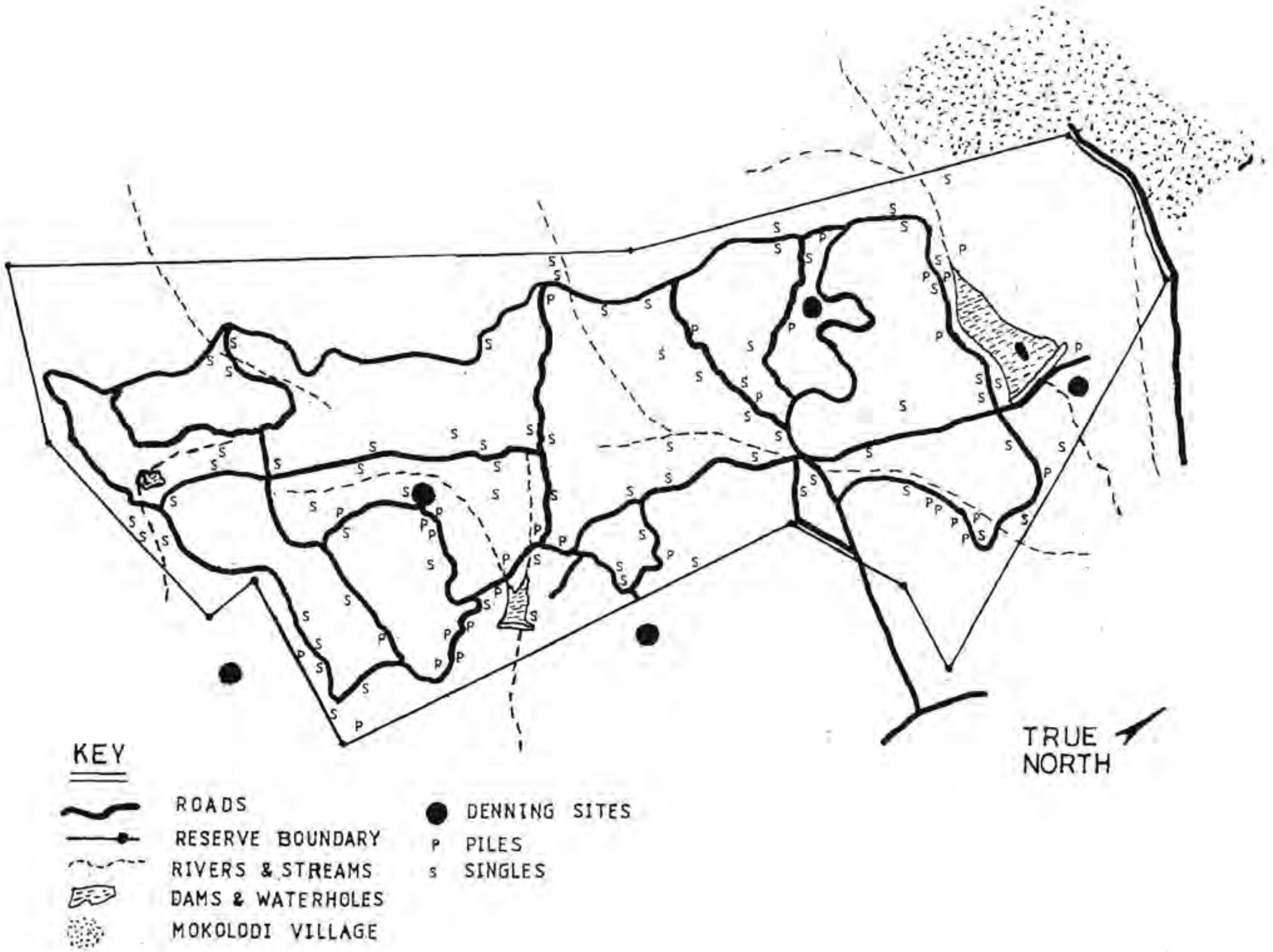

Fig. 7. Map showing the distribution of faeces in the study area as revealed by combing the area on foot. Locations of solitary faeces are distinguished from those where piles of faeces (middens) were found.

While recording the position of jackal droppings, I also noted whether they were on what could be judged as visually conspicuous objects, such as stones and tufts of vegetation. Single droppings were prominent (31 out of 52) compared to those in middens (25 out of 71). Possibly single deposits are positioned wherever prominent sites are found, whereas piles are put in specific locations, irrespective of the features of the terrain but according to social requirements, i.e. those of demarcating a boundary between group territories. The correspondence between the courses followed by piles, where the two jackal families were seen, and the locations of disputes between them suggested that the line of piles constituted a territorial border between the ranges of the two jackal families. At each pile only two scats were collected per monthly session for diet analysis to avoid altering the attractiveness or intrinsic utility of the pile.

Not much foraging was done during territorial marking; the jackals traversed the paths while trotting, and only stopped to urine-mark for a few seconds and immediately proceeded trotting. Prey encountered during these activities were however pursued with varying success (see Chapter Five). Rolling was also observed on five occasions when jackals wallowed in dust or in sandy and slightly gritty areas, and thereafter shaking their bodies from side to side vigorously. Sites where jackals had rolled in dust were frequently found associated with their tracks. Usually, such sites suggested that the activity involved more than a single animal, indicating that pairs or groups engaged in the activity in tandem.

Vocalisation

A total of 265 calls were recorded during the study period (Table 19). The incidence of vocalisation was highest during winter (34.3%, n = 265), followed by autumn (24.2%), whereas the frequency of calling during spring and the two summer periods were in similar proportions. Calling was thus relatively more frequent during the pairing-mating season (winter) than during the denning season (spring) ($\chi^2 = 5.78$, $d.f. = 1$, $p < 0.05$). Calls during the pairing-mating season were most frequent by groups (presumably the dominant territorial pairs) ($\chi^2 = 4.3$, $d.f. = 1$, $p < 0.05$) during the late afternoon (16h00-22h00) and in the early morning (04h00-06h00). Usually when one jackal called, others within hearing distance responded or joined in successively.

Denning

Dens were used by black-backed jackals for two different activities: 1) as resting sites during the non-active period (non-breeding dens), and 2) as sites for birth and rearing of pups (breeding dens). Dens were found by combing through the study site, following radio-tagged animals, and also by following jackal spoor, usually in well-drained sandy soils under the cover of shrubs and trees. Occupation of a den by a jackal was confirmed by direct observation. Jackals were also opportunistic with respect to den occupancy. They did not dig their own dens when other possibilities availed themselves. Denning sites were old excavations of warthog (*Phacochoerus aethiopicus*), springhaas (*Pedetes capensis*), aardvarks (*Orycteropus afer*) etc., to which the jackals may have added a couple of entrances. These were usually dug at the bases of inactive termite mounds. The number of den entrances varied from one to seven. The need for a variable number of entrances to dens is probably related to breeding status whereby breeding dens would have a higher number of entrances than non-breeding ones, and this may be related to the need to escape quickly into shelter when disturbed. However, this could not be conclusively ascertained due to small sample sizes, and the high turnover of den occupancy. Although jackals were observed excavating at times, the superficial nature of this undertaking suggested that this was probably for caching food or some other territorial function, rather than for den construction. The soils in MNR were generally shallow, and the difficulty for jackals to find or excavate suitable dens for breeding could explain their scarcity and random distribution. I consider that the distribution of dens was limited by the availability of suitable sites, moreso because in the adjacent commercial farms where soils were more well-developed, dens were plentiful even though access to such areas by the investigator was somewhat limited.

Table 19. Incidence of calling by black-backed jackals at Mokolodi Nature Reserve, Botswana

Time Period	**Summer 1995-96**	**Autumn 1996**	**Winter 1996**	**Spring 1996**	**Summer 1996-97**	**All Seasons**	**Relative % of calls**
16h00-18h00	4	16	27	10	9	**66**	24.9
18h00-20h00	6	21	18	10	2	**57**	21.5
20h00-22h00	3	7	9	2	4	**25**	9.4
22h00-00h00	2	3	1	1	0	**7**	2.6
00h00-02h00	0	0	0	0	0	**0**	0.0
02h00-04h00	5	2	4	2	3	**16**	6.0
04h00-06h00	6	6	12	10	8	**42**	15.8
06h00-08h00	3	5	7	7	7	**29**	10.9
08h00-10h00	1	2	5	0	2	**10**	3.8
10h00-12h00	0	0	0	0	0	**0**	0.0
12h00-14h00	0	0	0	0	0	**0**	0.0
14h00-16h00	2	2	8	0	1	**13**	4.9
Total	**32**	**64**	**91**	**42**	**36**	**265**	

Radio tracking of jackals resulted in avoidance behaviour to the extent that dens were sometimes vacated within days after I had located them. On the first occasion a den was vacated two days after locating it. This was probably caused by the detection of human activity around the den after I had collected some faecal material from around the den. As for the second occasion the jackal den was vacated because of heavy rainfall which inundated the area, filling up the den. The female initiated all changes in the location of the den but was assisted by the mate. No more jackals with young were thereafter located within MNR. Once abandoned, no holes were re-occupied for the duration of my field study.

The female of one collared pair showed signs of lactation but attempts to locate the denning sites were futile. Dens could have been relocated to areas of limited human interference (especially from tourists) such as within inaccessible Acacia thickets, and outside MNR in farms that were relatively undisturbed. This is quite plausible since radio tagged animals (and presumably the ones I frequented most) ended up being relocated outside MNR on the south-western part. These areas had limited through-routes and were consequently less disturbed relative to the much-traversed interior of MNR with its extensive network of roads. Some landowners in the surrounding farms were however loathe to allow people within their property at the 'awkward times' which typified peaks of jackal activity periods at MNR. This greatly hindered the collection of vital information on jackal behaviour on these farms. But whenever opportunities to enter such farms availed themselves, they were duly exploited although such activities were limited to daylight hours only. This effort resulted in the location of two more active dens in one of the farms (Lion Park).

Helping

My sample sizes were too small to detect any helper effects upon breeder survival, juvenile growth rates or inter-birth intervals, but these factors are important for cooperatively breeding mammals and birds. In the present study population, there was little sexual dimorphism, either physically or behaviourally. Although females are responsible for gestation and lactation, their mates provisioned them during the nursing period. The jackal family of the radio-collared female AFJ1 revealed some aspects of helping behaviour

(Moehlman, 1986) since its two surviving subadult young born in September 1995 were sighted with their parents on several occasions within the natal territory, even after reaching potentially reproductive age after 10 months of age. During November 1996 surveillance of dens revealed that these sub-adult young also took part in tending to the 1996 parental litter by bringing food back to the den, and also regurgitating food to pups on four occasions. Most interactions between yearling jackals and pups involved play behaviour that presumably had a social function. Several sightings of jackal groups consisting of the adult pair and one or two grown-up subordinates suggested that the incidence of helping behaviour could have been more prevalent in MNR than revealed by direct observations. In order to reveal helper effects in an exploited jackal population such as the one in MNR would require more detailed and rigorous assessments.

Discussion

Monogamy

Among black-backed jackals, the form of monogamy is strongly obligatory (Kleiman, 1977; Mock & Fujioka, 1990) with little sexual dimorphism, an equal sex ratio, mating exclusivity, predominantly intra-sexual aggression, similar behavioural roles and a high degree of behavioural synchrony including cooperative hunting and tandem marking. Jackals have affiliative behaviours such as grooming each other, sharing food, and feeding and protecting sick and injured partners (Moehlman, 1983, 1986). They tend to rest together and when individuals have been resting or hunting apart, they locate each other with contact calls before starting to forage. The presence of both members of the pair may be necessary to maintaining territory. Moehlman (1986) observed that when a male of a pair disappeared during the whelping season, the female and its pups all died. A high degree of affiliative behaviour, food sharing, synchrony of activity, year-round maintenance of the feeding territory, cooperative hunting, and intrasexual aggression maintained the monogamous bond and exclusive mating. The fitness of a female tolerating bigamy would potentially be lower than the reproductive success of monogamous females because of the division (or even the absence) of the male's parental investment.

Although the female parent bears heavy reproduction costs in terms of gestation, lactation, and regurgitation to pups, she is assisted by her mate and older offspring (helpers) when they are present. Moehlman (1983, 1986) found that when a pair without helpers raised a litter they had to divide their activity between staying at the den guarding the pups and foraging for food. Typically, adults do all their resting near the den such that when they are not guarding they are foraging. The presence of a single adult at the den constitutes protection for the pups. Adults both vocally warn pups (who run into the den) and threaten potential predators. Moehlman (1986) reported that the presence of one helper in black-backed jackal families led to a significant decline in the amount of time the parental pair spent at the den, allowing more time for foraging. Thus the presence of helpers may indirectly improve the provisioning of pups by allowing the parents to hunt as a pair and hence increase their hunting success rate on larger prey (Wyman, 1967; Lamprecht, 1978a,b). It may also allow the parental pair to defend, retain, and exploit carcasses killed or scavenged more successfully.

Selection for monogamy and long-term pair bonding may reflect both physiological and ecological constraints in black-backed jackals. Monogamy, especially in canids, is also closely associated with the occurrence of social groups (Moehlman, 1986). Black-backed jackals, like most canids, have a relatively large litter size and there is a long period of infant dependency (Kleiman & Eisenberg, 1973; Kleiman, 1977). Black-backed jackals at MNR are omnivorous and utilise small-sized abundant food resources that are energetically costly to collect. Paternal investment is critical to pup survival and if a male were to partition his care between several litters, then possibly no pups would survive and both male and female reproductive success would suffer (Moehlman, 1986). Domestic dogs (*C. familiaris*) can produce litters with multiple sires (Beach & Gilmore, 1949, in Moehlman, 1983). Thus maintenance of mating exclusivity may be important in all *Canis* species so that the monogamous male does not invest in offspring that he did not sire. Long-term pair bonds are also critical for territorial maintenance. I have already alluded to the fact that Moehlman (1983, 1986) reported that when one member of a pair dies or disappears during the whelping season, the remaining adult cannot sustain the pups and control the territory. The mate could potentially form another bond, but this was not observed in the present study, and single animals may not be able to retain a territory for very long. Several other potential benefits of monogamy accrue from retaining one's former partner (Mock & Fujioka, 1990): the former partner is known to be seasoned as a parent, may possess a suitable breeding site (or useful knowledge of the one used before), and is relatively familiar as an individual (which may help coordinate reproductive activities). Furthermore, because his/her qualities as a mate have been sampled personally, the partnership's past record may come into consideration.

When monogamy does occur it tends to be correlated with 1) minimal sexual dimorphism, 2) a long period of dependency in offspring, 3) high paternal investment, 4) delayed sexual maturation of juveniles in the family group, and 5) parental investment by juveniles in younger siblings (Eisenberg, 1966, in Kleiman, 1977). In species exhibiting long-term pair bonding such as black-backed jackals, there is often a reduction in the degree of sexual dimorphism, both behavioural and morphological (Kleiman, 1977). Black-backed jackals exhibit sequential urine marking of the same sites by bonded pairs, either initiated by the male or female. Along with a trend towards monomorphism in the frequency of scent marking, there is a tendency for dimorphism to be reduced in the behaviour patterns of scent marking, the development of scent glands, or both. Adult females in black-backed jackals use the modified leg lift when they urine mark. Thus the urine-marking movement is somewhat convergent with the typical leg lift of the male.

Group Size

Mated adult jackals often hunt in pairs and most young jackals are born during the winter and one of the parents (often the female during the suckling period) would be caring for the young. Hence fewer adult pairs and more single animals can be expected to be seen from July onwards (Rowe-Rowe, 1984). Furthermore, when an adult female jackal has a litter, immature animals from the previous litter may remain as 'helpers' (Moehlman, 1979, 1986), or become independent lone sub-adults, thereby increasing the number of single animals. Even those jackals that remain as helpers would be single animals, as sub-adults and unmated subordinate adults rarely hunt in pairs or larger groups. Since young jackals begin to forage with the adult female, or both parents, at the age of 14 weeks (Moehlman, 1980), therefore most groups of three or more can be expected from November onwards.

Seasonal differences in jackal group sizes have rarely been related to social organisation and reproduction (Rowe-Rowe, 1984). In black-backed jackals large group size is important during summer when pups must be fed and protected, but when pack members hunt alone. In a study on coyotes *Canis latrans*, which have similar social structure to black-backed jackals, Bekoff & Wells (1980) recorded group-size means of 1.3 in summer and 1.8 during winter. These authors attributed the differences to available food; during summer the coyotes lived chiefly on rodents, but mainly carrion was taken in winter, and the clumped food resource appeared to result in larger groups. Rowe-Rowe (1983) did not reach these findings in his study on jackals because in his study area carrion was usually consumed by vultures and so did not lie long enough to attract large numbers of jackals over a longer period.

It seems reasonable to propose that the social organisation of jackals may be an adaptation to the abundance and distribution of food, factors already held as determinants of many intra-specific differences in social organisation for various species of carnivores (Macdonald, 1979; Macdonald & Moehlman, 1983; Moehlman, 1986). But cooperative hunting does not seem to be an appropriate explanation for the groups of jackals observed in MNR. An alternative suggestion is that the highly clumped dispersion of the food supply presented an economically defensible resource. Furthermore, in black-backed jackals, benefits of living in a group can arise while members operate alone (e.g. provisioning pups with food by helpers).

Lamprecht (1979) indicated that one benefit of communal foraging becomes apparent when we consider patches of termites (Order: Isoptera), from which several individuals together can extract more food than one, because the resource is exhausted with time and not with consumption. Active harvester termites (*Hodotermes mossambicus*), an item in the diet of black-backed jackals in the present study, are commonly found teeming around their foraging holes wherein they take refuge when disturbed. Upon locating such a resource patch, an individual jackal can feed on the fleeing insects only for a limited time. A few other related animals cooperated in the defence of concentrated food against kleptoparasites. Kleiman & Brady (in Bowen, 1981) suggested that in species with a strong pair-bond such as black-backed jackals, variation in group size and social structure results from differences in the age of dispersal of young. Hence, delayed dispersal may result in a pack structure similar to other social canids.

Although there is evidence that prey size and seasonal variation in prey size in the diet may determine social organisation in canids (Bowen, 1981), other factors may also play a role in determining group size. However, when explaining inter- and intra-specific differences in ecology, causes are often difficult to distinguish from effects. Group living in carnivores appears to be widespread and occurs in a variety of environments (Macdonald, 1979). It is therefore unlikely that a single selective pressure has led to the evolution of sociality in all these of species, even though it is clear that pride size and cohesiveness in lions (*P. leo*) is very dependent on the absolute abundance of food (Schaller, 1972). In addition, a high population density resulting from abundant food and perhaps the inability to disperse may also influence group sizes in jackals independent of prey. Our inability to clearly characterise the social structure of canids may be due in part to heavy human persecution of these populations. Thus it may not be so surprising that where jackal populations are heavily hunted, group living is seldom reported as was the case in MNR.

The evolution of group life in the canids has probably been most strongly favoured by improved food acquisition (Kleiman & Eisenberg, 1973), for it has been shown for several species that hunts involving two or more individuals are more successful than a solitary hunting pattern. Bygott, Bertram, & Hanby (1979) showed that compared with singletons and pairs, male lions in groups of three or more can reliably gain tenure of female prides, retain tenure for longer, mate with more different females, and produce more surviving offspring; thus each individual has higher fitness through cooperation. Thus for lions, there is a marked increase in the inclusive fitness of a male the more related companions he has, such that inclusive fitness of a male in a large group is 5.7 times that of one male or of one of a pair.

Indeed, pair hunting in jackals may be an adaptation to overcome hunting problems because young antelopes such as impala lambs are often defended by their mothers (Schenkel, 1966; Jarman, 1976), and a pair of jackals can more easily cope with the double task of catching the lamb and distracting its mother. In the Serengeti, black-backed jackals lost almost 30%, golden jackals about 11%, of their self-caught hares and lambs to the much stronger spotted hyaenas (Lamprecht, 1978b). Several behavioural peculiarities are possibly adaptations to overcome this considerable competitive pressure: after a kill jackals were much more apprehensive than before. Large preys were hectically devoured while beetles or mice, too small to be snatched from them were chewed a long time before being swallowed. Hares and gazelle were torn in two, and the mates ate their portions some metres apart presumably that should one get robbed by kleptoparasites, they would share the other's piece (Lamprecht, 1978a, 1981).

The pair or family can share food from an unexpected localised food source when it has been discovered by only one individual in the group, even while foraging and feeding behaviour is typically individualistic. Pair hunting may also offset the considerable competitive pressure, as two jackals can eat a lamb much faster than one, thus lessening the risk of being robbed. This consequence may be the function of pair hunting in black-backed jackals, as pair hunting was no higher than for individuals, thus offering no support for the hunting hypothesis. There is however no correlation between hunting group size and prey type in jackals which could not also be explained by seasonal changes in social organisation (Lamprecht, 1981). When pups must be guarded, the parents must alternate at this, and hunt singly. But when the pair is not tied to a breeding den, the mere need to keep the mate available while on the move could lead to pair hunting, even though hunting, and consuming the kill would not require more than one jackal.

However, in as much as I appreciate the importance of diet in shaping the social structure of canids, I contend that social organisation (especially group size) in MNR is moulded to a greater extent by heavy man-induced mortality (i.e. 'predation' or hunting pressure) and intra-specific competition - and not even by intra-guild predation or interspecific kleptoparasitism, primarily due to the absence of the large social carnivores within MNR.

Home-range size appears not to be affected by hunting pressure at MNR. It is only in the absence of such persecution that the relationship between the jackal population and food abundance may apply. Thus, it is most likely that black-backed jackals at my study site reduced group size under an increased risk of 'predation' from humans, although in contrast, social groups of other species become more compact in the presence of predators (e.g. mongooses, *Mungos mungo*, pers. obs.). During any given day, an animal may fail to obtain a meal and go hungry, or it may fail to obtain matings and thus realise no reproductive success, but in the long-term, the day's shortcomings may have minimal influence on the lifetime fitness (Lima & Dill, 1990). Few failures, however, are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness. Predation may thus be a strong selective force over evolutionary time, and it has long been recognised as important in the evolution of adaptations, such as cryptic and aposematic coloration, protective armour, chemical defences, and asynchrony in activity periods. Predation has also been implicated in the evolution of sociality in both the breeding and non-breeding season (Bertram, 1978; Pulliam & Caraco, 1984). While predation pressure may vary little over evolutionary time, during ecological time (i.e. an animal's lifetime) the risk of being preyed upon may vary greatly on a seasonal, daily, or even minute by minute basis (Lima & Dill, 1990). Since an animal must accomplish more during its lifetime than simply avoiding predation, its antipredator adaptations should somehow be sensitive to the current level of predation risk (the 'risk of predation' - hereby intuitively defined as the probability of being killed during some time period). Such antipredator flexibility may be achieved by integrating gross morphological adaptations with the behavioural decision-making process.

A morphological or behavioural characteristic can be useful in various procedures, but it is not normally adapted to all of them. Large hunting groups, for instance, may be more advantageous than small ones in many ways, yet it is usually only one particular problem that actually requires groups of the observed size. Not even for a single species (e.g. lions, spotted hyaenas) is there only one particular consistent function of social hunting; it can differ with the ecological or social setting.

Territoriality

Territories were maintained directly by aggressive and agonistic interactions, and indirectly by scent marking (olfactory) and vocalisations (acoustic). Black-backed jackals at MNR exhibited territorial behaviour according to the following criteria: 1) stability of home ranges throughout the study period; 2) no overlap between pairs; 3) frequent inter-group boundary chases and clashes; 4) scent marking behaviour; and, 5) vocalisations.

Scent-marking

Resident pairs or groups appeared to be territorial, or at least intolerant of others, but as Lamprecht (1979) indicated, it was unclear whether they marked their territories as a signal to strangers or to familiarise themselves with the terrain. Jackal territorial boundaries were demarcated by piles of faeces as was found by Macdonald (1979) for golden jackals, although other workers have not mentioned finding black-backed jackal middens (e.g. Rowe-Rowe, 1976). Jackal territory is sometimes partly independent of feeding range and presumably has other functions such as breeding sites (Macdonald, 1979). The dense nature of the vegetation at MNR during the present study, coupled with the site's rugged topography provided few access routes for intruders; however, most of the main paths were well endowed with middens. The situation is confusing because the dry season climate favours the preservation of faeces for months, so part of the present day pattern may be an artefact of history. Several other species are known to use similar piles of faeces (Macdonald, 1979). The black-backed jackal is apparently territorial in some parts of southern Africa (Ferguson, Nel, & De Wet, 1983; Skinner & Smithers, 1990.) and East Africa (Moehlman, 1978,1979), but shows no sign of midden use and thus, when contrasted with the black-backed jackal population in the present study, constitutes another example of a canid species known to use middens in one territorial situation but which does not do so in a different, but still territorial, situation. Golden jackals in Israel (Macdonald, 1979) were found to use middens while in East Africa, midden use was not reported for the same species

When foraging with their mates, territorial individuals mark at almost twice the rate as when they are foraging alone (n =22). When travelling together they mark the same spot in tandem (n=80). The presence of scent from both members of the pair may advertise to potential intruders that they are both actively in residence (Moehlman, 1986). In wolves, boundaries of territories of neighbouring packs where contests take place have been referred to as buffer zones, and therefore 'regions of intraspecific strife' (Mech, 1994). Wolves were reported to run a greater risk of fatal encounters from adjacent conspecifics along the edges of their territories than in their centres. Like the jackals in MNR, wolves patrol the borders of their territories and scent mark the edges much more than the centres (Mech, 1994).

Among canids, scent-marking may serve as (Gese & Ruff, 1997 and references therein): a mechanism for territory maintenance or sex recognition; a signal of empty food caches; an indicator of sexual condition, maturity or synchrony, or internal information to orient members of the resident pack and to dispersing animals entering occupied territories. Individual recognition from urine marks has not been demonstrated for canids, but it has been shown that domestic dogs (*C. familiaris*) can detect a female's reproductive status (Beach & Gilmore, 1949, in Moehlman, 1983) and that chemical compounds found in male red fox (*V. vulpes*) urine are absent in female red fox urine (Macdonald, 1979). Scent marking is probably an alternative to agonistic interactions used by black-backed jackals for territorial defence. Findings from the present study are consistent with studies of mammalian scent marking in which the dominant pair marks the most and are the territorial owners (Randall, 1989).

Social Interactions

Boundaries and the internal area of the territory were actively defended against intruding conspecifics. All observed territorial conflicts involved aggression between individuals of the same sex (n=9) . The resident females threatened, attacked, and drove off intruding females while resident males looked on. The resident males threatened and drove off other intruding males (n=5). However, the presence of a clumped food resource such as a carcass or refuse dumping site attracted individuals from adjacent territories in such numbers that it was impossible to drive them all away (n=5). Nonetheless, aggregations of trespassers were usually short-term. Residents left their own territories to drink water and to scavenge elsewhere. They occasionally went on exploratory forays but were seldom off their territories for more than a few hours. It appears that in the time between the dissolution of the families and the pairing-mating season, pairs rove about more than usual, in search of suitable breeding grounds, so that they are more likely to meet, and there is an increased risk of altercation over favourable sites (Lamprecht, 1979). Encounters during the breeding season however, will probably be mainly with resident neighbours, known to each other, to whom less aggression will be directed as competition for living space is no longer acute.

Neighbours play a diverse role in territorial systems. They can be intruders, neutral, or even beneficial (Randall, 1989). At the least, neighbours can be friendly rivals, 'dear enemies' and tolerate each other. An established neighbour offers little threat, compared to an unsettled transient searching for a territory, so the gain from an agonistic encounter with a neighbour would be small (Maynard-Smith & Parker, 1976). Mutual avoidance rather than aggression probably contributes most to spacing in mammalian territorial systems. Social intolerance or aggression commonly increases after reproduction when population densities increase and juveniles disperse. High population densities should promote an increase in agonistic interactions, because individuals at high densities are less familiar with each other than at low densities (Bekoff, 1981, in Randall, 1989) and there is increased competition for territories.

Jackals were much more aggressive towards each other when there was competition for food (n=5). In these situations, the interactions between pair members were much friendlier than between other jackals. This suggests that the pair bond in black-backed jackals is strong (Ferguson, 1978). Lone animals live nomadically in large areas usually encompassing several family territories and rarely interact except during the breeding season or when loosely associating around a kill. The behavioural patterns of black-backed jackals during social interactions observed in the present study were consistent with those reported by Ferguson (1978) in the Kalahari Gemsbok National Park, save for the timid nature of the former at MNR. Direct aggression sometimes serves as a backup system when indirect territory maintenance such as scent marking and vocalisation fails. The distribution of scent-marks throughout the jackal's territory, their frequency of application, and the information that they contain help maintain the territory structure. Although scent-marks advertise an animal's location long after it has passed, they require direct and close scrutiny, and they fail to inform interested parties of their marker's current location.

Some overlap of group home ranges, especially at crucial spots such as watering holes or garbage sites, was observed for *C. mesomelas* in which the groups are normally mutually exclusive. In such instances, agonistic behaviour within the group is important in the development of social organisation, and the position of each group member in respect to others of the same group is relatively stable. In contrast, dominance relationships of an individual from one group with any member of another group cannot be expected to have been established. In some species, an individual or a pair may be dominant in the core area of its home range but not in the periphery. This tends to produce a regular dispersion by effectively excluding other individuals from breeding in the core without necessarily excluding their presence there as subordinates engaged in other activities (Brown & Orians, 1970).

Areas that were abandoned from one group range subsequently became part of a neighbour's range. High rates of range drift from February to April are likely to reflect (i) a reshuffling of the social hierarchy as yearling jackals disperse in autumn and early winter, followed by (ii) intense activity during pairing-mating in May to July (the relatively low rate of drift in May perhaps reflecting a staking out of territories by pairs, preparatory to mating), and (iii) subsequent changes to the range structure of denning females (Doncaster & Macdonald, 1991). The environment surrounding MNR, as well as within, to some extent is inherently disturbed by human activities such as road traffic, problem animal control operations, etc. These factors may act in concert, reducing the average life-span so that pairs have barely sufficient time to produce the first litter, but also causing rapid and unpredictable perturbations in the pattern of food availability (Doncaster & Macdonald, 1991). I suggest that drifting territoriality in MNR is largely a consequence of the social instability entailed by such abrupt changes to population structure and food availability brought about by intense disturbance and accelerated harvest. High population turnover may de-stabilise the dominance hierarchy and reduce the age difference of survivors (Doncaster & Macdonald, 1991). A likely outcome would be disruption of social mechanisms that under undisturbed populations prevent subordinate individuals from achieving breeding status (J.D. Skinner, pers comm.).

Within the jackal family, helpers have a subordinate status to the parents, and the former may experience suppression of endocrine function and reproductive behaviour (Moehlman, 1983, 1986; Creel & Macdonald, 1995). The reason for intrasexual aggression may be linked with reproduction. If a female permits another female on her territory, she may have to share the male. The male might then have two litters of pups to defend and feed. Since the male has finite paternal investment, fewer pups would survive if this investment were to be partitioned. Conversely, male intrasexual aggression ensures that the male alone will mate with the female, eliminating the possibility that he will care for pups that are not his own progeny.

Vocalisation

Vocalisation ('calling' or 'howling') by canids is believed to function primarily as a passive means of territory maintenance whereby neighbouring groups mutually advertise their locations over sufficiently long distances so as to warn each other and non-territorial transients where to avoid (Jaeger, Pandit, & Haque, 1996). Peaks in calling occur during the annual reproductive cycle when pairing and mating takes place, and following abandonment of dens when family groups become more mobile and use rendezvous sites within their territories. Calling diminishes at the end of the reproductive cycle when young are fully mobile. Calling is also low at the time of denning when it might endanger immobile young by signalling the location of their den site to rivals or other predators. A dynamic state of conflict therefore seems to occur among neighbouring territorial groups, which is probably mediated by changing needs to compete for resources.

There are three responses that dominant animals can conceivably use to defend their territories when intruders are known to be present (Jaeger *et al.*, 1996): vocalise and warn-off con-specifics; approach and confront; or howl followed by approach. Jackals, coyotes, and wolves all approach a source of broadcasted calling (Joslin, 1967; Skead, 1973). Available evidence suggests that it is territorial, dominant animals or groups that approach (Harrington & Mech, 1979). If calling functions to reduce confrontations and if elicited calling is higher during pairing-mating than during denning, we would expect approach and confrontation to be higher during denning than during pairing-mating. If calling conversely promotes confrontation, approaches would occur more frequently during mating; and if calling and confrontation were not directly associated, approaches would occur with equal frequency during both pairing and mating. This hypothesis was not tested in the present study but merits further investigation.

The difference in the frequency of calling between spring and winter may be because of the shorter nights in spring, but it also probably reflects seasonal differences in human activity. During winter, farmers retire earlier to their dwellings, whereas in spring and summer it was hot and humid and people tended to remain outdoors relatively late (pers. obs.). Because jackals were very wary of humans and avoided them at all costs, they restricted their activities (including calling) to those periods when humans were relatively less active (see Chapter Four). This is of adaptive value because broadcast calling in an environment where there is wholesale persecution would obviously attract humans to the position of the howling animal, which may subsequently be zeroed in and end up being killed. In addition, it was also evident in the field that howling jackals did not maintain the same position but also moved considerable distances during subsequent outbursts of calls.

The seasonal pattern of jackal calls, and of pair-wise or group calls in particular, is consistent with the hypothesis of a territorial function during the pairing-mating and denning seasons. These patterns showed the same annual trends reported for other canids, being relatively more frequent during pairing-mating when territories are being established and relatively low during denning when vulnerable young are present. This pattern is consistent with the explanation that it is territorial animals that call, and that calling functions primarily as a mechanism to advertise territorial occupancy and the location of dominant animals, so that confrontations with neighbouring pairs and transients can be reduced (Harrington &

Mech, 1979). The annual occurrence of territoriality is coincident with the reproductive season and probably an adaptation to rearing young. If transients call at the same level as territorial, breeding animals, we would expect no difference in the frequency of calls between separate stages of the breeding season, unless transients were relatively few in numbers.

Group or pair-wise calls further support a territorial function for calling because non-territorial, transient canids do not typically associate in groups (Harrington & Mech, 1979; Jaeger, *et al.*, 1996) other than when feeding on carcasses, refuse dumping sites, or other clumped food resources. Group or pair-wise calls (like tandem scent marking) may carry more authority, in terms of territory ownership, than howls by individuals (Harrington & Mech, 1979). In addition, mates are probably together more during pairing-mating than during denning when females are suckling young and males are out foraging. Dusk and dawn peaks in howling during pairing-mating are consistent with the findings of Skead (1973), who reported that spontaneous calling in the same species in the Transvaal during the mating season peaked during 19h00-23h00 and 04h00-07h00. Howling in wolves also peaks bimodally during 20h00-00h00 and 04h00-07h00 (Harrington & Mech, 1978), and in golden jackals (*C. aureus*) during 20h00-00h00 and 04h00-06h00 (Jaeger *et al.*, 1996).

Another explanation for the preponderance of calling in one of the seasons may be that, calling is high when territories are being established and that the need for territory advertisement diminishes during denning when neighbouring pairs (or groups) have learned one another's territory (Jaeger *et al.*, 1996). Furthermore, the effect of calling may even extend beyond pairing-mating and reduces trespassing by conspecifics during the subsequent denning period. It is possible that the inhibition of calling by adults during early development of pups has survival value for the pups, for by keeping silent the adults do not reveal the den site to potential intraguild predators.

Apart from intergroup communication, calling is also likely to function for intra-group communication (Harrington & Mech, 1978, 1979), which is supported by evidence from wolves for individually distinct vocalisations (Tooze, Harrington, & Fentress, 1990). The need to regroup probably is greater for large social carnivores such as clans of spotted hyaenas, lion prides, and wolf packs that cover large areas than it is for jackals at MNR. An intra-group function also offers an explanation why calling is low during denning (i.e. because a fixed and predictable den site precludes the need for howling) but one that is not mutually exclusive of territorial maintenance (Jaeger *et al.*, 1996).

Vocalisations, unlike scent-marks, provide instant information concerning the elicitor's current location, and in many species, vocalisations are important in territorial maintenance (Harrington, 1978; Harrington & Mech, 1979). Joslin (1967) felt that howling could serve this role in wolves, and thus keep packs aware of each other's locations so that near-fatal encounters could be avoided by modifying their movements. The same could be said for black-backed jackal vocalisation although this was not intensively investigated in the present study. In wolves, howling has been reported to play a role in intra-pack communication, especially in expediting and coordinating events such as departures, reunions, or movements (Joslin, 1967; Harrington, 1978). The progressive increase in howling in summer may reflect an increasing need for long-range, intra-pack communication as pups become more mobile, and packs begin the gradual abandonment of their predictable home site locations.

Territory holding by animals is seen as an adaptation to defend a limiting resource, often, although not always, a food resource (Davies & Houston, 1984; Carr & Macdonald, 1986). Since territoriality involves costs (e.g. defence against conspecifics) as well as benefits, territories are expected to be of the minimum size necessary to satisfy the requirements of the occupants. Enlargements would bring extra costs without net benefits. The defence of territories requires a not insignificant investment in terms of time and energy. In addition, by behaving in conspicuous ways, often involving vocalisations, the individual is probably subject to increased predation. For such behaviour to evolve there must be compensatory advantages so that the overall fitness of the individual is increased.

It is possible to find at least one common denominator for all of the diverse types of territorial behaviour. They can all be viewed as behavioural adaptations which are selected for in the course of evolution because they aid individuals in competing for the requisites for reproduction or survival (Dawkins, 1989). Territorial behaviour does not evolve because it has a function. Rather, it is favoured if individuals acting in that manner are more successful in surviving and reproducing than individuals behaving in other ways (Brown & Orians, 1970; Dawkins, 1989). Such a view is useful in generating testable hypotheses because it focuses attention on those aspects of the problem that must be studied, i.e. the ecological factors that determine fitness differentials among individuals who behave in different ways.

Denning

The number of breeding dens has been related to the number of canid breeding groups elsewhere (Hewson, 1986; Meia & Weber, 1992) and, in a similar vein, may thus be an indication of the number of resident jackal breeding pairs within MNR, especially given that jackals at MNR maintained exclusive home ranges. However, the estimation of jackal density is difficult because the number of jackals in an area also depends on the social organisation of the population: Jackals usually live in pairs or in groups according to habitat, prey availability, level of hunting pressure and the availability of immigrants. Hunting pressure may have an important influence on the number of breeding dens the following year. Jackals probably avoid breeding at sites with a history of high levels of human disturbance. However, although MNR provided a safe haven for breeding relative to surrounding farms, the unavailability of well-developed soil profiles and termitaria (termite mounds) militated against the establishment of dens in the predominantly rocky terrain that characterises a large proportion of the study area.

Burrowing or denning is an important behavioural adaptation for many organisms, for which this underground network provides a convenient refuge from the rigours of life on the surface (e.g. risk of predation). Soil is an excellent insulator against temperature extremes, and an animal resting just a few centimetres below the surface may comfortably survive the hottest day and coldest night. In a burrow, the humidity is relatively high and this helps animals reduce moisture loss. The humidity in an animal's breath - trapped in the burrows - also plays a part in keeping the tunnels humid and preventing moisture loss from the animal's body. Jackals whelp in dens and young typically spend most of their time in dens until they are weaned. Thus predation pressure is reduced and may allow jackals to produce more young in a more altricial state with a longer period of development. Since jackals also regurgitate food to their young, such behaviour enables them to efficiently and safely bring larger amounts of food to the den.

Helping

The young of several species of carnivores are often cared for by individuals that are not their parents. Tending to infants other than one's own is termed alloparental behaviour and may involve either 'helpers' with no young of their own, or adults with their own offspring who also tend to those of other parents. The presence of the parents' genes in future generations depends on the differential survival of their own progeny in comparison to those of other parents. Activities defined as 'helping' in mammals include feeding, grooming, baby-sitting, helping infants in distress, assistance in thermoregulation and allosuckling (Jennions & Macdonald, 1994 and refs. therein). In practice, 'helping' has been used to describe any activity directed towards infants or their parents which is likely to benefit the recipients and increase breeding success (e.g. alarm calling or provisioning a lactating female).

In the present study, it was difficult to document direct evidence of helping behaviour due to the highly secretive nature of the jackal population at MNR. In addition, it must be noted that the presence of helpers is partly dependent on the age of the parents because a pair with its first litter would not have any helpers anyway, unless the 'helpers' are not their own offspring. Besides, such facets of jackal behavioural ecology under human persecution pressures require a not insignificant allocation of time and resources to unearth. Thus direct evidence for helping behaviour would best be studied for at least two years, given that jackals breed once a year, and that the current progeny would most likely be helpers in the next breeding season. Although this was beyond the scope of the present study given its necessary brevity, the subject can hardly be ignored because of its theoretical interest and importance.

The incidence of 'helping' is partly related to the onset of dispersal in jackals. First, juveniles disperse in some cases because they have to: They are forced to disperse by their parents or other resident adults, when they are perceived by these as becoming a threat in the competition for resources (e.g. food, shelter, and mates). Those that are not strong or fit enough to resist eviction are forced to leave. On the other hand, juveniles disperse because they can: By leaving their natal range they may increase their chances of breeding successfully and perhaps avoid inbreeding. They do this if suitable areas are available to disperse into, and if they are fit enough to compete for a new home range. In other words, the fitter individuals disperse. These two categories correspond to the 'Resident Fitness Hypothesis' and the 'Emigrant Fitness Hypothesis' respectively, defined by Anderson (1989) with respect to rodents. According to the former hypothesis, juveniles are fundamentally philopatric, settling on their natal sites if permitted to do so. Dispersal is driven by the aggressive behaviour of adults and intragroup aggression increases under food stress (Kruuk & Parish, 1982; Anderson, 1989).

Four factors may be considered by an offspring who chooses between dispersing and attempting to breed independently, or postponing departure and remaining as a non-breeder with the parental group (Emlen, 1982a): the cost (risk) of dispersal itself; the probability of successful establishment on a suitable territory or area following dispersal; the probability of obtaining a mate; and the likelihood of successful reproduction once 'established'. The paradox of why animals have similar social organisations in seemingly opposite ecological situations was extensively treated by Emlen (1982a, b). In addition, dominance interactions among littermates may determine who remains on the home territory (Moehlman, 1986). Dominant pups tend to be more independent and better foragers; they might have a higher rate of reproductive success when they emigrated, if one or more of their siblings stayed and helped. However, if successful emigration was difficult (e.g. if the jackal population was at high density) then a pup might improve its fitness by remaining with its family for an additional year. Thus if emigration was not feasible, dominant pups could remain on the home territory and possibly force siblings out (Moehlman, 1986).

It is also likely that there is a reproductive advantage of delayed dispersal and increased group size. Moehlman (1979) showed that 'helpers' assisting the parents increase the survival of black-backed jackal pups. In her study, Moehlman (1979) found that helpers contributed food directly to the pups and also regurgitated food to the mother during the period of lactation. Helpers also contributed by guarding the pups while the parents were absent. Families with more adults (i.e. those with helpers) had an attendant adult at the den most of the time, thus providing greater protection to the pups against potential intraguild predators. Hence Moehlman (1979) found that the number of helpers positively correlated with pup survivorship (r=.967). On average each helper added 1.5 surviving pups to the litter. The presence of helpers was found to be independent of food density, and the critical factor in pup survival was deemed to be the number of provisioning adults that can capture prey and make it available to the pups.

An animal's 'inclusive fitness' (Hamilton, 1964; Dawkins, 1989) is the sum of its direct fitness, derived from its own offspring, and indirect fitness, derived from the offspring of its relatives, with which it shares genes. Inclusive fitness examines the lifetime effect of an individual's behaviour on the next generation's gene pool, not only in terms of her own reproduction but that of related individuals. Jackal helpers are as closely related to their full siblings as they would be to their own offspring. As their contributions as helpers increase pup survivorship, their own inclusive fitness is enhanced by kin selection until such a time that breeding is attempted. In fact, an adult helper gains more (yield one pup per adult) by being a helper of its parents than by finding a mate (yield 1/2 pup per adult). Helpers have also been reported in red foxes (Macdonald, 1979; Von Schantz, 1984a), wolves (Mech, 1970, in Bowen 1981), golden jackals and wild dogs (Van Lawick & Van Lawick-Goodall, 1970), and coyotes (Bekoff & Wells, 1980). Thus, helpers may derive benefits through inclusive fitness. Although helpers may have a low probability of obtaining breeding positions on their own, but by taking care of related individuals, they increase their inclusive fitness.

The fact that an individual is closely related to its full siblings as it is to its offspring prompts the question of when to breed. The answer to the question of whether an individual should begin to breed or persist in alloparenthood may lie in the calibration of costs and benefits by environmental factors. For example, if a young jackal has the option of remaining at home as a helper or leaving to attempt to become a breeder, the pros and cons of the alternatives are largely determined by ecological circumstances. If conditions are such that the chances of becoming established as a breeder elsewhere are very low, then the long-term prospects of inheriting the natal territory and the immediate advantages of hunting prey and avoiding danger in a familiar terrain may be added to the possibility of helping rear siblings whilst gaining in both experience and inclusive fitness. These may all combine to favour staying at home. In the case of black-backed jackals studied by Moehlman (ignoring the costs of helping), helpers delayed reproduction for one year and potentially increased their inclusive fitness on average by 0.87 pups. Gittleman (1982, in Macdonald & Moehlman, 1983) also found that across the Carnivora, the relative birth weight and litter sizes are greater among species showing paternal and /or alloparental behaviour, but neither increase with group size alone. This may indicate that alloparental behaviour does in general represent an increased investment in the young.

If the cost of helping is high (i.e. food shortage), then it is unlikely to occur, and so is 'an epiphenomenon of delayed reproduction, occurring under ecological conditions making the cost of helping low' (Harrington & Mech, 1980; in Macdonald & Moehlman, 1983). However, the age-status of helpers (i.e. whether they are yearlings or adults) may have an important impact on the provisioning of pups. Wild dog adults allow yearlings to eat first at a kill. During periods of scarce resources, yearlings will not only have first access to carcasses but also steal regurgitations from pups. Hence their provisioning is favoured over pups, to the extent that in four wild dog packs with yearlings, no pups were successfully raised (Macdonald & Moehlman, 1983). More importantly, we could expect the opportunities for, and consequences of, alloparental behaviour in any species to be tempered by prevailing ecological circumstances. Consequently, there is no necessary incompatibility between studies, even to the same species, which find conflicting indications of the consequences of alloparental behaviour.

Several potential benefits have been hypothesised to explain the behaviour of helpers in all species where helpers have been found (Von Schantz; 1984a,b; Jennions & Macdonald, 1994; Creel & Macdonald, 1995). These include:

1. Increased chances of survival by remaining as a subordinate in a group rather than by dispersing. Remaining in a natal group leads to benefits of increased foraging

efficiency and predator detection while avoiding the high mortality associated with dispersal in relatively unfamiliar and potentially hostile terrain.

2. Increased chance of filling a reproductive niche in the future. If suitable breeding sites or territories are extremely limited, an individual can wait until a breeding vacancy occurs in the natal group, or may be able to bud a territory from the natal territory.

3. Increased reproductive success when helpers can reproduce. Helpers may acquire skills in infant care-taking, foraging ability, predator detection, and defence that leads to greater reproductive success as a result of deferring reproduction instead of reproducing immediately.

Parents in turn benefit from the presence of helpers through increased reproductive success as parents accrue more reproductive benefits by helpers investing in their pups (degree of relatedness, $r = 1/2$) than by helpers investing in their own pups (grandpups, $r = 1/4$). Thus it is in the parent's best interest to accommodate helpers. However, the available food resources potentially mediate retention of helpers. The food requirements of secondary animals may be lower than those of primaries since additional group members, perhaps through lower status, might not reproduce and, if the alternative were emigration (and increased risks of starvation and death), might accept a lower than optimal nutrition rate (Carr & Macdonald, 1986). The phenomenon of reciprocal altruism involves one individual aiding another, who subsequently is helpful in return, when the need arises. Although such a symbiotic arrangement would benefit members of trustworthy coalitions, it seems susceptible to cheating (Maynard-Smith, 1976; Dawkins, 1989). However, Axelrod & Hamilton (1981) have shown that reciprocity could evolve as a stable stratagem if an individual's reaction mirrored its partner's action (i.e. tit for tat).

Theoretical Considerations

The proximate mechanism underlying the regulation of group size is complex and imperfectly understood (Zimen , 1976; Messier, 1985). An increase in prey abundance seems to produce a direct increment in the within-group recruitment and survival rates (Keith, 1983, in Messier, 1985). Moreover, group size may be related to the dispersal strategy of group members. As prey abundance increases, the territory mosaic becomes progressively saturated (lower territory vacancy) which could provoke delayed dispersal (Messier, 1985). Thus given the rarity of vacant areas, a maturing jackal may benefit more by trying to obtain reproductive status within its natal area than by dispersing; i.e. a non-disperser could take advantage of the ability of the whole pack to defend space in which it may eventually breed. This advantage can be crucial under highly saturated conditions. Variation in black-backed jackal social structure has led to a maximisation of its resource base. Sociality is surely a strategy allowing access to large prey without sacrificing the advantage that smaller body size gave it in the efficient use of small prey (Bowen, 1981). This, in part, may explain the singular success of black-backed jackals in most parts of Africa in the face of human persecution, unlike its larger carnivorous counterparts.

Caraco & Wolf (1975) also contended that selection has favoured the capacity for social animals to adjust group size in response to a hierarchy of ecological factors, primarily temporal and spatial patterns of resource availability. These patterns influence foraging efficiencies, mating probabilities, and reproductive success. But predation pressure also often constitutes another important factor determining social tendencies, as is the suggested scenario for the social organisation of jackals in the present study. Group size will be optimised in response to the most important environmental characteristics, in an attempt to maximise the total benefit-to-cost ratio for individual group members. Even within broadly similar habitats there is room for considerable intraspecific variation in the basic parameters of carnivore social organisation, i.e. group size and home range size.

Creel & Macdonald (1995) summarised studies on a variety of social carnivores, noting that tolerance of other animals provides benefits by allowing cooperative hunting and defence, and promoting a reduced vulnerability to predation. Large groups meet the costs of reproduction by providing alloparental care that leads to a greater number of litters, larger litters, and increased survival of offspring. Litter mass and litter growth is higher in species with communal or biparental care. Because there is high within-group relatedness in social carnivores, non-reproductive or minimally reproductive helpers are able to benefit from increased inclusive fitness.

It has already been noted that two main selective pressures that have been invoked to explain why some of the Carnivora live in groups are the need for assistance in hunting and killing large prey, and the need for defence against attacks by other predators (Lamprecht, 1981). However, neither of the above selective pressures explains why some species live in groups but travel and hunt alone (Macdonald, 1983). Benefits, which vary according to the species or population, do not only come from cooperative hunting, defence of territory and prey, and defence against predators. They also derive from the opportunity to learn from other group members' experiences, division of labour, care of the young and sick, and other advantages associated with alloparental behaviour. However, all the many benefits of group living must operate within a framework of constraints determined largely by the dispersion and abundance of available resources (Lamprecht, 1981; Macdonald, 1983; Kruuk & Macdonald, 1985). Considering the great diversity of social systems in the Carnivora, both inter- and intra-specific variations in the ecological costs of sociality are as relevant as is variation in the behavioural benefits. Hence resource (particularly food) dispersion is fundamental to the spacing and structure of carnivore society in that it may set the limits to the group and territory sizes within which other combinations of selective pressures operate.

Another theoretical paradigm that explores the influence of an animal's foraging ecology on its social life is the Resource Dispersion Hypothesis (RDH, Macdonald, 1983; Doncaster & Macdonald, 1992). According to this hypothesis the smallest home range with an economically defendable configuration which will reliably support a basic social unit (a pair of animals) may sometimes support additional individuals. These are tolerated in numbers and at times when any costs to the basic pair due to their presence are outweighed by the overall benefits. This may happen when resources are spatially and temporally heterogeneous. Such additions are governed by the patterns of resource dispersion, and presumably where resources may be prey, mates, breeding sites, etc. In this case RDH suggests that territory size is constrained by the dispersion of patches of available (food) resources, whereas group size is independently limited by the richness of these patches (e.g. Kruuk & Parish, 1982). The RDH thus provides an ecological explanation of how, at minimum costs to themselves members of a pair could incorporate additional group members into even the smallest economically defendable territory that will sustain them. Kruuk & Macdonald (1985) indicated that while some animals, termed 'contractors' might defend such minimum territories, others, termed 'expansionists', might benefit from forming larger groups and thereby defending larger territories in excess of minimal requirements for breeding. The distinction between contractors and expansionists is important in so far as it may help in understanding the processes underlying the adjustment of population density, group sizes and range sizes to the availability of resources [see Kruuk & Macdonald (1995) for an in-depth analysis]. Knowledge of the processes involved allows prediction of the outcome of the management of carnivore populations. In cases where jackals are persecuted in an attempt to forestall predation on small livestock and game as in the agricultural areas around MNR, it is important to know how jackals living adjacent to eradication areas will behave, e.g. what will happen to the territories (and sizes thereof) of those groups adjoining an eradicated group. Since it appears that jackals at MNR are contractionists, Kruuk & Macdonald (1985)'s predictions would be that the neighbours of evacuated territories will continue to cover the same range, as before. However, the situation is further compounded by the fact that by creating vacua in otherwise 'saturated' habitats, satellite, transient or dispersing individuals may immigrate into vacated territories (see Chapter Four and Chapter Eight).

Macdonald (1983) concluded that once group-living in carnivores has evolved as an adaptation to resource dispersion then other benefits accruing from sociality *per se* (e.g. cooperative hunting and defence of kills) further moulds the social organisation in each population or species and that 'the balance of these contemporary benefits is not necessarily the same as that which originally selected for group living'. Predictions from the RDH about spatial organisation require information about three features of a territory (Doncaster & Macdonald, 1992): (i) its food security, (ii) its defensibility, and (iii) the social behaviour of its components. Food security and defence costs are both affected by the spatial and temporal pattern in which food is available, and further consequences of members of a social group arise from the benefits of cooperation and the costs of dispersal.

Von Schantz (1984) proposed an alternative but still compatible model, the Constant Territory Size Hypothesis (CTSH). This hypothesis also requires environmental heterogeneity, but in this case habitat quality is hypothesised to fluctuate in the long term. Territories have fixed boundaries over long periods of time and encompass areas sufficient to support an individual or breeding pair through the worst periods. The model predicts that as food abundance increases, the territory owners, for example the breeding pair, take advantage of this resource surplus by allowing their offspring to remain at home, thereby increasing the group size. When food abundance decreases the subordinate group members will be evicted from the territory by the breeding pair. Hence in any given territory of say, jackals or foxes, group size will be positively correlated with the annual food abundance whereas territory size will be constant from year to year. Von Schantz (1984) argued that if territory quality fluctuated over periods which were long, but less than the lifetime of the animal concerned (and considering the disadvantages of repeated symmetrical border disputes), territories would have to be large enough to accommodate the primary pair in the worst circumstances. In a study of pied wagtails (*Motacilla alba*), Davies & Houston (1981) found that territory owning wagtails varied their tolerance of satellites so as to maximise their own daily feeding rate. When food was very abundant the owners gave up defending their territories altogether and ignored intruding wagtails, but if the food supply decreased again, normal territorial behaviour was quickly resumed. Under the conditions that an owner tolerates a satellite, the owner enjoys an increased feeding rate because the benefits gained through help with defence outweigh the costs incurred through having to share the food supply with another bird.

Von Schantz (1984c) argued that RDH is severely limited because he believed that it depends on the existence of 'bottleneck' periods when only one patch is available in a territory and is therefore not applicable to groups whose members regularly forage in different patches simultaneously. However, Macdonald (1984) asserted that RDH could apply to territories within which several patches were fruitful simultaneously and that whether or not group members forage together simultaneously, will depend on the selective pressures moulding their sociality. He saw the scenario of inter-annual variation in resource availability as being compatible with RDH, rather than as an alternative to it.

In conclusion, many variations exist on the general theme of black-backed jackal social behaviour. As similar intra-specific variation is emerging for other carnivores, it seems unhelpful to wax mystical about *the* social organisation of the black-backed jackal or any other species. Rather we should stress the dynamic nature of the species' *social systems* (Macdonald, 1979) and examine intraspecific variations in terms of the selective pressures acting on different classes of individuals within each society. With sufficient information about the intra-specific variations in social behaviour for different species, the limits of flexibility for social systems of each could be defined and thereafter compared. Such comparisons could shed some light on the evolutionary significance of puzzling differences between social systems (Macdonald, 1979). It should be emphasised that many factors influence the social organisation of a species and that, under different ecological conditions, a population may stray from what is considered to be the species' modal social system in an optimum habitat (Kleiman, 1977).

CHAPTER EIGHT

CONSERVATION AND MANAGEMENT

Introduction

Since earliest times canids, especially the black-backed jackal *C. mesomelas*, the red fox *Vulpes vulpes*, the coyote *C. latrans*, and the wolf *C. lupus* and its domesticated descendants, have had a significant impact on human populations. The success of black-backed jackals, and their close association with humans, has meant that all feature prominently in the mythology of indigenous Africans. It is interesting to note that those canids that have had the greatest impact on human culture in the past are also the very species that still pose some of the most complex wildlife management problems today. In particular, in many areas, extensive canid population control operations are undertaken, yet few of these programmes seem to have achieved their desired goals.

There is one indisputable fact about the problem of jackals in game ranches and small livestock farming areas. Killing the jackals alone is incapable of containing the problem. Despite impressive records in the number of problem animals killed by farmers, the problem is on the increase. In some areas small livestock losses have been so severe that farmers have abandoned the enterprise (e.g. Fair, 1994). Small livestock farmers who are experiencing heavy losses to predators should consider applying several control measures. Electric fencing may be very effective in keeping marauders out of selected areas or farms, but it is important to realise that there is no single simple solution to the problem and that each control method has its strong and weak points. Understanding these is vital for success.

Game and livestock farmers hit by stock losses through depredations on stock by black-backed jackals might feel justified in trying to kill the suspected culprits. But farmers and the human society at large are party to the predator problem. The supplanting of a wide spectrum of wildlife species and their natural habitats with farmland and domestic animals has set the scene for the predator 'problem'. Farmers in particular must accept that their farmland was once the home of a variety of species on which the black-backed jackals preyed (as carrion or as live animals). I suggest that society comes to terms with the black-backed jackal. This animal is often the only survivor of the medium-to-large carnivores in vast areas of sub-Saharan Africa.

Jackal control has been practised for many decades in many parts of Botswana and southern Africa (particularly in South Africa) in general. Although it might have had good short-term results, no study of its long-term effects on ecosystems seems to have been made. The importance of selective elimination that deals with culprits cannot be overemphasised for cost-effective control of problem animals. This chapter examines some methods of jackal population control, and the possible impacts of management actions on their ecology. In particular, the discussion focuses on the effects of jackal population reductions, since this is the most common of jackal control methods currently being used. Although emphasis will be on black-backed jackals, the ideas equally apply to other canids or mammalian carnivores in general.

Population Reductions

Canid population reduction is attempted for a variety of reasons (Van Heerden, 1988; Harris & Saunders, 1993; Reynolds & Tapper, 1996):

1. To prevent disease spread from canids to (a) man, e.g. rabies; and (b) livestock and/or companion animals, e.g. sarcoptic mange.

2. To prevent predation on (a) human populations; (b) livestock; (c) endangered indigenous species; and (d) vulnerable populations of nesting birds.

3. To prevent competition with, or predation on, rare species of canid.

4. To reduce crossbreeding with endangered species of canid.

5. To prevent competition with human populations by hunting game species.

In addition, canid populations are hunted for a variety of reasons not directly related to population reduction or problem animal control:

1. Commercial harvest, usually for furs

2. Recreational hunting of (a) indigenous species; and (b) non-indigenous species introduced for hunting purposes.

3. Traditional harvesting/hunting by indigenous people for medicinal purposes and other societal obligations.

Management Strategies for Jackal Populations

Society is demanding that administrative and decision-making processes involve the public and, where possible, satisfy a variety of public interests. Conservation plans should therefore seek to; (1) maintain sufficient wildlife use and value to compete more effectively with alternative land uses destructive of ungulate-predator systems, e.g. domestic animal production, or agriculture; (2) assure the long-term security of predators in most managed areas; and (3) provide sufficient wildlife to satisfy many non-consumptive and consumptive uses of predators and their ungulate prey. It is envisioned that management following this plan will help fulfil wildlife desires for people living in areas adjacent to parks.

When predation limits the growth of ungulate populations, wildlife managers have three options: (1) wait for a more-or-less natural change of events, (2) reduce or eliminate harvest by man during critical periods for prey populations, or (3) hasten the increase in prey by reducing predators (Gasaway *et al.*, 1983). Considering the lengthy period (may be decades) that may be required for natural events to produce a major increase in numbers of ungulates, Option I is not viable due to impatience on the part of wildlife users. Option II, decreasing or eliminating harvest does not specifically apply to the situation in MNR since there has been insignificant impala harvest ever since the park was established. If harvest had been practised, its elimination could forestall jackals limiting impala but it is unlikely to prevent it. Reducing or eliminating harvest will have little effect once predators exert sufficient control to cause a prey decline or to maintain prey at low densities; therefore control of harvest is best used in conjunction with other options rather than alone.

Artificial predator reduction in conjunction with reduction in harvest of prey is the most viable management option to increase impala populations over short time intervals. In general, as the ungulate population grows, predator removal can be reduced and harvest of prey by man increased. Increased predation and harvest will reduce the growth rate of the ungulate population, and eventually predation will again become a major limiting factor. Therefore, when exploitation and moderate densities of the prey population are to be maintained, predators must be managed (Gasaway *et al.*, 1983). Predator management, which includes the periodic reduction of predator numbers, can ensure a sustained long-term sharing of the ungulate resource between man and predators, while avoiding low prey densities that support few predators, exploiters, or wildlife tourists. The contention that wildlife should pay its way to ensure its conservation has much relevance to predator management. In most rural settings in Africa, society is finding it difficult to accept that predators should be conserved for the simple reason that predators are viewed as competitors utilising a potential resource that could have been utilised by people instead.

Hence there is need to search for a socially acceptable predator management system. Cooperation between wildlife users can produce conservation plans that will reduce the divisiveness of predator-prey management. Area-specific plans can address wildlife values and use ranging from natural densities with little or no harvest to increased abundance and higher harvests of wildlife. Conservation plans can define what is acceptable management in specific areas. Maximum lamb-rearing success is attained when mature mothers predominate in the breeding population (see Chapter Six). Management of harvest to produce such an age structure may be an important strategy where predation on neonates markedly reduces impala recruitment, particularly in areas where other options (e.g. predator control) are limited and predators and hunters compete significantly.

In principle, one can seek to reduce the losses to predators by reducing the number of predators (lethal control) or by reducing their access to, or availability of, the prey (non-lethal control). In practice, predator reduction is much the most common approach and, on first principles, much the least promising. Jackals can be killed in a number of ways, each with its advantages and disadvantages. From the point of view of conservation, lethal methods that are not species specific (e.g. trapping and poisoning) frequently result in the inadvertent killing of 'non-target' animals. In areas where common predators coexist with rarer animals, non-specific lethal control results in what can only be called the reckless endangerment of the rare and vulnerable species.

Several means of jackal population control are currently used or under consideration:

1. Poisoning: This includes the use of poisoned baits, gin traps, toxic collars, etc.

The killing of non-target species by these methods has disastrous effects with possibly wide-ranging ecological effects. The killing of bat-eared foxes *Otocyon megalotis* and aardvarks *Orycteropus afer*, for example, has resulted in the loss of other important allies in the farmer's battle against harvester termites (Van Heerden, 1988). The use of poison collars (livestock protection collars - LPC) although not 'humanely acceptable' to animal rights activists offer some promises. Jackals usually go for the throat of their prey. The collar protects the sheep, but in puncturing the collar the predator is given a lethal dose of poison, killing it instantly. The collars contain a quick acting poison under pressure that kills the jackal almost instantaneously on puncturing it. Once a collar has been punctured it is removed from the sheep and sent back for repair. The collars come from Livestock Protection Company in Mariental, Namibia and cost about ZAR100 each. Where various predators such as caracal (*Caracal caral*) and jackals are sympatric, lambs as well as adult stock should be collared because of differential selectivity of predators particularly with respect to prey size. For example, jackals commonly go for the small sheep or lambs while caracal prefer larger lambs or adult sheep (Byford-Jones, 1994).

2. Trapping - cage traps, leg-hold traps, snares, etc.

First, jackals should be caught before they get moonstruck, mate and produce offspring from May up to July. If this has failed, location of dens with pups should be embarked upon mainly during July, August and September. Finally, if nothing has worked thus far, emphasis should be directed to catching the inexperienced youngsters who should start running around from September onwards because they are relatively easy to catch. Preventive control during the dispersal period (February to April) would mostly remove many non-resident transient jackals that would normally be absent in the control area during the jackal breeding period. Preventive control during May to July would be more efficient because resident territorial jackals (i.e. the local breeding population) would most likely be removed. The reproductive period and its associated activities imposes an energetic constraint on breeding jackals such that there is a tendency for such individuals to kill more prey during this period so as to meet their own energetic requirements, in addition to that of the current progeny.

However, it must be borne in mind that studies with some radio-collared canids (e.g. coyotes) have revealed that individuals are relatively invulnerable to capture within their territories or home ranges (Windberg, 1996, and references therein) and, by extension, this implies that capture success for jackal territory owners or holders would be minimal in most cases. Lures used with capture devices generally rely on the food seeking, curiosity, or social behaviours of jackals to elicit attraction. The behavioural responses of animals to novel stimuli involve the combined effect of attraction or aversion, which appears to be influenced by the familiarity with the site where the stimuli are encountered (Harris, 1983; in Windberg, 1996). In experiments with captive coyotes (*C. latrans*), Harris (1983) demonstrated that coyotes exhibit neophobic behaviour toward novel stimuli, and showed that neophobic responses occur most frequently in familiar environments (i.e. territories and home ranges). My experiences while trapping jackals in the field in MNR further suggest that it may even be possible that some individuals may have learned to avoid (human) odours associated with trap-sets. Often, after a lapse of about one week during trapping in MNR, baits were found to undergo a gradual decline in luring ability. If the composition of the bait was slightly modified, however, trap visits (but not subsequent catches) would increase again. Thus, the use of techniques for surveying, capturing, or otherwise manipulating jackals should include a consideration of their potential for generating neophobia toward novel visual stimuli. Acting on these biological aspects of predator control may pay dividends in the final analysis.

3. Hunting with dogs - digging out dens with terriers, pursuit with hounds, etc.

Hunting using packs of foxhounds, greyhounds, and foxterriers, has been successful in combating the black-backed jackal on the Transvaal Highveld during summer, while hunt clubs usually employ a variety of farm dogs (Van Rensburg, 1965). The use of foxhounds is however limited as they rely on their sense of smell and the dispersion of animal scent, which in turn is dependent on the amount of moisture present. Foxhounds may thus find it difficult to trace an animal on its scent in dry weather such as prevails during the greater part of the year in southern Botswana. Feral or vagrant dogs which cannot be controlled by means of foxhounds are also suspected of being responsible for a considerable percentage of small livestock lost through predation such that effective control may eventually, depend upon destroying these animals in addition to the black-backed jackals.

Organised jackal hunts sometimes involving horses and packs of dogs, often result in the indiscriminate killing of anything on four legs that may be intercepted in the veld. The use of hunting dogs is however recommended for removing residual populations of medium-sized problem animals after other forms of control have ceased to be effective. In theory, hunting dogs could catch or corner jackals that have become bait- or trap-shy, or those that avoid being seen using other methods, e.g. from a helicopter. Hunting with dogs is ineffective for the large-scale reduction of jackal density, compared with poisoning. Therefore hunting dogs are highly successful in capturing and cornering solitary jackals encountered and provides an alternative technique for removing residual jackals from an area after large-scale reduction by another method.

4. Shooting - night-shooting, aerial shooting, etc.

5. Use of calls to attract canids to guns or waiting hounds: The use of calling (mostly scrubhare/rabbit distress calls and lamb bleats) is one of the oldest hunting methods, and is well-developed in Europe and the USA. Black-backed jackals are usually called in to sites where they can be shot. The best calling times are the early morning or late afternoon when activity is high. Effectiveness can be increased by conducting nighttime calling, using

powerful infra-red search lights. Farmers who cannot master the art of calling can use tapes which are played over loudspeakers (Schneekluth, 1995).

6. Gassing of dens and using smoke to bolt animals from dens.

7. Chemically, surgically, immunologically, or hormonally reducing birth rates in predators can reduce growth rates in predator populations.

8. Habitat destruction - removal of harbourage, destruction of dens, removal of garbage, etc.

9. Habitat manipulation - giving a competitive edge to canids less inimical to local needs.

Alternative strategies that may be used in an attempt to reduce jackal impact are:

1. Exclusion fencing, such as electric fences.

Relocation coupled with physical exclusion of predators just before lambing can improve impala survival in small and enclosed areas such as in MNR. Jackal-proof fences help restrict the movements of black-backed jackals and, if used in conjunction with foxhounds, can be a fairly effective control method. Apart from the fact that jackal-proof fences are expensive and difficult to erect and maintain in rugged terrain as in MNR, they are frequently undermined by burrowing mammals such as porcupines *Histrix africaeaustralis*, aardvarks *Orycteropus afer*, bushpigs *Potamochoerus porcus*, warthogs, *Phacochoerus africanus*, as well as black-backed jackals, and springhaas *Pedetes capensis*. When holes are dug under these fences they become ineffective for jackal control and maintenance costs are increased. In South Africa, government standards specify that at least 150 mm of the fence netting must be laid flat on the ground and covered with stones or pinned to the ground with wire staples, or 100 mm of the netting wire should be buried vertically and packed with stones on both sides. Notwithstanding these efforts, in certain localities, chacma baboons (*Papio hamadryas*) remove these stones from the bottom of the fences during their foraging activities.

As a result of jackal-proof fences being undermined, the game or livestock farmer not in many cases effectively reduces black-backed jackal depredation on small stock, despite a costly outlay on fencing. This in turn leads to unselective gin trapping by farmers, as it is most common for these traps to be placed in holes under the fences. Individual farmers will even launch an extensive extermination campaign against burrowing animals. The aardvark *O. afer* is often the culprit and so has been a target of farmers. But killing aardvarks has lost the farmer an important ally in the fight against termites. Another animal that may also suffer severely because of its tendency to ram fences is the ostrich. For example, on many northern Cape farms in South Africa, where once large flocks occurred, ostrich numbers have dwindled (Van Heerden, 1988). In addition, jackal-proof fencing may create isolated populations of animals such as the grey duiker and steenbok, and may aid potential predators, including domestic dogs, in preying on such enclosed animals (Heard & Stephenson, 1987). Where there is evidence of animals digging under nature reserve fences as in MNR, entering neighbouring farmlands and raiding crops or stock, it frequently happens that the neighbouring farming community develops negative attitudes towards nature conservation and the reserve in particular.

2. Aversive conditioning, such as the use of lithium chloride to reduce predation on sheep. Conditioned taste aversion is a natural phenomenon of feeding behaviour, but here individuals learn rapidly at the subconscious level to avoid by taste foods associated with illness: following consumption of a poisonous food and its unpleasant effects, all food with the same taste will evoke strong avoidance behaviour. Learning is rapid, and a single experience can suffice to create a lasting avoidance. Research on this is however in its exploratory phase.

3. Increasing alternate prey may reduce predation on the resident impala population in MNR. Interestingly, jackal foraging ecology espoused in the present study reflects the availability of a wide variety of food items and the differential vulnerability of prey. The dramatic seasonal shift by jackals to feeding on indigenous fruits, when they were abundant, and consumption of insects in significant amounts, when other foods were available, suggests that fruits and insects may substantially buffer predation on other species. Hence, it may be possible to predict the intensity of jackal predation on vertebrate prey through routine monitoring of fruit and insect abundance (Andelt & Kie, 1987). The high consumption of fruits also suggests the

potential, in some areas, for strategic plantings of appropriate fruiting species to buffer predation on desirable species, or possibly to lure jackals to areas where they might be easily captured.

4. Diversionary feeding of predators on or near impala lambing grounds for 4-5 weeks may reduce predation on neonates.

5. Habitat enhancement (e.g. through fire management) may increase impala numbers through improved impala physical condition and reproductive rate.

6. Vaccination against diseases such as rabies, or fumigation of burrows to kill parasitic mites in order to reduce the prevalence of sarcoptic mange in areas where canids are prized for their pelts.

7. Compensation for stock losses or the adoption of alternative enterprises less susceptible to canid predation.

8. Timing livestock production in adjacent agricultural and wildlife properties to minimise predation.

9. Using guard dogs to protect livestock.

10. Using light or sound stimuli, or other scarers, to reduce predation.

11. Removal of carrion (and human refuse), so that canids are not attracted to these areas.

In many parts of semi-arid Botswana, black-backed jackals are undoubtedly the most problematic predators. But not all jackals kill small livestock and game. It is no longer necessary to wage a war against the jackal in an attempt to eliminate them from farming properties. The truth is that such wars are rarely successful; more often than not they are costly and futile campaigns, and non-problem jackals are seen as allies in the management of problem animals (Fair, 1994). Jackals serve an important function in controlling caracal

(*Caracal caracal*), dassies (*Procavia capensis*), and rodents, all of which can cause heavy losses to farmers. In most cases in Southern Africa, killing jackals has resulted in the increase of caracal numbers in particular, primarily because jackal predation on caracal helps maintain caracal populations at low levels (J.D. Skinner, pers. comm.). Jackal eradication is therefore not only senseless but also foolish. Eradication is also senseless because jackals are incredibly resistant to it. They counter when put under a downward population pressure, by increasing not only the number of litters they produce per year, but also the number of pups per litter (Van Heerden, 1988). The answer lies in dealing on a selective basis, with individual killer animals (Fair, 1992). A strategic problem animal control plan is one that focuses on eliminating only the culprits (J.A.J. Nel, pers. comm). Such a plan allows the existence of a non-sheep-killer-predator-population, because they keep potential killers out of their territory (see Chapter Seven). The use of the livestock protection collar (LPC) on farms has proved that not all jackals kill small livestock and game - it is only a relatively small number that do the killing.

Goats and sheep are particularly vulnerable to predation by jackals, while cattle for the most part, are relatively immune. The choice of the type of livestock to be raised in a particular area may be influenced by various factors: market demand, the type of forage available, cultural traditions, or historical accident. However, in areas where a particular species of predator is causing problems with a particular species of livestock, one option is to remove the predator. But where it is culturally, ecologically, and economically possible, a simpler solution might be to raise a different type of animal. This is all very well from the perspective of the conservationist. But the peasant farmer who loses part of his meagre small stock to jackals would be in a far different position had a similar number of livestock been lost to a commercial farmer (for example) since sheep and goats are the poor man's cattle in most parts of rural Botswana.

The lucid reality of all this is that, no matter what the method of lethal control is employed, reducing predator numbers is an expensive process that requires a long-term commitment on the part of government or private producers. When deciding to manage an abundant canid population, three major factors need to be considered before embarking on a management programme:

1. The cost-effectiveness and/or cost:benefit ratios of predator control and/or management

2. The effects of control operations on canid populations

3. The non-target effects of control programmes in (a) increasing the number of prey species, which in turn may be pests; and (b) the ecological/environmental impact of population reduction techniques. For this presentation, emphasis will be on item (2) and (3) above, since these are essentially of biological interest.

Predation

Traditionally, biologists have attributed a major decline in ungulate numbers to starvation, whereas in reality this represents the tip of the iceberg. Failure to detect and gauge natal mortality could pose grave bio-sociological problems especially where the need for such information led to the wrong management strategy.

Some of the factors which may predispose livestock property and small game to jackal predation include; an abundance of suitable habitats to provide harbourage, autumn/winter lambings during the main jackal dispersal period, low availability of alternative food types, and individual livestock properties lambing out of sequence. It is true that a high proportion if not all, of the prey taken by jackals possess some trait that predisposes them to predation. Many factors that predispose prey to predation by jackals are obvious, such as senility due to poor nutrition, injuries, parasites, diseases, and merely being relatively small in size, or simply being newborn. However, many traits predisposing prey to predation are far subtler and not easily measured by biologists. For instance, the 'grandmother effect', in which the nutritional state of an individual's grandmother becomes a factor in its survival, is a good example (Mech *et al.*, 1991; Paquet, Nelson, & McRoberts, 1991).

The very contest between carnivore and prey seems to imply that far more prey will escape than get caught and that usually the least fit individuals will succumb easily to predation. However, beneficial effects of this culling by carnivores are not immediately obvious. Philosophically one can argue that an ecosystem that includes its full complement of carnivores is more natural and therefore better. Certainly, the nature of the energy flow and biogeochemical cycling in a carnivore-free ecosystem would be different from that in an ecosystem with its natural carnivore complement. The problem is the time scale. Carnivores like other orders of mammals have exerted their influence in ecosystems in minuscule increments over millennia.

Keith (1974) provided the following guidelines for evaluating the relative importance of a factor that may affect populations;

a) Identify its immediate demographic effects and compare its impact with other factors

b) Describe its interaction with other factors in terms of additive (the effects of two factors sum up), compensatory (a change in the magnitude of one factor produces the opposite change in magnitude of another so that their combined effect on the population is unchanged), or modifying effects; and

c) Characterise its action in relation to population density.

However it is difficult to detect interactive effects in the absence of experimental manipulation. We also need to know how predation rates vary with prey densities (Boutin, 1992), and whether predation rates are limiting or regulatory as described by Sinclair (1989). One can assess the degree of limitation imposed by a factor by studying a population at a single density using Keith's criteria, or by removing the factor of interest experimentally and observing subsequent changes in population density relative to control areas. However populations of varying densities are required to determine if a factor is regulatory.

Experimental studies potentially reveal so much more about dynamic relationships than descriptive studies. Predator removal/restocking experiments are the classic example of such manipulations. Unfortunately, simple predator removal experiments must be followed for a long time to try to separate experimental effects on equilibria and stability - which is a difficult separation to make (Taylor, 1984). Instead, one could also investigate the influence of predation by altering *prey* densities - which is precisely the design advocated by Nicholson (1957) and Murdoch (1970) as the most direct way of detecting population regulation. In this case it is important to acknowledge that both predation and dispersal, motivated by intra-specific aggression, must play critical roles (Slade & Balph, 1974). These two factors may also interact to form a complex that is too interrelated to be treated as merely the additive or multiplicative effects of predation and dispersal considered alone (Mitchell *et al.*, 1992). Notwithstanding time and budgetary constraints, the manipulative experiment that would adequately investigate predator-prey relationships would conceivably consist of a factorial arrangement of enhanced, diminished and control prey populations compounded with enhanced, diminished and control predator populations (Taylor, 1984).

The Carnivora, as the name implies, are generally predatory, and to a greater and lesser extent, all canids live by killing prey. This ecological/evolutionary truism raises three related questions in the context of conserving and managing wild canids (Ginsberg & Macdonald, 1990):

(1) To what extent does their prey limit the populations of canids, and to what extent do they limit the numbers of their prey?

(2) With respect to valuable prey, is the impact of predation by canids in general disadvantageous to people?

(3) Where predation by canids throws them into conflict with people, how might such conflict be resolved?

As previously indicated, problems are likely to arise with predation on three categories of prey: domestic stock, wild game, and endangered species, although in reality the delineation is less distinct. Nearly every species of canid has been implicated in livestock damage. Ginsberg & Macdonald (1990) reported that of the 34 canid species, 21 have been implicated to kill livestock or poultry at least occasionally. By virtue of their numerical ascendancy, black-backed jackals find themselves in circumstances under which their predation is economically significant, especially to the low-income sectors of society who depend on small livestock for their livelihood. Goats and sheep are the poor man' s cattle in many parts of Africa, especially in the moisture limited Kalahari ecosystem where other forms of agriculture are difficult to embark upon. In Botswana, whose rural populace inhabits most parts of the dry Kalahari, it is black-backed jackals that are usually blamed for excessive predation on small domestic stock.

When a farmer encounters a dead lamb being eaten by a jackal, or when a game hunter sees a pack of wild dogs devouring an ungulate carcass, they commonly feel a wrath born of competition: both farmer and hunter had wanted the prey for themselves (albeit for different purposes). But underlying such anger, is the assumption rather than proof of competition. Had the lamb or ungulate carcass been eaten as carrion, then it would already have been valueless. Livestock seen being consumed by a predator may have died of natural causes and, subsequently, been scavenged by the predator. Equally, if the predators had singled out sickly individuals that were nevertheless destined to die, then the measure of competition with man would be unimportant (Ginsberg & Macdonald, 1990; Boutin 1992; Gasaway *et al.*, 1983). If preys are destined to die from starvation, and a predator's feasting is confined to the proportion destined to perish, then the predator only acts as the hangman! Only if predation affects the breeding stock that could have otherwise survived could predation be said to be limiting a natural population. For example, during my study on jackals at Mokolodi Nature Reserve, Botswana, I documented pairs of jackals moving among the female ungulates presumably inspecting them for signs of lambing during the calving/lambing season. These jackals fed on both domestic and wild ungulate afterbirths almost immediately after expulsion. In fact, what happened in certain cases is that jackals occasionally attacked ungulates when the latter were recumbent during parturition. In such instances the partly born calf or lamb would be eaten, while the vulva of the female may also be eaten, with the result that the dam or cow may subsequently be destroyed. It is in such cases when jackal predation could potentially limit population growth and be a source of conflict.

Evidence that predators eat a given prey is not evidence that by doing so they are a pest. To evaluate pest status, much must be known of the circumstances, including both biological and economic information (Ginsberg & Macdonald, 1990; Harris & Saunders, 1993). After ascertaining the magnitude of the problem, then the costs and benefits of proposed solutions require careful assessment, and such assessment should be instituted in the perspective of local economies. If the concern is over live prey, then the evaluation of damage must exclude those that were eaten as carrion. In a similar vein, if predators take sickly individuals, the cost of their predation must be devalued by what it would have cost to care for the ailing prey.

How then, do we measure the magnitude of livestock losses that are caused by canids? Most field studies of canid feeding ecology are made from the perspective of the predator, not the prey. They give some indication of the proportion of livestock in an animal's diet. From this, if one knows the population density of the carnivore being studied, an estimate can be made of the numbers of sheep, goats, or chicken that might be lost to that particular population of canid. However, Ginsberg & Macdonald (1990) argue that when measuring the impact of canids on livestock production, "the question we need to answer is not 'what percent of the diet is composed of livestock?' or even 'how many sheep are eaten by canids?' but 'what effect does canid predation have on total livestock production?'

Basically, calves are eaten at higher rates than cattle, lambs more frequently than sheep, and predation on lambs is more common than on adult ungulates. This suggests that canid predation will be the greatest problem at times when livestock are bearing and raising young. Of course, at other times of the year, jackals are surviving on other types of food. Hence if young animals can be protected, jackals may well stop eating livestock, and switch to more easily acquired foods. Clearly the influence of jackals on domestic livestock will depend on the interactions between jackals and their wild prey. The extent of predation on livestock may be related to the quantity or quality of other prey species, from a jackal's point of view.

It is often assumed that canid predation on wildlife reduces the amount of wildlife available for human consumption and sport. Before such an assumption can be made, data must be collected on the following questions (Ginsberg & Macdonald, 1990):

(1) Is the consumptive utilisation of the prey species by humans on a scale with that of jackals or canids in general? If, for the most part, humans are the major

predators in a system, removing other causes of predation may result in only a marginal increase in human harvests.

(2) If jackals and other canids are removed from an ecosystem, or reduced in number, does the prey they eat become available to man or do these animals die from other causes? For example, black-backed jackals often specialise on young prey animals. If removal of jackals results in a greater rate of predation by other predators (e.g. caracal, birds of prey, feral dogs, etc.) or increased natal mortality from starvation and disease, canid reduction alone is unlikely to result in greater human harvests of adult animals.

The above analysis assumes that the important question to ask is how to mitigate the cost of depredation of livestock by canids. However, in many circumstances, the costs of predation may be irrelevant. Most of the time when wild predators kill domestic animals, people react instinctively, rather than logically. Despite some infinitesimal losses that may be incurred, it is those few incidents that may provoke dispirited public controversy. Such an outcry would not have occurred had domestic dogs been responsible for the losses, or had a few sheep died of starvation or disease. Predation by wild carnivores in such cases is seen as a loss that can and should be controlled; not an act of God, but the result of negligence on the part of the wildlife or game managers.

Effects of Control Operations

Predator control by humans is as old as livestock husbandry. The deliberate, often organised destruction of many mammalian predator species has been a feature of human development in Europe - and later in countries to which Europeans spread - for centuries (Reynolds & Tapper, 1996). Destruction to the point of extinction was basically practised for purposes of protection of life and commodities (livestock, game, fur, etc.). Reduction of predator numbers specifically to allow an increased harvest of some game species was mainly a nineteenth century development, while the adoption of predator control to benefit endangered species for their own sake belongs to recent decades.

Wildlife scientists and managers are fond of calling Aldo Leopold (1949) the father of wildlife management. However, many professionals overlook or ignore one of his central messages, as embodied in one of his most famous quotations: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong if it tends to do otherwise." Leopold saw a distinction between the true sustained-yield management, in which wildlife systems are harvested only selectively in a way that tries to ensure their underlying structural and functional integrity, and what I would refer to as 'farming' of these systems. Similarly, the 'precautionary principle' (Myers, 1993) also counsels us that conservation or other action should not be undertaken unless it can be shown not to be damaging.

Carnivore biologists, wildlife and farm managers regularly assume that jackal populations can be reduced without significant biological impact. 'Biological impact' is typically defined solely as numerical status: The impact is considered negligible if the jackal populations either maintains or soon recovers to about the same size. Little more than the number of animals is considered, and sometimes not even this standard is maintained. Some biologists seem willing to accept almost any behavioural variation as 'inherent'. Scavenging of dead ungulates is an important supplemental foraging activity by jackals, but should garbage eating, largely solitary maize-field canids really be regarded as jackals? Or are they the products of a lengthy subtle process of altering jackal behaviour through human persecution and habitat/prey displacement? Some examples of 'adaptability 'may instead actually serve as a warning about the pitfalls of watching for numerical signals of endangerment while ignoring virtually all else about the biology of the animals. To understand the impact of heavy ongoing public killing, and short-term government control on jackal populations and why, in general, this makes little biological sense, requires an understanding of jackal social organisation. Social behaviour is strongly influenced by inheritance (Plomin, 1990) and is therefore very much within the realm of biology.

One of the factors that will affect the efficacy of a canid control operation is the behaviour of the target animals. In a species such as the black-backed jackals where there are territorial and transient animals, it is logical to assume that the territorial and hence reproductive individuals may pose the greater risk to some agricultural interests, since the provisioning of pups is a stimulus to depredation, and the removal of the pups may as well end the problem. However, the younger and transient animals would presumably be easier to capture than territory holders within the interior of their ranges. Thus jackal control operations would be most effective after dispersal and immediately before the whelping season. Any mortality would then be additive and also limit production the following season.

Black-backed jackals are territorial animals, and territories being specific defended areas, are often considered as spatially consistent throughout the life-span of an individual (e.g. Brown & Orians, 1970; White & Garrott, 1990). However, in some circumstances territory size and configuration may be adjusted to incorporate changes in occupancy of neighbouring territories or changes in the distribution of certain limiting resources (Kruuk & Macdonald, 1985; Doncaster & Macdonald, 1991). Relative values of mortality for dominant animals rather than overall values are likely to be of greatest significance for territory stability since these are the individuals which spend most of their time in active territory maintenance and defence. (White, *et al.*, 1996). Hence any mortality of dominant animals will act to destabilise existing social hierarchies, and consequently, surviving animals may make opportunistic adaptations to their behavioural patterns to exploit resources in neighbouring territories made available by the death of a dominant animal. In cases where mortality rates of dominant animals are high, such destabilisation will be more frequent, and spatial organisation will be unstable as a result.

Heavy, indiscriminate harvest or control of a highly social species could hardly be expected not to reduce and fragment its sociality and eventually produce less selectivity in other important aspects of behaviour (Haber, 1996). Similarly it is difficult to imagine that such killing would not add greatly to the natural variations in territory boundaries and overall territory mosaics and that it would not simplify homesite traditions within these territories. Greater variability in prey kill rates and territory-size versus group-size relationships is probably also explained to a large measure by social changes and by the increased availability of temporary vacancies within territorial mosaics, which allows for more expansion of both surviving and new territories. It is difficult to dissect the impacts of jackal exploitation because detailed comparative information on behaviour from both exploited and protected jackal populations is scarce. Major differences in prey types can greatly influence the degree of sociality (Bowen, 1981) and consequently, foraging behaviour.

Under conditions of moderate to heavy exploitation, with frequent replacement of key individuals, it would be difficult for jackals to maintain stable, well-defined dominance relationships such as has been reported in other studies (Ferguson, 1978; Moehlman, 1983, 1986; Rowe-Rowe, 1986; J.D. Skinner, pers. comm). There would likely be more overall variation in most relationships, dominance and otherwise. Territorial behaviour and hunting would be determined more by interactions of various jackals than by the behaviour of the same core of high-ranking group members. Competition would be less restrained, and when group size continued to increase, there would probably be less of a difference in consumption rates among adults, lower average per-adult rates of consumption per prey kill, and shorter refractory periods leading to more time spent hunting, a continuing increase in kill rates, and probably more of a tendency for the group to try and expand its territory (Haber, 1996). With heavy exploitation, especially ongoing harvest, there is bound to be much less opportunity for well-established groups to persist in relative isolation from each other.

Additional kill rate differences reported for exploited populations might involve subtler social or other types of distortions. Hayes *et al.* (1991, in Haber, 1996) suggested that the sharp increase in kill rates (by wolves *C. lupus* on moose *Alces alces*) they observed for groups reduced to pairs following heavy control was due to two factors: 1) The unusually large territories that colonising pairs were able to occupy initially provided them with an increased selection of potentially vulnerable prey. 2) Higher per-kill losses to competitors, especially ravens, prompted them to spend more time hunting. It is also quite plausible that heavy broadcast harvest or control implies a greater likelihood that pairs can settle into area and hunt sizeable territories with less risk of attack from nearby established groups.

In those situations where jackals have been shown to depress ungulate population levels, the most frequent management response is to kill the jackals. But jackals, like many canids can be very productive (Van Heerden, 1988). Yearly variations in reproductive output may primarily be a function of changes in pregnancy rates, especially yearlings, in addition to changes in litter size, and post-natal survival of young pups may have an important influence on recruitment. In many areas canid populations may be food-limited, and this may be a major factor limiting pup survival. An increase in the proportion of young animals is frequently recorded in canid populations following substantial levels of harvest. The combination of density-dependent effects on reproduction, mortality, and dispersal makes it nearly impossible to reduce abundant canid populations in anything except local areas. For example, a wolf pack usually produces one relatively large litter of five to six pups. When populations are not saturated, 22-41% of all wolf packs produce multiple litters (Harrington *et al.*, 1982; in Ginsberg & Macdonald, 1990). In other areas, only 10% of the packs may produce multiple litters. Hence reducing wolf numbers may result directly in a large number of young wolves (Ballard, Whitman, & Gardner, 1987). What this means is that even when suffering an annual mortality of 50%, a wolf pack can remain stable in its numbers. Storm (1977) also found that when the density of foxes was reduced to 0.04 km^{-2} by control, dispersal was responsible for repopulating areas to a density ten times that level within four years. Thus, although reduction may result in reduced numbers, it can also lead to several new waves of immigration and an increase in births. Nature abhors a vacuum, and carnivores appear to be no exception to natural laws. Jackals are frequently killed as control measures in areas where ecological factors such as abundant food have made them a pest. But for every predator killed, there may be another just waiting to move into such prime habitat. A local lethal control for wolves in Canada did not decrease wolf numbers but led to an increase in immigration with new wolves moving into the area to compensate for artificially low densities (Ballard *et al.*, 1987). This clearly shows that even total removal will only result in a temporary respite from canid predators unless an area is completely isolated.

Other likely impacts of harvest and control include disruption of learning, increased population-wide mixing, and different within- and between-group genetic patterns, all of which would be difficult to identify with the sketchy comparative information available. However, these impacts might be among the most important. Disruption in the flow of learning from generation to generation would result in fewer, simpler learned behavioural traditions and in general a diminished role of these behaviours (Haber, 1996) that help adapt individual family groups to the specific resources and other unique features of each area.

Jackals commonly live 6-7 years or more in well-established family groups subjected to little or no hunting or trapping (Lombaard, 1971; Moehlman, 1983, Rowe-Rowe, 1986). In contrast, few jackals live for more than 4-5 years in exploited populations. This implies a high rate of turnover and young age-structure. Consequently there is much less opportunity for jackals in these populations to accrue and transfer information from one generation to the next via the prolonged dependency period and complex learning sequences important to jackals under natural conditions (Moehlman, 1983, 1986).

Jackal social behaviour may be remarkably adaptable, but the adaptations are primarily for food acquisition, not defence against sustained, heavy predation. It does not necessarily follow that jackals will be able to survive heavy exploitation and control just because they have held their own numerically against heavy killing for the past century or so. A few decades of heavy killing amount to the blink of an eye compared with the far longer period of evolutionary time over which jackals have evolved in response to the opposite pressures.

It surely is surprising how we seldom practice what we preach. We have managed to artificially select for particular breeds of stock in agriculture for centuries, but we shy away from the fact that by killing jackals for control purposes, we may be unwittingly doing the same. In the longer term natural selection operates against controlled killing: only jackals that survive the cull can breed, which selects for individuals less easy to kill. And these may well be the extant jackal populations that we find most difficult to control today because, relative to those who perished, their behavioural repertoire allows them to withstand the vagaries of human persecution.

Effects on Animal Population Densities

The effects of control on canid numbers are particularly difficult to evaluate, since there are a few absolute and relatively few reliable comparative density estimates for canids. Hence there have been few attempts to measure long- or short-term canid population changes. Density estimates based on the number of social groups per square kilometre are generally of little use for evaluating the effects of control unless the actual number of animals is known.

The primary objective of predator reduction was to safeguard domestic livestock and poultry, but also to promote human safety and to benefit game species (Reynolds & Tapper, 1996). As time went by, and larger predators became increasingly uncommon or even extinct, attention shifted to smaller predators. It is possible that in general the removal of top predators allowed smaller predators to increase numerically and expand their geographical distribution, because predation within 'guilds' of predators (or 'intra-guild predation') is increasingly proving to be important in shaping predator communities (Polis, Myers, & Holt, 1989; Palomares, Gaona, Ferreras, & Delibes, 1995). In any case, small predators certainly benefited from changes in land-use.

Large mammalian carnivores may help control populations of medium-sized, opportunistic predators in landscapes with some degree of habitat fragmentation. Soule' (1988) suggested that mesopredator release is a general phenomenon and that smaller omnivores and predators undergo population explosions, when large dominant predators are extirpated. In Yellowstone National Park (Wyoming, USA), coyotes *Canis latrans* expanded in population after extirpation of wolves (*C. lupus*) and assumed many of the ecological characteristics and functions, including pack formation and predation on large ungulates (Noss, Quigley, Hornocker, Merrill & Paquet, 1996). Furthermore, in at least one instance (Sargeant *et al.*, 1994, in Reynolds & Tapper, 1996) it is clear that the destruction of coyotes (*C. latrans*) to protect livestock in the North American prairie pothole region changed the distribution, abundance and predation impact of yet another smaller canid, the red fox (*V. vulpes*). In a similar vein, in sub-Saharan Africa, black-backed jackals have also been implicated as being capable of assuming the predatory role of large African pure predators, where the latter have been extirpated (Estes, 1967). In particular, an increase in the numbers of caracals (*C.caracal*) after extensive eradication campaigns of jackals has been observed in southern Africa (J.D. Skinner, pers. comm.), simply because the latter usually suppresses the population of the former through intra-guild predation.

Although the idea of 'predator pits' (Newsome, 1990), i.e., that there is a limited range of population densities at which a predator can control a prey population remains theoretical, it is of extreme practical importance for the control of canid populations since injudicious control may result in unwanted numbers of other pests. Newsome, Parer & Catling (1989) found no effect of fox predation on rabbit population declines that were due to arid conditions and poor pastures. However, after rabbit numbers collapsed, foxes were important in suppressing population growth. Newsome *et al.* (1989) then introduced the concept of environmentally modulated predation. Sinclair, Olsen & Redhead (1990) also came to very similar conclusions with mouse (*Mus domesticus*) populations in Australia; at lower prey densities, the impact of predators was density-dependent and regulated prey densities, whilst at higher densities the total predator response was inversely density-dependent and predators were unable to regulate the mouse population.

Furthermore, generalist predators may have a stabilising influence on prey numbers, since they include a considerable proportion of rodents in their diet only when rodents are common, and switch to other prey during periods of rodent scarcity (Andersson & Erlinge (1977).

Epidemiology of Jackal Rabies

Since black-backed jackals have also been implicated in the transmission of rabies in southern Africa (e.g. Meredith, 1982; Bingham & Foggin, 1993; Alexander, *et al.*, 1994), the transmission of the rabies virus from infectious to susceptible jackals is a direct consequence of the social behaviour of the infectious individuals. An understanding of the ecology of the reservoir animal population is basic to the development of an effective rabies control programme. The persistence of rabies and the success of attempts to control it depend fundamentally on a measure known as the contact rate (Bacon & Macdonald, 1980; Macdonald, 1980a, 1982). The contact rate for a population is the average number of susceptible individuals infected by each diseased animal (Prozesky, 1982; Bailey, 1975, in Ginsberg & Macdonald, 1990; White, Harris & Smith, 1995). Although radio-tracking has enabled the movements of jackals to be studied in detail, quantifying the contact behaviour of such an elusive species as the black-backed jackal requires more than one individual to be radio-tracked continuously and simultaneously with a high degree of accuracy. The need for many animals in a relatively small area to be captured and radio-collared, combined with the fact that simultaneous, continuous radio-tracking is a very labour-intensive operation, has meant that such work has not been undertaken so far on any vertebrate host (White *et al.*, 1995). Contact rate is not constant, but a complicated function of the social organisation and density of vectors, and thus of the frequency of meetings between them. From basic biological premises, many factors could influence the rise and fall of the disease: the number of jackals, the density of the population, their contact rate; the virulence and incubation period of the infection (Bacon & Macdonald, 1980; Macdonald & Bacon, 1982; Prozesky, 1982), etc. Using computer simulations it is possible to get a fair idea of what is actually happening in nature. But most of these parameters (e.g. reproductive rate and contact rates) depend on vector (in this case, jackals) behaviour; if we are to understand how jackal rabies spreads, and how, rationally, to stop it spreading, we must understand jackal sociobiology.

Human Perceptions

People possess certain basic values toward animals and nature that inevitably affect their perceptions of individual species. Second, people's attitudes are significantly influenced by the physical and behavioural attributes of a species, including the animal's size, perceived intelligence, morphology, mode of locomotion, cultural and historical associations, and other factors. Third, people's knowledge and understanding of a species can influence attitudes, including factual, conceptual, and conservation awareness. Finally, perceptions are affected by past and present interactions with particular species, including conflict, recreational use, property relationships, and management status (Kellert, Black, Rush & Bath, 1996).

Why should carnivores be conserved if their activities conflict those of man? Ginsberg & Macdonald, (1990) offered an appealing explanation: "Perhaps it is insight into their individualism won through our association with domestic dogs, perhaps it is the ability of some of them to withstand the worst that man can throw at them, perhaps it is that we see some reflection of ourselves in their opportunism, or perhaps it is simply the transfixing elegance of their jaunty grace. Whatever the pot-pourrie of reasons that blend into their appeal, the 34 species that comprise the family Canidae are special. They are special because they have, as perceived friend and foe, preoccupied the imaginations of mankind for millennia. They are special because the breadth of their adaptations makes them enthralling to science. They are special because the contradictory facets of their relations with people perplex the conservationist. The possibility that we are heedlessly, perhaps needlessly, mismanaging many of them is saddening; the probability that our negligence will force several more to extinction should fill us with bottomless dismay".

The relationship between jackals and humans has never been amicable due to predation on game and livestock. Farmers and ranchers have consistently expressed the most negative attitudes towards predators, a sentiment generally motivated by fear of economic loss. Still, perception is often stronger than reality, and depredation by any predator of an individual rancher's stock can inflict severe emotional, financial, and political consequences. The path of least resistance to a state resembling harmonious coexistence of predators and livestock producers involves limiting the opportunity for conflict. Improvement in animal husbandry may not be costly and may produce significant results. Proper disposal of livestock carcasses, either those killed by predators or those resulting from other causes of natural mortality, appears to reduce subsequent predation. Confining animals at night, or during their infancy, when they are most vulnerable, also reduces losses to predation. Proper disposal of garbage limits jackals access to otherwise easily accessible food resources, eventually restricting the ability of jackal populations to increase.

Why are so many losses that appear to be due to natural causes, or other predators blamed on a particular species like lions and wild dogs? In many cases, the blame for such misreporting is, in part, due to abuses of policies developed to protect those larger carnivores. In many parts of the world, where large predators are rare or endangered, farmers and game ranchers are compensated for losses due to lions and wild dogs (e.g. in Botswana and Zimbabwe), but not for other causes of livestock mortality. Hence kills known to have been made by black-backed jackals, foxes, and feral dogs are called wild dog kills so that a farmer can collect compensation (Ginsberg & Macdonald, 1990; Reynolds & Tapper, 1996; pers. obs.). However, compensation is not a form of predator control, but a form of governmental recognition that the costs of predation should be borne by the public at large. Compensation spreads the risk to individual farmers, which can be considerable even if regional losses are low. As noted above, compensation without confirmation of canid depredation can lead to abuse of the system, rather than justified claims for compensation.

Some carnivore species, such as lions have been protected to the point that they are threatening trailists in national parks or people living in proximity to parks. Still, others like black-backed jackals have adapted so well to human development, which often removed their competitors and enemies, that they are now more numerous than ever. So, we are entering an era which may be more contentious than in the past because when carnivores interfere with human activities, they aren't merely an aggravation like impala eating grain on fields; they also eat livestock (Mills, 1991). In most cases, conflicts of people with carnivores represent a more serious and urgent problem to management agencies than other kinds of complaints. This may clearly more than offset the creature's charisma, an attribute sometimes advanced for their conservation. When these factors are added to the growing trend towards wildlife management by public referendum, inequities and conflicts are inevitable. For example, the multitude of voters in cities who are unaffected by any of the negative impacts of carnivores can simply outvote rural residents who bear the brunt of the damage. It is ironic that this simple majority-rule type of wildlife management is basically the same approach that extirpated carnivores many years ago. There may not have been public referendums at that time, but there were bureaucrats acting contrary to scientific opinion but bending to public will.

Any effort to conserve biodiversity is bound to be difficult at a time when the human population is growing exponentially, and everyone worldwide wants to live like the rich, extravagant members of our species in most parts of the Northern Hemisphere. Conservation requires compromises and concessions from everyone and is nearly always accompanied by biological tragedy (Noss, 1996). Even the most stubborn optimists know in their hearts that unless some plague or other factor brings human population and consumption down to sustainable levels, and unless the prevailing attitudes of humans towards nature changes radically soon, mass extinction is probably unavoidable. Some species will almost certainly go extinct whether or not we try to save them; other species may go extinct if we do nothing to help them but may survive regardless of what we do. So, it makes sense to focus conservation programmes on the middle group of species, those that are in trouble but have a good chance of surviving if we help them.

The ultimate challenge is changing human attitudes, and the proximate challenge is offering these animals sufficient security until human attitudes change. But changing human attitudes through education may take generations to have an effect inasmuch as attitudes towards the animals have been moulded for hundreds of years. Conservation of carnivores and other demanding species will always be inconvenient (Noss, 1996). It will always be violently opposed by some people, and therefore politically volatile. Conserving animals that are capable of spreading disease, killing, and eating us and that need large, wilderness areas requires great commitment on the part of conservation biologists, activists, land managers, and political leaders, and a good bit of tolerance on the part of the people who live, work, and play in carnivore habitat. Hence the predatory activities of black-backed jackal on domestic stock has functioned as a particularly powerful barometer of changing and conflicting attitudes towards wildlife in most parts of Sub-Saharan Africa. It is evident that the management of MNR and livestock owners perceived that they had a significant problem with predation on smaller ungulates and livestock, respectively. An economic loss of this magnitude while perceived as a problem by small livestock owners, may not be great enough to warrant action by the government. Such a programme might be more costly than the total annual loss to the herds, though from the standpoint of public relations such a programme may be desirable. Most methods of jackal control are available albeit at a cost.

The following criteria are a suggested blueprint for the conservation and management of black-backed jackals in particular, and other mammalian predators, in general. First, field research must play a primary role. Without baseline information on the status of the species, its principal prey, and its range and habitat requirements, sound conservation planning and management are impossible. Secondly, once baseline biological data are available, it then becomes essential to expand the conservation equation to include relevant cultural, economic, and political factors. Conservation does not occur in a vacuum, and understanding the broader context is essential to long-term success. Thirdly, based on such a broad understanding, it is then possible to design and implement more comprehensive approaches to conservation. Finally, there should be monitoring and feedback. Good conservation is a dynamic process. Techniques must be developed and personnel trained to replicate initial surveys and provide updated information, not only on status of the predatory/prey populations, but also on habitat conditions, and the broader socio-economic context. Such information must then be made available to decision-makers so that they may adapt their management plans and practices. Without such monitoring and feeback, conservation is reduced to mere crisis management. But conservation biology or wildlife management should not become a science of doom.

The foreregoing discussion illustrates two points: a) that there are substantial management problems concerning species such as jackals which are not endangered, and b) that modern techniques offer ecologically exciting solutions to wildlife management problems. I fully recognise that the particular propositions I have propounded have far greater conceptual than prescriptive power. However, prescriptions and cookbook approaches should be avoided in conservation biology and wildlife management because the systems with which we work are specific and endlessly varied in time and space. No single detailed prescription can be of much use for more than a single system.

SUMMARY

The objective of the present study was to investigate black-backed jackal behavioural ecology at Mokolodi Nature Reserve (MNR), Botswana, with particular emphasis on movements and jackal predation on impala. An offshoot of the present study also sought to explore the prevalence of jackal rabies in MNR and adjacent agricultural areas. Radio telemetry (supplemented by direct observations) was selected as the tool for studying behaviour, movements, social organisation, and also to assist in estimating jackal density in the reserve. Faecal analysis (supplemented by analysis of stomach contents), based on the identification of prey remains in faeces, was chosen as the method to determine jackal diet.

Spatial Utilisation and Activity

Jackal behavioural activity patterns were investigated during standard circuit surveys, through focal animal sampling, and opportunistically. The number of black-backed jackals fluctuated between months and on a seasonal basis (Table 1 & Figure 1). Generally it increased throughout winter and decreased during summer. Fewer jackals were seen between October and February. "Hunting/foraging" (28.7%, n = 181) was observed significantly more often than any other behavioural activity, followed by "locomotion" (23.8%), "flight" (21.2%), “resting” (14.4%), and “interactions”, in that order.

Jackals in MNR exhibited a bigeminous activity pattern (crepuscular and nocturnal periods). Periods of activity occurred from 17h00 to 22h00, and also from 05h00 to 08h00, with peaks around 18h00 and 06h00. In general, the frequency of occurrence of each activity type differed according to the part of day (24-h period) it was recorded. Peaks of activity suggested that jackals synchronised their activity with the activity of their animal prey, and the relative inactivity of their major predator (man) as field observations revealed. The apparent persecution of jackals by farmers in the surrounding areas could account for the enhanced vigilance behaviour of the former. There was a seasonal change in the general activity periods of jackals at MNR and this was probably for thermoregulatory purposes. Total activity was more pronounced for winter (27.2%), followed by spring (21.7%) and autumn (20.8%). The two summers (1995-96 and 1996-97) revealed similar proportions of total jackal activity.

Home-range size was determined through radio-tracking of known individuals, and the programme CALHOME (Kie et al., 1994) was used to analyse range-size using the minimum convex polygon (MCP) method (Mohr, 1947). The mean aggregate home-range size for the 3 radio-collared animals was 15.9 km^2. Seasonal home-range sizes differed between seasons with a tendency for range expansion during the dry winter months. Mean seasonal home-range size was also highest for the winter period (20 km^2). On the basis of social organisation (Rowe-Rowe, 1982) and the mean of the minimum seasonal home-range estimate of 8.2 km^2 it is suggested that MNR supports a jackal population of at least 13 individuals - a density of 0.4 jackals/km^2. The overall seasonal density estimates based on nightlighting sessions (Meia & Weber, 1992, 1996) lay between 0.1 and 1.8 individuals per km^2.

Black-backed jackals in MNR utilised wooded cover for denning, predator avoidance, and foraging purposes. They did not use habitats according to their proportional availability in any season. In all seasons jackals used open savanna grassland, Croton/Combretum tree savanna, and seasonal floodplains less than expected from their availability, and used tree and bush savanna, semisweet mixed bushveld and agricultural areas much more than expected, the latter increasingly so during the spring and summer months. Agricultural areas were used more than expected during both the 1995/96 and 1996/97 summer seasons, and less than expected during the intervening autumn, winter and spring seasons.

More jackals were killed by trapping and hunting outside of their home ranges than along the periphery and no residents were killed within their respective home ranges. This suggests that young dispersing jackals may be more susceptible to hunting than resident jackals because they are away from familiar terrain. However, avoidance of roads and hunters during daylight hours are learned responses, and younger jackals may be more susceptible to hunting primarily in early autumn. Vulnerability may be more a function of lack of experience rather than unfamiliarity with the surrounding territory (Roy & Dorrance, 1985). Extra-territorial excursions were commonly witnessed in this study area particularly those directed towards the surrounding farming areas and human settlements. Food stress upon groups entailed hazardous extraterritorial movements and may have caused some human-related deaths (i.e. concealed natural mortality). Possibly, human-caused mortality altered group dynamics of some families but not sufficiently to invalidate the description of jackal social organisation discussed in the present study.

In the family pairs of jackals observed in the present study, the home ranges of individuals did not overlap totally, but corresponded more closely to the situations observed by Ferguson et al., (1983) who noted that subordinate individuals only use a small part of the group range. There was no overlap between the ranges of adjacent pairs, but it appeared that jackals entered the range of adjacent groups to access some rich feeding patches such as anthropogenic food sources and carcasses.

Foraging Ecology

Potential animal and plant food available to jackals varied throughout the year because of its seasonal character. Jackals were observed foraging during 37.1% of 786 hours of focal animal observations (including 62.9% of those in which the jackal was foraging when the observation began) and opportunistically in many other instances. It is quite evident that jackals strayed from their territories to devour fresh kills or carrion elsewhere. Hunting accounted for 76.0% (n = 355) of all foraging observations. Scavenging was observed 43 (9.2%) times, while gathering accounted for 14.8% (n = 69) of all feeding observations. Jackals were observed attempting to kill prey on 355 occasions, successfully killing and eating prey on 101 (28.5%) occasions. Of all feeding instances, 21.1 % were kills of rodents. Catches of rodents accounted for 36.6% (n = 45) of all successful hunting attempts.

During the calving/lambing season of ungulates, pairs of jackals could be seen moving among the females presumably inspecting them for signs of lambing. Jackals at MNR fed on both domestic and wild ungulate afterbirths almost immediately after expulsion. In addition, concealed lambs were killed by pairs of jackals searching through impala lambing grounds, probably using olfactory cues. Impala lambs were captured due to total exhaustion after persistent attacks, by being bitten under the neck, and then persisting with the pressure. Mostly, the jackals waited until the female had given birth and then worked as a team; one of the pair distracting the female, while the other attacked the young. However, attacks on parturient impala dams were also documented. Frequently, only lamb remains in the form of uneaten portions of legs were found. Most causes of lamb mortality were difficult to determine in MNR because remains of lambs (when there were any) were located a long time after the lamb's death and were badly mangled and had begun to decompose. Jackal predation on neonatal impala as well as on yearlings and emaciated or senile adults, indicates jackal potential to limit impala population increase in MNR, particularly through natal recruitment, but this merits further investigation. At a conservative estimate, overall, at least half of the annual calf crop fell prey to jackals during the 1996/97 lambing period alone. The number of impala lambs that succumbed to jackal predation therefore constitutes a significant proportion of the impala population, and in conjunction with other natal and adult mortality factors, can considerably limit, or even depress population levels.

Furthermore, scat analysis revealed that mammals were the most common food resource (32.4%, n = 518), followed by anthropogenic items (14.8%), fruits (12.9%), invertebrates (10.8%), birds (8.5%), unidentified items (3.5%), and reptiles (1.4%). Jackals changed their diets when prey species became vulnerable to predation. For example, impala lambs were most vulnerable when less than two weeks old. Jackals took advantage of this vulnerability, as field observations suggested. Seasonality of prey occurrence in scats was pronounced for small mammals, miscellaneous fruits and invertebrates: Small mammals (mostly rodents) were more frequently eaten in the dry season and fruits during the wet season.

Because little to no detailed information is available on the interrelationships between jackals and prey prior to the increase in modern man's influence on wildlife and habitats, the character of that relationship under pristine conditions remains to a large degree speculatory. As human encroachment and agriculture continue to reduce wildlife habitat in Botswana and much of sub-Saharan Africa, management decisions must be founded on a precise understanding of wildlife ecology and population dynamics. In particular, one important aspect of ungulate ecology is the extent and causes of lamb mortality. Although it is usually impractical to eliminate or even reduce the major factors in lamb mortality, an understanding of these factors is necessary to further our understanding of herd dynamics and improve the predictive capabilities of wildlife managers (Kunkel & Mech, 1994). Although the general effects of predation on ungulate populations are difficult to assess without intensive studies, monitoring prey with radio telemetry is a more direct method of measuring losses to predation. Collaring dams and lambs for prompt relocations of dead and live animals as indicated by radio signals (mortality sensors) can provide better tally of losses to predation or other mortality factors, thus improving diagnostic opportunities.

Jackal foraging ecology reflects the availability of a wide variety of food items and the differential vulnerability of prey. Given the addition of anthropogenic food resources and altered habitats in human settlements, black-backed jackals' diet at MNR was more diverse and differed from that reported in relatively undeveloped areas (Wyman, 1967; Hall-Martin & Botha, 1980; Smithers, 1971; Lamprecht, 1978a; Rowe-Rowe, 1983). Direct observational data and scat analysis reported here indicate that jackals are opportunistic feeders, that eat carrion as well as practically any animal they can easily overpower. Jackals are highly adaptable animals being able to exist as predators on small game and livestock, scavengers, eat insects or rodents, and as indicated in the present study, also feed on anthropogenic food sources, wild fruits and agricultural crops. The relative importance of scavenging and predation in the lives of jackals varies according to both time and place. Where pure predators and their prey are plentiful, jackals may live largely as scavengers if they themselves are not too numerous to engage in intraspecific competition (Estes, 1967). Where pure predators are scarce, as is the case in MNR, jackals become very active hunters; in fact they have been implicated to even partially fill a pure predator's vacated niche. Like other predators, jackals behave so as to maximise their fitness, which is often done by maximising their net energy intake. In fact, a predator's prey choice is not only a consequence of prey energy content, but it also depends on the predator's success in finding, handling, and consuming its prey. Other studies on jackals' diet have revealed similar feeding behaviour (e.g. Wyman, 1967; Bothma, 1971; Smithers, 1971; Rowe-Rowe, 1976), albeit with some deviations from the findings of the present study.

Social Behaviour and Organisation

Direct observations revealed that there was little evidence of jackal groups and I believe social structure in MNR mostly comprised solitary residents, transients, and members of resident pairs. Jackal groups were uncommon probably because of heavy persecution by humans and a food base independent of large prey. Hunting of jackals by man may depress group sizes both directly and by creating vacant territories and so reducing the costs of dispersal. Seasonal variation was also observed in the number of single animals, two's, and groups of 3 to 4 individuals. Seasonal differences were quite pronounced for single animals and groups of two, and followed a pattern that was related to reproduction and social behaviour. Family groups usually consisted of two parents and from 1 to 3 young. Most sightings of single animals were recorded during autumn. Pairs were most numerous in winter and this was probably the pairing-mating season, as the first cubs were seen during August-September

Social encounters within pairs or family groups included social grooming, play fighting, and running play. Intra-group aggression was in connection with incidents involving ano-genital sniffing of females by males, and sometimes some attempts at mounting. The social status of helpers was always submissive with respect to the parents, and these subordinates did assist their same-sex parents in territorial defence against same-sex conspecific intruders. Encounters between heterosexual individuals of different groups never ended in biting and/or chasing, whereas this seemed to be the rule in encounters between two strange females, and between two strange males. Encounters between neighbours were less aggressive than between apparently strange groups.

Territories were maintained directly by aggressive and agonistic interactions, and indirectly by scent marking (olfactory) and vocalisations (acoustic). Black-backed jackals at MNR exhibited territorial behaviour according to the following criteria: 1) stability of home ranges throughout the study period; 2) no overlap between adjacent pairs; 3) frequent inter-group boundary chases and clashes; 4) scent marking behaviour; and, 5) vocalisations. Dens were used by black-backed jackals for two different activities: 1) as resting sites during the non-active period (non-breeding dens), and 2) as sites for whelping and rearing of pups (breeding dens).

Finally, the importance of understanding jackal social behaviour and organisation in the epidemiology of jackal rabies is also underscored. Furthermore, conservation and management options are discussed in relation to their likely impact on jackal behavioural ecology, effects on the ecology of other species, and the role of the human dimension. Broadcast killing of jackals clearly is of limited value in the long-term. And the paradox remains - that an attempt to reduce jackal impact through reducing numbers may so disrupt the jackals' social milieu, by creating vacua and promoting movement - and this could theoretically increase jackal impact even at lowered densities. Some recommendations and suggestions are then offered for a holistic approach to the conservation and management of predator populations.

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