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*),

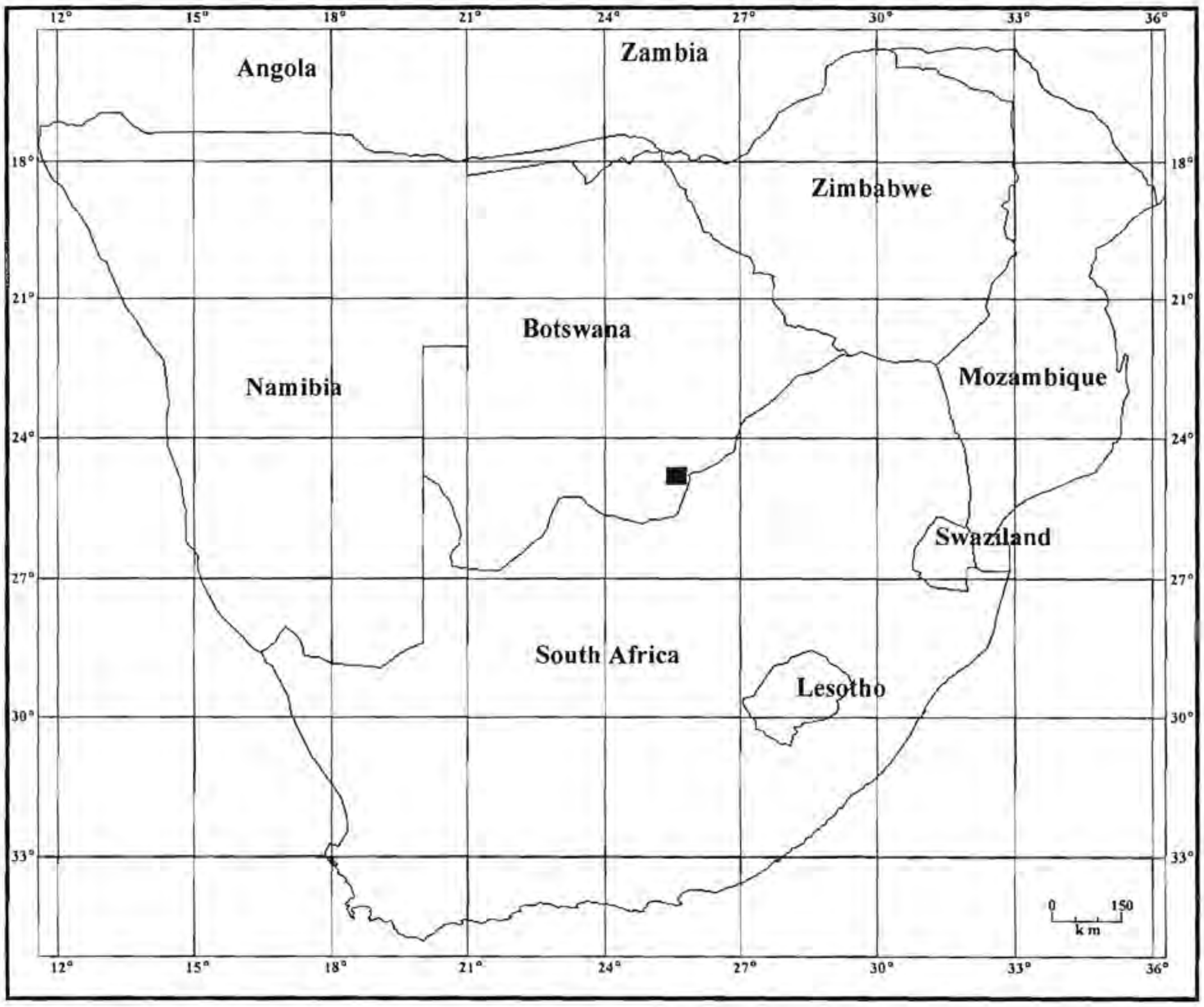

Fig. 1. Geographical location of Mokolodi Nature Reserve in Botswana, Southern Africa.

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 ($\chi^2 = 33.9$, *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).

Month/Year	**Sampling Period**				**Mean no. of jackals per session**
	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	

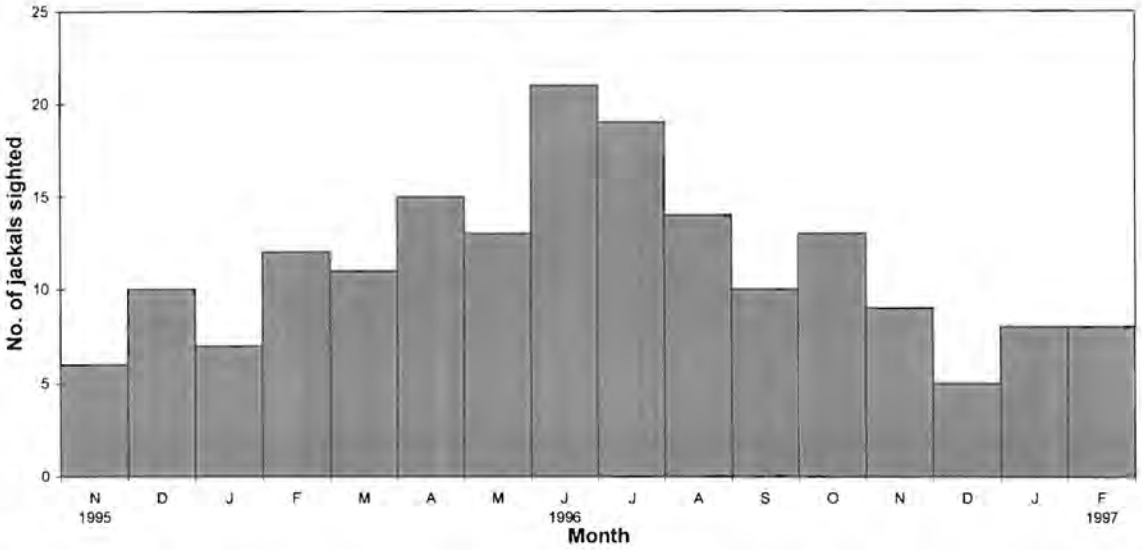

Fig. 2. Monthly sightings of black-backed jackals in Mokolodi Nature Reserve during standard circuit censuses

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).

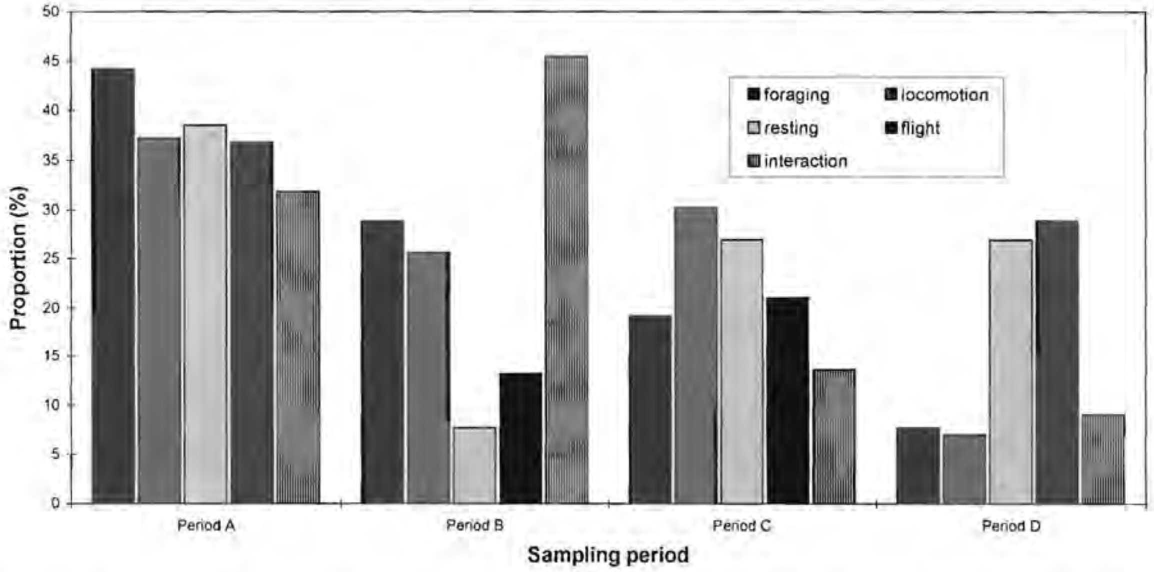

Fig. 3. Frequency of occurrence (%) of different activity types during the four sampling periods (A: 16h00-22h00; B: 22h00-04h00; C: 04h00-10h00; D: 10h00-16h00).

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.

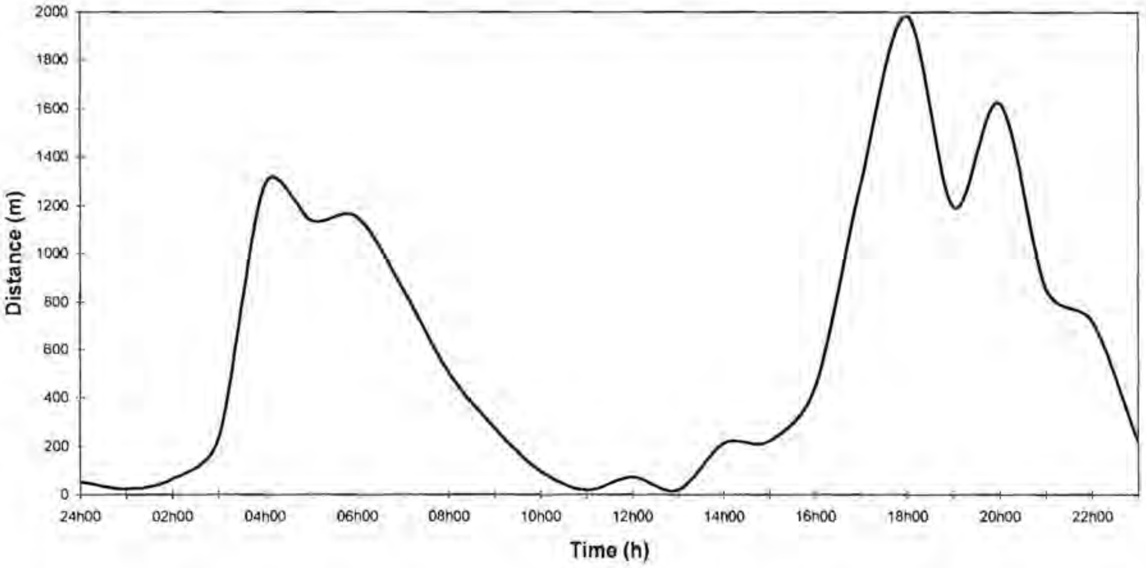

Fig. 4. Combined average activity patterns of two radio-collared black-backed jackals in MNR, estimated as the mean distance (m) travelled by hour, as a function of time of day (n = 10, 24-h tracking periods).

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).

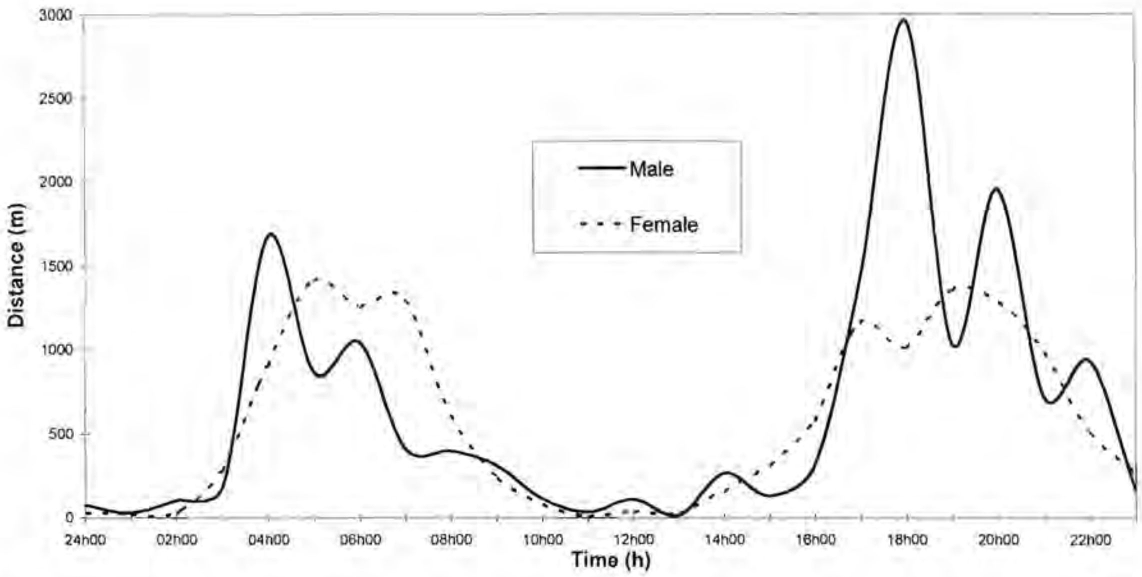

Fig. 5. Diurnal and nocturnal activity patterns of two radio-collared jackals at Mokolodi Nature Reserve

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, $home\ range = 0.11 \times body\ weight^{1.36}$ (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).