Behavioural ecology of the caracal in the Kgalagadi Transfrontier Park, and its impact on adjacent small stock production units

by

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Abstract

A study, to investigate the behavioural ecology of the caracal and to try to quantify the potential effect that these medium sized felids have on small stock on Namibian farms bordering the Kgalagadi Transfrontier Park, was undertaken from June 2000 to August 2002. It was necessary to capture caracals, which had ranges in the vicinity of the Namibian border, to fit them with radio-collars to facilitate the monitoring of their movements. Although many studies on small predators have been conducted, the methods of capture are constantly being modified and refined. Nine caracals were caught during 632 trap nights. Refinements of the methodology applied in the use of cage traps for the capture of small carnivores and the immobilisation of the captured animals are described. These refinements include the use of a crush plate in conjunction with a hand held syringe to immobilise animals caught inside cage traps. Non-target animals were frequently caught in cage traps set for caracals, demonstrating the non-specific nature of such trapping efforts. Data relating to the numbers of non-target animals caught during this study were included to illustrate the potential of this capture technique for the capture of other small carnivores.

The movements of radio-collared caracals were monitored, not only to establish whether the range sizes of caracals in the Kalahari are larger than those of caracals in more mesic regions, but also to determine whether caracals, with ranges in the vicinity of the Namibian border, transgressed this border. It seems, from the data gathered, that caracals in the Kalahari do have larger ranges than those in other areas in southern Africa. Additionally, it is clear that caracals do transgress the Namibian border and that the ranges of caracals in this region are contiguous with those in Namibia.

The spoor of caracals were followed with the assistance of an experienced Kalahari San tracker. Much insight into the ecology of elusive and principally nocturnal predators can be gained by spoor-tracking such animals and recording their behaviour based on the evidence and imprints that they leave in the soft sand of the Kalahari. Data gathered whilst spoor-tracking caracals was used to analyse the habitat selection and behaviour of these animals.

Although the vegetation of the southern Kalahari is described as homogeneous, there is definite stratification of the vegetation throughout the dune-veld. By quantifying this

vegetation stratification it was possible to investigate whether caracals showed a preference for any vegetation component. Caracals tended to use the dune streets less than would be expected if they were using all the vegetation components in proportion to their availability.

One of the primary activities of any predator is hunting. By spoor tracking caracals it was possible to stratify the hunting behaviour of caracals into a series of component behaviours including, crawling, stalking, crouching, taking-off, chasing and pouncing. Based on these records of hunting events the hunting behaviour of caracals in the Kgalagadi Transfrontier Park was modelled and a logical sequence of behaviours that were most likely to result in a successful hunt was defined. All hunting events were stratified according to their component behaviours and the relative hunting success for each sequence was recorded. It appears that caracals in the Kalahari tend to lie in ambush for their prey rather than employ prolonged stalks while hunting.

The diet of caracals was analysed based on faecal analysis and on records of kills. This analysis was conducted to establish what caracals in the Kalahari prey upon and whether caracals, that have ranges in the vicinity of the Namibian border, prey upon small stock. It was found that caracals prey primarily on small mammals, especially rodents. Additionally, it was found that caracals prey upon a variety of small and medium sized predators. Although there is an abundance of avian prey available, caracals did not exploit this resource to any great extent. Caracals do prey on small stock, especially during the colder months.

Brant's whistling rats are common in the Kgalagadi Transfrontier Park and as such it was anticipated that they would contribute substantially to the diet of caracals. In this case

caracals might actively attempt to forage optimally for Brant's whistling rats. Data were gathered by conducting a series of transects and recording the occurrence of Brant's whistling rat colonies within these transects. These data were compared to those of the incidence of caracals encountering Brant's whistling rat colonies during their movements. It seems that caracals may employ an optimal foraging strategy relative to Brant's whistling rats during the hot season but not in the cold season.

Spoor density is an index of predator population density. Spoor counts were done to determine whether the caracal spoor density along the Namibian border was greater than that in the interior of the Kgalagadi Transfrontier Park. Long distance transects were done to investigate the relative spoor densities in three 10 km wide zones relative to the Namibian border. It is likely that caracals use the areas in the vicinity of the Namibian border more intensively and move across the border more frequently in the cold season than in the hot season.

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Research is not feasible without a strong support structure in place. I was fortunate that throughout this project I had such support. I would therefore like to take this opportunity to thank those people and institutions that contributed substantially to the successful completion of this project.

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- Outdoor Warehouse

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CHAPTER 1

INTRODUCTION

The caracal *Caracal caracal* is a solitary, predominantly nocturnal felid. Schreber described the first specimen from the southwestern Cape region of South Africa, in 1776. Caracals preferentially inhabit the dry open savanna regions of southern Africa (Skinner & Smithers 1990, Estes 1995, Bothma & Walker 1999). Caracals have, however, been recorded in most major habitat types in southern Africa (Stuart & Wilson 1988). The areas from which they are excluded include the Namib Desert of Namibia (Stuart & Wilson 1988) and the coastal forests of KwaZulu-Natal (Von Richter 1972). Outside the southern African region caracals are found throughout Africa, excluding the tropical forests of West and Central Africa and the Sahara Desert. Beyond Africa, caracals are found throughout the Arabian Peninsula, north into Kazakhstan and southeast into India (Bothma & Walker 1999).

Caracals are medium-sized cats, weighing up to 20 kg (Skinner & Smithers 1990), that feed on a broad spectrum of prey including insects, reptiles, birds and mammals up to the size of a springbok *Antidorcas marsupialis* and mountain reedbuck *Redunca fulvorufula* (Grobler 1981, Stuart 1981, Stuart 1982, Moolman 1986, Palmer & Fairall 1988, Stuart & Wilson 1988, Skinner & Smithers 1990, Stuart & Hickman 1991, Estes 1995, Avenant & Nel 1997, Bothma & Walker 1999).

Caracals are physically robust cats with muscular back legs that are longer than the front legs (Skinner & Smithers 1990). They are reddish in colour, with soft white fur on their bellies. The uniform red pelage has led to the caracal being called rooikat (red cat) in

Afrikaans. Due to caracals having long, tufted black ears and short tails relative to their body length, they have often erroneously been called lynxes. Caracals are, however, not closely related to either the Old or the New World lynxes beyond the two superficial, morphological attributes mentioned above (Bothma & Walker 1999).

In southern Africa, caracals frequently prey on small domestic livestock, and for this reason they are considered problem animals by small livestock farmers. In South Africa and Namibia legislation is in place that classifies caracal as vermin and allows farmers to hunt, trap and destroy them (URL: http://lynx.uio.no/catfolk/ssacr01.htm). However, in the more northerly African and Asian distribution zones caracals are considered endangered, and they have been classified as a CITES Appendix II species (URL: http://lynx.uio.no/catfolk/ssacr01.htm).

Notwithstanding their wide distribution and problem animal status, little is known of the ecology and behaviour of caracals (Grobler 1981, Moolman 1986, Bothma & Walker 1999). This is probably due to caracals being notoriously difficult to study in the wild because of their nocturnal, solitary behaviour and cryptic colouration (Estes 1995, Van Heezik & Seddon 1998). Many of the studies to date have investigated the prey selection of caracals based on stomach or faecal contents, and behavioural studies based on observations of captive animals.

There is often conflict between conservation institutions and small livestock farmers especially where parks or nature reserves that maintain predator populations are adjacent to small livestock areas. The conflict arises due to the contention by farmers that the conservation agencies protect predators that prey upon domestic stock, and hence indirectly contribute to their own stock losses. Such a situation exists on the western border of the Kgalagadi Transfrontier Park where it borders on Namibia. The motivation for the present study is to gain insight into the behavioural ecology of free-ranging caracals in the Kgalagadi Transfrontier Park, and to try and determine whether they have an impact on small livestock on the neighbouring agricultural land in Namibia.

To investigate the caracal behaviour and their potential impact on the small livestock farms, a multi-faceted research approach was necessary to answer the following key questions:

- Do the ranges of caracals in the Kgalagadi Transfrontier Parks extend into Namibia?
- Do caracals in the Kalahari show any habitat preferences?
- How do caracals hunt their prey?
- Do caracals utilise small livestock as prey?
- Are there higher densities of caracals near to the Namibian border than elsewhere in the Park?

It is intended that the results of this work be published as a series of articles in various peer-reviewed scientific journals. To this end, each chapter is an entity unto itself and complies with the stylistic regulations of the intended publication. The tables and figures are labelled consecutively within each chapter. Literature cited in each chapter is referenced at the end of that chapter and a full list of citations is included at the end of the thesis. The methodology for each component study is described within the individual articles. However, general methods and a brief summary of the methods employed in each of the chapters appear in Chapter 3. The study area remained the same throughout the study and this results in a certain amount of repetition regarding the description of the study area in various chapters of this dissertation. An extended description of the study area has also been included (Chapter 2). The final chapter discusses general management recommendations based on the conclusions drawn from the research.

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CHAPTER 2

STUDY AREA

Introduction

The study was conducted in the southwestern portion of the Kgalagadi Transfrontier Park in an area where the Park shares a common border with Namibia (Fig. 1). The Kgalagadi Transfrontier Park was officially proclaimed at a ceremony on 12 May 2000 (Donaldson 2000). Prior to the amalgamation the two components of the Kgalagadi Transfrontier Park the Kalahari Gemsbok National Park (South Africa) and the Gemsbok National Park (Botswana), had been managed as separate entities even though there was never any fence between the two parks. The Nossob River forms the border between South Africa and Botswana, and although this political boundary is in place for humans, there is no fence and it therefore has no effect on the movement of wild animals. The agreement ratified by the combining of the Parks stipulates that the whole area is to be managed according to the same management plan with the same goals, as opposed to two separate Parks with separate focuses and goals.

Location

The Kalahari system is a sand-covered area that stretches from 29° S on the Orange River to 1 ° N in the Democratic Republic of Congo. From east to west the Kalahari extends from 32° E in Zimbabwe to 11° E in Angola (Cooke 1957, in Thomas & Shaw 1991). The Kgalagadi Transfrontier Park covers an area of 36 200 km^2 in the southwestern portion of this system.

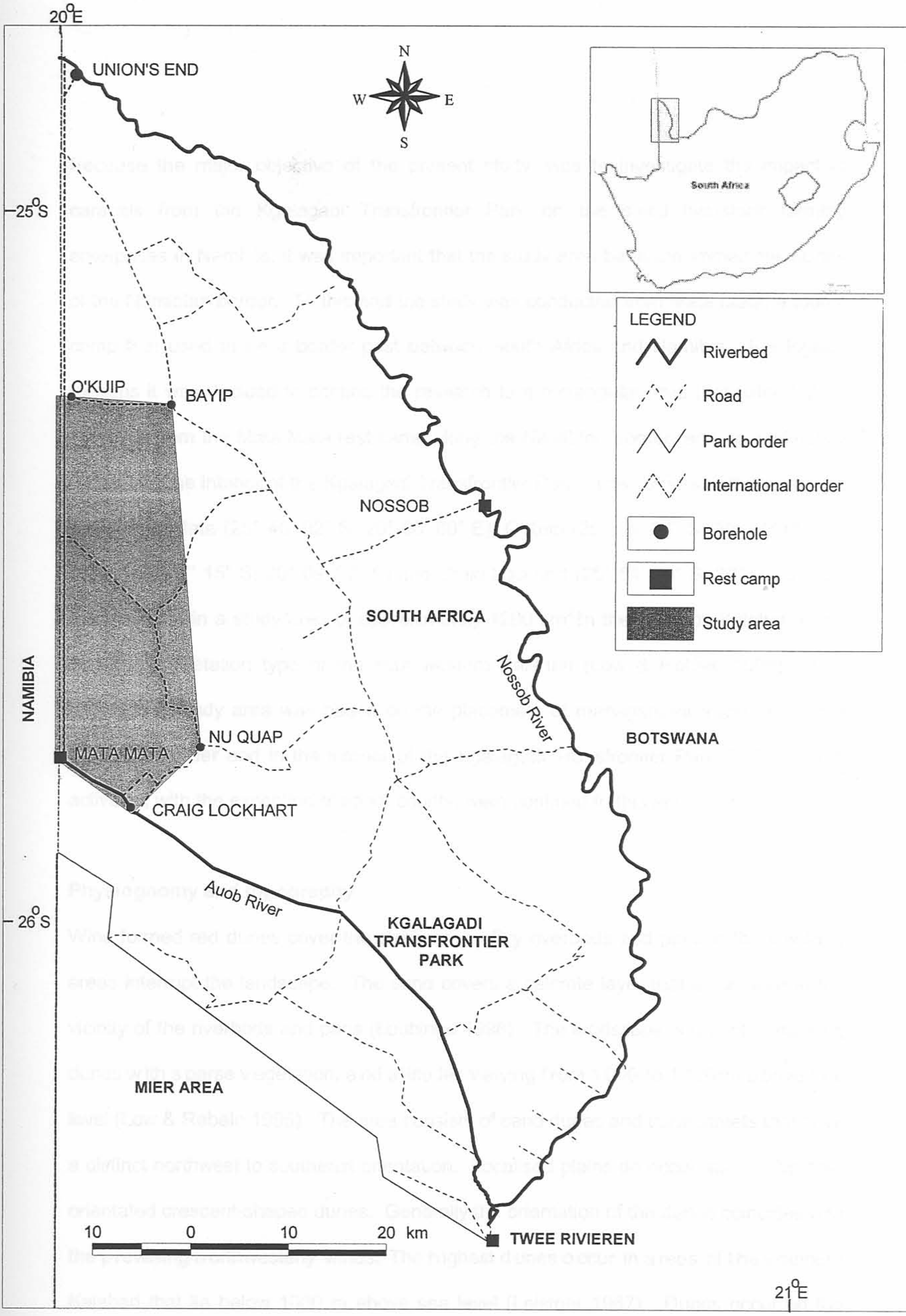

Figure 1: Position of the study area within the Kgalagadi Transfrontier Park.

Because the major objective of the present study, was to investigate the impact of caracals from the Kgalagadi Transfrontier Park on the small live-stock farming enterprises in Namibia, it was important that the study area be in the immediate vicinity of the Namibian border. To this end the study was conducted from Mata Mata, a tourist camp that used to be a border post between South Africa and Namibia. For logistic reasons it was decided to confine the research to a rectangular area that extended 60 km north from the Mata-Mata rest camp along the Namibian border, and approximately 20 km into the interior of the Kgalagadi Transfrontier Park. The corners of this rectangle were Mata Mata (25° 46' 02" S; 20° 00' 00" E), O'Kuip (25° 16' 28" S; 20° 00' 00" E), Bayip (25° 17' 15" S; 20° 09' 37" E) and Craig Lockhart (25° 51' 56" S; 20° 06' 07" E). This resulted in a study area of approximately 1200 km^2 in the Shrubby Kalahari Dune Bushveld vegetation type of the southwestern Kalahari (Low & Rebelo 1996). This rectangular study area was based on the placement of management tracks along the Namibian border and in the interior of the Kgalagadi Transfrontier Park. All research activities, with the exception of spoor counts, were confined to this area.

Physiognomy and topography

Wind formed red dunes cover the study area. Dry riverbeds and pans in the low-lying areas interrupt the landscape. The sand covers a calcrete layer that is exposed in the vicinity of the riverbeds and pans (Lubbinge 1998). The landscape is one of undulating dunes with sparse vegetation, and altitudes varying from 1 000 to 1 100 m above sea level (Low & Rebelo 1996). The area consists of sand dunes and dune streets that have a distinct northwest to southeast orientation. Localised plains do occur, as do atypically orientated crescent-shaped dunes. Generally the orientation of the dunes coincides with the prevailing northwesterly winds. The highest dunes occur in areas of the southern Kalahari that lie below 1000 m above sea level (Leistner 1967). Dunes occur on the westerly and northwesterly banks of the Nossob and Auob rivers, while the underlying calcrete layer is exposed to a distance of approximately 500 m from the rivers on the southeasterly riverbanks (Leistner 1967).

Crescent-shaped dunes are distinguished by their shape and the upwind orientation of the arms of the crescent (Mckee 1983). The sand depth, in the vicinity of crescent–shaped dunes, varies from 3.5 to 35 m (Parris 1984). These dunes are usually formed as a result of a combination of two factors, fallen trees on dune crests and wind action (Eriksson *et al.* 1989).

The areas between the dunes are known as dune streets or dune valleys. The sand layer in these lower-lying areas is relatively shallow, especially in the north and west of the South African portion of the Kgalagadi Transfrontier Park. In some cases the sand is so shallow that the calcrete substratum is exposed (Leistner 1967).

Although the highest dunes are taller than 30 m, the mean vertical distance between dune crests and the floor of dune streets is 8.2 m. The distance between dune crests varies from 100 to 500 m with a mean of 228.5 m. Most of the dunes have flat crests that can be up to 9.1 m wide. The longest continuous, unbranched dune is 3.2 km long, but single dunes can stretch over distances of over 14.5 km.

Drainage

The Kgalagadi Transfrontier Park is situated in a huge land depression in southern Africa with a gradual southerly gradient. As a result of this, the fossil riverbeds follow the southward gradient. The four rivers that historically drained the southern Kalahari are the Nossob, Auob, Molopo and Kuruman Rivers. They all formed part of the Orange

River catchment basin. As far as it can be determined, the one that ceased flowing most recently is the Molopo, but it has not flowed consistently for at least the past 1000 years. Even in seasons of abnormally high rainfall, such as 1999 to 2000, none of the rivers flows to reach the Orange River. Of the above four rivers, only the Auob and Nossob Rivers pass through the Kgalagadi Transfrontier Park.

The Nossob and Auob Rivers originate in the highlands of Namibia and their lower riverbeds pass through the Kgalagadi Transfrontier Park. The Molopo and Kuruman Rivers originate in the east (Leistner 1967). Although neither the Nossob nor the Auob Rivers flow, even in years of exceptionally high rainfall, sporadic flooding of portions of the riverbeds ensures the replenishment of the water table and prevents the river courses from being blocked by dune formation (Leistner 1967). The Auob River floods locally more frequently than the Nossob River. The Auob River last flooded in March 2000 while the two most recent recorded floodings of the Nossob River occurred in 1934 and 1963 (Van Rooyen 2001).

Pans

There are numerous pans in the Kgalagadi Transfrontier Park (Van Rooyen 2001). They usually form circular depressions of varying sizes, with hard bases. They are created by wind erosion and periodically contain water (Lubbinge 1998, Van der Walt & Le Riche 1999). The bases of the pans can lie up to 20 m below the surrounding plains (Van der Walt & Le Riche 1999). Wild animals often congregate near the pans to take advantage of the water that accumulates in these depressions after rain (Van der Walt & Le Riche 1999, Van Rooyen 2001).

Van Rooyen (2001) differentiates between two basic pan types, those that are vegetated with grass and those that are bare. Van der Walt & Le Riche (1999) included a third category of pans that have a hard limestone floor.

The soils of the pans are more varied than in the surrounding dune veld, and a gradient of changing soil chemical composition exists between the centre of the pan and the dunes that surround the pan. The soil in the pans is generally more compacted and has a higher mineral content than that of the surrounding vegetation (Parris 1976). Due to the high mineral content, animals often use areas on the pan floor as natural salt licks (Parris & Child 1973, Parris 1976, Van der Walt & Le Riche 1999). The gradient of changing chemical composition also leads to the concentric zonation of vegetation as it merges from the centre of the pan into the surrounding veld (Leistner 1967, Parris & Child 1973, Van Rooyen 2001).

Geology

The geological formations of the Kgalagadi Transfrontier Park form part of the Kalahari Group (Malherbe 1984). Information relating to the pre-Kalahari formations was obtained while drilling boreholes and is made up of dolerite or sedimentary formations of the Karoo-sequence. Seven distinct geological formations have been identified in this area and include the Wessels, Budin, Lonely, Eden, Mokalanen, Goeboe Goeboe and Gordonia Formations. The Eden, Mokalanen and Goeboe Goeboe Formations are usually confined to the riverbeds and pans while the Gordonia Formation underlies the duneveld and areas surrounding the rivers and pans (Malherbe 1984, Main 1987).

Soil

The Kalahari sand is not simply a homogeneous unit, but varies greatly in colour, composition and texture (Thomas & Shaw 1991). The colour variation of the sand is a result of varying degrees of leaching (Van der Walt & Le Riche 1999). The sand layer in the Kalahari can be up to 30 m thick and is of aeolian origin (Thomas 1984). The soils can be divided into two primary groups, coarse and fine-textured soils that can be further divided into seven basic groups (Leistner & Werger 1973). The vast majority of the soil particles consist of sand grains that are primarily quartzite. The red colour of the sand grains is a result of ferrous oxide adhering to the grains. The only soils that differ are those white sands that occur in the low-lying areas such as riverbeds and pans. These areas act as dams for organic material and mineral nutrients. In the dunes the Hutton soil form dominates but further north and east into Botswana, the Clovelly form prevails (Van der Walt & Le Riche 1999). The soils of the riverbeds and pans fall into one of five forms namely; Oakleaf, Dundee, Valsrivier, Swartland and Mispah (Van Rooyen 1984).

Climate

The southern Kalahari is an arid savanna with a mean annual rainfall that varies from 150 mm (Fig. 2) in the southwest to 300 mm in the north (Leistner 1967, Low & Rebelo 1996, Lubbinge 1998, Van Rooyen 2001). The area falls between the 200 and 250 mm isohyets and is characterised by low irregular annual rainfall (Mills & Retief 1984). The rainfall is highly variable and can vary from < 100 mm to > 700 mm per year (Van Rooyen 2001). Van der Walt and Le Riche (1999) distinguished three distinct climatic phases;

- A wet phase when the rainfall is far above the annual mean.
- An arid phase when the rainfall is far below the annual mean.
- A transitional phase when the rainfall varies around the annual mean.

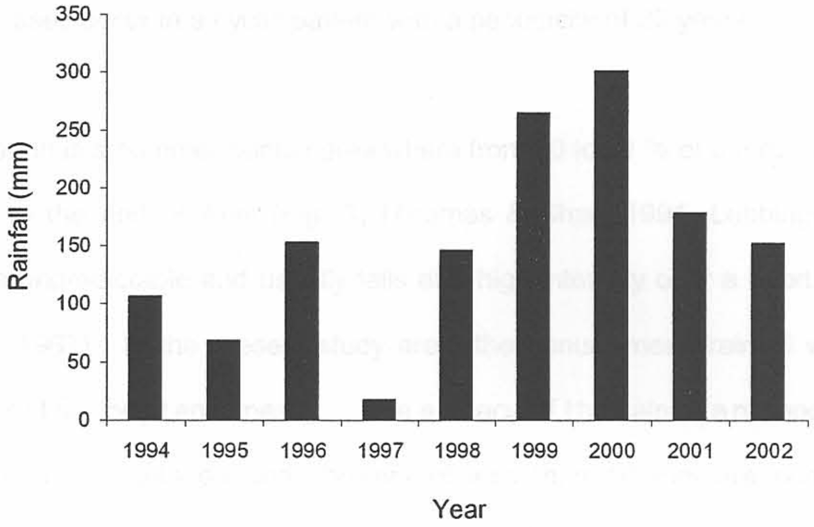

Fig 2: Recent annual rainfall for Mata Mata rest camp in the Kgalagadi Transfrontier Park from 1994 to 2002, where the mean annual rainfall is 152.3 mm.

These phases occur in a cyclic pattern with a periodicity of 20 years.

The Kalahari is a summer rainfall area where from 80 to 91 % of the rain falls from early October to the end of April (Fig. 3) (Thomas & Shaw 1991, Lubbinge 1998). The rainfall is unpredictable and usually falls at a high intensity over a short period of time (Leistner 1967). In the present study area, the annual mean rainfall was 153.5 mm (84.3 % of the long term mean). The efficacy of the rain is an important factor in relation to the vegetation and showers of less than 10 mm are considered to be ineffectual for the germination of seeds (Leistner 1967). The evaporation rate plays a huge role on the efficacy of the rain because the evaporation rate is 10 times that of the mean annual rainfall (Lubbinge 1998).

The Kalahari is subjected to some of the most extreme temperatures in southern Africa with a maximum daily temperature of 45.4° C and a minimum of – 10.3° C (Low & Rebelo 1996, Van Rooyen 2001). January is usually the hottest month with the lowest temperatures being recorded in June and July (Fig. 4) (Leistner 1967, Lubbinge 1998).

Vegetation

The vegetation is characterised by the trees *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca* trees, a shrub layer of *Grewia retinervis* and *Rhus tenuinervis,* and a well-developed grass layer consisting mainly of *Stipagrostis amabilis*, *Eragrostis lehmanniana, Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996).

The Kgalagadi Transfrontier Park forms the southern part of the greater Kalahari ecosystem. Because of the arid nature of the area, many of the plants there are

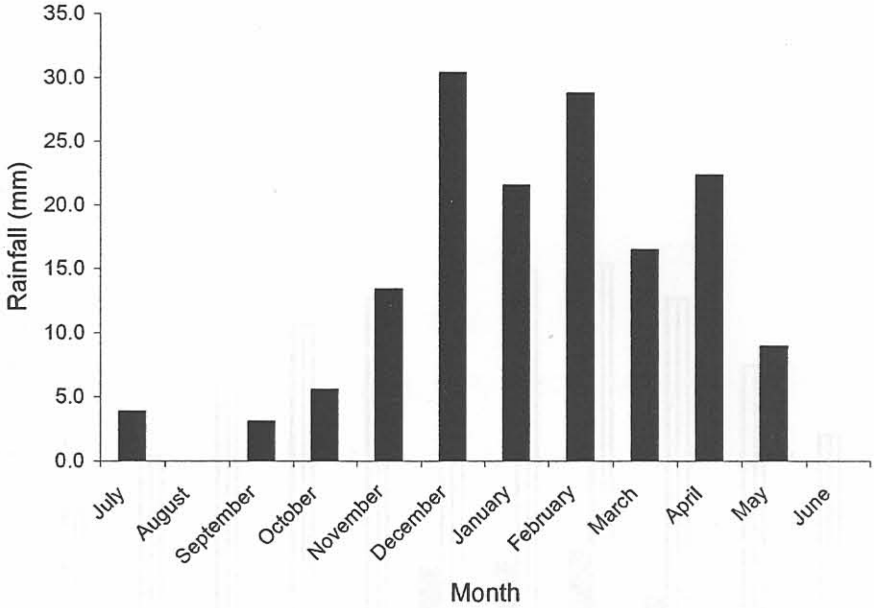

Fig 3: Mean monthly rainfall at Mata Mata rest camp in the Kgalagadi Transfrontier Park from 1994 to 2002

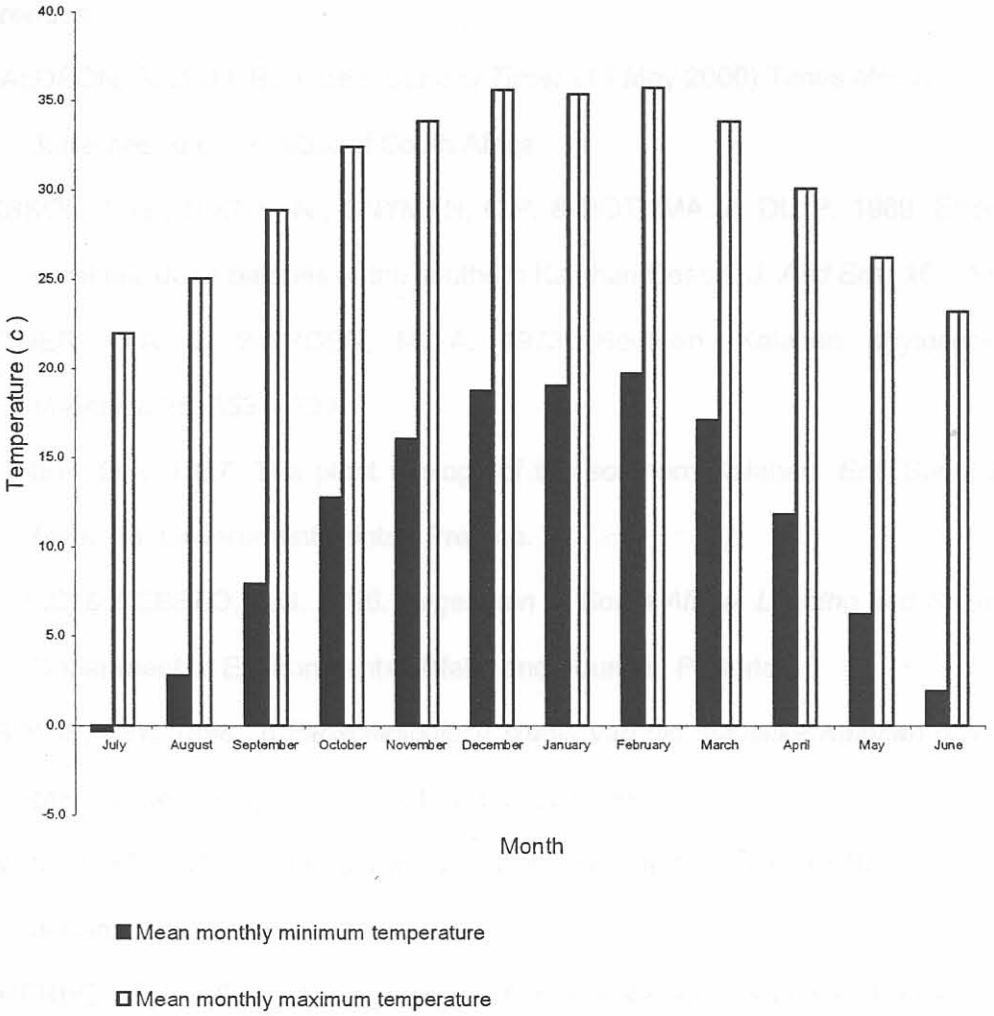

Fig 4 : Mean maximum and minimum temperatures for Mata Mata rest camp in the Kgalagadi Transfrontier Park from 1994 to 2002.

ephemeral. After sufficient rain, these plants germinate quickly to complete their life cycles in a short time (Eloff 1984).

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CHAPTER 3

METHODS

Introduction

To answer the questions posed, a study was done during two years of fieldwork in the Kgalagadi Transfrontier Park, from June 2000 to July 2002. Caracals were captured and radio transmitters were fitted to research animals. These animals were then radio-tracked to gather range use data. The spoor tracking technique (Eloff 1984, Bothma & Le Riche 1984, Stander et al. 1997) was used to gather behavioural, habitat selection and prey selection data relating to caracals in the Kgalagadi Transfrontier Park. Faecal samples were collected and analysed to determine what prey caracals selected and whether caracals utilised sheep as prey. Spoor counts (Stander 1998, Funston *et al.* 2001) were conducted to investigate the relative caracal densities in the interior of the park and along the Namibian border.

The results of this study were prepared as a set of independent journal articles, and each article contains a description of the methods that were used for that investigation. Therefore, the general methods that were used during the present study are discussed briefly here. In most instances the data were analysed on a seasonal basis with a hot season from October to March, and a cool to cold season from April to September (Bothma & Bothma 2004). It was not viable to conduct seasonal analyses of the prey selection of caracals due to the small sample size available for the hot season.

Capture, collaring, care and release of caracal.

To fit caracals *Caracal caracal* with radio collars, it was necessary to capture a number of animals and immobilise them. Box traps were used to capture caracals in the Kgalagadi Transfrontier Park. The macro and micro positioning of the box traps were important to optimise the chances of capturing caracals (Boddicker 1988). Various combinations of different lures and baits were used to attract caracals into the cages. These worked with varying degrees of success. The trap line was patrolled on a daily basis to ensure that non-target animals could be released and that the caracals were immobilised before being subjected to unnecessary heat stress (Brand 1993). Modifications were made to the standard box trap design to allow for the introduction of a crush into the trap. When a caracal was caught, the crush was placed into the box trap. An assistant would then use the crush to physically restrain the caracal inside the box trap. It was then possible to administer the immobilising drug, Zoletil [Virbac RSA (Pty) Ltd. 1996], to the captive animal by using a hand-held syringe. Once immobilised, the caracals were removed from the box traps, to be checked for any injuries and external parasites, weighed, measured and fitted with Telonics radio-collars. In high ambient temperatures, immobilised caracals were doused with water to prevent overheating. Because there is no reversing agent for Zoletil the immobilised caracals were placed back inside the box traps and the trapdoor was closed once they had been fitted with radio collars. The trap with the caracal inside was left in a cool area to allow the immobilising agent to wear off (Stander & Morkel 1991). Once the caracals had fully recovered from the immobilising agent, they were released.

Range use

Caracals were fitted with 250 g Telonics radio-collars, transmitting on individual frequencies within the 148.80 to 148.89 MHz. frequency range. After release the collared caracals were radio-tracked on a weekly basis. This interval of at least a week between consecutive locations avoided underestimation of range size due to auto-correlation of the locations (Swihart & Slade 1985, Reynolds & Laundre 1990). Radio tracking was done from the ground by using high vantage points to locate the radio signals. Occasionally aerial tracking was used to supplement the ground tracking. To avoid the errors inherent in basing locations on triangulation, the individual caracals were physically located to get a visual confirmation of their positions (Macdonald & Amlaner 1980, Nams & Boutin 1991). The positional fixes for each individual were recorded with GPS equipment and were then used to calculate the range sizes for the caracals. Two range estimation programs, Ranges V (Kenward & Hodder 1996) and Animal Movement (Hooge 1999), were used to calculate the minimum convex polygon, the kernel and the harmonic mean range for caracals that generated sufficient data points to ensure meaningful results from statistical analysis (Mizutani & Jewell 1998, Broomhall 2001). Two alternative analysis programs were used to give a less biased reflection of the range sizes of caracals and to improve the flexibility of the results for comparison with future studies.

Habitat selection

To facilitate the study of habitat selection by caracals in the Kgalagadi Transfrontier Park it was necessary to redefine certain terms that are usually associated with habitat selection so that their application in relation to the present study was relevant. Habitat selection was based on dividing the shrubby Kalahari dune bushveld into a number of subdivisions including habitat components (dune crests, dune slopes and dune streets), dune slope aspects, and plant association (Van der Walt 1999, Van Rooyen 2001). To stratify the shrubby Kalahari dune bushveld into habitat components, the non-mapping method (Marcum & Loftsgaarden 1980) was preferred to the traditional mapping method because of its ability to stratify vegetation on a fine scale.

Caracal spoor were followed according to the method of Eloff (1984), Bothma &Le Riche (1984) and Stander *et al.* (1997) to gain an insight into the behaviour of these animals. This method involved patrolling the roads within the study area at 10 km per hour with the tracker scanning the road from a tracking chair that was bolted to the front bumper of the research vehicle. On detecting fresh caracal spoor, the tracker started to walk, following the spoor, describing the behaviours that could be identified from the spoor. The behavioural observations were recorded on field forms. In addition to behavioural observations, habitat utilisation observations were recorded and linked to GPS locations, to facilitate habitat selection analysis. The behaviours were categorised as either involving movement or being stationary. Many of the stationary behaviours could be related to specific plant species within each habitat component.

Baseline vegetation frequency data were collected by using 100 m step-point transects in each of the habitat components (Mentis 1981). The data were converted to reflect the plant frequencies in each habitat component. These frequencies could then be compared with the plant utilisation that caracals displayed while performing various stationary behaviours. This reflected the microhabitat selection that caracals displayed.

Chi-squared tests were used to establish whether caracals selected or avoided various habitat components and plant species within the defined habitat components. Where significant levels of selection were indicated, the Bonferroni approach was used to establish whether specific plant species or habitat components were selected or avoided

(Marcum & Loftsgaarden 1980, Moolman 1986, Caley 1994, Alvarez-Cardenas *et al.* 2001).

Hunting behaviour

The spoor tracking method of Eloff (1984), Bothma & Le Riche (1984) and Stander *et al.* (1997) was used to collect data related to the hunting behaviour of caracals. From the spoor, a Kalahari San tracker could distinguish six individual component behaviours related to hunting; stalk, crouch, take-off, chase, pounce and kill. Although Schaller (1972) defined minimum distances for component behaviours of hunts as they related to lions *Panthera leo,* it was necessary to redefine these distances as they relate to caracals because the distances that relate to lions are too great to apply directly to caracals.

For analysis purposes, the prey were separated into two distinct categories with large adult prey having a mean body mass of > 1 kg and small prey one of 1 kg or less. Prey that left visually faint or undetectable spoor were assumed to be small prey because the spoor of larger prey would be clearly visible and identifiable. Correspondence analysis (SAS 1999) was used to model the sequence of hunting behaviours most likely to result in a kill.

Prey selection

Two methods were used to analyse the prey selection by caracals in the Kgalagadi Transfrontier Park. Traditional scat (faecal) analysis was used as the primary method, and records of known and attempted kills detected from spoor tracking were used to supplement these data as was done by Bothma & Le Riche (1984) for leopards *Panthera pardus.*

Caracal scats were identified by their association with caracal spoor (Bothma & Le Riche 1984, Emmons 1986, Oli *et al.* 1993) and their typical segmented appearance (Norton *et al.* 1986, Stuart & Hickman 1991). On collection, scats were placed in labelled paper bags and air-dried (MacDonald & Nel 1986). On completion of the fieldwork the contents of the scats were analysed in a laboratory. The scats were washed to remove all water-soluble components. Only the macroscopic particles of the scat then remained, including; tooth fragments, hair, bones, plant material, hoofs and insect carapaces. These remnants were used to determine what prey the caracals had been utilising.

Gelatine imprints of the hair cuticle patterns were made and compared with the cuticle patterns on reference slides made from hair samples from known species. Additionally the cuticle patterns were compared with existing keys (Dreyer 1966, Perrin & Campbell 1979, Keogh 1983, Keogh 1985). Cross sections of the hairs in the scats were made (Douglas 1989) and compared with cross-sections of the hairs of known species, and with a photographic record held at the Centre for Wildlife Management.

While spoor tracking, all hunting attempts were recorded. Where possible the intended prey was also identified from spoor. In many instances, however, the prey animal could not be identified and was recorded as unknown for prey selection analysis.

Possible optimal foraging for Brant's whistling rats

To determine whether caracals were employing an optimal foraging approach when searching for Brant's whistling rats *Parotomys brantsii*, it was necessary to compare the incidence of Brant's whistling rat colonies along a random path with their incidence along caracal movement paths. A vehicle was used to conduct 20 straight line transects of 10 km each. Observations on the presence or absence of Brant's whistling rat colonies were made at 0.5 km intervals along the length of each transect. This gave a base line (expected) frequency of the occurrence of Brant's whistling rat colonies within the study area. Whilst spoor tracking caracal according to the method of Eloff (1984), Bothma & Le Riche (1984) and Stander *et al.* (1997) observations on the occurrence or absence of Brant's whistling rat colonies were made every 0.5 km along each set of caracal tracks. The base line frequency of Brant's whistling rat colonies was then compared with the frequency observed along the caracal tracks to determine whether caracals selected paths with a relatively high incidence of Brant's whistling rat colonies using the CATMOD procedure (SAS 1999).

The effect of small stock farming in Namibia on caracal density in the neighbouring Kgalagadi Transfrontier Park.

Spoor density is directly related to the density of that species in an area (Tyson 1959, van Dyke, Stander 1998, Funston *et al.* 2001). Spoor counts were conducted along management tracks in the study area to determine whether there was a higher caracal spoor density along the border than in the interior of the Kgalagadi Transfrontier Park. Two long-distance transects were used, one along the Namibian border and one in the interior of the Park. The interior transect was conducted along a route that diverged away from the Namibian border. At its furthest point, this route lay 30 km away from the Namibian border. Both routes were completed on consecutive days of each month. A tracker sat on a tracking chair mounted to the front bumper of the research vehicle and indicated every incidence of caracal spoor. These incidences were noted, in conjunction with their position, distance for which they were visible on the track, and their orientation (transverse or longitudinal) relative to the track. Only fresh spoor, as indicated by the tracker, were included in the data set. Because the aim was to try to detect a cline of caracal activity between the interior of the Park and the areas along the border, the interior transect was divided into three strips, 0 – 10 km, >10 - 20 km and >20 - 30 km, relative to their perpendicular distance from the Namibian border. The density, length and orientation of the spoor recorded along the strips in the interior were compared with those recorded along the border.

Questionnaire survey

To investigate the perceptions by the Namibian farmers of the extent of the impact of predators on small stock production, questionnaires were distributed to farmers at various farmers union meetings. Due to the low number of respondents, these data are too sparse to warrant further analysis. Where the opinion of the Namibian farmers is referred to in the text, it is based on the responses of 15 farmers to the questionnaires, five of whom own land that borders directly on the Kgalagadi Transfrontier Park.

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CHAPTER 4

THE CAPTURE, COLLARING, CARE AND RELEASE OF CARACAL

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ABSTRACT

During a research project in the Kgalagadi Transfrontier Park, caracals *Caracal caracal* were captured and fitted with radio collars. Over a two-year period, 632 nights of trapping were completed. During this time, 152 animals were captured in cage-traps, of which nine were caracals. Three caracals were immobilised by using estimated doses of Zoletil based on the recommended standard dose of 3 to 5 mg of Zoletil per kg of body mass. A further six caracals were immobilised by using a standardised dose of 50 mg Zoletil. Use of a standard dose of immobilising agent was found to be more practical under field conditions than trying to estimate the mass of the captured animals. Chicken-based baits were found to be effective for a broad spectrum of small carnivore species. Modifications to the conventional, single-door cage design were made to accommodate a crush plate. The use of the crush plate in conjunction with a handheld syringe was found to be the most effective method of immobilisation, and it reduced the stress to which the captured animals were subjected. Recommendations for the post-capture handling of small predators are made, based on field experience.

Keywords: Caracal, capture, cage-traps, immobilisation, handling, Kalahari

Submitted to *Koedoe*

INTRODUCTION

To study animals by using radio telemetry it is necessary to capture the animals and fit them with radio collars from time to time. It is essential that any animal that is captured for study purposes be released in a fit and healthy condition. The study animals should be subjected to as little stress as possible during the capture, immobilisation, collaring, and subsequent recovery and release procedures. The success of the capture and release of an animal is not merely determined by the capture of the animal but it is rather determined by how the animals are handled, transported and kept after capture (Ebedes, Du Toit & Van Rooyen 1993). The capture of predators is a time consuming process, requiring patience and persistence. If the correct capture and care procedures are not followed, the stresses induced by these procedures may result in injury or death of the study animals (Ebedes *et al.* 1993).

To fit caracals with radio collars in the present study it was necessary to use both physical (trapping) and chemical (immobilisation and tranquillisation) capture techniques. Mechanical restraints consisting of traps or cages of various designs are generally used to capture or hold animals initially, but chemical restraint is necessary for detailed examination and manipulation (Jessup 1982). Certain carnivores can be darted while free-living, but this is not the case with caracal that must be trapped first before chemically immobilising them (McKenzie & Burroughs 1993).

This paper elaborates on the methods that are employed in the capture of small carnivores generally for research purposes, and highlights the practical problems that were experienced and possible solutions that were developed during the capture of caracals for research in the Kgalagadi Transfrontier Park.

STUDY AREA

This study was done in an area along the Namibian border near Mata-Mata in the southwestern portion of the Kgalagadi Transfrontier Park. For logistic reasons it was decided to confine the research activities to an area that extended 60 km north from the Mata-Mata rest camp along the Namibian border, and approximately 20 km into the interior of the Kgalagadi Transfrontier Park.

The Kalahari Gemsbok National Park was proclaimed in 1931, but it only became a reality in 1935 when a number of farms along the southern bank of the Aoub River were acquired. Today, the Park exists in much the same state as it was then (Van Wyk & Le Riche 1984). An agreement to formally combine the Kalahari Gemsbok National Park (South Africa) with the bordering Gemsbok National Park (Botswana) to form the Kgalagadi Transfrontier Park was signed by representatives of the governments of South Africa and Botswana in 1999. This agreement was ratified at an amalgamation ceremony held on the 12 May 2000 (Donaldson 2000).

The Mata-Mata area lies in the Shrubby Kalahari Dune Bushveld vegetation of the Savanna Biome (Low & Rebelo 1996). This area is an arid savanna with temperatures varying from –10 ° C to 45 ° C in the shade, with an annual mean rainfall of 153.5 mm that occurs mainly in the summer. The landscape is one of undulating dunes with sparse vegetation, and altitudes varying from 1000 to 1100 m above sea level (Low & Rebelo 1996).

The vegetation is characterised by the trees *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca*, with a shrub layer of *Grewia retinervis* and *Rhus tenuinervis* and a well-developed grass layer consisting mainly of *Stipagrostis amabilis*, *Eragrostis lehmanniana*, *Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996). There is little variation in the soil forms because the area is predominantly covered by aeolian sand overlying calcrete (Low & Rebelo 1996).

The Kgalagadi Transfrontier Park forms the southern part of the greater Kalahari ecosystem. Because of the arid nature of the area, many of the plants there are ephemeral. After sufficient rain, these plants germinate quickly to complete their life cycle in a short time (Eloff 1984).

Because of the harshness of the environment, the southern Kalahari is an area that is only sparsely inhabited by humans. This above any other factor contributes to the uniqueness of the area, and it enhances the value of the area for field research in wildlife management and conservation.

METHODS

Both mechanical and chemical capture techniques were used to capture caracals. Mechanical capture of caracals involved trapping by using cages (box traps), while chemical capture involved the immobilisation of the caracals once they had been trapped mechanically.

A number of lethal and non-lethal methods have been described for the capture of smaller carnivores and furbearers (Boddicker 1999). Non-lethal methods are the only ones that are appropriate for application in such a field ecological study. Commonly used non-lethal methods such as cage traps and leg-hold traps have been used in numerous research projects worldwide. Although the use of leg-hold traps was considered for this project, it was decided to use cage traps exclusively after consultation with the ethics committee of South African National Parks. This decision was based on the fact that leg-hold traps that are set for the capture of caracal could also injure smaller non-target animals that will also be trapped (Boddicker 1999).

Physical capture

Cage design:

The two basic cage designs that have been used for the capture of caracal to date are the single-door design and the double-door design (Moolman 1986). Only single-door cage traps (Bothma 1975) with certain modifications for the use of a capture crush were used in this project (Figs. 1, 2 & 3). The cages were designed and constructed within the parameters laid down by the ethics committee of South African National Parks. The cages (Figs. 1, 2 & 3) were constructed with internal measurement of 1.5 m long, by 0.5 m high by 0.5 m wide (Finch 2000, pers. comm.[1]). This configuration ensured that a caracal could not be injured by the falling trapdoor (Bothma 1975; Harthoorn 1976) and that the trapped animal would not be able to turn around and escape from the cage before the trapdoor had closed.

The cage frame was covered with a double layer of 40 mm precision-welded mesh, ensuring that the mesh was secured in such a fashion that no sharp points were

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[1] Mr. J.Finch: Varmint & Game Safari's Africa cc, 6 Cradock Ave, Eldoraigne, 0157

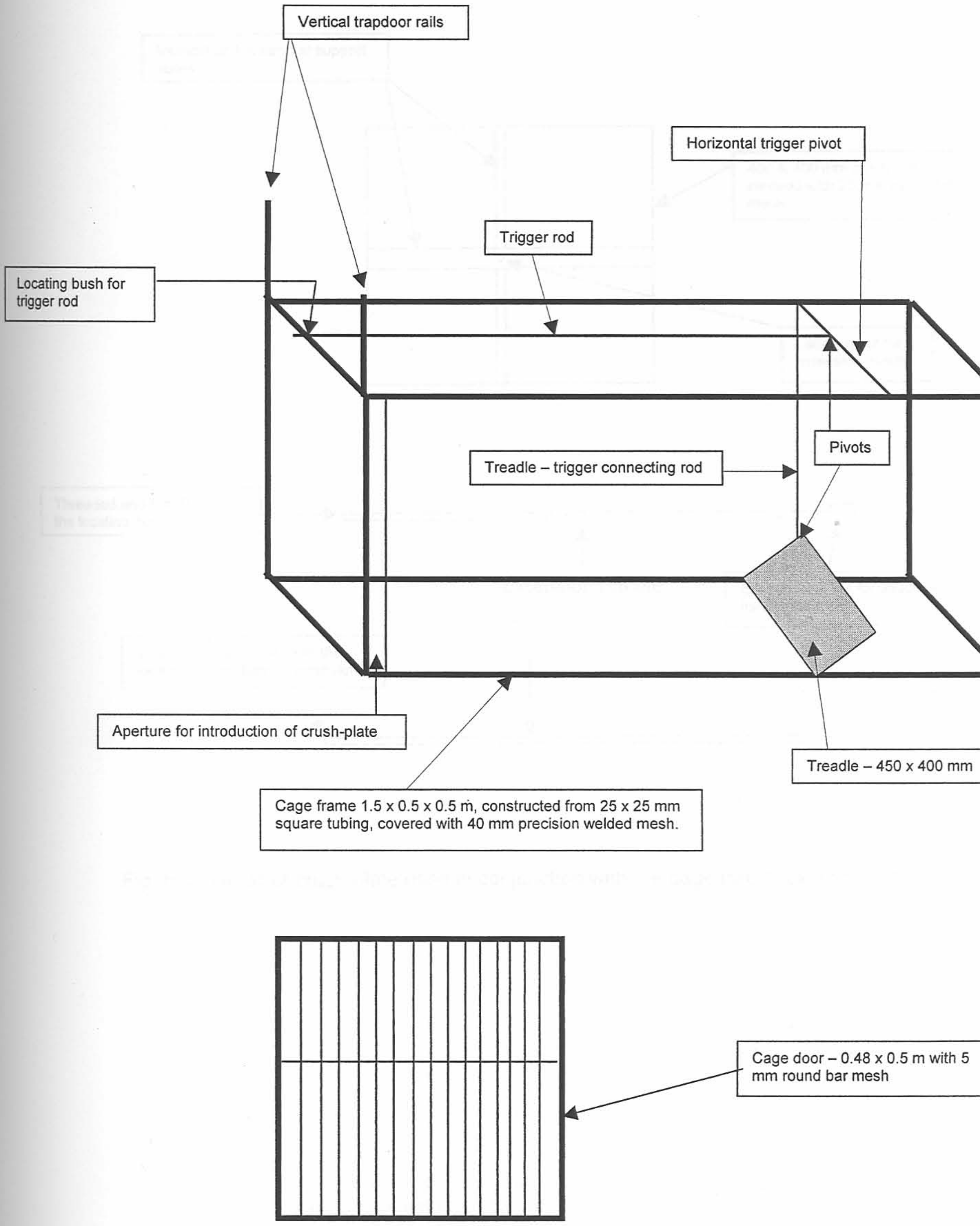


Figure 1: The design of cage traps used for capture of caracals in the Kgalagadi Transfrontier Park

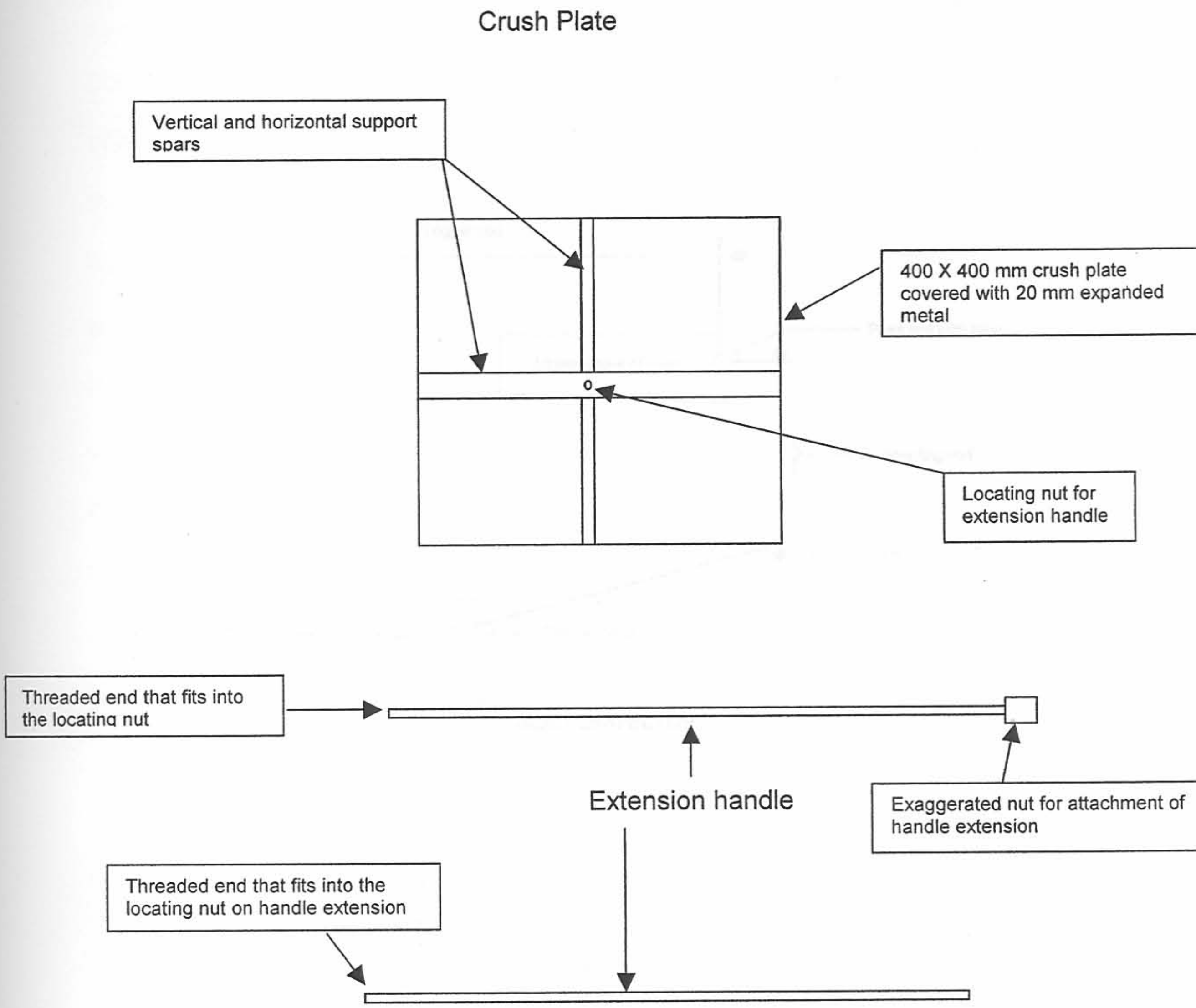
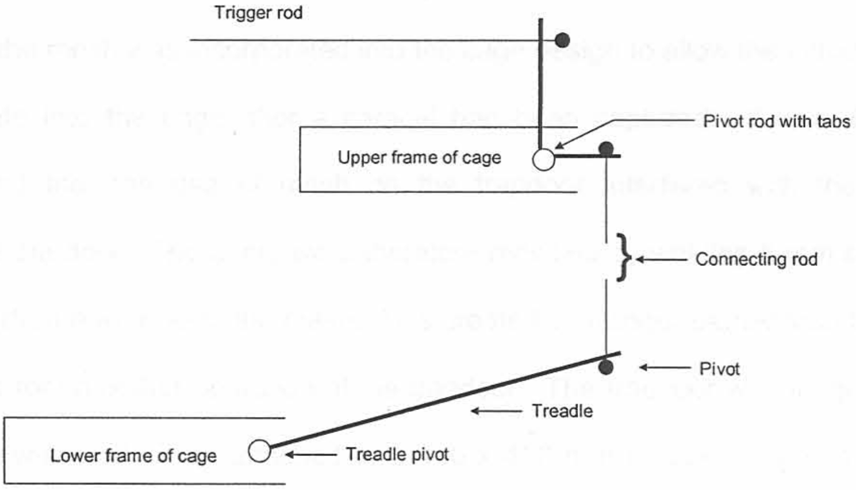
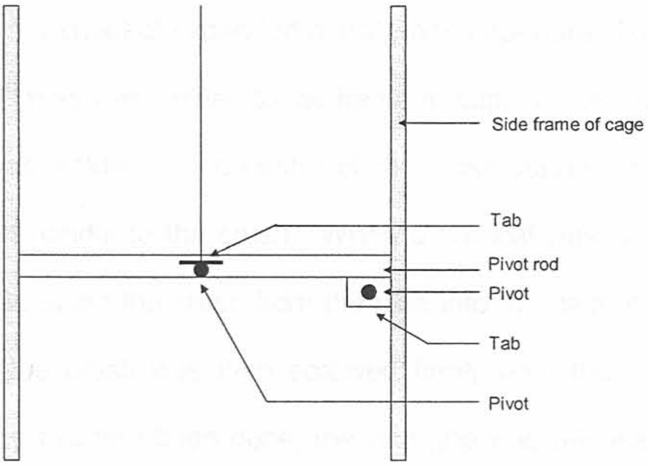


Figure 2: Detail of crush plate used in conjunction with the cage trap shown in Figure 1.



SIDE PERSPECTIVE



AERIAL PERSPECTIVE

Figure 3: Detail of trigger mechanism and pivot rod of cage traps used for the capture of caracals in the Kgalagadi Transfrontier Park

pointing into the cage (De Wet 1993). The mesh was overlapped to reduce the effective mesh diameter to 20 mm. A single layer of mesh was used on the back of the cage to allow for hand injection of captured animals. A 30 mm wide vertical aperture in the mesh was incorporated into the cage design to allow the introduction of a crush plate into the cage after a caracal had been captured. It was, however, initially found that the use of mesh on the trapdoor interfered with the smooth operation of the door. The doors were therefore modified by welding 5 mm steel bars into the doorframe to replace the mesh. This created a stronger barrier than the mesh and allowed for smoother operation of the trapdoor. The trapdoor was triggered by a system of levers and pivots attached to a 400 x 450 mm treadle, hinged 1 m away from the door of the cage (Finch 2000 pers. comm).

A crush plate was designed that could be introduced into the cage through the vertical aperture in the side of the cage. The crush plate consisted of a square steel frame of 400 x 400 mm, covered with a sheet of expanded metal whose aperture diameter was 20 mm. An additional steel cross was welded to the frame to support the centre of the expanded metal. A nut was welded to the centre of the cross support to allow the attachment of an extension handle to the crush. When a caracal was captured, an assistant used a vice-grip to insert the crush from the side into the cage through the aperture. The handle of the crush was then screwed firmly onto the crush plate through the trapdoor. Once this had been done, the vice-grip was released and the crush plate could be used.

The concept is that an assistant introduces the crush plate into the cage and uses it to gradually reduce the internal volume of the cage in which the captive animal can move, eventually pressing the animal firmly against the back of the cage, preventing the animal from moving. Once the animal is so restrained it is possible to administer an exact dose of immobilising agent to the captive animal by using a hand-held syringe.

Setting the cage

It is important to set cages in the correct manner and places (Mills 1996), where the animals are known to be active (De Wet 1993). Much research into optimising trapping success has been done in the United States of America. It has been suggested that the selection and preparation of the trap site and cage set-up are vital factors to consider when trapping predators. Correct trap locations are normally productive for the entire spectrum of target species (Boddicker 1999). The aim of positioning a trap selectively is to try and ensure that all the possible target animals will encounter the trap (Boddicker 1988).

Micro and macro positioning are the two aspects of trap location that contribute to the effectiveness of trapping (Boddicker 1999). Macro positions are locations that take landscape position, habitat type and obvious routes and wildlife trails into consideration. Cages should be placed in preferred habitat types, next to frequently used trails and features that cause predators to concentrate in an area (Bothma 1975).

Micro-positioning refers to the final positioning of the cage, its proximity to a road or trail and bushes, and it takes variables such as wind direction into consideration. Ideally the prevailing wind should blow away from the cage against the direction of travel of the target animal (Boddicker 1999). The ideal micro-position in the Kalahari study area was on a dune crest in a tall *Stipagrostis amabilis* grass clump, at a distance of < 1 m from a permanent track. In the present study, cages were always set in areas of known caracal activity as was indicated by fresh tracks, and/or where evidence of recent caracal urine or faeces was found (Brand 1993).

Having decided on an optimal location for the trap, the cage is set. In preparation, the ground upon which the cage is to be set is first levelled with a spade. This is done for two reasons. A cage that is unstable on the ground might move as the animal steps into the cage. This would startle the animal and it will not continue to enter the cage. When a cage is set up with one end elevated, it might prevent the sliding trapdoor from operating as effectively as it should.

Once in position, the treadle of the cage is covered with a woven white plastic sheet. The sheet covers the treadle and a portion of the floor of the cage in front of and behind the treadle. This prevents sand from building up under the treadle and stopping it from operating properly. Once the sheeting is in position, a shallow layer of soil is sprinkled over the floor of the cage and over the plastic sheeting (De Wet 1993). The plastic sheet should be sufficiently slack to allow for the setting of the treadle. In addition, the sand load on the treadle must be sufficient to cover and hide the treadle, but it should not cause the trapdoor to close without an animal stepping onto the treadle.

The bait or lure, hereafter referred to as bait, is next secured inside and at the back of the cage (Brand 1993). This ensures that any animals that are attracted to the bait have to step on to the treadle to get to it. If the bait were attached behind the cage, some animals can reach the bait without being trapped.

Once the bait is in place, the cage is camouflaged, but it is not necessary to hide the cage completely. Some authors feel that it is also not necessary to make any attempt to conceal the cage (Bothma 1975, Verdoorn pers. comm.[2]). However, Brand (1993) suggests that although caracals are not as sensitive to human scents and trap odours as jackals, the cages should still be camouflaged when trapping a caracal.

The back end of the cage should be made inaccessible to predators by positioning it in a dense bush, or by placing branches in such a way that predators are prevented from trying to remove the bait from the back of the cage without entering it (De Wet 1993). It is also important that any animals that approach the cage should be able to see through it from the front. No material should be packed on top of the cage but the sides should be packed with sufficient vegetation to obscure the hard lines of the frame of the cage. None of the camouflage material should protrude into the cage because any sharp object such as a branch can injure a captured animal (De Wet 1993).

To ensure that an animal will step onto the treadle, guide sticks are positioned in such a manner that the animal has to step over them on to the treadle when approaching the bait. Predators generally tend to avoid stepping on sticks, stones and other items (Boddicker 1999).

Nothing should obstruct the smooth operation of the trigger mechanism. It is therefore important to check the operation of the cage thoroughly before leaving it set. Branches should not obstruct the free fall of the trapdoor, there should be no obstruction under the treadle, and vegetation that is used to camouflage the cage should not interfere with the operation of the trigger mechanism or the closing trapdoor.

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Auditory, visual and olfactory attractants

Predators use a combination of sight, smell and hearing while hunting (Boddicker 1999). It is these senses that the trapper depends upon to coax animals into traps. Lures and baits are perhaps the most important aspect of trapping. Auditory attractants include squeakers and recordings of distress calls of prey species (Boddicker 1999). Brand (1993) suggests that the positioning of a squeaker device in bushes immediately behind the trap might increase the efficiency of trapping attempts.

Visual attractants such as feathers, fur, bones and various other articles that are suspended from the back of the cage draw target predators into a cage by pandering to the natural curiosity of predators (Brand 1993; Boddicker 1999). In the present study, small cardboard cards of 20 x 40 mm were covered with silver foil and were then suspended in the back of the cage as a visual attractant.

Olfactory attractants (baits) appeal to the sense of smell of the target animals. These attractants can be divided into the following four basic categories (Boddicker 1999):

- Food attractants such as fresh and rotten meat, eggs, fruits, and fish.
- Territorial attractants such as urine and faeces that predators use to scent-mark.
- Curiosity attractants that might not be naturally encountered by the target animals but are known to attract them purely out of interest. These include substances such as catnip and anise.
- Sex lures based on the urine of females in oestrus, and the sex glands and their extracts.

Baits are commonly used to entice animals into traps. Various types of and recipes for bait have been recommended for caracal trapping. They include Number 9 bait cage to provide a cooler environment and to calm the animal down (De Wet 1993) and assistance was called for by radio. Once assistance had arrived, the caracal was physically restrained inside the cage by using the crush plate as described above. The appropriate dose of 3 to 4 mg per kg of Zoletil (Virbac RSA (Pty) Ltd. 1996) (McKenzie & Burroughs 1993) was then administered intramuscularly by using a handheld syringe.

Once the drug had taken full effect, the caracal was removed from the cage, weighed, various measurements were taken and the animal was fitted with a radio collar. Having completed these procedures the cage was re-positioned in a shady area, and the floor was covered with sand. The caracal was then put back into the cage with its eyes covered to protect them from desiccation by exposure to the elements (Stander & Morkel 1991). Under hot conditions, captured caracals were doused with cold water to reduce their body temperature whilst they were recovering (Meyer pers. comm.[4]). The cage door was then shut and the shade net was replaced. The caracal was left inside the cage until it had recovered fully from the effects of the immobilising drug. Once the animal was alert again and had regained full motor control, it was released.

Trapping efficiency was calculated by dividing the total number of animals trapped by the number of trap-nights (Stander & Morkel 1991).

RESULTS

Physical capture

From 2 July 2000 to 4 April 2002, a total of 632 trap-nights were completed by using four single-door box traps (Figs. 1, 2 & 3). The traps were set for 14 days of each

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month. Nine caracals were caught at various locations at a 1.4% capture success rate. Various bait and lure combinations (Table 1) were used with varying degrees of success. The baits can broadly be divided into two categories, those including chicken and those excluding chicken. Chicken-based baits were used for 525 trap-nights, and resulted in 132 captures of which six were caracals. This converts to a trapping success rate of 25.1% for all species and 1.1% for caracals. The baits that excluded chicken were used for 106 trap-nights, resulting in 19 captures of which two were caracals for a total trapping success rate of 17.9% and 1.9% for caracals. The ninth caracal was captured by using a cage that was positioned in the mouth of the burrow of an aardvark *Orycteropus afer* in which the caracal had taken refuge.

The non-selective nature of this trapping technique is emphasised by the fact that of the 152 successful trap-nights, caracal were only captured on nine occasions. Furthermore, 94.0 % of the animals that were captured were non-target species (Table 1, Fig. 4). No collared caracal were recaptured during the study period.

Chemical capture.

In three cases, single doses of 60 mg (twice) and 65 mg (once) of *Zoletil* (CI-744), which consists of a 1:1 combination of the anaesthetic tiletamine hydrochloride and the sedative zolazepam hydrochloride, was administered intramuscularly to the captive caracals, based on a visual estimation of the body weight of the animal (Table 2). In six cases caracals were injected with a single standardised dose of 50 mg of Zoletil (0.5 cc at 100 mg per cc) (Meyer pers. comm.). In all cases a single dose of Zoletil was sufficient to immobilise the caracals for the time that was required to fit radio collars and to take all the necessary measurements.

(Schellingerhout 1978), caracal faeces and urine, fish heads, and striped polecat *Ictonyx striatus* carcasses (Moolman 1986), dead or live chickens and guinea fowl *Numida meleagris*, springbok *Antidorcas marsupialis* and sheep *Ovis aries* (Norton & Lawson 1985), fish, shellfish and fresh meat baits (Boddicker 1999), live domestic cats *Felis silvestris* (Verdoorn pers. comm.), rotten ostrich *Struthio camelus* eggs (Myburgh pers. comm.[3]) and fresh caracal kills (Brand 1993).

Lures depend on the innate curiosity of predators to attract target animals into a trap. These lures include scent, sight and olfactory stimuli (Finch, pers. comm). Many visual lures (feathers, silver foil on suspended cards, and animal hair) and scent lures (catnip oil, anise, and bobcat *Felis rufus* glands) were recommended by Finch (pers. comm).

A number of food, territorial, curiosity and sexual attractants were used during the trapping attempts in the present study. The primary bait used was fresh chicken, but both fresh and rotten fish were also used. In addition, urine and faeces were used as territorial lures. Both catnip and anise extract were used as curiosity lures and the sexual glands of the bobcat were used as a sexual attractant.

Handling captured animals

Because of the non-selective nature of trapping (Mills 1996), one of the criteria that was set into the trap design was that non-target species could be released with the minimum of stress and injury (Brand 1993). Traps were inspected daily before 10:00 to ensure that any captured animals were not subjected to unnecessary heat stress. Non-target animals were checked for injury before being released. Fortunately no animals were injured whilst confined in the cages and they were released immediately. After a caracal had been caught, shade netting was placed over the

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Table 1: *The capture success achieved by using various bait and lure combinations to capture caracals in the Kgalagadi Transfrontier Park from June 2000 to March 2002.*

Bait	Trap-nights	Number of animals trapped	Capture success (percentage of total trap-nights)	Capture success (percentage of bait-specific trap-nights)	Caracal	African wild cat	Cape fox	Black-backed jackal	Other animals
Bobcat gland & catnip	28	2	1.32	7.14	2	0	0	0	0
Caracal carcass	14	8	5.26	57.14	0	0	0	5	3
Caracal urine	14	2	1.32	14.29	0	0	1	1	0
Caracal urine & scat	1	1	0.66	100.00	0	1	0	0	0
Chicken	124	22	14.47	17.74	3	3	3	10	3
Chicken & bobcat gland	8	0	0.00	0.00	0	0	0	0	0
Chicken & feathers	7	4	2.63	57.14	0	0	0	4	0
Chicken & silver ball	243	77	50.65	23.46	2	8	10	52	5
Chicken, anise & feline fix	10	2	1.32	20.00	0	0	0	1	1
Chicken, bobcat gland & urine	31	4	2.63	12.90	0	2	0	2	0
Chicken, bobcat gland & catnip	23	3	1.97	13.04	0	3	0	0	0
Chicken, catnip & feline fix	13	1	0.66	7.69	0	0	0	0	1
chicken, catnip & urine	18	7	4.61	38.89	0	1	0	6	0
Chicken, Peters 2 & catnip	13	3	1.97	23.08	0	0	0	0	3
Chicken, urine & bobcat gland	17	3	1.97	17.65	1	2	0	0	0
Chicken, urine & feline fix	18	6	3.95	33.33	0	1	0	0	5
Dove	1	1	0.66	100.00	0	0	0	1	0
Fish & silver ball	41	4	2.63	9.76	0	0	0	3	1
Ground squirrel carcass	5	1	0.66	20.00	0	0	0	0	1
At an aardvark burrow	1	1	0.66	100.00	1	0	0	0	0
Peters no 2 & bobcat gland	2	0	0.00	0.00	0	0	0	0	0
Total	632	152	100	na	9	21	14	85	23

Table 2: *The efficiency of Zoletil in the immobilisation of caracals in the Kgalagadi Transfrontier Park from June 2000 to March 2002*

Caracal number	Gender	Dose in mg	Effective dose in mg per kg	Time injected	Time down	Time lucid	Time of release	Time lapse in hours between immobilisation and release	Body mass in kg
148.21	Male	60	4.62	08:15	08:25	10:30	11:50	3.58	13.00
148.81	Female	50	4.55	08:10	08:19	09:55	11:00	2.83	11.00
148.82	Male	65	6.50	07:33	07:40	10:35	13:33	5.00	10.00
148.87	Female	60	6.32	11:05	11:10	14:22	16:50	5.75	9.50
148.89a	Male	50	4.76	08:20	08:25	10:00	13:20	5.00	10.50
148.88	Male	50	4.00	09:38	09:45	10:40	12:55	3.28	12.50
148.84a	Male	50	3.57	14:00	14:10	14:45	16:00	2.00	14.00
148.84b	Male	50	4.55	12:45	12:48	14:00	15:05	2.33	11.00
148.89b	Female	50	6.25	10:20	10:25	12:52	13:50	3.50	8.00

DISCUSSION

Two factors that have the greatest bearing on the success of a trapping programme are the efficiency and the selectivity of the trapping effort (Boddicker 1999). Trapping efficiency is the number of captures relative to the number of trap-nights used. Trapping selectivity is the proportion of the captured animals that are target animals. It is possible to have a high trapping efficiency with a poor trapping selectivity.

Trapping should be as selective as possible so as to optimise time and expenditure and to avoid unnecessary stress or injury to animals (Boddicker 1999). It is possible to improve the selectivity of trapping by utilising the most selective equipment. For caracals, making box traps specifically designed for them are required to do this. This largely precludes animals that are significantly larger than caracals from being caught when trapping for caracals because they are physically too large to enter the cages (Table 1). The size of the cage door used here ensured that predators such as lions *Panthera leo*, brown hyaenas *Parahyaena brunnea* and spotted hyaenas *Crocuta crocuta* could not enter the cages. However, the size of the cage did not prevent lions, brown hyaenas and spotted hyaenas from investigating the cages and setting them off by nudging them. Selectivity to prevent animals smaller than caracals from getting trapped can be improved by setting the weight required to activate the trapdoor so that it requires a relatively heavy tread to trigger it (Boddicker 1999). Using cage traps, it is preferable to set the treadle finely and to accept that a high number of non-target animals will be caught rather than to set the treadle too coarsely and losing a possible caracal capture because the chances of injuring non-target species in box-traps are minimal. Positioning cages in areas of high caracal activity increases the selectivity of the trapping effort for caracal (Boddicker 1999).

Using specific baits will increase the selectivity of trapping too. The only non-predatory animals that were caught during the present study were an aardvark and three porcupines *Hystrix africaeaustralis* (Fig. 4). This shows that the choice of bait or lure largely precludes non-predators from being captured.

Baits and lures

Due to the conditions under which the present research was conducted, the use of live baits was not possible. It is important that the well-being of the animal that serves as bait be considered when using such a strategy. When the ambient temperature rises above 30°C it is not humane to leave an animal confined and unsheltered. Additionally, it was not practical or viable in the present study to patrol the trap line twice a day, once to check the traps and a second time in the late afternoon to reset the traps and to replace the live bait. It would not have been ecologically sound to use domestic cats as live bait because they are able to crossbreed with the African wild cats *Felis silvestris*, which occur in the Kgalagadi Transfrontier Park, if the bait animal should escape into the wild.

A number of bait and lure combinations were used during the study, but it was found that the most economic, practicable and effective combination of bait consisted of fresh frozen chicken pieces in conjunction with a visual lure (Table 1). Olfactory lures were also used with varying degrees of success (Table 1).

Trapping success

Although the 1.4 % trapping success rate that was achieved in this study seems low, it compares well with the results that were achieved for caracal in other studies where the capture success ranged between 0.2 and 2.2 % (Stuart 1982; Norton & Lawson

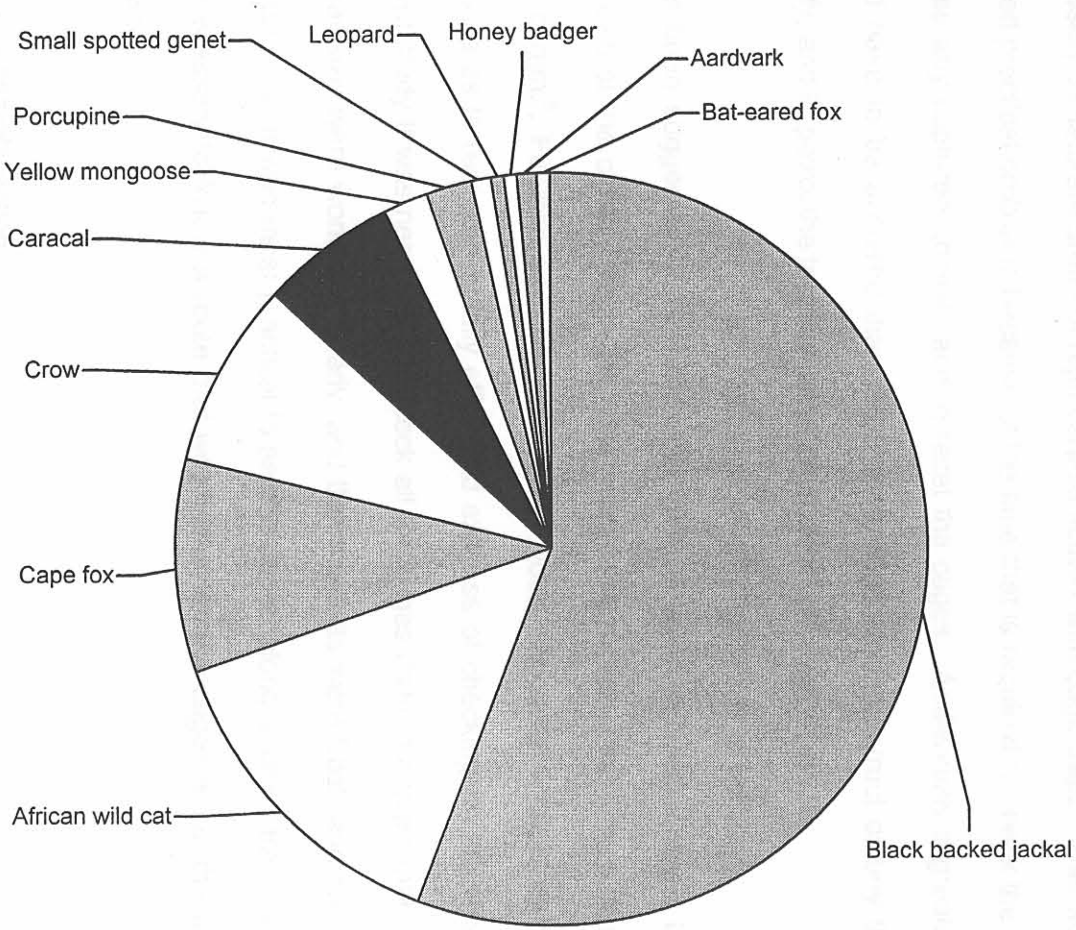

Figure 4: Relative trapping success achieved when using cage traps in the Kgalagadi Transfrontier Park to trap animalsfrom June 2000 to March 2002.

1985; Moolman 1986; Avenant & Nel 1998). This merely emphasises that caracal are inherently difficult animals to trap alive.

To reduce the time required to capture more animals in any study, it would have been necessary to saturate areas of high caracal activity with cage traps. This would have created practical problems because of the time that is required to check the cages, to release any captured animals and to reset the cages. Additionally a greater budget would have to be acquired than what was available to construct or buy the cages initially, and to patrol the trap line on a daily basis.

It has been suggested that radio collars can be attached to the cages in such a manner that the closing trapdoor would trigger the collars to start transmitting (Mills pers. comm.[5], Funston pers. comm.[6]). This would require the prioritisation of the cages so as to reduce the daily effort and expense of checking the trap-line. In the present study it was necessary to check all the cages daily to ensure that the trigger mechanisms were working properly, and that the baits were fresh and had not been disturbed. As it was most practical to set the cages along existing tracks or roads it was necessary to follow a route that would pass all the cages along the trap-line in one visit.

Chemical immobilisation

To fit caracals that were captured in the wild with radio collars, and to measure and weigh them it is necessary to immobilise them chemically (Brand 1993). A number of methods have been developed to administer immobilising drugs to captured wild

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animals. Commonly used methods include dart guns, blowpipes, pole-syringes and conventional syringes (Ebedes *et al.* 1996).

It is not feasible to dart a wild caracal in a cage trap with a dart gun because of the likelihood of injuring the captured animal even when the dart gun is set to its lowest muzzle velocity. The movement of caracals in the cage as humans approach it also precludes the effective use of blowpipes. In the present study a pole-syringe was used to administer drugs to captured caracals on two occasions. However, this was an inefficient way of immobilising them because a portion of the drug dose was wasted when the caracals moved around as the pole-syringe was introduced into the cage in an attempt to inject the animal. It was also found that even when using poles or sticks (Brand 1993, McKenzie & Burroughs 1993) to prevent the movement of a captured animal, it was not possible to immobilise caracals in cages with the minimum of stress or injury.

A crush plate to immobilise seven caracals, and one leopard in the traps was used without any resultant injuries to the study animals or the capturers. Equipment of this nature can be used on any caged animal that has to be immobilised. The prerequisite is that the capture equipment (cage and crush) be constructed with the target species in mind. In the case of larger predators it would be necessary to have more than one assistant available to control the crush plate properly.

McKenzie & Burroughs (1993) suggested using a dose of 3 to 4 mg per kg of Zoletil for the immobilisation of caracals. In the present study it was found that the prolonged human presence while estimating the body mass of a caracal caused unnecessary stress to the animal. Moreover the estimated mass was often inaccurate, and time was wasted in preparing a syringe according to the relevant estimate. It was preferable to use a standard dose of 50 mg of Zoletil (Virbac 1996) (Meyer pers. comm) for the immobilisation of caracals in cages. Animals with a body mass that varies from 8 to 14 kg were successfully immobilised when using this standard dose, and no supplementary dose was necessary.

Post capture handling of caracals

In most cases of carnivores being immobilised with Zoletil, the animal is positioned in a cool place once the work on the animal has been completed. The capture team then withdraws to keep watch over the recovering animal from a distance so as to ensure that the recovering animal is not attacked or incapacitated. The narcosis wears off slowly (Table 2) because there is no antidote for Zoletil (Burroughs 1993).

Of the nine caracals that were immobilised in the present study, one died as a result of heat stress that had induced capture myopathy. This death might partially have been caused by the differing elimination half-lives of tiletamine and zolazepam, as has been seen to be the case in domestic cats (Anon. not dated) and in lions (Stander & Morkel 1991). Subsequent to this mortality it was decided to replace all the immobilised caracals in their cages and to cover the cages with shade netting to create a suitably shaded and cool area for the duration of their recovery. No further mortalities occurred.

CONCLUSIONS

When set correctly, cage traps can be used effectively for the capture of caracals. Because the caracal is a low-density animal, the trapping success relative to the trapping effort will always be low. However, ways to increase the degree of species selectivity has to be researched. The only currently known way to achieve a higher degree of selectivity and efficiency in caracal trapping is to position the cage traps in areas of high caracal activity, and to investigate more caracal-specific lures and baits.

When a caracal is captured, it is essential to ensure that it is subjected to as little stress as possible. The animal should be immobilised as quickly as possible by using the best techniques available. If new ways can be found to reduce the stress on the captured animal, or to improve the efficiency of the capture technique they should be applied.

Wherever caracals are captured for research purposes, they should always be returned to their wild state in a condition and under circumstances that will ensure their survival. In the case of all small predators it is strongly recommended that the captured animals be returned to a cage trap until they have entirely recovered from any drug effects before being released.

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CHAPTER 5

RANGE USE BY THE CARACAL IN THE KGALAGADI TRANSFRONTIER PARK

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ABSTRACT

Two female and three male caracals *Caracal caracal* were radio-collared in the Kgalagadi Transfrontier Park and their ranges were calculated. Only three of the caracals produced sufficient data points for satisfactory harmonic mean and kernel analysis of their range sizes, but those of the other two were analysed with the minimum convex polygon procedure. The three statistically verifiable ranges were for two males and a female. The range sizes of males one and two, when calculated with the kernel method, were 312.8 and 92.3 km^2 respectively for 95 % of the points, and that of female one was 66.9 km^2. Range estimates of male three and female two could not be determined statistically. The reasons for the discrepancies in the range sizes are discussed, along with possible reasons for them. Nevertheless the ranges for caracals in the Kgalagadi Transfrontier Park are considerably larger than those calculated for caracals elsewhere in southern Africa.

Keywords: Caracals, *Caracal caracal*, radio-tracking, minimum convex polygon, kernel analysis, harmonic mean

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INTRODUCTION

The orientation of animals in relation to each other is determined by the availability of resources within the habitat in which they occur. The resources in question are not only those of food and shelter, but also the proximity of potential mates. Dispersion of animals in an environment tends to maximise the reproductive success of the individual (Davies 1991). In the case of solitary predators where the male plays no parental role, it seems that the ranges of the females are related to food resource distribution and those of the males to mate acquisition (Davies 1991, Bailey 1993). To maximise reproductive success a male's range tends to overlap with the ranges of a number of females. Ranges of solitary predators are strongly influenced by habitat quality, sex and age. In areas characterised by low prey densities, predators are likely to have larger ranges than in areas that have an abundance of prey (Bailey 1993).

Lawrence (1998) defined the range of an animal as that area within which an animal seeks its food. However, generally the broader definition is accepted that the range is that area in which an animal normally lives. The concepts of territoriality and range are often, mistakenly, used interchangeably. A territory is part or all of a range, being defined as that area within a range that is actively defended by the occupier against animals of the same species (Lawrence 1998). Burt (1943) distinguished between an animal's range and its territory as follows: a range is that area that an animal occupies, whereas a territory is an area within the range that is actively and aggressively defended. Pitelka (1959) suggested that the territory of an animal is that area within an animals' range that is used exclusively by that animal. It is the concept of range rather than territory that is the focus of the present study.

In many cases, intra-specific overlaps in range use occur, because many animals do not occupy exclusive ranges (Smith 1990). Burt (1943) summed up the concept by defining the range of an animal as that area that an animal utilises for its basic life requirements of feeding, breeding, and resting.

The range of an animal is not a simple uni-dimensional area because animals use the space within the boundary of their range disproportionately at different times. Areas of high utilisation within the range are known as core areas of use (Samuel, Pierce & Garton 1985). The identification of a core area of use within a range is important because it contributes to the understanding of the ecological factors that dictate range use. Core areas of use generally contain home sites, refuges and dependable food sources (Burt 1943; Kaufmann 1968; Ewer 1962). It is accepted that while ranges may overlap, core areas of use never do so (Ewer 1962). The core areas of use are also used more intensively than what might be expected under an equal-use pattern (Samuel *et al.* 1985).

The basic hypothesis that is investigated here is that the range size of the caracal *Caracal caracal* in arid areas where the prey base is variable and the hunting cover is sparse (Kruuk 1986), is indeed larger than that of caracal elsewhere, as has been suggested by Gittleman & Harvey (1982) and Bothma & Le Riche (1994). This hypothesis has been supported in other felids by research on the bobcat *Lynx rufus* (Litvaitis *et al* 1986), Canadian lynx *Lynx canadensis* (Sandell 1989) and leopard *Panthera pardus* (Bothma *et al.*1997). The following two specific key questions were examined here:

1. What is the range size of the caracal in this arid region?
2. Do the ranges of caracals near the Namibian border in the Kgalagadi Transfrontier Park extend across the border into Namibia?

STUDY AREA

This study was done in an area along the Namibian border near Mata-Mata in the southwestern portion of the Kgalagadi Transfrontier Park. For logistic reasons it was decided to confine the research activities to an area that extended 60 km north from the Mata-Mata rest camp along the Namibian border (20° 00' E longitude), to approximately 20 km into the interior of the Kgalagadi Transfrontier Park.

The Kalahari Gemsbok National Park was proclaimed in 1931, but it only became a reality in 1935 when a number of farms along the southern bank of the Aoub River were acquired. Today, the Park exists in much the same ecological state as it was then (Van Wyk & Le Riche 1984). An agreement to formally combine the Kalahari Gemsbok National Park (South Africa) with the bordering Gemsbok National Park (Botswana) to form the Kgalagadi Transfrontier Park was signed by representatives of the governments of South Africa and Botswana in 1999. This agreement was ratified at an amalgamation ceremony that was held on the 12 May 2000 (Donaldson 2000).

The Mata-Mata area lies in the Shrubby Kalahari Dune Bushveld of the Savanna Biome (Low & Rebelo 1996). This is an arid savanna with temperatures varying from –10° C to 45° C in the shade with an annual mean rainfall of 153.47 mm occurring mainly in the summer. The landscape is one of undulating dunes with sparse vegetation at altitudes varying from 1000 to 1100 m above sea level (Low & Rebelo 1996).

The vegetation is characterised by the trees *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca*, a shrub layer of *Grewia retinervis* and *Rhus tenuinervis*, and a well-developed grass layer consisting mainly of *Stipagrostis amabilis*, *Eragrostis lehmanniana, Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996). There is little variation in the soil forms because the area is predominantly covered by aeolian sand overlying calcrete (Low & Rebelo 1996).

The Kgalagadi Transfrontier Park forms the southern part of the unique greater Kalahari ecosystem. Because of the arid nature of the area, many of the plants there are ephemeral. After sufficient rain, these plants germinate quickly to complete their life cycle in a short time (Eloff 1984).

Because of the harshness of the environment, the southern Kalahari is an area that is only sparsely inhabited by humans. This above any other factor contributes to the uniqueness of the area, and it enhances the value of the area for field research in wildlife management and conservation.

METHODS

Three adult male and two adult female caracals were captured with cage traps from July 2000 to April 2002, and were fitted with 250 g Telonics radio-collars transmitting in the 148.80 to 148.89 MHz. ranges. Three individuals (male 1, male 2 and female 1) provided sufficient data points for meaningful statistical analysis of their range sizes with the harmonic mean and kernel methods. The other two individuals (male 3 and female 2) only generated sufficient data points to calculate range size with the minimum convex polygon method. Nevertheless, these results are given here for comparative purposes only. No attempt was made to measure range overlaps because not all the caracals in a particular area could be monitored.

All the captured caracals were judged to be adults by inspection of their teeth (Stuart 1982) and because they had achieved a weight consistent with an adult (Bernard & Stuart 1987). Notwithstanding the adult status attributed to all three male caracals, it is probable that male 3 was a young adult because his movements indicated that he was still attempting to establish a permanent range. The difference in body weight and canine length (Table 1) between male 1 and male 2 indicates that male 2 was a younger individual, weighing less and with less evidence of wear on the canine teeth than in male 1.

After their release, the radio-collared animals were radio-located on a weekly basis, where possible. The intermittent nature of the consecutive observations ensured that the positional locations were independent of one another and of the disturbance caused to the animal when it was tracked before (Reynolds & Laundre 1990; Swihart & Slade 1985). The tracking regime therefore avoided auto-correlation of positional data and the resultant underestimation of range size (Swihart & Slade 1985). Most locations were obtained by ground tracking, because an aircraft was not available during the final year of the project.

Radio-tracking

Radio-tracking was done primarily from the ground, but it was occasionally supplemented with aerial tracking. Positional fixes were based on the global

Table 1: *The range sizes and age determination of the caracals that were radio-tracked in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Collar frequency in MHz	Period collared in months	Gender	Range size in km^2: 95 % MCP estimate	Range Size in km^2: 95 % kernel estimate	Age	Mass in kg	Total body length in mm	Canine length in mm			
								Right upper	Right lower	Left upper	Left lower
148.82	5.00	Male	765.7		Adult	10.0	1150	15.0	12.0	14.5	11.7
148.87	1.00	Female	2.7		Adult	9.5	985	9.2	0.0	10.0	0.0
148.88	12.00	Male	168.8	312.8	Adult	12.5	1100	15.4	13.6	15.6	13.0
148.84	7.00	Male	57.1	92.3	Adult	11.0	1175	17.0	13.4	17.8	13.2
148.89	5.00	Female	62.4	66.9	Adult	8.0	1004	13.4	11.2	12.0	10.5

MCP: Minimum convex polygon method

positioning system (GPS). Traditionally, radio-collared animals are located by triangulation (Lindzey & Meslow 1977, Stuart 1982, Don Bowen 1982, Litvaitis, Sherburne & Bissonette 1986, Moolman 1986, Kaunda 1998, Mizutani & Jewell 1998). However, there are limitations inherent in the use of triangulation as there may be discrepancies between the animal's true position and the position that is eventually calculated for it (Macdonald & Amlaner 1980, Nams & Boutin 1991). To obviate these errors it was decided to visually locate the radio-collared animals first and then to determine their positions with GPS equipment.

Animals were radio-tracked by using the crests of high dunes as vantage points to listen for radio signals. The direction from which the signal was being transmitted was determined by using a directional antenna in conjunction with a magnetic compass, ensuring that other sources of magnetism did not cause false deflection of the compass (Kenward 1987). Due to the nature of the terrain in the Kgalagadi Transfrontier Park it was possible to travel directly towards the radio signal through the veld. That the correct direction was being followed was confirmed by regularly taking further bearings towards the signal from vantage points en route. In principle, as the distance between the receiver and the transmitter decreases the perceived signal strength increases. Once the signal was judged to be within walking range of the vehicle, the radio-collared animal was approached on foot until visual contact with the animal was made. It was preferable to follow this procedure during the heat of the day, because the radio-collared animal was then less likely to flee before a visual location could be confirmed. In cases where animals did flee before a positive visual location could be done, the onset point of a set of fresh tracks was used to indicate the caracal's original position.

Occasionally, aerial tracking was used to supplement ground tracking. Aerial tracking was done from a high-wing Cessna 182 aircraft with directional antennas attached to the wing struts on either side of the aircraft. Radio-tracking followed the conventional method (P. Funston pers comm.[1]; Kenward 1987). After running some tests it was established that radio-locations taken from the aircraft were accurate to within a grid of 10 000 m^2.

Calculation of range size and identification of core areas of use

If an animal's position is sampled at intervals over a period of time, a plot including all those fixes represents the animal's range for that period of time (Kenward 1987). Positional fixes for radio-collared animals were recorded and used to calculate the range of caracals in the Kgalagadi Transfrontier Park.

Three methods of range analysis were applied to the data, a parametric method (the minimum convex polygon method) and two non-parametric ones (the kernel analysis method and the harmonic mean method). The non-parametric methods of data analysis were selected because they do not impose false probabilistic circles or ellipses, or require assumptions of normal distribution on the range data calculations (Zar 1984, Kenward 1987). The data were subjected to these analyses by using two different computer programs because it has been found that different programs give different range size estimates for the same data set, even while applying the same analysis protocols (Gallerani Lawson & Rodgers 1997). Consequently the Ranges V program (Kenward & Hodder 1996) was used as the primary range estimator, and the Animal Movement Extension of the widely used ArcView Global Information System package, (Hooge 1999), as the secondary estimator. .

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Minimum convex polygon method

The simplest and most widely used method of assessing the range size of an animal is the minimum convex polygon method because it is the smallest area polygon that includes all the location points (Worton 1987). The limitations of this method are that the range size is highly correlated with the number of observations, and that it includes areas that are never visited by the animal in question. Therefore the limited sample sizes available here could only be used for rough indications of range size. The method also does not allow the calculation of the intensity of range use because it only takes the outermost locations into consideration (Worton 1987, Gallerani Lawson & Rodgers 1997). The greatest benefit of this method is that it is the only one that is comparable between studies (Harris *et al.* 1990) because all the other range size estimators use a different algorithm for their estimation of range size.

Outlying location points may be a result of occasional excursions outside the range, and the inclusion of these points could exaggerate the size of the range when computed by using the minimum convex polygon method (Mizutani & Jewell 1998). To take this into consideration, a process of peeling is suggested that involves disregarding 5 % of the location plots that lie furthest away from the arithmetic mean centre of the range, and calculating the area of the minimum convex polygon on the remaining 95 % of the locations (Kenward 1987, Mizutani & Jewell 1998, Broomhall 2001). However, removal of any outliers must be done judiciously because their possible biological relevance cannot be underestimated (Linn & Key 1996).

The core area of use of the range has been defined as an area of obvious clumping of locations (Stuart 1982, Moolman 1986, Bothma 1994). Bothma (1994) found that 13 of the 18 locations (72.2 %), for a collared male caracal in the Kgalagadi

Transfrontier Park, were included in the core area. Based on this it was decided to construct 75 and 50 % contours for the current data to give an indication of the core areas of range use.

Harmonic mean method

The harmonic mean method estimates the density distribution of fixes and equates this to the probability of encountering the animal. The resultant contours indicate the centres of activity or core areas of use. The method is therefore useful when determining the intensity of habitat use, but not as useful for determining total range size (Worton 1987, Mituzani & Jewell 1998). This calculation method allows the isolation of more than one centre of activity, which can be beneficial when calculating core areas of use (Harris *et al.* 1990).

The harmonic mean method allows the calculation of ranges that relate closely to the distribution of the location fixes, but it includes areas that are not frequented by the animal. It is therefore advisable to use an 80 % isopleth to give a more accurate estimation of the range (Harris *et al.* 1990).

The harmonic mean method should not be used to compare mean range sizes between studies statistically because the various computer programs use different algorithms and grid cell sizes upon which to base the calculations (Harris *et al.* 1990). Using the harmonic mean method it has been suggested that the 50 % isopleth gives a suitable indication of core areas of use for many species (Harris *et al.* 1990). It was therefore decided to analyse the current data according to this guideline.

The kernel method

The kernel method relies on placing a probability density on each location point. Each probability density is known as a kernel (Worton 1989, Erran Seaman & Powell 1996). The advantages of kernel methods are that they are not based on parametric assumptions and facilitate the smoothing of location data. Additionally, kernel methods have consistent statistical properties (Worton 1989). The selection of a smoothing parameter is important when using the kernel method (Worton 1989), and generally, the least-squares cross-validation approach is considered appropriate (Silverman 1986). A number of options are available when using kernel analysis to investigate range use by animals. In cases where accuracy is not critical, a fixed kernel method gives sufficient information. However, where accuracy is important, such as in arid environments where range size might be used to calculate the size of viable conservation areas, an adaptive kernel method should be used in conjunction with a least-squares cross-validation (Worton 1989). This is the approach that was followed for the analyses that were done in the present study.

Many authors feel that the kernel method with a 95 % isopleth gives a reliable representation of the range size of many species (Jaremovic & Croft 1987, Mizutani & Jewell 1998, Broomhall 2001). It was therefore decided to use this method upon which to base the range size estimates of the caracals (male 1, male 2 and female 1) for which sufficient data points were recorded in the present study to ensure meaningful results.

The 95 % isopleth was used in both the harmonic mean and kernel analyses to remove the effect of outliers on the calculation of range size (Jaremovic & Croft 1987, Mizutani & Jewell 1998, Broomhall 2001). To define the core areas of use, 75 and 50 % isopleths were drawn.

RESULTS

For those caracals for which sufficient locations were obtained to facilitate meaningful analyses (≥ 25 locations) (Mituzani & Jewell 1998, Broomhall 2001) the results appear in Figs. 1 to 6. In addition, the 100 % minimum convex polygon and the peeled (95 %) minimum convex polygon results appear in Fig. 7. Where appropriate, the core areas of use as determined with the harmonic mean method (75 and 50 % isopleths) (Ranges V) appear in Figs. 1, 3 and 5.

Male 1 was located on 40 occasions from 10 August 2001 to 21 August 2002 (Table 1). Synthesis of these data showed that he had a range of 312.8 km^2 (95 % kernel analysis) (Fig. 1), with core areas of use of 94.0 km^2 (75 % harmonic mean) and 51.5 km^2 (50 % harmonic mean) (Fig. 2). The 50 % harmonic mean core area of use equates to 16.5 % of the total range. With the minimum convex polygon method, the 50 % core area of use comprises 22.5 % of the total range area as calculated with the 95 % minimum convex polygon method.

Male 2 was located on 30 occasions. Synthesis of these data gave a range estimation of 92.3 km^2 (95 % kernel analysis) (Fig. 3), with core areas of use of 27.9 km^2 (75 % harmonic mean) and 24.2 km^2 (50 % harmonic mean) (Fig. 4). The core area of use (50 % harmonic mean) equates to 15.3 % of the total range. Based on the minimum convex polygon method, the core area of use represents 40.4 % of the total range.

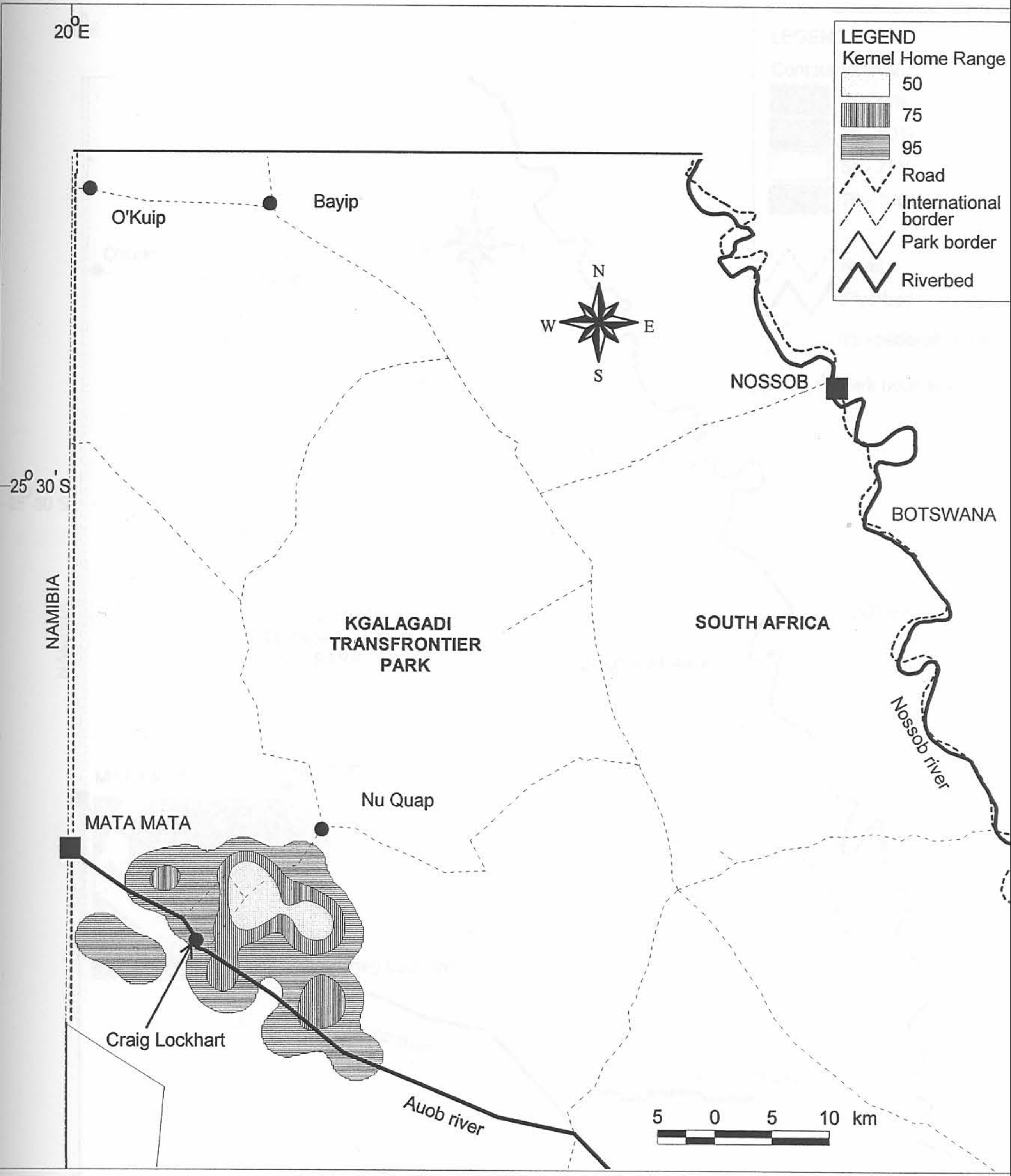


Figure 1: Range use of male 1 using the kernel home range method in the Kgalagadi Transfrontier Park from June 2000 to July 2002.

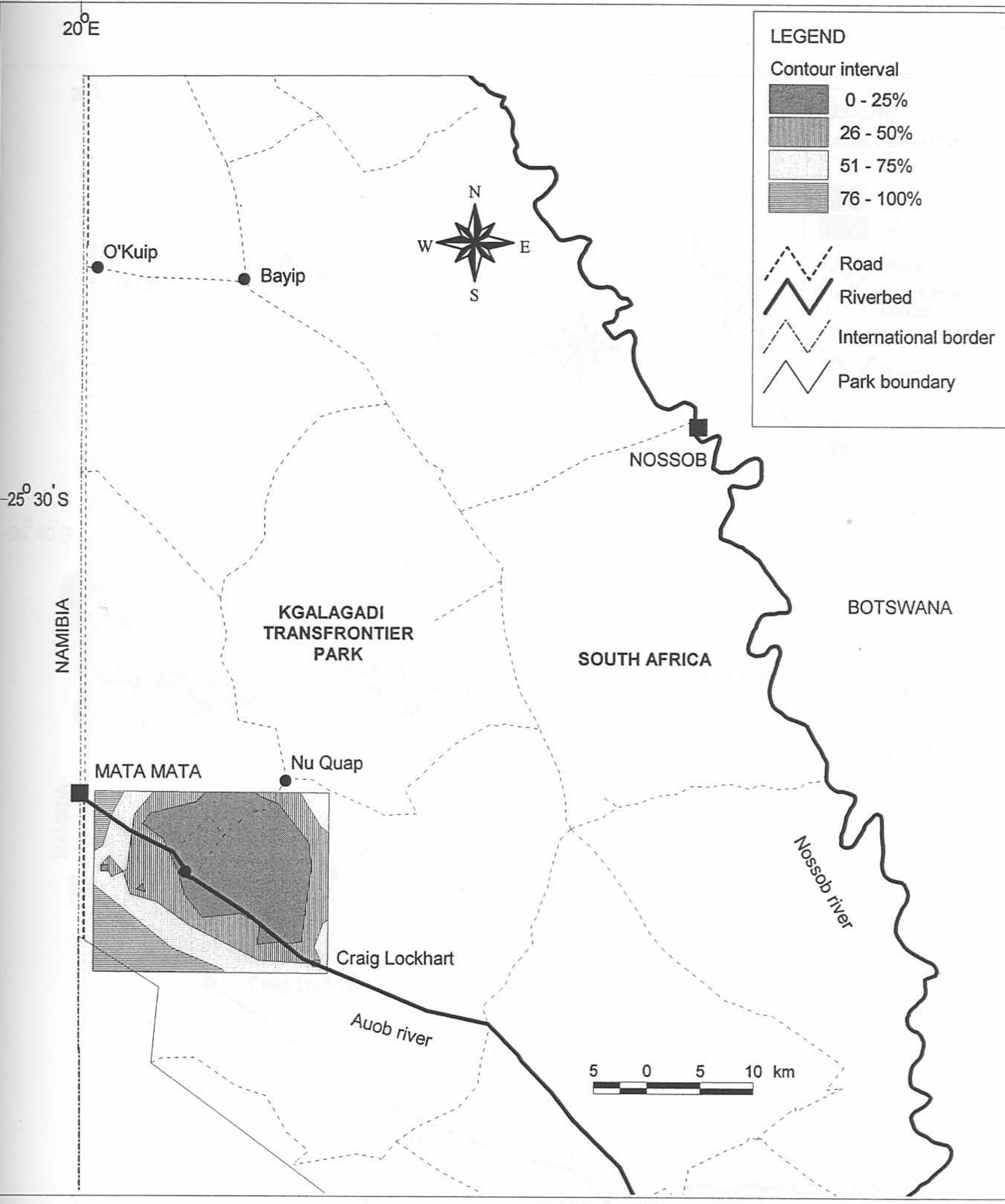


Figure 2: Range use of male 1 using the harmonic mean method in the Kgalagadi Transfrontier Park from June 2000 to July 2002.

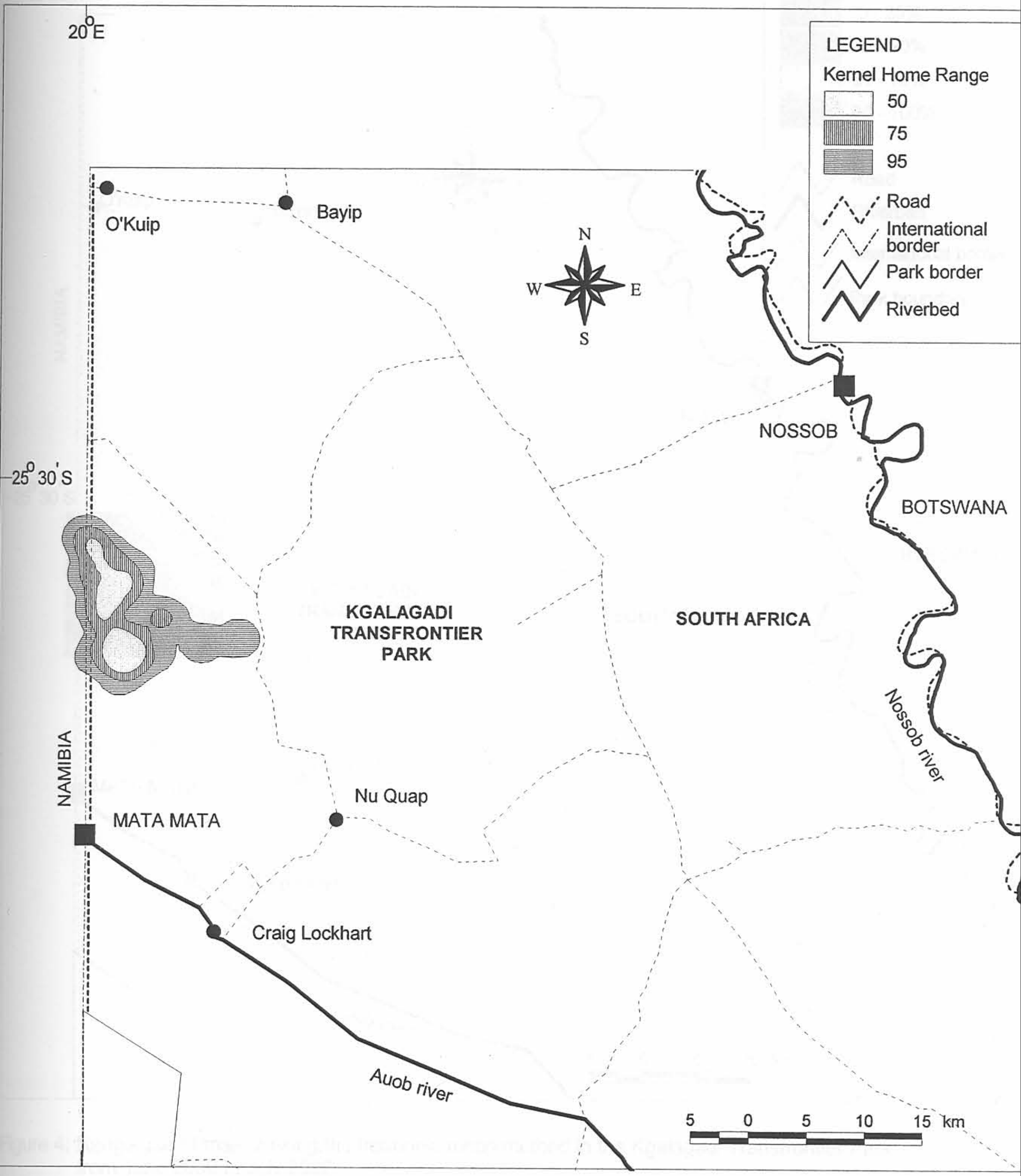


Figure 3: Range use of male 2 using the kernel home range method in the Kgalagadi Transfrontier Park from June 2000 to July 2002.

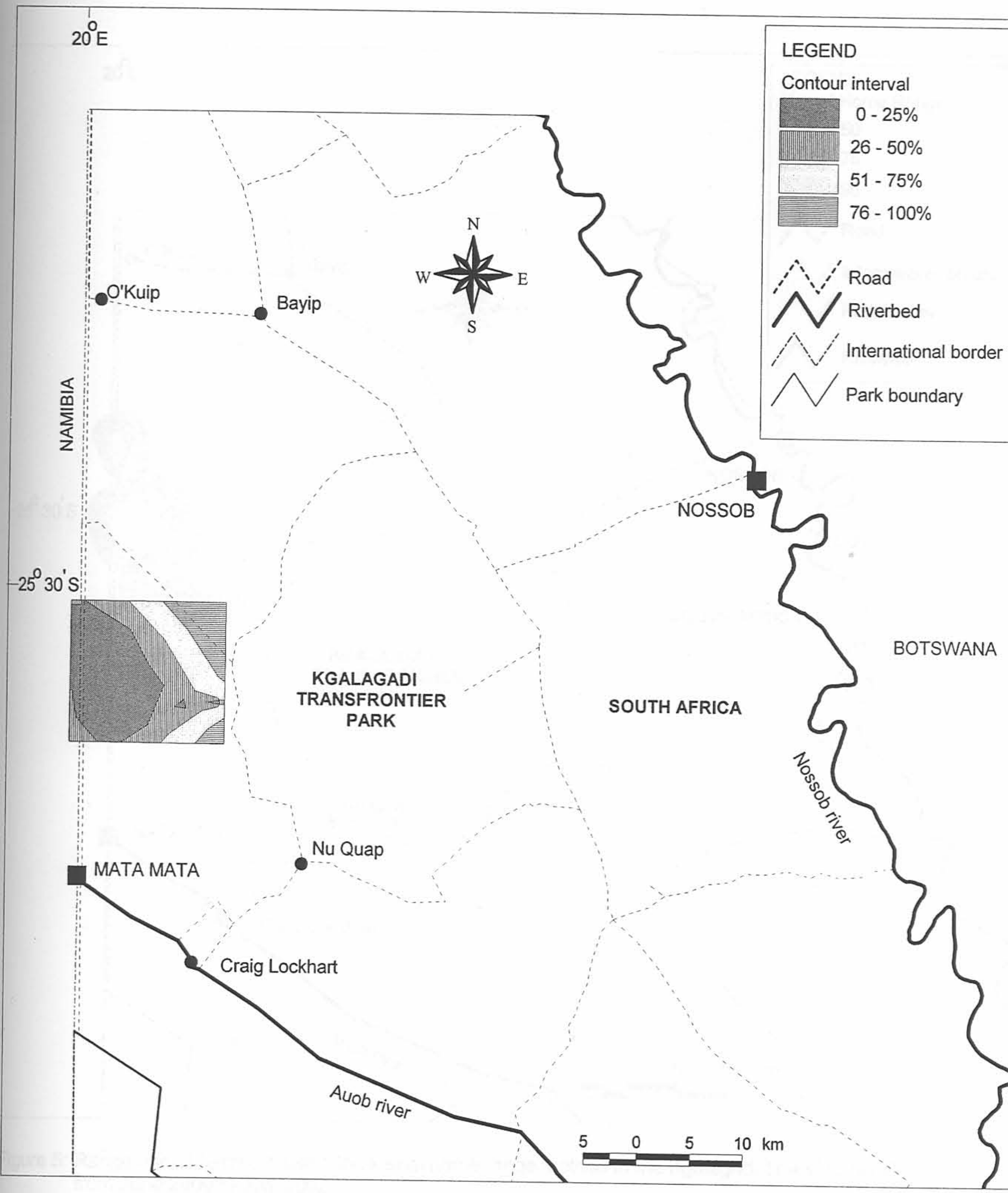
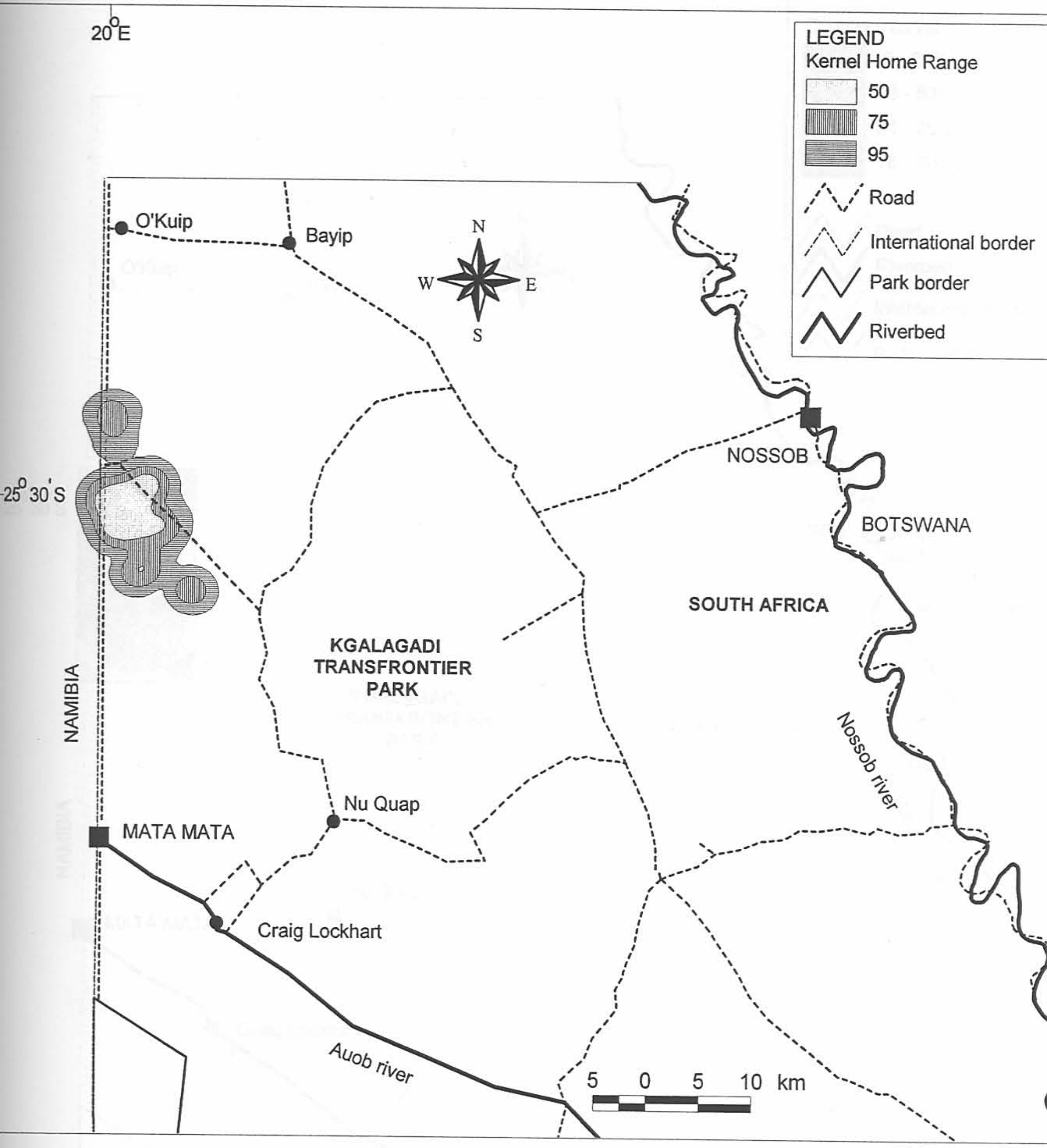


Figure 4: Range use of male 2 using the harmonic mean method in the Kgalagadi Transfrontier Park from June 2000 to July 2002.



gure 5: Range use of female 1 using the kernel home range method in the Kgalagadi Transfrontier Park from June 2000 to July 2002.

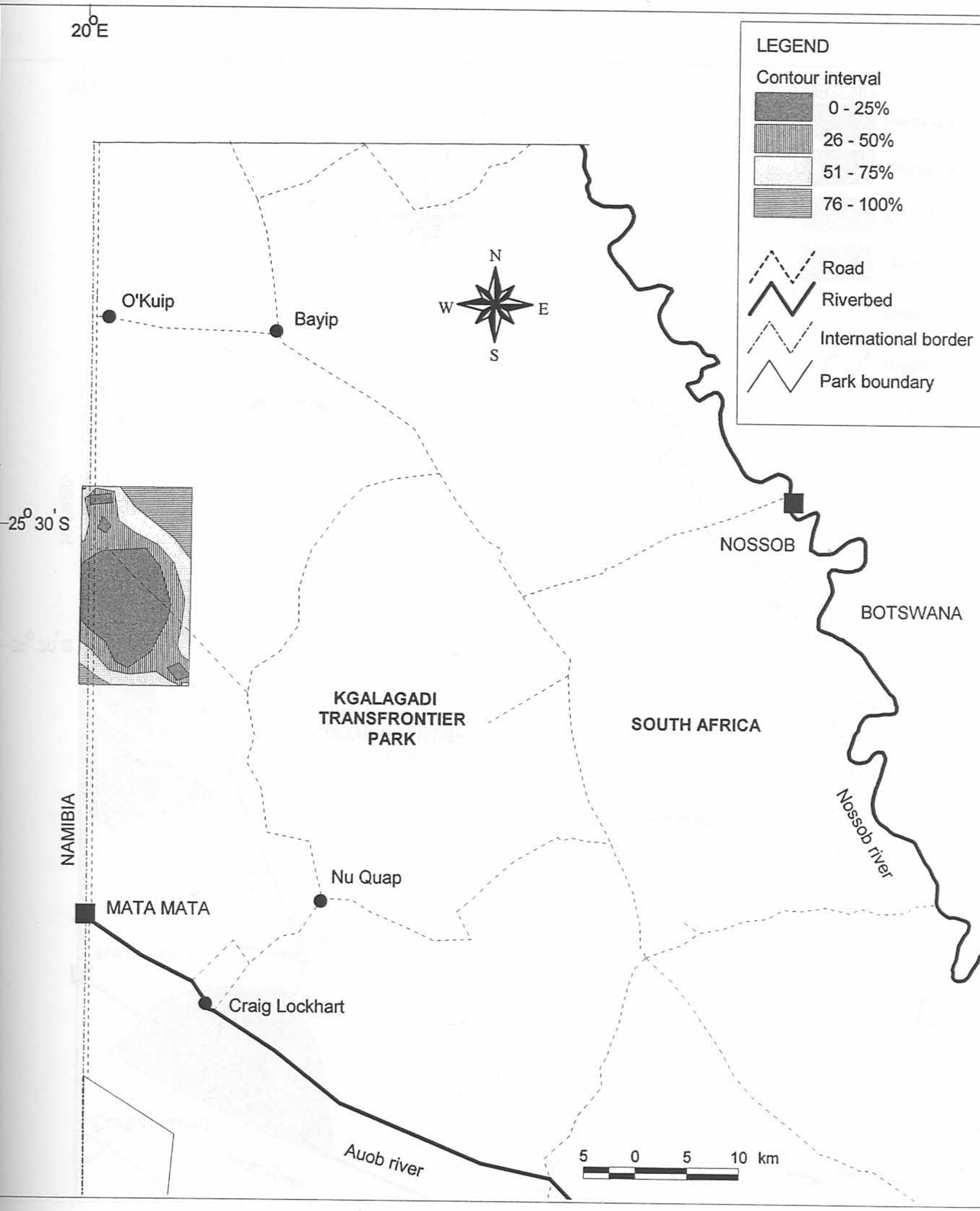
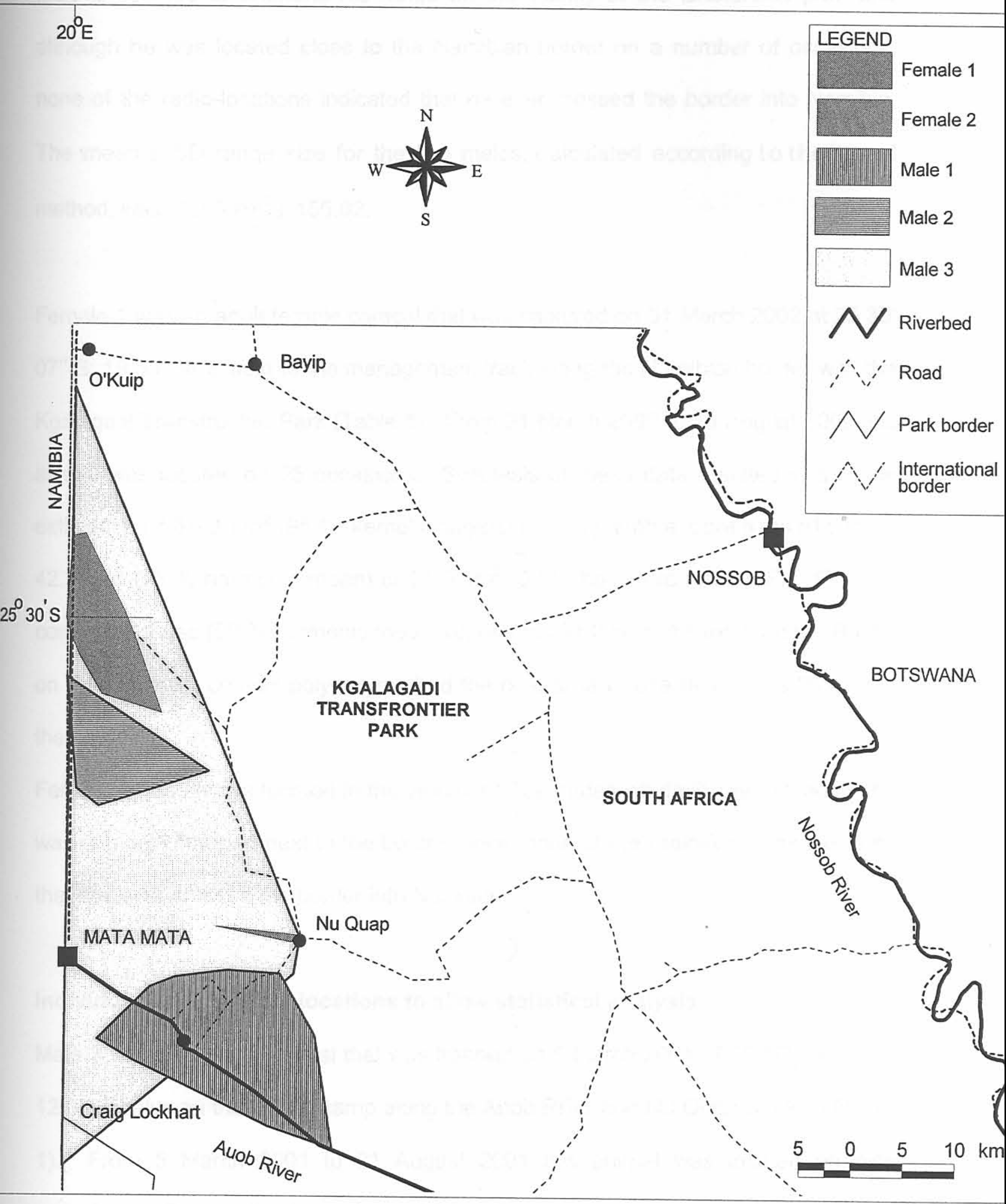


Figure 6: Range use of female 1 using the harmonic mean method in the Kgalagadi Transfrontier Park from June 2000 to July 2002.



gure 7: Range use of all radio-collared caracal determined by the minimum convex polygon method in the Kgalag
Transfrontier Park from June 2000 to July 2002.

Male 2 seemed to orientate his range on the vicinity of the Driefendas pan, and although he was located close to the Namibian border on a number of occasions, none of the radio-locations indicated that he ever crossed the border into Namibia. The mean ± SD range size for the two males, calculated according to the kernel method, was 202.5 km^2 ± 155.92.

Female 1 was an adult female caracal that was captured on 31 March 2002 at 25 30' 07" S: 19 59' 56"E next to the management track along the Namibian border with the Kgalagadi Transfrontier Park (Table 1). From 31 March 2002 to 19 August 2002 this animal was located on 25 occasions. Synthesis of these data resulted in a range estimation of 66.9 km^2 (95 % kernel analysis) (Fig. 5), with a core area of use of 42.2 km^2 (75 % harmonic mean) or 21.5 km^2 (50 % harmonic mean) (Fig. 6). The core area of use (50 % harmonic mean) represents 31.0 % of the total range. Based on the minimum convex polygon method the core area of use represents 26.4 % of the range.

Female 1 was always located in the vicinity of Driefendas windmill, and although she was originally trapped next to the border fence, none of the radio-locations indicated that she ever crossed the border into Namibia.

Individuals with too few locations to allow statistical analysis

Male 3 was a 10.0 kg caracal that was trapped on 5 March 2001 at 25 46' 14" S: 20 12 07 E between the giraffe camp along the Auob River and Nu Quap windmill (Table 1). From 5 March 2001 to 21 August 2001 this animal was located on nine occasions. Due to the low number of locations, the only appropriate method for range analysis was the minimum convex polygon method. According to this method the range size of male 3 was 765.7 km^2 (95 %) (Fig.7). The resultant core areas of use, derived by constructing 75 and 50 % contours, were 118.2 and 21.7 km^2 respectively. Male 3 was eventually shot by a Namibian farmer when it crossed into Namibia from the Kgalagadi Transfrontier Park.

Female 2 was a 9.5 kg caracal captured at Nu Quap windmill (25 46' 17" S: 20 12' 09" E) on 15 June 2001 (Table 1). During the period from 15 June 2001 to 19 July 2001 this animal was located on seven occasions. This animal died on 19 July 2001 and the collar was retrieved. The condition of the collar on recovery suggests that another predator had killed the caracal. The minimum convex polygon method (95 %) was applied to this small sample and gave a range size of 2.7 km^2 (Fig.7). The resultant core areas of use were 0.3 and 0.2 km^2 respectively when the 75 and 50 % minimum convex polygon contours were calculated. For the period that female 2 was collared, she remained in a small area in the vicinity of the Nu Quap windmill.

The ranges and core areas of use for male 3 and female 2 are represented in Tables 2 and 3 for completeness only but they should not be considered representative of the mean range size and core areas of use of caracals in the Kgalagadi Transfrontier Park, nor were they used for this purpose.

Namibian farmers bordering the Kgalagadi Transfrontier Park shot three research animals that were originally captured and radio-collared in the Kgalagadi Transfrontier Park. It is therefore clear that the caracals do cross into Namibia from the Kgalagadi Transfrontier Park. Due to the loss of these animals it was not possible to assess whether the movement of caracals into Namibia was due to stock raiding or whether it simply indicated that the ranges extended beyond the borders of the Park, as do those of leopards (Bothma *et al.* 1997).

DISCUSSION

Because of the small sample size and the highly variable results (Table 2) it was decided to discuss the range of each caracal independently. Moreover, the ranges of the animals that generated meaningful results when using statistical methods are discussed separately from those upon which it was only possible to perform minimum convex polygon analyses.

Male 1 was collared for the longest period of time, and hence he produced in the highest number of location points. This animal also had the largest range of all the animals that could be located on sufficient occasions to facilitate statistical analysis of the range data. After collaring, the animal remained in a stable range area, to the extent that after locating the animal on six separate occasions it was possible to go to one of two vantage points within the range and be sure of picking up a signal from the animal. All attempts to locate the animal were successful. This animal was never located in the vicinity of the Namibian border. Although the possibility exists that the animal made excursions to areas outside the stable range area, no such behaviour was detected by radio-tracking.

When the range of male 1 is compared with that of the male studied by Bothma & Le Riche (1994) in the Kgalagadi Transfrontier Park there is an obvious difference in range size. The range of an adult male caracal as calculated by Bothma & Le Riche (1994) was 308.0 km^2 when calculated according to the minimum convex polygon method using 100 % of the locations. In comparison the male 1 had a range of 194.3 km^2 (Ranges V) or 194.2 km^2 (Animal movements) when calculated according to the minimum convex polygon method. This is 63.1 % of the range size of the adult male caracal that Bothma & Le Riche (1994) studied. Kernel analysis (95 %) of the range

Table 2: *Range sizes calculated by two range programs as applied to data collected for caracals in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Item	Range method	Range size in km^2				
Animal number:		Male 1	Male 2	Female 1	Male 3	Female 2
Collar frequency:		148.88	148.84	148.89	148.82	148.87
Gender:		Male	Male	Female	Male	Female
Number of radio locations:		40	30	25	9	7
Ranges V	MCP 100	194.3	71.3	66.7	765.7	2.7
	MCP 95	168.8	57.1	62.4	765.7	2.7
	MCP 75	97.1	39.8	32.3	118.2	0.3
	MCP 50	37.9	23.1	16.5	21.7	0.2
	Harmonic 100	283.0	120.0	95.7	-	-
	Harmonic 95	219.3	51.0	89.8	-	-
	Harmonic 75	94.0	27.9	35.3	-	-
	Harmonic 50	51.5	14.1	20.8	-	-
	Kernel 100	400.1	161.6	102.8	-	-
	Kernel 95	312.8	92.3	66.9	-	-
	Kernel 75	139.3	44.2	42.2	-	-
	Kernel 50	55.7	24.2	21.5	-	-
Movement	MCP 100	194.2	71.3	66.6	765.6	2.7
	MCP 95	-	-	-	-	-
	MCP 75	-	-	-	-	-
	MCP 50	-	-	-	-	-
	Kernel 95	268.9	120.3	138.1	-	-
	Kernel 75	88.4	56.1	69.2	-	-
	Kernel 50	29.1	23.1	26.6	-	-
	Harmonic 100	-	-	-	-	-
	Harmonic 95	-	-	-	-	-
	Harmonic 75	-	-	-	-	-
	Harmonic 50	-	-	-	-	-

Ranges V: Kernel analysis using a tail weighted adaptive kernel and least-squares cross-validation of male 1 estimates the range of this caracal at 312.8 km^2 which is 61.0 % larger than the range estimated according to the minimum convex polygon method. Different environmental conditions, and hence food resources, may have played a role here.

Male 2 generated sufficient locations to allow for meaningful statistical analysis and had a range of 71.3 km^2, when calculated according to the 100 % minimum convex polygon method. This equates to 23.1 % of the range size recorded by Bothma & Le Riche (1994) and 36.7 % of the size of the male 1.

Although male 2 had a considerably smaller range than male 1 on two occasions when radio-tracking was attempted, no signal was detected. On all occasions when this male was successfully radio-located, a signal was detected from one of three high vantage points within the defined range. It is possible that on those occasions when this animal could not be detected, he may have been on excursions outside the known area of its range. The reasons for these excursions may be that he was trying to extend his range. Another possibility is that he had gone across the border into Namibia. This does not, however, explain why a signal was not detected, because vantage points along the border were used for radio-tracking purposes. Kernel analysis (95 %) resulted in a range size estimation of 92.3 km^2 that is 29.4 % larger than the range estimated according to the minimum convex polygon method for male 2.

Female 1 provided sufficient locations to allow for meaningful results from statistical analysis of the range size. She was frequently recorded in the vicinity of the Namibian border. As no other females were trapped and collared in the Kgalagadi

Transfrontier Park, it is impossible to compare these results with that of other females. The kernel method (95 %) estimated the female's range at 66.9 km^2, which is to all purposes identical to that when estimated by the minimum convex polygon method (66.7 km^2).

The young Male 3 was limited to a core area of use (minimum convex polygon 75 %) of 118.2 km^2 for the first month after capture (Table 1). Thereafter he moved over large distances which made regular radio-tracking impossible. This animal first moved northwest from where he was captured near Nu Quap (25 46' 15" S: 20 12' 05" E) to an area near Driefendas windmill (25 28' 20" S: 20 01' 01" E) a distance of 40 km. Over a period of two months he then moved 36 km further to the north and was located near O'Kuip (25 16' 28" S: 20 00' 57" E). He was finally shot in Namibia on a farm 25 km south of Mata Mata rest camp at 25 57' 53" S: 19 59' 50" E. It is believed that this animal was moving out of its natal range and was trying to establish a range of its own as is known to happen in larger predators (Bothma 2002). The range of 765.7 km^2 (100 % minimum convex polygon) for the period over which he was tracked would then not have been stable. This range is 248.6 % larger than the range established for an adult male caracal in the same area by Bothma & Le Riche (1994) and 576.7 % larger than the mean male range (100 % minimum convex polygon) of the other males in this study.

Female 2 was located within a small area for a period of a month. On capture, this animal seemed to be in a good physical condition. It was obvious that she was old because there was evidence of extensive tooth wear (Table 1). This female remained in a range of 2.7 km^2 (100 % minimum convex polygon). However on the 19 July 2001 the collar was located 300 m from Nu Quap Windmill, and it was evident from the condition of the collar that the caracal had died and had been consumed by another predator. Therefore this range area is not indicative of the mean range size of female caracals in the Kgalagadi Transfrontier Park.

Comparison with other studies

When compared with other studies of caracal ranges (Table 3) it is evident that even when the minimum convex polygon method is applied for comparative purposes, the range sizes of caracals in the Kgalagadi Transfrontier Park are far larger than those in other areas. The only study area that has revealed a larger range size for an individual male caracal was in Saudi Arabia, a true desert with a concomitant low prey density. The peeled range (95 % minimum convex polygon) for the individual in Saudi Arabia was 865.4 km^2. The 100 % minimum convex polygon method for the animal in Saudi Arabia gave a range of 1116.0 km^2 (Van Heezik & Seddon 1998).

Rodents form a significant portion of the diet of a caracal (Stuart 1982, Moolman 1986, Avenant 1993). The relatively smaller range size of males 1 and 2 (Tables 1 and 2), when compared with the results from Bothma & Le Riche (1994), could be related to the higher prey abundance as a result of two consecutive years of rainfall far above the mean for the study area during the study period. Rodent populations tend to track increased rainfall closely, with a gradual build-up and rapid decline (Nel *et al.* 1984). The population densities of small predators tend to change in synchrony with prey population dynamics (Brand *et al.* 1976). The ranges of small predators tend to expand as prey densities decline (Ward & Krebs 1985, Litvaitis *et al.* 1986).

There is no evidence from other studies that the range size of female caracals is related to the range size of male caracals according to a specific ratio. However,

Source	Study area	Animal	Gender	Number of locations	MCP 100 (km^2)	MCP 95 (km^2)
Stuart (1982)	Caledon	1	male	67	48.0	-
	Caledon	2	male	4	N.A.	-
	Eastern Robertson Karroo	3	female	43	11.8	-
	Eastern Robertson Karroo	4	female	17	26.7	-
	Eastern Robertson Karroo	5	female	12	22.4	-
	Coastal sandveld	6	female	25	11.9	-
Norton & Lawson (1984)	Stellenbosch	1	male	63	65.0	-
Moolman (1986)	Mountain Zebra National Park	1	male	28	16.7	-
	Mountain Zebra National Park	2	male	30	16.0	-
	Mountain Zebra National Park	3	male	35	15.8	-
	Mountain Zebra National Park	4	male	66	12.2	-
	Farm next to Mountain Zebra National Park	5	male	41	30.6	-
	Farm next to Mountain Zebra National Park	6	male	26	21.5	-
	Farm next to Mountain Zebra National Park	7	male	23	5.1	-
	Mountain Zebra National Park	8	female	46	6.5	-
	Mountain Zebra National Park	9	female	45	6.3	-
	Mountain Zebra National Park	10	female	27	5.1	-
	Mountain Zebra National Park	11	female	24	3.9	-
Bothma & Le Riche (1994)	Kgalagadi Transfrontier Park	1	male	18	308.0	-
Avenant & Nel (1997)	West Coast National Park	1	male	298	27.5	-
	West Coast National Park	2	male	352	26.4	-
	West Coast National Park	3	female	52	5.6	-
	West Coast National Park	4	female	558	8.9	-
	West Coast National Park	5	female	375	7.7	-
van Heezik & Seddon (1998)	Saudi Arabia	1	male	74	1116.0	865.4
Melville (current study)	Current study	1	male	40	194.3	168.8
	Current study	2	male	30	71.3	57.1
	Current study	3	male	9	765.7	765.7
	Current study	4	female	25	66.7	62.4
	Current study	5	female	7	2.7	2.7

MCP: Minimum convex polygon method

Sandell (1989) suggests that in solitary carnivores, the ranges of males are approximately 2.5 times that of females. There is evidence, however, that the ranges of female caracals are considerably smaller than those of males (Stuart 1982, Moolman 1986, Avenant & Nel 1993). This seems to be true for the Kgalagadi Transfrontier Park too, but this observation is only based on one female that provided sufficient locations to allow statistical analysis of her range use. Male 2 had a range size similar to that of female 1, but it is thought that this was due to his still being young and subdominant, whereas male 1 was considered to be mature and dominant. The differential range size of these two individuals agrees with Sandell's (1989) contention that dominant males roam over larger areas than subdominants.

CONCLUSIONS

It is clear, even from such a small sample, that the range sizes of caracals in the Kgalagadi Transfrontier Park are considerably larger than those recorded for caracals elsewhere in South Africa. This supports the hypothesis that in arid areas with low prey densities, the ranges of caracals are larger than those in more mesic regions with higher prey densities (Gittleman & Harvey 1982). This has implications for conservation in arid areas because it indicates that larger areas are required to sustain viable predator populations in arid areas than in more mesic regions.

To gain further insight into the range use and range size of caracal in the Kgalagadi Transfrontier Park it would be necessary to capture and collar a larger sample of both male and female caracals, both in the interior of the Park and along the border with Namibia. The only way to gauge how far caracals from the Park move into Namibia and *vice versa* is to persuade farmers in the vicinity to cooperate more actively with research attempts. Based on current data, the population of caracals in the

Kgalagadi Transfrontier Park is contiguous with that of Namibia and should be managed as a megapopulation.

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CHAPTER 6

HABITAT SELECTION BY THE CARACAL IN THE KGALAGADI TRANSFRONTIER PARK.

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Abstract

Caracal habitat selection was studied in the semi-arid Kgalagadi Transfrontier Park. It was necessary to stratify the homogeneous vegetation of the shrubby Kalahari Dune Bushveld into its components by using a non-mapping method. During the study, caracals were tracked by spoor for 537.9 km with the assistance of an experienced Kalahari San tracker to interpret observable behaviour patterns. Behaviour patterns relative to habitat components were recorded and analysed to determine whether caracals displayed habitat component selection. Information regarding the behaviour in specific plant associations by caracals was recorded and analysed, based on vegetation data that were collected by using foot-point transects. Caracals do not select dune crests and dune slopes for specific activities more than expected, but the dune streets are used less frequently than expected, except when killing prey. Caracals also show a definite selection for dune slope aspect in relation to specific types of behaviour.

Keywords: Caracal; habitat component selection; shrubby Kalahari dune bushveld; spoor tracking; plant association selection

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Introduction

Use of the environment is central to the study of the ecology of animals, particularly with regard to the habitats that they occupy (Johnson 1980). Habitat is defined here as the environment in which an animal lives (Lawrence 1998). The habitat selection that an animal displays enables it to use those areas that cater for its fundamental needs to feed, reproduce and rest (Brewer 1994). Habitat selection is a function of active selection and enables animals to persist in certain habitats. The extent of habitat use is dependent on the quality and abundance of both the biotic and abiotic resources present in an area (Boyce & McDonald 1999).

The caracal *Caracal caracal* is found throughout Africa, and across the Arabian Peninsula into central Asia. On a broad scale, caracals occur in a spectrum of habitats ranging from montane forests in the southern Cape region of South Africa, to the arid desert fringes in Saudi Arabia and Kazakhstan (Bothma & Walker 1999). The areas from which they are excluded include the coastal forests in KwaZulu-Natal in South Africa, areas along the western seaboard of southern Africa, the tropical forests of central Africa and the hyper arid regions of the deserts that fall within it's area of distribution (Stuart & Wilson 1988; Skinner & Smithers 1990; Estes 1995). There is a high degree of intra-habitat variation within the broad habitat types mentioned above. Therefore, to gain a better insight into the finer aspects of its ecology, an investigation into the habitat selection and utilisation of the caracal on such a finer scale is important.

In previous caracal studies, habitats were stratified according to plant community boundaries (Norton & Lawson 1985; Moolman 1986; Van Heezik & Seddon 1998). The current study was conducted in the shrubby Kalahari Dune Bushveld (Van Rooyen 2001) of the Kgalagadi Transfrontier Park. Although a homogeneous vegetation type covers the entire study area, there is distinct, localised, recurrent vegetation stratification over short distances within this vegetation type. The current study aims to determine whether caracals in the Kgalagadi Transfrontier Park display a higher than expected use pattern for certain components of this dune bushveld habitat. The hypothesis that was tested was that caracals in the Kgalagadi Transfrontier Park are expected to use all the habitat components in proportion to their availability.

Study area

This study was done in an area along the Namibian border near Mata-Mata in the southwestern portion of the Kgalagadi Transfrontier Park. For logistic reasons it was decided to confine the research to an area that extended 60 km north from the Mata-Mata rest camp along the Namibian border (20° 00' E longitude) to approximately 20 km into the interior of the Kgalagadi Transfrontier Park.

The Kalahari Gemsbok National Park was proclaimed in 1931, but it only became a reality in 1935 when a number of farms along the southern bank of the Aoub River were acquired. Today, the Park exists in much the same ecological state as it was then (Van Wyk & Le Riche 1984). An agreement to formally combine the Kalahari

Gemsbok National Park (South Africa) with the bordering Gemsbok National Park (Botswana) to form the Kgalagadi Transfrontier Park was signed by representatives of the governments of South Africa and Botswana in 1999. This agreement was ratified at an amalgamation ceremony that was held on the 12 May 2000 (Donaldson 2000).

The Mata-Mata area lies in the Shrubby Kalahari Dune Bushveld of the Savanna Biome (Low & Rebelo 1996). This area is an arid savanna with temperatures varying from –10° C to 45° C in the shade with an annual mean rainfall of 153.47 mm occurring mainly in the hot season. The landscape is one of undulating dunes with sparse vegetation at altitudes varying from 1000 to 1100 m above sea level (Low & Rebelo 1996).

The vegetation is characterised by the trees *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca*, a shrub layer of *Grewia retinervis* and *Rhus tenuinervis,* and a well-developed grass layer consisting mainly of *Stipagrostis amabilis, Eragrostis lehmanniana, Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996). There is little variation in the soil forms because the area is predominantly covered by aeolian sand overlying calcrete (Low & Rebelo 1996).

The Kgalagadi Transfrontier Park forms the southern part of the greater Kalahari ecosystem. Because of the arid nature of the area, many of the plants there are ephemeral. After sufficient rain, these plants germinate quickly to complete their life cycle in a short time (Eloff 1984).

Because of the harshness of the environment, the southern Kalahari is an area that is only sparsely inhabited by humans. This above any other factor contributes to the uniqueness of the area, and it enhances the value of the area for field research in wildlife management and conservation.

Methods

In this study it was necessary to use potentially ambiguous terminology to describe the divisions and subdivisions of the habitat in which the research was conducted. To avoid confusion, the following definitions were applied to the habitat subdivisions that were used in this study:

- Habitat : The broad habitat type in which the study was conducted is known as the Shrubby Kalahari Dune Bushveld (Van Rooyen 2001).
- Habitat component : This is a subdivision of the habitat, and it includes the dune crests, the dune slopes and the dune streets. For the purposes of this study, this is the first and most coarse habitat subdivision that was used (Fig. 1).
- Dune crest : The sparsely vegetated top portion of a dune that is a transitional area between the two opposing sides (slopes) of the same dune. This habitat component has no directional aspect (Fig. 1).
- Dune slope : The dune face that is transitional between the dune crest and the dune street. This habitat component has a directional orientation or aspect. Dune slopes vary in gradient with the southwest-facing slopes being steeper than the northeast-facing ones (Van der Walt & Le Riche 1999) (Fig. 1).
- Dune street : The mostly flat area between two dunes that is transitional between the opposing dune slopes of two adjacent dunes. This area usually

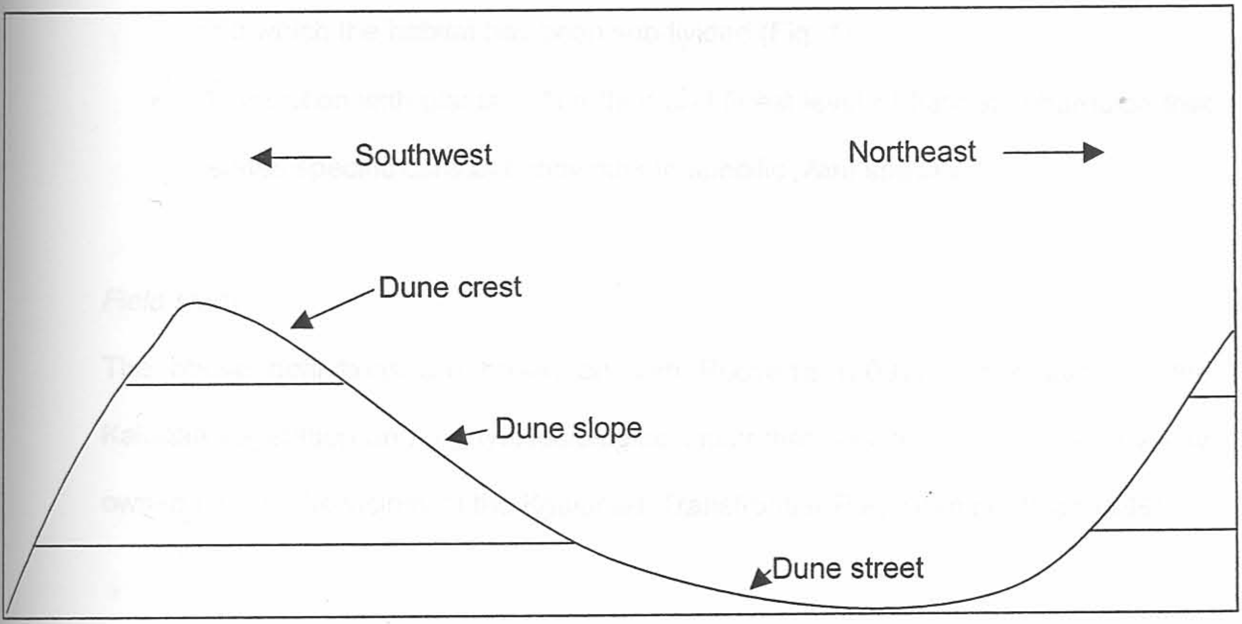

Fig. 1. The stratification of the habitat components, in relation to the dunes that was used in the present study in the Kgalagadi Transfrontier Park. The southwest-facing dune slopes are markedly steeper than the northeast-facing ones.

has a more compact soil and is dominated by the grass *Schmidtia kalihariensis* and the low shrub *Rhigozum trichotomum* (Van Rooyen 2001) (Fig. 1).

- Aspect : The directional orientation of the dune slope. In most cases this orientation is either northeast or southwest (Van der Walt & Le Riche 1999). However, some dunes are orientated differently, and in these cases the dune slopes also have different orientations. The orientation of the dune slopes towards or away from the sun causes the northeast-facing slopes to be warmer than the southwest-facing ones. This is the second, less coarse level into which the habitat has been subdivided (Fig. 1).
- Association with plants : The third and finest level of habitat subdivision that relates specific caracal behaviours to specific plant species.

Field study

The above definitions are based on Van Rooyen's (2001) classification of the Kalahari vegetation and a phytosociological study that was conducted on a privately owned farm in the vicinity of the Kgalagadi Transfrontier Park (Van der Walt 1999)

In previous caracal studies (Moolman 1986, Norton & Lawson 1985) it was possible to stratify the habitats according to distinct vegetation units that could be clearly defined by using mapping techniques. In the present study this approach was not feasible because of the low level of macro-habitat variation within the Shrubby Kalahari Dune Bushveld (Van Rooyen 2001).

Because the use of mapping techniques for the stratification of the separate components of the Shrubby Kalahari Dune Bushveld was not practical, it was decided to use the non-mapping technique that was proposed by Marcum & Loftsgaarden (1980) to stratify the habitat components of the study area. In the present study, where obvious habitat stratification occurs within a designated vegetation type over a short distance, the non-mapping method is superior to the conventional mapping method. An aerial photograph on a scale of 1:50 000 and a point grid overlay was used to determine the ratio in which the habitat components occurred in the study area, and upon which the analyses of habitat selection were based. A computer random number generator was used to define randomised grid coordinates upon which the habitat ratio was calculated (Marcum & Loftsgaarden 1980).

Spoor-tracking data for caracal were collected according to the method of Bothma and Le Riche (1984) and Stander *et al.* (1997). A high number of habitat selection observations linked to global positioning system (GPS) locations were made based on 154 separate sets of caracal tracks over a total spoor tracking distance of 537.9 km. Radio-location data are less useful than spoor tracking data for this purpose because the errors involved in radio-tracking tend to lead to an underestimation of preference in habitats that occur in small patches (White & Garrot 1986). Moreover, because of the richness of the spoor-tracking data and the relative paucity of the radio-tracking data in the current study, it was decided to base the habitat selection analysis on the spoor-tracking data only.

While tracking spoor, several aspects of caracal behaviour were recorded that could be incorporated into the habitat use data. The tracking data were divided into two components, movement and stationary data, for the purposes of analysis. The caracal movements were recorded as strings of habitat components encountered while moving between consecutive stationary types of behaviour. Additional factors that related to the various types of behaviour, including dune slope aspect and plant relationships, were recorded.

Baseline vegetation frequency data were collected by conducting ten step-point transects of 100 m each in each of the defined habitat components (Mentis 1981) (Table 1). The results from the vegetation transects were converted into a vegetation ratio of occurrence against which plant association data could be compared. The results from the vegetation transects were compiled to reflect the relative plant frequencies in each habitat component, and as a combined plant frequency across all three habitat components (Table 1).

Data analysis

Chi-squared analyses were used to establish whether a significant selection for or against using a specific habitat component or plant species was shown by caracals. In those cases where significant values were found, the Bonferroni approach was used to establish which habitat components or plant species were selected or avoided (Marcum & Loftsgaarden 1980; Moolman 1986; Caley 1994; Alvarez-Cardenas *et al.* 2001). The flexibility of this method allowed it to be used not only for the analysis of habitat component selection but also for the detection of specific plant association use. The data were analysed seasonally for the hot season (October to March) and the cold season (April to September), and on a combined seasonal basis.

e 1: *The percentage contribution of various plant species in the specific vegetation parameters of the Kgalagadi Transfrontier Park from June 2000 to August 2002, based on step-point transects.*

Plant	Percentage contribution over all habitat components	Percentage contribution on dune crests	Percentage contribution on dune slopes	Percentage contribution on dune streets
Acacia erioloba	0.0	0.0	0.1	0.0
Acacia haematoxylon	0.5	0.8	0.3	0.4
Acacia mellifera	0.1	0.0	0.2	0.0
Acanthosicyos naudinianus	2.5	4.1	2.8	0.7
Aristida meridionalis	0.8	1.1	1.2	0.1
Asparagus spp.	0.0	0.0	0.1	0.0
Bare patch	35.3	42.1	35.6	28.5
Boscia albitrunca	0.3	0.7	0.1	0.0
Brachiaria glomerata	0.7	0.7	1.2	0.1
Bulbostylis hispidula	0.3	0.1	0.2	0.5
Centropodia glauca	2.0	1.2	1.8	3.0
Chenopodium album	0.1	0.1	0.2	0.0
Crotalaria sphaerocarpa	0.2	0.0	0.5	0.0
Crotolaria spartioides	0.1	0.2	0.0	0.0
Dicoma spp.	0.0	0.0	0.1	0.0
Elephantorrhiza elephantina	0.5	0.0	0.5	1.0
Eragrostis lehmanniana	11.6	8.1	16.2	10.7
Eragrostis porosa	0.4	0.0	0.9	0.5
Eragrostis trichophora	0.1	0.2	0.0	0.0
Gisekia africana	0.8	1.2	0.6	0.6
Harpagophytum procumbens	0.7	0.0	0.0	1.9
Heliotropium ciliatum	7.4	8.3	7.3	6.7
Hermannia burchelli	0.4	0.4	0.6	0.3
Hermannia tomentosa	1.7	0.9	1.6	2.4
Hermbstaedtia fleckii	0.5	0.1	1.3	0.0
Hirpicium gazanioides	0.1	0.3	0.0	0.0
Indigofera alternans	0.4	0.2	0.4	0.6
Indigofera auricoma	0.2	0.3	0.4	0.0
Indigofera flavicans	0.2	0.4	0.1	0.1
Limeum argute-carinatum	0.1	0.2	0.0	0.0
Limeum fenestratum	0.5	0.6	0.4	0.5
Limeum sulcatum	0.5	0.1	0.3	1.1
Lycium boscifolium	0.0	0.1	0.0	0.0
Merremia verecunda	0.0	0.0	0.1	0.0
Monechma divaricatum	0.0	0.0	0.1	0.0
Monechma incanum	0.2	0.0	0.6	0.1
Nolletia arenosa	0.0	0.0	0.1	0.0
Oxygonum delagoense	1.5	2.5	2.2	0.0
Pergularia daemia	0.1	0.0	0.2	0.0
Phyllanthus angolensis	0.1	0.1	0.1	0.0
Phyllanthus maderaspatensis	0.2	0.6	0.0	0.0
Phyllanthus sericeus	0.0	0.0	0.1	0.0
Plinthus sericeus	0.2	0.4	0.3	0.0
Requienia sphaerosperma	1.5	1.5	1.2	1.6
Rhigozum trichotomum	5.6	1.4	3.1	12.0

Table 1: *Continued*

Plant	Percentage contribution over all habitat components	Percentage contribution on dune crests	Percentage contribution on dune slopes	Percentage contribution on dune streets
Rhus tenuinervis	0.0	0.0	0.1	0.0
Salsola spp.	1.4	2.8	1.2	0.3
Schmidtia kalihariensis	10.0	1.2	10.3	18.2
Senna italica	0.1	0.0	0.1	0.3
Sericorema remotiflora	0.1	0.0	0.2	0.0
Sesamum triphyllum	0.3	0.4	0.3	0.2
Stipagrostis amabilis	6.2	12.9	1.9	3.9
Stipagrostis ciliata	1.0	2.2	0.1	0.6
Stipagrostis hirtigluma	0.4	0.0	0.3	1.0
Stipagrostis obtusa	0.1	0.0	0.3	0.0
Stipagrostis uniplumis	0.8	0.0	1.3	1.1
Tribulus zeyheri	0.9	1.2	1.1	0.6
Xenostegia tridentata	0.5	0.8	0.3	0.5
	100.0	100.0	100.0	100.0

Where caracal behaviours were recorded on the dune slopes, the aspect of each slope was recorded. The percentage use of the various behaviours on each dune slope aspect is reflected in Table 2.

All stationary behaviour data were combined into a single database comprising 6200 independent GPS locations that were related to specific behaviours. The proportional occurrence of the stationary types of behaviour in each of the defined habitat components was also calculated. Once these data had been analysed together, the data were separated into independent stationary types of behaviour. The same analysis protocol was then applied to the individual behaviours to test whether behaviour specific habitat component selection occurred.

The variable distance between dune crests (Van der Walt & Le Riche 1999) and the resultant variability in the distances that caracals could travel within each vegetation component necessitated the weighting of the movement data. The weighting was done by dividing the number of habitat component observations recorded for each set of caracal tracks by the distance for which that caracal spoor was followed during the tracking session. The unweighted and weighted data sets were both subjected to analysis. For the analyses, each habitat component within each movement string was regarded as an independent observation

Caracal behavioural patterns were associated not only with habitat components but also with specific plant species. Therefore, whenever a specific type of behaviour was noted to occur within 100 mm radius of a plant, based on the position of the spoor track, the behaviour was considered to be associated with that plant. Where no plant was observed within 100 mm of the spoor track, the behaviour was regarded

Table 2: *The percentage utilisation of variously orientated dune slopes, by caracals in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Type of behaviour	Season	Aspect															
		N	NNE	NE	ENE	E	ESE	SE	SSE	S	SSW	SW	WSW	W	WNW	NW	NNW
Combined behaviours	SW	0.8	-	54.3	-	2.5	0.6	0.7	-	0.7	0.0	37.5	0.0	1.8	-	0.9	-
Combined behaviours	S	1.1	-	55.4	-	1.7	-	0.3	-	0.5	-	38.2	-	1.6	-	1.2	-
Combined behaviours	W	0.6	-	53.3	-	3.2	1.2	1.1	-	0.8	0.1	37.0	0.1	2.0	-	0.7	-
Standing	SW	1.0	-	53.4	-	1.7	0.3	0.3	-	0.6	-	40.3	-	1.3	-	1.2	-
Standing	S	1.5	-	54.9	-	1.0	-	-	-	0.8	-	38.8	-	1.2	-	1.8	-
Standing	W	0.5	-	52.1	-	2.2	0.5	0.5	-	0.5	-	41.5	-	1.4	-	0.8	-
Sitting	SW	1.2	-	-	-	7.4	2.0	3.9	-	1.2	-	77.0	-	5.5	-	2.0	-
Sitting	S	0.8	-	-	-	4.8	-	2.4	-	-	-	85.6	-	5.6	-	0.8	-
Sitting	W	1.5	-	-	-	9.9	3.8	5.3	-	2.3	-	68.9	-	5.3	-	3.0	-
Lying-up	SW	1.5	-	47.8	-	2.0	-	0.5	-	1.0	-	41.4	-	5.9	-	-	-
Lying-up	S	2.5	-	41.0	-	2.5	-	0.8	-	-	-	48.4	-	4.9	-	-	-
Lying-up	W	-	-	58.0	-	1.2	-	-	-	2.5	-	30.9	-	7.4	-	-	-
Urinating	SW	-	-	67.6	-	5.4	-	-	-	-	-	27.0	-	-	-	-	-
Urinating	S	-	-	60.0	-	-	-	-	-	-	-	40.0	-	-	-	-	-
Urinating	W	-	-	72.7	-	9.1	-	-	-	-	-	18.2	-	-	-	-	-
Defecating	SW	-	-	43.8	-	-	-	-	-	-	-	43.8	-	12.5	-	-	-
Defecating	S	-	-	66.7	-	-	-	-	-	-	-	33.3	-	-	-	-	-
Defecating	W	-	-	38.5	-	-	-	-	-	-	-	46.2	-	15.4	-	-	-
Rolling	SW	-	-	68.8	-	6.3	6.3	-	-	-	6.3	12.5	-	-	-	-	-
Rolling	S	-	-	75.0	-	-	-	-	-	-	-	25.0	-	-	-	-	-
Rolling	W	-	-	66.7	-	8.3	8.3	-	-	-	8.3	8.3	-	-	-	-	-
Clawing and scraping	SW	9.1	-	59.1	-	13.6	-	4.6	-	-	-	9.1	4.6	-	-	-	-
Clawing and scraping	S	-	-	75.0	-	12.5	-	-	-	-	-	12.5	-	-	-	-	-
Clawing and scraping	W	14.3	-	50.0	-	14.3	-	7.1	-	-	-	7.1	7.1	-	-	-	-
Crouching	SW	0.8	-	52.5	-	2.5	-	*	-	0.8	-	41.7	-	0.8	-	0.8	-
Crouching	W	0.8	-	52.5	-	2.5	-	*	-	0.8	-	41.7	-	0.8	-	0.8	-
Starting a run	SW	-	-	50.0	-	1.8	-	1.8	-	1.8	-	42.9	-	1.8	-	-	-
Starting a run	W	-	-	50.0	-	1.8	-	1.8	-	1.8	-	42.9	-	1.8	-	-	-
Killing	SW	-	-	53.9	-	15.4	7.7	-	-	-	-	23.1	-	-	-	-	-
Killing	S	-	-	85.7	-	-	-	-	-	-	-	14.3	-	-	-	-	-
Killing	W	-	-	16.7	-	33.3	16.7	-	-	-	-	33.3	-	-	-	-	-
Eating	SW	-	-	50.0	-	16.7	16.7	-	-	-	-	16.7	-	-	-	-	-
Eating	S	-	-	71.4	-	-	-	-	-	-	-	28.6	-	-	-	-	-
Eating	W	-	-	20.0	-	40.0	40.0	-	-	-	-	-	-	-	-	-	-

SW :- both summer and winter
S :- summer
W :- winter

to be associated with a bare patch. The same analysis protocol as above was applied to indicate whether caracals tended to select or avoid specific plants for specific types of behaviour. The number of potential plant associations differed according to each behaviour pattern. It was necessary, therefore, to apply different critical chi-squared values to the chi-squared calculations for each of the behaviours.

Results

The proportional representation of the various habitat components when using the non-mapping method of Marcum & Loftsgaarden (1980) in the study area is 12.7% dune crests: 53.8% dune streets: 33.5% dune slopes. If the caracals used the habitat components in their frequency of occurrence, this then will be the expected proportion of use for the various types of behaviour in each of the three habitat components. This expected ratio was also used as the basis for further habitat selection analyses.

Habitat component selection

Analysis of the stationary behaviour on a year-round basis indicated that the caracals tended to select or avoid certain habitat components (chi-square = 14.98; df = 2; $P \leq 0.05$). When subjected to further analysis to determine which habitat components were selected or were avoided, the Bonferroni confidence intervals (0.91) (Marcum & Loftsgaarden 1980) that were calculated were (-0.17, -0.03) for the dune crests, (-0.182, 0.22) for the dune slopes and (0.08, 0.30) for the dune streets. This indicates that caracals utilise the dune crests in greater proportion than expected, the dune slopes as expected and the dune streets less than expected (Table 3). For the non-movement data 22.8 % of the observations were on a dune crest, 41.6 % were on a

Table 3: *Habitat component selection displayed by caracals, in the Kgalagadi Transfrontier Park, based on a chi-squared analysis in conjunction with 91% Bonferroni confidence intervals, from June 2000 to August 2002*

Behaviour	Both seasons combined				Significance conclusion
	Chi-squared value	*P*-value	Habitat	Confidence interval	
Unweighted movement	10.78	≤0.05	Dune	(-0.198; -0.008)	+
			Slope	(-0.235; -0.005)	+
			Street	(0.124; 0.336)	-
Weighted movement	8.36	≤0.05	Dune	(-0.119; -0.067)	+
			Slope	(-0.147; -0.073)	+
			Street	(0.16; 0.24)	-
Total non-movement	14.98	≤0.05	Dune	(-0.17; -0.03)	+
			Slope	(-0.182; 0.022)	=
			Street	(0.08; 0.3)	-
Standing	7.42	≤0.05	Dune	(-0.23; 0.006)	=
			Slope	(-0.22; 0.08)	=
			Street	(0.03; 0.33)	-
Sitting	12.8	≤0.05	Dune	(-0.261; -0.023)	+
			Slope	(-0.25; 0.05)	=
			Street	(0.09; 0.39)	-
Lying-up	2.18	≤0.05	Combined	No selection	
Urinating	11.06	≤0.05	Dune	(-0.28; -0.04)	+
			Slope	(-0.156; 0.124)	=
			Street	(0.03; 0.33)	-
Defecating	7.91	≤0.05	Dune	(-0.234; -0.0002)	+
			Slope	(-0.21; 0.07)	=
			Street	(0.04; 0.34)	-
Rolling	18.83	≤0.05	Dune	(-0.32; -0.06)	+
			Slope	(-0.04; 0.2)	=
			Street	(-0.03; 0.25)	-
Clawing and scraping	3.3	≤0.05	Combined	No selection	
Crouching	8.53	≤0.05	Dune	(-0.086; 0.085)	=
			Slope	(-0.28; -0.04)	+
			Street	(0.04; 0.3)	-
Starting a chase	26.24	≤0.05	Dune	(-0.069; 0.035)	=
			Slope	(-0.23; -0.09)	+
			Street	(0.1; 0.24)	-
Killing	6.32	≤0.05	Dune	(0.004; 0.17)	-
			Slope	(-0.26; 0.04)	=
			Street	(-0.13; 0.17)	=
Eating	9.5	≤0.05	Dune	(-0.055; 0.133)	=
			Slope	(-0.38; -0.08)	+
			Street	(0.04; 0.34)	-

Table 3: *Continued*

Behaviour	Summer				Significance conclusion
	Chi-squared value	*P* value	Habitat	Confidence interval	
Unweighted movement	9.14	≤0.05	Dune	(-0.187; 0.033)	=
			Slope	(-0.29; 0.01)	=
			Street	(0.06; 0.36)	-
Weighted movement	5.68	≤0.05	Combined	No selection	
Total non-movement	11.12	≤0.05	Dune	(-0.113; 0.027)	=
			Slope	(-0.22; -0.02)	+
			Street	(0.05; 0.27)	-
Standing	10.77	≤0.05	Dune	(-0.128; 0.022)	=
			Slope	(-0.21; -0.01)	+
			Street	(0.06; 0.28)	-
Sitting	18.19	≤0.05	Dune	(-0.013; 0.026)	=
			Slope	(-0.28; -0.06)	+
			Street	(0.11; 0.33)	-
Lying-up	1.59	≤0.05	Combined	No selection	
Urinating	10.96	≤0.05	Dune	(-0.247; 0.009)	+
			Slope	(-0.24; 0.059)	=
			Street	(0.07; 0.32)	-
Defecating	11.66	≤0.05	Dune	(-0.186; 0.04)	=
			Slope	(-0.32; -0.02)	+
			Street	(0.04; 0.34)	-
Rolling	26.61	≤0.05	Dune	(-0.62; -0.24)	+
			Slope	(0.05; 0.37)	-
			Street	(0.02; 0.42)	-
Clawing and scraping	1.36	≤0.05	Combined	No selection	
Crouching	NA		NA	No summer records	
Starting a chase	NA		NA	No summer records	
Killing	2.88	≤0.05	Combined	No selection	
Eating	5.83	≤0.05	Combined	No selection	

Table 3: *Continued*

Behaviour	Winter				Significance conclusion
	Chi-squared value	*P* value	Habitat	Confidence interval	
Unweighted movement	12.48	≤0.05	Dune	(-0.25; -0.011)	+
			Slope	(-0.26; 0.04)	=
			Street	(0.09; 0,39)	-
Weighted movement	11.43	≤0.05	Dune	(-0.169; 0.051)	=
			Slope	(-0.26; 0.04)	=
			Street	(0.02; 0.32)	-
Total non-movement	20.01	≤0.05	Dune	(-0.21; -0.07)	+
			Slope	(-0.16; 0.04)	=
			Street	(0.09; 0.31)	-
Standing	18.214	≤0.05	Dune	(-0.22; -0.072)	+
			Slope	(-0.15; 0.05)	=
			Street	(0.05; 0.35)	-
Sitting	30.41	≤0.05	Dune	(-0.29; -0.13)	+
			Slope	(-0.14; 0.08)	=
			Street	(0.15; 0.35)	-
Lying-up	5.12	≤0.05	Combined	No selection	
Urinating	11.02	≤0.05	Dune	(-0.29; -0.09)	+
			Slope	(-0.09; 0.19)	=
			Street	(-0.005; 0.29)	=
Defecating	7.62	≤0.05	Dune	(-0.25; -0.01)	+
			Slope	(-0.17; 0.1)	=
			Street	(0.02; 0.32)	-
Rolling	0.35	≤0.05	Combined	No selection	
Clawing and scraping	1.74	≤0.05	Combined	No selection	
Crouching	8.53	≤0.05	Dune	(-0.086; 0.085)	=
			Slope	(-0.28; -0.04)	+
			Street	(0.04; 0.3)	-
Starting a chase	26.24	≤0.05	Dune	(-0.069; 0.035)	=
			Slope	(-0.23; -0.09)	+
			Street	(0.1; 0.24)	-
Killing	14.57	≤0.05	Dune	(0.055; 0.199)	-
			Slope	(-0.27; 0.03)	=
			Street	(-0.155; 0.145)	=
Eating	17	≤0.05	Dune	(-0.05; 0.178)	=
			Slope	(-0.44; -0.16)	+
			Street	(0.08; 0.38)	-

+ :- component used in greater proportion than its expected occurrence
- :- component used in smaller proportion than its expected occurrence
= :- component used in the same proportion as its expected occurrence

dune slopes and 35.6 % in a dune street. These frequencies differ significantly ($P \leq 0.05$) from the observed and therefore expected habitat component ratio (Table 4).

The behaviour-specific analyses are summarised in Table 3. The data indicate that caracals do select or avoid various habitat components when performing certain types of behaviour, but not other types.

There are also seasonal habitat component use patterns. In hot season the dune crests are used in proportion to their expected occurrence, the dune slopes are used more often than what would be expected, and the dune streets are used less often so. In the cold season the dune crests are used more often than expected and the dune slopes as expected in proportion to their occurrence (Table 3). In both the hot season and the cold season, the dune streets are therefore used less often than expected, which indicates definite avoidance of this habitat component (Table3).

Caracals utilise the northeast-facing dune slopes more often than the southwest-facing ones for a number of types of behaviour (Table 2). Of all types of behaviour, 54.3 % of the observations on the dune slopes were done on the northeast-facing slopes, while 37.5 % occur on the southwest-facing dune slopes. The rest occur on other, less prevalent dune slope aspects (Table 2).

Analysis of the movement data indicates that the caracal selects or avoids certain habitat components (unweighted data: chi-square = 10.78, df = 2, $P \leq 0.05$; weighted data : chi-square = 8.36, df = 2, $P \leq 0.05$). The weighted and unweighted habitat frequency analysis results differed from those of the stationary behaviour aspects. The caracals utilise the dune crests and dune slopes more often than would be

The percentage use by caracals of various habitat components across seasons and seasonally whilst ning specified types of behaviour in the Kgalagadi Transfrontier Park from June 2000 to August 2002

Behaviour	Season	Habitat component use		
		Dune crest	Dune slope	Dune street
General habitat ratio		12.7	33.4	53.8
Combined unweighted	SW	23.3	45.3	31.4
	S	20.4	46.8	32.8
	W	25.8	43.9	30.3
Combined weighted	SW	22.2	43.7	34.1
	S	18.7	44.2	37.1
	W	25.2	43.3	31.5
Combined behaviours	SW	22.9	35.5	41.6
	S	17.4	37.8	44.9
	W	27.3	33.7	39.0
Standing	SW	23.8	40.1	36.1
	S	18.2	44.4	37.4
	W	27.5	37.9	34.6
Sitting	SW	27.0	42.7	30.3
	S	18.1	49.9	32.0
	W	34.5	36.6	29.0
Lying-up	SW	15.2	41.5	43.4
	S	10.5	42.0	47.5
	W	21.1	40.2	38.8
Urinating	SW	29.1	35.0	35.9
	S	25.5	42.6	31.9
	W	32.1	28.6	39.3
Defecating	SW	24.4	40.0	35.6
	S	20.0	50.0	30.0
	W	25.7	37.1	37.2
Rolling	SW	33.3	42.4	24.2
	S	55.9	32.4	11.8
	W	9.4	53.1	37.5
Clawing and scraping	SW	12.5	41.7	45.8
	S	16.7	38.9	44.4
	W	10.0	43.3	46.7
Crouching	SW	12.8	49.6	37.6
	W	12.8	49.6	37.6
Starting a chase	SW	20.9	35.7	43.4
	W	20.9	35.7	43.4
Killing	SW	4.0	44.0	52.0
	S	7.1	42.9	50.0
	W	0.0	45.5	54.6
Eating	SW	8.8	55.9	35.3
	S	11.1	50.0	38.9
	W	6.3	62.5	31.3

SW :- Summer and winter combined
S :- Summer
W :- Winter

expected, and the dune streets less often than expected (Table 3). When represented as a ratio, both the unweighted frequencies of use for the movement behaviours (23.3 % for the dune crests, 45.3 % for the dune slopes, and 31.4 % for the dune streets) and the weighted frequencies (22.2 % for the dune crests, 43.7 % for the dune slopes, and 34.1 % for the dune streets) do not differ significantly from those of the stationary behaviour (unweighted data : chi-square = 0.42, df = 2, $P \leq 0.05$; weighted data :chi-square = 0.092, df = 2, $P \leq 0.05$).

When analysed on a seasonal basis the unweighted movement data (chi-square = 9.14, df = 2, $P \leq 0.05$) indicate that dune crests and dune slopes are being used in proportion to their occurrence, while the dune streets are being used less often than expected (Table 3). The weighted movement data (chi-square = 5.68, df = 2, $P \leq 0.05$) show no specific habitat component preference in the hot season (Table 3). However, in the cold season the unweighted movement data (chi-square = 12.48, df = 2, $P \leq 0.05$) indicate that the caracals use the dune crests more often than expected, the dune slopes are used in proportion to their occurrence as expected, and the dune streets are used less often than expected (Table 3). The weighted data (chi-square = 11.43, df = 2, $P \leq 0.05$) show that caracals use the dune crests and dune slopes in proportion to their occurrence, and the dune streets less often than expected (Table 3).

Selection of dune slope aspect

Van der Walt & Le Riche (1999) stated that the two predominant dune slope aspects in the southern Kalahari are those that face northeast and southwest. The southwest-facing dune slopes are steeper and cooler than the northeast-facing dune slopes. Baseline data on the contribution of the various dune slope aspects to the dune slope habitat component could not be calculated and statistical analysis of the dune slope aspect data could therefore not be done. The extent to which caracals utilise certain dune slope aspects is therefore represented here as a percentage of the total number of observations of particular types of behaviour within the dune slope habitat component.

When all types of stationary behaviour are combined, caracals used the northeast-facing dune slopes more often than the southwest-facing ones all year round, but there was no evidence of any seasonal variation in dune slope aspect selection (Table 2). The trend of using northeast-facing dune slopes in preference to southwest-facing ones held for most types of behaviour. However, there were notable exceptions when sitting, defecating, killing and eating. Sitting was never recorded on northeast-facing slopes. When defecating, the year-round trend was for caracals to use the northeast-facing and southwest-facing dune slopes in proportion to their occurrence. However, in the hot season, the northeast-facing slopes were used most often but in the cold season southwest-facing slopes were used most often. Killing and eating of prey on a year-round basis was mainly done on the northeast-facing dune slopes. The selection for northeast-facing dune slopes when killing and eating is especially strong in the hot season. In the cold season, the northeast-facing dune slopes are not used much for killing and eating prey (Table 2).

Plant associations

The caracals stopped and stood close to 52 different plant species during this study. In most cases, the caracals did so in proportion to the frequency of occurrence of these plant species, but *Acacia erioloba*, *Acacia haematoxylon*, *Acacia mellifera*, *Aptosimum elongatum*, *Boscia albitrunca*, *Citrullus lanatus*, *Enneapogon* *cenchroides*, *Grewia flava*, *Helichrysum argyroshaerum*, *Hermannia tomentosa*, *Lycium boscifolium* and *Rhus tenuinervis* were used significantly ($P \leq 0.05$) more often than expected, based on their frequency of occurrence. The only plant species that was used less often than expected was *Schmidtia kalihariensis* ($P \leq 0.05$). This annual grass forms dense stands, which makes moving through them difficult (Table 5).

When sitting, there was no evidence of any significant association with specific plant species on the dune crests. On the dune slopes, the caracals sat close to 29 plant species. Of these species, *Acacia haematoxylon*, *Acacia mellifera*, *Boscia albitrunca* and *Helichrysum argyrosphaerum* were associated with more often than expected ($P \leq 0.05$), and no plant species was associated with less often than expected. In the dune streets the caracals also sat close to 29 plant species, of which *Acacia haematoxylon*, *Boscia albitrunca*, *Helichrysum argyrosphaerum* and an unidentified *Salsola* species were associated with more often than expected ($P \leq 0.05$), while *Schmidtia kalihariensis* was again the only plant species that was associated with less often than expected ($P \leq 0.05$) (Table 5).

When lying-up on the dune crests, caracals associated with 15 different plant species. The only plant species that was associated with more often than expected ($P \leq 0.05$) was *Boscia albitrunca*, and no plant species association was recorded less often than expected. On the dune slopes, *Boscia albitrunca* and *Rhigozum trichotomum* were associated with more often than expected ($P \leq 0.05$), and *Schmidtia kalihariensis* and *Tribulus zeyheri* were associated with less often than expected ($P \leq 0.05$). In the dune streets the caracals associated with 23 plant species when lying-up, but the only plant species that was associated with more

Table 5: *The plant utilisation by caracals in the Kgalagadi Transfrontier Park from June 2000 to August 2002, as determined by using chi-squared analysis in conjunction with 95 % Bonferroni confidence intervals.*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Standing	Combined components	52	79.08	108.39	2.448	*Acacia erioloba*	(-0.015; -0.004)	+
						Acacia haematoxylon	(-0.084; -0.044)	+
						Acacia mellifera	(-0.037; -0.019)	+
						Acanthosicyos naudinianus	(-0.019; 0.057)	=
						Aptosimum elongatum	(-0.013; -0.005)	+
						Bare patch	(-0.01; 0.21)	=
						Boscia albitrunca	(-0.107; -0.073)	+
						Centropodia glauca	(-0.029; 0.039)	=
						Chascanum pumilum	(-0.0037; -0.0001)	+
						Chenopodium album	(-0.0085; 0.0065)	=
						Chrysocoma obtusata	(-0.0029; 0.0001)	=
						Citrullus lanatus	(-0.0037; -0.0001)	+
						Crotalaria spartioides	(-0.014; 0.0064)	=
						Crotalaria sphaerocarpa	(-0.0069; 0.0053)	=
						Dimorphotheca polyptera	(-0.0041; 0.0043)	=
						Ehretia rigida	(-0.0019; 0.0003)	=
						Elephantorrhiza elephantina	(-0.015; 0.019)	=
						Enneapogon cenchroides	(-0.0037; -0.0001)	+
						Eragrostis lehmanniana	(-0.047; 0.111)	=
						Geigeria ornativa	(-0.00097; 0.00041)	=
						Gisekia africana	(-0.014; 0.029)	=
						Grewia flava	(-0.0072; -0.0018)	+
						Harpagophytum procumbens	(-0.0134; 0.026)	=
						Helichrysum argyrospaerum	(-0.015; -0.0067)	+
						Heliotropium ciliatum	(-0.015; 0.113)	=
						Hermannia burchellii	(-0.012; 0.019)	=
						Hermannia tomentosa	(-0.12; -0.06)	+
						Hirpicium echinus	(-0.0073; 0.0075)	=
						Indigofera alternans	(-0.0151; 0.0165)	=
						Indigofera flavicans	(-0.0094; 0.012)	=
						Limeum sulcatum	(-0.012; 0.021)	=
						Lycium bosciifolium	(-0.012; -0.0012)	+
						Monechma incanum	(-0.023; 0.0016)	=
						Nolletia arenosa	(-0.0102; 0.00003)	=
						Oxygonum delagoense	(-0.02; 0.037)	=
						Phaeoptilum spinosum	(-0.001; 0.009)	=
						Plinthus sericeus	(-0.01; 0.012)	=

Table 5: *Continued*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Standing	Combined components					*Asparagus* spp.	(-0.004; 0.004)	=
						Other	(-0.06; 0.056)	=
						Radyera urens	(-0.001; 0.009)	=
						Requienia sphaerosperma	(-0.023; 0.034)	=
						Rhigozum trichotomum	(-0.044; 0.07)	=
						Rhus tenuinervis	(-0.015; -0.0036)	+
						Schmidtia kalihariensis	(0.001; 0.147)	-
						Senecio eenii	(-0.0034; 0.000003)	=
						Senna italica	(-0.0076; 0.0094)	=
						Serecoricorema remotiflora	(-0.0056; 0.0063)	=
						Sesamum triphyllum	(-0.0092; 0.01)	=
						Stipagrostis amabilis	(-0.025; 0.093)	=
						Stipagrostis ciliata	(-0.02; 0.028)	=
						Stipagrostis uniplumis	(-0.032; 0.0127)	=
						Terminalia sericea	(-0.0015; 0.0004)	=
						Tribulus zeyheri	(-0.015; 0.031)	=
						Xenostegia trdentata	(-0.013; 0.021)	=
Sitting	Dune crest	27	40.11	39.37		No evidence of plant associations		
Sitting	Dune street	30	43.77	84.63	2.448	Bare Patch	(-0.17; 0.09)	=
						Acacia erioloba	(-0.017; 0.003)	=
						Acacia haematoxylon	(-0.072; -0.014)	+
						Acacia mellifera	(-0.036; 0.03)	=
						Acanthosicyos naudinianus	(-0.017; 0.026)	=
						Aptosimum elongatum	(-0.017; 0.003)	=
						Asparagus spp.	(-0.0085; 0.0035)	=
						Boscia albitrunca	(-0.029; -0.0002)	+
						Centropodia glauca	(-0.031; 0.057)	=
						Chascanum pumilum	(-0.007; 0.003)	=
						Citrullus lanatus	(-0.007; 0.003)	=
						Crotalaria sphaerocarpa	(-0.017; 0.003)	=
						Eragrostis lehmanniana	(-0.064; 0.104)	=
						Grewia flava	(-0.007; 0.003)	=
						Helichrysum argyrospaerum	(-0.069; -0.019)	+
						Heliotropium ciliatum	(-0.04; 0.09)	=
						Hermannia burchellii	(-0.0138; 0.0142)	

Table 5: *Continued*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Sitting	Dune street	30	43.77	84.63	2.448	*Hermannia tomentosa*	(-0.0423; 0.0417)	=
						Indigofera alternans	(-0.026; 0.019)	=
						Limeum fenestratum	(-0.016; 0.0218)	=
						Monechma incanum	(-0.03; 0.002)	=
						Nolletia arenosa	(-0.007; 0.003)	=
						Other	(0.006; 0.144)	-
						Oxygonum delagoense	(-0.013; 0.0036)	=
						Requienia sphaerosperma	(-0.036; 0.034)	=
						Rhigozum trichotomum	(-0.019; 0.145)	=
						Salsola spp.	(-0.111; -0.075)	+
						Schmidtia kalihariensis	(0.054; 0.246)	-
						Stipagrostis amabilis	(-0.019; 0.077)	=
						Stipagrostis ciliata	(-0.019; 0.0224)	=
						Stipagrostis uniplumis	(-0.035; 0.023)	=
Sitting	Dune slope	30	43.77	72.32	2.448	*Acacia erioloba*	(-0.0243; 0.0021)	=
						Acacia haematoxylon	(-0.048; -0.006)	+
						Acacia mellifera	(-0.035; -0.001)	+
						Aptosimum elongatum	(-0.0059; 0.0025)	=
						Asparagus spp.	(-0.0147; 0.0104)	=
						Bare patch	(-0.23; 0.01)	=
						Boscia albitrunca	(-0.077; -0.029)	+
						Centropodia glauca	(-0.025; 0.041)	=
						Citrullus lanatus	(-0.015; 0.001)	=
						Crotalaria sphaerocarpa	(-0.023; 0.015)	=
						Cucumis africana	(-0.0059; 0.0025)	=
						Enneapogon cenchroides	(-0.0059; 0.0025)	=
						Eragrostis lehmanniana	(-0.01; 0.17)	=
						Grewia flava	(-0.015; 0.0015)	=
						Helichrysum argyrospaerum	(-0.023; -0.001)	+
						Hermannia tomentosa	(-0.042; 0.026)	=
						Indigofera alternans	(-0.0157; 0.0163)	=
						Lycium bosciifolium	(-0.0095; 0.0025)	=
						Monechma incanum	(-0.028; 0.015)	=
						Nolletia arenosa	(-0.012; 0.007)	=
						Other	(0.033; 0.227)	-
						Oxygonum delagoense	(-0.019; 0.053)	=

Table 5: *Continued*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Sitting	Dune slope	30	43.77	72.32	2.448	*Acanthosicyos naudinianus*	(-0.016; 0.064)	=
						Requienia sphaerosperma	(-0.0366; 0.0234)	=
						Rhigozum trichotomum	(-0.067; 0.027)	=
						Rhus tenuinervis	(-0.017; 0.005)	=
						Salsola spp.	(-0.058; 0.008)	=
						Schmidtia kalihariensis	(-0.005; 0.145)	=
						Stipagrostis amabilis	(-0.03; 0.04)	=
						Stipagrostis ciliata	(-0.017; 0.005)	=
						Stipagrostis uniplumis	(-0.021; 0.037)	=
Lying-up	Dune crest	16	26.3	44.37	2.446	Bare patch	(-0.13; 0.23)	=
						Acacia erioloba	(-0.039; 0.029)	=
						Acacia haematoxylon	(-0.12; 0.022)	=
						Acanthosicyos naudinianus	(-0.032; 0.084)	=
						Boscia albitrunca	(-0.219; -0.021)	+
						Enneapogon cenchroides	(-0.048; 0.02)	=
						Eragrostis lehmanniana	(-0.045; 0.128)	=
						Hermannia tomentosa	(-0.074; 0.034)	=
						Monechma incanum	(-0.048; 0.02)	=
						Other	(0.102; 0.298)	-
						Oxygonum delagoense	(-0.066; 0.058)	=
						Requienia sphaerosperma	(-0.044; 0.046)	=
						Rhigozum trichotomum	(-0.117; 0.031)	=
						Rhus tenuinervis	(-0.048; 0.02)	=
						Salsola spp.	(-0.148; 0.032)	=
						Stipagrostis amabilis	(-0.05; 0.17)	=
						Stipagrostis ciliata	(-0.086; 0.05)	=
Lying-up	Dune street					*Citrullus lanatus*	(-0.027; 0.007)	=
						Other	(0.17; 0.39)	-
						Oxygonum delagoense	(-0.017; 0.007)	=
						Rhigozum trichotomum	(-0.107; 0.097)	=
						Stipagrostis amabilis	(-0.046; 0.066)	=
						Stipagrostis uniplumis	(-0.047; 0.029)	=
						Tribulus zeyheri	(-0.017; 0.007)	=

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Lying-up	Dune slope	28	41.34	82.529	2.447	Bare patch	(-0.17; 0.11)	=
						Acacia erioloba	(-0.078; 0.07)	=
						Acacia haematoxylon	(-0.058; 0.006)	=
						Acacia mellifera	(-0.0273; 0.0107)	=
						Aptosimum elongatum	(-0.0169; 0.0071)	=
						Aristida meridionalis	(-0.037; 0.031)	=
						Boscia albitrunca	(-0.163; -0.055)	+
						Centropodia glauca	(-0.047; 0.035)	=
						Enneapogon cenchroides	(-0.017; 0.007)	=
						Eragrostis lehmanniana	(-0.053; 0.153)	=
						Grewia flava	(-0.017; 0.007)	=
						Helichrysum argyrospaerum	(-0.017; 0.007)	=
						Heliotropium ciliatum	(-0.001; 0.129)	=
						Hermannia burchellii	(-0.021; 0.023)	=
						Hermannia tomentosa	(-0.028; 0.042)	=
						Lycium hirsutum	(-0.017; 0.007)	=
						Monechma incanum	(-0.042; 0.016)	=
						Nolletia arenosa	(-0.0181; 0.0099)	=
						Other	(0.04; 0.2)	-
						Oxygonum delagoense	(-0.021; 0.055)	=
						Requienia sphaerosperma	(-0.028; 0.034)	=
						Rhigozum trichotomum	(-0.136; -0.004)	+
						Rhus tenuinervis	(-0.018; 0.0099)	=
						Salsola spp.	(-0.071; 0.015)	=
						Schmidtia kalihariensis	(0.021; 0.169)	-
						Stipagrostis amabilis	(-0.06; 0.03)	=
						Stipagrostis ciliata	(-0.042; 0.006)	=
						Stipagrostis uniplumis	(-0.028; 0.036)	=
						Tribulus zeyheri	(0.068; 0.122)	-
Urinating	Dune crest	10	18.31	63.48	2.44	*Acacia haematoxylon*	(-0.12; 0.061)	=
						Aptosimum elongatum	(-0.125; 0.051)	=
						Boscia albitrunca	(-0.12; 0.06)	=
						Eragrostis lehmanniana	(-0.066; 0.154)	=
						Grewia flava	(-0.125; 0.051)	=
						Heliotropium ciliatum	(-0.064; 0.156)	=
						Hermannia tomentosa	(-0.58; -0.14)	+

Table 5: *Continued*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Urinating	Dune crest	10	18.31	63.48	2.44	Other	(0.28; 0.68)	-
						Oxygonum delagoense	(-0.17; 0.08)	=
						Salsola spp.	(-0.29; 0.05)	=
						Stipagrostis amabilis	(-0.024; 0.21)	=
Urinating	Dune street	12	21.03	70.54	2.44	Bare patch	(-0.09; 0.29)	=
						Aptosimum elongatum	(-0.11; 0.07)	=
						Centropodia glauca	(-0.077; 0.081)	=
						Crotalaria spartioides	(-0.35; 0.024)	=
						Eragrostis lehmanniana	(-0.066: 0.174)	=
						Helichrysum argyrospaerum	(-0.35; 0.024)	=
						Hermannia tomentosa	(-0.56; -0.16)	+
						Other	(0.2; 0.42)	-
						Oxygonum delagoense	(-0.14; 0.058)	=
						Requienia sphaerosperma	(-0.086; 0.074)	=
						Salsola spp.	(-0.148; 0.042)	=
						Schmidtia kalihariensis	(0.04; 0.26)	-
						Stipagrostis amabilis	(-0.071; 0.082)	=
Urinating	Dune slope	8	15.51	75.33	2.44	*Acacia haematoxylon*	(-0.09; 0.042)	=
						Bare patch	(0.082; 0.422)	-
						Centropodia glauca	(-0.081; 0.063)	=
						Heliotropium ciliatum	(-0.091; 0.129)	=
						Hermannia tomentosa	(-0.64; -0.24)	+
						Other	(0.28; 0.58)	-
						Requienia sphaerosperma	(-0.137; 0.053)	=
						Salsola spp.	(-0.297; 0.001)	=
						Stipagrostis amabilis	(-0.132; 0.061)	=
Defecating	Dune crest	7	14.07	128.52	2.44	Bare patch	(-0.42; 0.36)	=
						Acacia erioloba	(-0.303; 0.121)	=
						Acanthosicyos naudinianus	(-0.26; 0.16)	=
						Hermannia tomentosa	(-0.288; 0.14)	=
						Other	(0.24; 0.48)	-
						Oxygonum delagoense	(-0.276; 0.144)	=
						Schmidtia kalihariensis	(-0.725; 0.575)	=
						Stipagrostis amabilis	(-0.181; 0.259)	=

Table 5: *Continued*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Defecating	Dune street	7	14.07	30.72	2.44	*Salsola* spp.	(-0.18; 0.077)	=
						Bare patch	(-0.52; 0.17)	=
						Hermannia tomentosa	(-0.363; 0.071)	=
						Indigofera alternans	(-0.18; 0.08)	=
						Other	(0.38; 0.62)	-
						Oxygonum delagoense	(-0.182; 0.07)	=
						Schmidtia kalihariensis	(-0.12; 0.26)	=
						Senecio eeni	(-0.183; 0.075)	=
Defecating	Dune slope	6	12.59	49.98	2.44	Bare patch	(-0.28; 0.34)	=
						Citrullus lanatus	(-0.22; 0.08)	=
						Hermannia tomentosa	(-0.53; 0.026)	=
						Other	(0.46; 0.7)	-
						Requienia sphaerosperma	(-0.44; 0.06)	=
						Rhigozum trichotomum	(-0.19; 0.12)	=
						Sesamum triphyllum	(-0.22; 0.1)	=
Rolling	Dune crest	2	5.99	15.13	2.42	Bare patch	(-0.59; -0.09)	+
						Other	(0.33; 0.57)	-
						Stipagrostis amabilis	(-0.33; 0.13)	=
Rolling	Dune street	8	15.51	40.13	2.44	Bare patch	(-0.63; -0.15)	+
						Acacia haematoxylon	(-0.11; 0.05)	=
						Citrullus lanatus	(-0.12; 0.048)	=
						Eragrostis lehmanniana	(-0.04; 0.188)	=
						Grewia flava	(-0.122; 0.05)	=
						Helichrysum argyrospaerum	(-0.19; 0.05)	=
						Other	(0.29; 0.59)	-
						Rhigozum trichotomum	(-0.03; 0.198)	=
						Stipagrostis uniplumis	(-0.113; 0.087)	=
Rolling	Dune slope	3	7.81	31.33	2.43	Bare patch	(-0.73; -0.31)	+
						Aptosimum elongatum	(-0.2; 0.08)	=
						Helichrysum argyrospaerum	(-0.2; 0.08)	=
						Other	(0.54; 0.76)	-

Table 5: *Continued*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Clawing and scraping	Dune crest	3	7.81	75.8	2.43	*Acacia erioloba*	(-1.1; -0.04)	+
						Acacia haematoxylon	(-0.63: 0.25)	=
						Bare patch	(-0.24; 0.68)	=
						Other	(0.552; 0.588)	-
Clawing and scraping	Dune street	3	7.81	49.99	2.43	*Acacia erioloba*	(-1.06; -0.74)	+
						Bare patch	(0.08; 0.4)	-
						Other	(0.57; 0.78)	-
						Stipagrostis amabilis	(-0.14; 0.12)	=
Clawing and scraping	Dune slope	3	7.81	93.51	2.43	*Acacia erioloba*	(-0.98; -0.55)	+
						Acacia haemotoxylon	(-0.307; 0.047)	=
						Bare patch	(0.083; 0.457)	-
						Other	(0.526; 0.758)	-
Crouching	Dune crest	7	14.07	33.28	2.44	Bare patch	(-0.49; -0.03)	+
						Boscia albitrunca	(-0.22; 0.04)	=
						Chenopodium album	(-0.1; 0.039)	=
						Crotalaria sphaerocarpa	(-0.103; 0.043)	=
						Eragrostis lehmanniana	(-0.048; 0.146)	=
						Other	(0.227; 0.459)	-
						Requienia sphaerosperma	(-0.21; 0.048)	=
						Stipagrostis amabilis	(-0.007; 0.207)	=
Crouching	Dune street	17	27.59	45.994	2.44	*Acacia erioloba*	(-0.034; 0.0144)	=
						Bare patch	(-0.34; 0.003)	+
						Centropodia glauca	(-0.044; 0.062)	=
						Elephantorrhiza elephantina	((-0.034; 0.0339)	=
						Enneapogon cenchroides	(-0.037; 0.017)	=
						Eragrostis lehmanniana	(-0.23; 0.03)	=
						Helichrysum argyrospaerum	(-0.056; 0.016)	=
						Heliotropium ciliatum	(-0.058; 0.1)	=
Crouching	Dune street	17	27.59	45.994	2.44	*Hermmania tomentosa*	(-0.07; 0.051)	=
						Indigofera alternans	(-0.035; 0.028)	=
						Monechma incanum	(-0.055; 0.017)	=
						Other	(-0.042; 0.166)	=

Table 5: Continued

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Crouching	Dune street	17	27.59	45.994	2.44	*Requienia sphaerosperma*	(-0.036; 0.046)	=
						Rhigozum trichotomum	(-0.004; 0.17)	=
						Salsola spp.	(-0.38; 0.34)	=
						Schmidtia kalihariensis	(0.06; 0.26)	-
						Stipagrostis ciliata	(-0.034; 0.027)	=
						Stipagrostis uniplumis	(-0.076; 0.03)	=
Crouching	Dune slope	18	28.87	43.493	2.446	Bare patch	(-0.34; -0.04)	+
						Acacia erioloba	(-0.0306; 0.0144)	=
						Acacia mellifera	(-0.0308; 0.0158)	=
						Boscia albitrunca	(-0.045; 0.013)	=
						Centropodia glauca	(-0.043; 0.045)	=
						Citrullus lanatus	(-0.062; 0.01)	=
						Enneapogon cenchroides	(-0.028; 0.012)	=
						Eragrostis lehmanniana	(-0.1; 0.137)	=
						Helichrysum argyrospaerum	(-0.029; 0.0122)	=
						Heliotropium ciliatum	(-0.014; 0.126)	=
						Hermannia tomentosa	(-0.069; 0.033)	=
						Other	(0.086; 0.27)	-
						Oxygonum delagoense	(-0.041; 0.051)	=
						Requienia sphaerosperma	(-0.058; 0.03)	=
						Rhigozum trichotomum	(-0.075; 0.049)	=
						Schmidtia kalihariensis	(-0.01; 0.156)	=
						Stipagrostis ciliata	(-0.062; 0.012)	=
						Stipagrostis uniplumis	(-0.0436; 0.036)	=
						Tribulus zeyheri	(-0.03; 0.034)	=
Killing	Combined components	8	15.51	23.14	2.44	Bare patch	(-0.4; 0.14)	=
						Acacia mellifera	(-0.133; 0.055)	=
						Other	(0.27; 0.51)	-
						Oxygonum delagoense	(-0.265; 0.055)	=
						Requienia sphaerosperma	(-0.081; 0.029)	=
						Rhigozum trichotomum	(-0.094; 0.126)	=
						Salsola spp.	(-0.124; 0.072)	=
						Schmidtia kalihariensis	(-0.25; 0.13)	=
						Stipagrostis amabilis	(-0.089; 0.133)	=

Table 5: *Continued*

Type of behaviour	Habitat component	Degrees of freedom	Critcal chi-squared value [0.05]	Calculated chi-squared value	Z value [0.05]	Plant	Confidence interval	Significance
Eating	Combined components	14	23.68	61.79	2.44	*Acacia haematoxylon*	(-0.24; 0.024)	=
						Aptosimum elongatum	(-0.159; 0.039)	=
						Bare patch	(-0.054; 0.354)	=
						Boscia albitrunca	(-0.159; 0.043)	=
						Cucumis africana	(-0.1; 0.041)	=
						Helichrysum argyrospaerum	(-0.157; 0.039)	=
						Heliotropium ciliatum	(-0.049; 0.139)	=
						Hermannia tomentosa	(-0.241; 0.033)	=
						Lycium bosciifolium	(-0.098; 0.042	=
						Other	(0.243; 0.477)	-
						Oxygonum delagoense	(-0.242; 0.032)	=
						Rhigozum trichotomum	(-0.115; 0.109)	=
						Salsola spp.	(-0.09; 0.06)	=
						Schmidtia kalihariensis	(-0.08; 0.16)	=
						Tribulus zeyheri	(-0.096; 0.048)	=

+ :- Plant used in greater proportion than its expected occurrence
- :- Plant used in smaller proportion than its expected occurrence
= :- Plant used in the same proportion as its expected occurrence

often than expected there ($P \leq 0.05$) was *Acacia haematoxylon*. In addition, bare patches were used significantly more often ($P \leq 0.05$) than expected when lying-up. Only *Heliotropium ciliatum* was associated with less often than expected ($P \leq 0.05$) by caracals in dune streets when lying-up (Table 5).

When urinating on dune crests the caracals urinated close to 10 plant species, compared with 11 plant species in the dune streets and seven on the dune slopes. Across all the three habitat components, the caracals only associated with *Hermannia tomentosa* more often than expected ($P \leq 0.05$) when urinating. On the dune crests and dune slopes, no plant species were associated with less often than expected when urinating. In the dune streets, *Schmidtia kalihariensis* was associated with less often than expected ($P \leq 0.05$) for urination, and on the dune slopes bare patches were used less often than expected ($P \leq 0.05$) (Table 5).

When defecating, the caracals associated with six plant species on the dune crests and the dune streets and with five on the dune slopes. No plant species was associated with more or less often than expected for defecation. When caracals roll on the dune crests, only the tufted grass *Stipagrostis amabilis* was associated with this behaviour. On the dune slopes, two plant species were associated with rolling, while in the dune streets it was seven. In the three habitat components, bare patches were used significantly more often ($P \leq 0.05$) than expected when caracals rolled (Table 5).

When clawing trees and scraping the ground during scent-marking, caracals did so in association with two plant species in each of the habitat components. Across the three habitat components the only plant species that was associated with behaviour more often than expected ($P \leq 0.05$) was *Acacia erioloba*. On the dune slopes and in the dune streets bare patches were used less often than expected ($P \leq 0.05$) (Table 5) for such scent-marking.

Crouching was associated with six plant species on the dune crests, 16 plant species in the dune streets and 17 plant species on the dune slopes. In these three habitat components, caracals crouched more often than expected ($P \leq 0.05$) on bare patches. The only plant species that was associated with less often than expected when crouching ($P \leq 0.05$) was *Schmidtia kalihariensis* in the dune streets (Table 5).

Seven plant species in the three habitat components were present in the proximity of kills, but none of them were associated with killing more or less often than expected. Thirteen plant species in the three habitat components were recorded in association with eating prey by caracals, but none of them were used more or less often than expected (Table 5).

Discussion

The habitat component ratio that was calculated with the non-mapping method (Marcum & Loftsgaarden 1980) differed greatly from the one that was calculated by Van der Walt (1999). According to Van der Walt (1999) the dune crests contributed 2 %, the dune slopes contributed 22 % and the dune streets 69 % to the total habitat, with two additional components making up the surface area deficit of 7 % in the area that study.

Habitat component selection

Proportionally, the dune streets form the highest component proportion of the habitat that is available to caracals in the Kgalagadi Transfrontier Park, contributing 53.8 % of the habitat available in the current study area, with the dune crest and dune slope habitat components contributing 12.7 % and 33.5 % to the available habitat respectively. Caracals, however, tend to select for the two latter habitat components rather than the larger dune street component. Therefore, in effect they only use 46.1 % of the total available habitat area to any great extent (Table 3).

There are a number of possible explanations for the use of the dune slopes and crests in a higher than expected proportion. The most obvious explanation is that the elevation of the dune slopes and the dune crests provides natural vantage points from which caracals can scan the surrounding area for potential prey and other predators as was found for domestic cats (Leyhausen 1979) and leopards (Bothma & Le Riche 1989). Moreover, sufficient cover for hunting is available on the dune slopes and the dune crests and the vegetation density there does not inhibit the movements of a caracal, as much as the higher vegetation density in the dune streets would do. Moolman (1986) and Van Heezik & Seddon (1998) suggested that caracals select certain habitat types based on the availability of cover. The suitability of the habitat for successful hunting seems to be a prerequisite for habitat selection by caracals. The dense stands of *Rhigozum trichotomum* shrubs and the annual grass *Schmidtia kalihariensis* that occur in the dune streets (Table 1) will make the dune streets less suitable for hunting than the other habitat components, especially because it impares both sight and movement.

The high percentage of caracal behaviour that was observed on the dune slopes is believed to be partially attributable to the presence of rodents there where they naturally occur in higher densities. Rodents are also abundant on dune slopes but they are largely absent from the dune crests (Nel *et al.* 1984). Moreover, rodents form an essential component of a caracal's diet in the Kgalagadi Transfrontier Park (Melville *et al.* 2004). For hunting, the dune slopes are therefore preferable to the dune streets for a caracal. This is further substantiated by the preference that is shown by caracals when they start to run from a stationary or crouching position at the onset of a chase (Table 3). Moolman (1986) suggested that caracals in the Mountain Zebra National Park utilise certain habitat types because of the high incidence of their preferred prey there. In Saudi Arabia, caracals also prefer habitats that support large prey populations (Van Heezik & Seddon 1998).

An additional reason for the selection of the dune slopes and the dune crests is that caracals may avoid *Schmidtia kalihariensis*, a highly aromatic annual grass that exudes an acidic substance that can affect animals negatively, and that at times may form dense and almost impenetrable stands that inhibit movement (Van Rooyen 2001). *Schmidtia kalihariensis* occurs in a higher frequency in the dune streets than on either the dune slopes or the dune crests (Table 1). It forms 1.2 % and 10.3 % of the vegetation on the dune crests and the dune slopes respectively, and 18.1 % in the dune streets (Table 1). The southwest-facing dune slopes are possibly used less often than the northeast-facing ones because the southwest-facing slopes have steeper slip-faces than the northeast-facing ones (Van der Walt & Le Riche 1999). The mobility of caracals on steep slopes is probably inhibited by the sheer gradient. A combination of all these factors may therefore cause caracals to use the dune streets less often than expected, and the dune slopes and crests more often than expected.

Association with plants

The association of specific plants with specific types of behaviour is difficult to quantify, and it is important to note that there are definite limitations to the method that was applied in this study. To obtain base-line data for the frequency of occurrence of vegetation, foot-point transects were done. Due to the nature of this type of data collection, not all the plant species that are potentially available for association by the caracals were recorded in each habitat component. When caracals were associated with plant species that were not recorded in the vegetation transects, the actual value that was used in the statistical analysis for missing plants was zero. This zero value tended to bias the level of preference displayed for association with certain plant species when executing certain behaviours in certain habitat components. The base-line data were collected for all the plant species, but the caracals only associated with specific plants when conducting certain types of behaviour. The plants that were not involved in such association were clumped in the category "other" in the preference calculations (Table 5). This clumping exaggerated the chi-squared values for certain types of behaviour relative to certain plant species. The fact that the caracals do associate with certain plant species suggests a level of positive selection for the presence of that plant, even in cases where the statistical tests are not conclusive.

Standing

Standing is a type of behaviour that involves stopping and pausing while moving about normally. It is possible that stopping on the dune slopes and the dune crests is linked to hunting and the use of vantage points to locate prey as in leopards (Bothma & Le Riche 1989) or to locate and avoid other predators. A differential habitat component use pattern was found, with the caracals stopping on the dune slopes by preference in the hot season, and on the dune crests in the cold season. This could be explained by the fact that during the hot season, the prey of a caracal is more abundant and readily available than in the cold season when prey becomes more limited (Begg 2001). In the hot season this may cause the caracals to utilise the dune slopes more often because that is where their prey is more likely to occur then (Nel *et al.* 1984). In the cold season, however, it may be necessary for caracals to utilise the higher vantage points that are provided by the dune crests to locate their prey as in domestic cats (Leyhausen 1979) and leopards (Bothma & Le Riche 1989).

The preferential use of the northeast-facing dune slopes is probably related to a higher density of rodent burrows or colonies on these slopes. The higher rodent density on the northeast-facing dune slopes may be due to a denser substrate on the shallower northeast-facing dune slopes than on the steeper southwest facing dune slopes. A dense substrate is ideal for the excavation of burrows (Nel, pers. comm.)[1]. The higher ambient temperatures on the northeast-facing dune slopes, in the southern hemisphere may also influence the rodent density there. Habitat selection based on thermal conditions is alluded to in Lovegrove (1993) in a paper on the thermoregulation of endotherms. *Acacia mellifera* shrubs occur exclusively on the northeast-facing dune slopes in the study area, and these areas are used extensively by a number of rodent species, but especially by Brant's whistling rat *Parotomys brantsii* for burrowing or nesting (Van Rooyen, pers. comm.)[2]. This rodent is also abundant in the diet of caracal (Melville *et al* 2004). The presence of these rodents

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may influence the preference that is shown by the caracals for the northeast-facing dune slopes. The preference for associating with certain trees, and dense shrubs and forbs suggests that the caracals use these plants as cover when hunting, and for shade when moving around in the early morning and late afternoon when they are known to be active in the daylight (Avenant & Nel 1998).

Occasionally a caracal was observed to stand near a rodent burrow. These caracals were possibly waiting for potential prey to emerge from the burrows. Caracals also stood near the entrance or even to go into aardvark *Orycteropus afer* and porcupine *Hystrix africaeustralis* burrows, either to hunt or to lie-up for the day. Caracals also frequently stopped to investigate springhare *Pedetes capensis* faecal deposits but the reason for doing so is obscure.

Sitting

Sitting can be part of resting or hunting. The same trends were found for sitting as were found for standing, with the dune crests and the dune slopes being used more often than expected, and the dune streets less often than expected (Table 3). A similar seasonal pattern of variation in the use of these habitat components was found for sitting as was found for standing, with the dune crests being utilised more often in the cold season, and dune slopes more often in the hot season. A characteristic of the sitting behaviour of caracals is that they use the southwest-facing dune slopes more often than expected for sitting (Table 2). This especially, happened in the hot season, when 85 % of all observed incidences of caracals sitting on a dune slope were on southwest-facing ones. Although caracals are predominately nocturnal, a certain amount of diurnal behaviour does occur (Avenant & Nel 1998). The northwest to southeast orientation of the dunes leaves the southwest-facing dune slopes in the shade for longer in the morning. Consequently they are cooler in the hot season than the northeast-facing ones. When sitting on a southwest-facing dune slope, a caracal may well be resting in a cooler part of its habitat, especially during the hot season. A further environmental factor that could be contributing to the selection of the southwest-facing dune slopes is the prevailing northwesterly wind (Van der Walt & Le Riche 1999) from which the southwest-facing dune slopes will be sheltered. This would also reduce the chances of prey animals detecting the scent of hunting caracals. When sitting during a hunt, the caracals that sat near rodent burrows probably waited for prey to emerge.

Lying-up

Caracals utilise all three of the habitat components in proportion to their occurrence when lying-up on a year-round basis. However, on a seasonal basis, the dune crests are used more frequently than expected during the cold season (Table 4). This pattern is probably related to thermoregulation because the dune crests are more exposed to direct sunlight than the more shaded southwest-facing dune slopes or the more heavily vegetated dune streets. Caracals may use the dune crests as vantage points from which to locate potential prey or to detect other predators as happens in leopards (Bothma & Le Riche 1989). Because caracals are known to display some diurnal behaviour in cool, overcast conditions (Avenant & Nel 1998), a hunt could presumably be initiated in the cold season from a position where a caracal is lying-up.

Caracals utilise the predominant southwest-facing and northeast-facing dune slopes in similar proportions in the hot season, but the increase in the use of the northeast-facing dune slopes during the cold season (Table 2) is probably related to thermoregulation as in leopards (Bothma & Le Riche 1984). Because of the cold southerly winds of the cold season, caracals probably utilise the northeast-facing slopes then to shelter from that wind, and to make use of the warmer north-easterly orientated dune slopes as lions and leopards do.

Caracals prefer *Boscia albitrunca* trees when lying-up, on the dune crests and on the dune slopes, but not in the dune streets (Table 5). The low frequency of use of *Boscia albitrunca* in the dune streets is related to the low frequency of occurrence of this tree in that habitat component (Table 1). In the two habitat components in which *Boscia albitrunca* does occur fairly abundantly, the caracals utilise these trees more often than expected to lie up under because they provide cover for escape from the heat and from prey when hunting as happens in leopards in the same region (Bothma & Le Riche 1984). The bare patches that are used in the dune streets to lie-up in are probably used as temporary resting sites when moving about rather than as places to lie-up for extended periods of rest. In the early morning, caracals frequently lie in the shade of plants with sparse shade. Due to the orientation of the sun and the proximity parameter of ≤100 mm that was imposed on the method of data collection when measuring associations with plants, these caracals were often recorded as lying-up on a bare patch when they were actually lying in the morning shade of particular plants.

Caracals were only recorded to lie-up near *Schmidtia kalihariensis* grass tufts on the dune slopes, but even there they used this plant less often than expected (Table 5). This is probably due to the characteristics of *Schmidtia kalihariensis* that would affect caracals negatively (Van Rooyen 2001). The low ground creeper *Tribulus zeyheri* was also only associated with on the dune slopes for lying-up, but less often than expected (Table 5), probably because of the spiky nature of the fruit that it produces (Van Rooyen 2001) which would make lying-up on these plants uncomfortable.

On five occasions during the present study the caracals used aardvark burrows to lie-up in, in the same manner as leopards (Bothma & Le Riche 1984) and brown hyaenas *Parahyaena brunnea* (Mills 1990). This behaviour was only recorded in the hot season. These burrows provide ideal cover from other predators, and they provide protection from the intense daytime heat of the hot season.

Urinating

Caracals often use scent-marking by urination as a form of olfactory communication (Stuart 1981; Estes 1995) in the same manner as other felids do (Schaller 1972; Verberne & Leyhausen 1976; Bothma & Le Riche 1984, Bothma 1998). This is also the case in the Kgalagadi Transfrontier Park. For urination, the caracals utilise the dune crests more often than expected in both seasons, possibly to optimise the use of the prevailing winds to distribute the scent over a long distance.

When caracals urinate on the dune slopes there is a tendency to utilise the northeast-facing dune slopes more often than the southwest-facing ones (Table 2). This pattern is more pronounced in the cold season than the hot season. The increased utilisation of the northeast-facing dune slopes in the cold season may be to take advantage of the prevailing southerly wind then to distribute the scent. Also, the desiccation effect will not be as pronounced on the northeast-facing dune slopes as on the southwest-facing ones. Consequently, the lifespan of such a scent will be increased.

Although caracals were observed to urinate on various plant species, the only species that was used consistently and more often than expected in all the habitat components was the low shrub *Hermannia tomentosa* (Table 5). This selection may be related to the dense and hairy nature of the foliage of this plant that would trap the scent for long periods (Van Rooyen 2001). The only habitat component in which caracals were observed to associate with *Schmidtia kalihariensis* when urinating, was the dune slopes, and even there it was used less often than expected (Table 5). The reason for avoiding *Schmidtia kalihariensis* when urinating is probably linked to the highly aromatic nature and acidic exudates of this grass species (Van Rooyen 2001). Caracals were also observed to urinate repeatedly against various tree trunks, especially *Boscia albitrunca* trees, which may indicate the use of scent posts to mark the boundaries of the ranges of an individual caracal.

Stuart (1981) reported that caracals occasionally scrape their feet through their own urine. This was also found in the Kgalagadi Transfrontier Park where this type of behaviour involved a caracal depositing urine on a pile of leaf litter and then scraping its hind paws through the wetted litter. It is generally regarded as an alternative form of scent-marking.

Defecation

Faecal deposition is known to contribute to olfactory communication in caracals (Estes 1995). The preferential deposition of faeces on the dune crests (Tables 3 & 4) probably enhances the distribution of the scent by the prevailing winds. Caracals deposit faeces in exposed positions throughout the year. In the hot season, however, the caracals utilise the dune slopes more often than expected when defecating, but the dune crests were used in proportion to their occurrence when doing so (Table 3). The preferred use of the northeast-facing dune slopes in the hot season when defecating increases the rate of desiccation and reduces the effective lifespan of the scent of the faeces. There is no evidence that specific plant species are selected in association with defecation (Table 5). It has been suggested that the deposition of exposed faecal deposits by caracals may only be related to the scent-marking of range boundaries (Stuart 1981; Stuart & Wilson 1988). In the present study caracals were never observed to use faecal middens or latrines, to deposit their scats in open scrape marks, nor to bury their scats.

Rolling

Estes (1995) suggested that rolling might contribute to olfactory communication in felids. In the present study, the caracals regularly rolled on bare patches of sand. This behaviour occurred more often on the dune crests than in any other habitat component. There was a strong seasonal difference in rolling behaviour. In the cold season, there was no significant habitat component selection for rolling, but in the hot season there was a distinct preference for rolling on the dune crests (Tables 3 & 4). Caracals also occasionally rolled in old carcasses.

Clawing and scraping

Stuart (1981) and Stuart & Wilson (1988) suggested that clawing and scraping might have a territorial marking function. Caracals in the Kgalagadi Transfrontier Park clawed trees in much the same manner as leopards (Bothma 1998). Additionally, caracals were observed to scrape the ground with their hind feet without urinating, and this behaviour was included with the analysis of clawing and scraping. In the present study, caracals were not observed to display any significant habitat component selection when clawing and scraping (Table 3). There was, however, a selection for *Acacia erioloba* trees when clawing trees (Table 5). This is probably related to fact that the coarse, deeply furrowed bark (Palgrave 1993; Van Rooyen 2001) is more abrasive on the claws (Estes 1995), and the flaking nature of the bark leaves a more visible mark on these trees than on other tree species. Caracals also tended to claw trees growing on the northeast-facing dune slopes and scraped the ground there more often than on other dune aspects, especially in the hot season. The clawing marks were generally found on the northeast side of the trees.

Crouching

Crouching was often a precursor to a caracal starting to chase a prey animal. Caracals preferred the dune slopes to the other habitat components when crouching, and this is probably linked to the high prevalence of rodents on the dune slopes (Nel, *et al.* 1984). The use of bare patches in which to crouch suggests that an unobstructed terrain from which to launch an attack on prey may be important in the hunting strategy of caracals (Table 5). There is no evidence that caracals favoured either of the predominant dune slope aspects when crouching (Table 2).

Starting a run

The act of starting a run flows from crouching within the context of hunting, and it is therefore logical that the selection of habitat component for this type of behaviour mirrors that of crouching. Of the habitat components that the caracals use, prey animals are found in the highest density on the dune slopes. There is no significant selection for any dune slope aspect when starting a run. No associations with plant species are relevant here because, in this case, the start of a run was related to movement rather than specific point on the ground.

Killing

There is some evidence that caracals avoid the dune crests when killing prey, and that they tend to utilise the other habitat components in proportion to their occurrence for the killing of prey (Tables 3 & 4). It is logical that the least number of kills were made on the dune crests because few prey animals will try to escape by running up a dune or along a dune crest. Moreover, the highest density of rodents occurs on the dune slopes and in the dune streets (Nel *et al.* 1984). It is for these reasons that the highest percentage of kills that were recorded also occurred on the dune slopes and in the dune streets. The northeast-facing dune slopes were used more often than the southwest-facing ones when killing prey, particularly in the hot season. This is probably because prey animals occur in higher densities on the northeast-facing dune slopes (Lovegrove 1993, Van Rooyen pers. comm.), and the less steep gradient of these dune slopes. No specific plant associations were noted in conjunction with caracals making kills. This was expected because of the great degree of chance inherent in killing prey. Therefore any active habitat selection related to this behaviour is unlikely.

Eating

Over the whole year and the cold season the dune crests were used less often than expected for eating. This is probably because of caracals eating their prey wherever they catch and kill them. The dune streets were also used less often than expected for eating, but the dune slopes were used more often than expected (Table 3). This probably relates to the occurrence of prey animals within the latter habitat component (Nel *et al.* 1984). No evidence of habitat component selection when eating was found in the hot season (Tables 3 & 4). High frequencies of observations of caracals eating were found on the northeast-facing dune slopes. In the hot season 75 % of all the records of a caracal eating its prey were on the northeast-facing dune slopes. This pattern is related to the proportionally high number of kills that are made on the northeast-facing dune slopes. Both these patterns probably also relate to a higher density of rodents occurring on the northeast-facing dune slopes (Nel, pers. comm.). There is no evidence that specific plant species were associated with when eating prey, and those plants that are present there were in proportion to their occurrence (Table 5).

Conclusions

Even in the apparently homogeneous habitat of the Kgalagadi Transfrontier Park, caracals display a level of habitat component selection across the full spectrum of variation. On a coarse habitat component level, the caracals tend to select the dune crests and dune slopes, while avoiding the dune streets. On a finer scale, the dune slopes with various aspects were used preferentially for a range of behavioural patterns. Caracals also display some degree of selectivity when associating with specific plant species for particular behavioural patterns. The overall conclusion is that caracals do not utilise the available habitat in proportion to its occurrence, but rather that they select specific components of it for specific types of behaviour.

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CHAPTER 7

HUNTING BEHAVIOUR OF THE CARACAL IN THE KGALAGADI TRANSFRONTIER PARK

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ABSTRACT

Caracals were spoor-tracked in the Kgalagadi Transfrontier Park with the assistance of a Kalahari San tracker to investigate their general ecology and behaviour. Observations relating to caracal hunting behaviour were made based on large and small prey categories. Caracals use a flexible hunting technique and their hunting methods are adapted to specific circumstances. They hunt larger prey more with a higher degree of success than smaller ones. There is a logical sequence of hunting behaviour that is likely to result in a kill.

Keywords: caracal, *Caracal caracal*, spoor-tracking, hunting, Kalahari

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INTRODUCTION

There is a paucity of data relating to the hunting behaviour of nocturnal, solitary felids in general (Bothma & Le Riche 1989) and caracals *Caracal caracal* in particular. The ability to hunt and kill prey is central to the survival of any predator. Felids are among the most highly specialised carnivores (Kruuk 1986), and are killers *par excellence* (Ewer 1973). The evolutionary fitness of any animal is dependent on the quality and quantity of its diet (Griffiths 1975). Predatory strategies are designed to optimise nutrient intake within an environment that is governed by a complex system of ecological factors (Sunquist & Sunquist 1989). In the semi-arid Kgalagadi Transfrontier Park, stringent ecological constraints necessitate the refinement of hunting tactics by predators to increase their chances of survival (Bothma *et al.* 1997). Factors such as the availability, abundance, size, vulnerability and behavioural response to predation of prey animals all influence a predator's prey selection and hunting success (Bothma *et al.* 1997). Of the carnivore families, the Felidae is the family that is most specialised for the capture of vertebrate prey. However, felids prey selectively on prey animals whose size is commensurate with their own body size (Kruuk 1986).

Due to the sandy nature of the substrate in the Kgalagadi Transfrontier Park it was possible to use the spoor-tracking methods as described by Eloff (1984), Bothma & Le Riche (1984) and Stander *et al.* (1997) to study the hunting behaviour of the caracal in the Kgalagadi Transfrontier Park, and to investigate the hunting success achieved by caracals in this semi-arid environment. Different authors have variously described how a hunt consists of several component behaviours. Kruuk (1972) suggests that all predator hunts are comprised of a search and an approach, followed by the immobilisation and eating of the prey animal. Mills (1990) suggests that a hunt is any interaction between a predator and a potential prey, where the predator moves towards the prey at an increased speed, in the absence of any carrion. Schaller (1972) and Bothma & Le Riche (1984) suggest that hunts by large felids consist of at least a combination of any of three primary hunting behaviours: a stalk, a chase and a kill. Caro (1994) extended this list of behaviours to include, trotting, crouching and rushing. According to Estes (1995) all cats have the same basic hunting motivation, namely to capture, kill and eat its prey.

To investigate the hunting behaviour of caracals in the Kgalagadi Transfrontier Park the following three hypotheses were tested here:

1. Caracals display a variable hunting technique.
2. Larger prey items are hunted more vigorously than smaller ones.
3. There is an ideal sequence of behaviours that is most likely to result in a successful hunt.

STUDY AREA

This study was done in an area along the Namibian border near Mata-Mata in the southwestern portion of the Kgalagadi Transfrontier Park. For logistic reasons it was decided to confine the research to an area that extended 60 km north from the Mata-Mata rest camp along the Namibian border (20° 00' E longitude) to approximately 20 km into the interior of the Kgalagadi Transfrontier Park.

The Kalahari Gemsbok National Park was proclaimed in 1931, but it only became a reality in 1935 when a number of farms along the southern bank of the Aoub River were acquired. Today, the Park exists in much the same ecological state as it was then (Van Wyk & Le Riche 1984). An agreement to formally combine the Kalahari Gemsbok National Park (South Africa) with the bordering Gemsbok National Park (Botswana) to form the Kgalagadi Transfrontier Park was signed by representatives of the governments of South Africa and Botswana in 1999. This agreement was ratified at an amalgamation ceremony that was held on the 12 May 2000 (Donaldson 2000).

The Mata-Mata area lies in the Shrubby Kalahari Dune Bushveld of the Savanna Biome (Low & Rebelo 1996). This area is an arid savanna with temperatures varying from –10° C to 45° C in the shade with an annual mean rainfall of 153.47 mm occurring mainly in the hot season. The landscape is one of undulating dunes with sparse vegetation at altitudes varying from 1000 to 1100 m above sea level (Low & Rebelo 1996).

The vegetation is characterised by the trees *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca*, a shrub layer of *Grewia retinervis* and *Rhus tenuinervis,* and a well-developed grass layer consisting mainly of *Stipagrostis amabilis*, *Eragrostis lehmanniana, Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996). There is little variation in the soil forms because the area is predominantly covered by aeolian sand overlying calcrete (Low & Rebelo 1996).

The Kgalagadi Transfrontier Park forms the southern part of the greater Kalahari ecosystem. Because of the arid nature of the area, many of the plants there are ephemeral. After sufficient rain, these plants germinate quickly to complete their life cycle in a short time (Eloff 1984).

Because of the harshness of the environment, the southern Kalahari is an area that is only sparsely inhabited by humans. This above any other factor contributes to the uniqueness of the area, and it enhances the value of the area for field research in wildlife management and conservation.

METHODS

Field data collection

The spoor-tracking method as described by Eloff (1984), Bothma & Le Riche (1984) and Stander *et al.* (1997) was used. An experienced Kalahari San tracker was employed to identify and interpret the caracal spoor on a step-by-step basis. All behavioural patterns observed were recorded, and from these observations the data relating to hunting behaviour were extracted. Due to the variation in the compaction of the sand, the small size of a caracal and, hence, the variable clarity of the spoor, caracals could seldom be tracked for an entire 24-hour activity period. The data presented here are therefore random observations of the behaviour of several caracals that were tracked for variable distances and intervals from June 2000 to August 2002.

A division of hunts simply into the components of a stalk, chase and kill (Schaller 1972) was too coarse to describe the hunting behaviour of caracals fully. Therefore, it was decided to expand these behavioural components to include a crouch, a take-off, and a pounce. A hunt was therefore recorded when the tracker indicated any one of the following behaviours: a stalk, a crouch, a take-off, a chase, a pounce and a kill. Hunting success was indicated by clear evidence that the prey animal had been killed. This evidence was usually in the form of a carcass, visceral remains, hair, feathers or blood. In the absence of such evidence, a hunt was considered to have been unsuccessful. However, this might underestimate the hunting success of caracals because in some cases caracals are known to consume small prey entirely without leaving any visible evidence of a kill (Stuart & Hickman 1991). This is also known to happen in other small cats like the serval *Leptailurus serval* (Geertsema 1985).

Schaller (1972) defined minimum distances for each of the components of hunting behaviour. However, he determined these distances for lions *Panthera leo* and consequently they are too long to be directly applicable to the caracal. The following definition of a stalk and a chase was therefore used in the present study: a chase was any determined rush of 1 m or more towards a potential prey animal, while a stalk was any approach towards a potential prey item in a stalking posture for a distance ≥ 1 m. A take-off happens when a caracal begins to chase a potential prey item, and it is the transitional stage between a stationary or slow-moving activity to a full chase. This behaviour could be initiated from a crouched position, or from a stationary (standing) one, or whilst walking. However, it involves a discernible rapid acceleration towards a potential prey item. A pounce is a leap towards a prey animal. It occurs either from a stationary or a crouched position while walking about normally or when chasing prey. A hunt is defined as any response of a caracal to a potential prey animal (Bothma & Le Riche 1984). The distances covered whilst performing any of these behaviours, and the intended prey involved in any of these behavioural components were also recorded. The distance of a hunt as used here is the total distance over which a hunt takes place, including all the component distances involving stalking, chasing and pouncing that make up the behavioural sequence of a hunt.

The data were interpreted on a year-round and a seasonal basis. The seasonal analysis was based on a hot season from October to March, and a cold season from April to September.

Data analysis

For the purposes of analysis the prey animals of the caracals were separated into two distinct size classes, with large prey having a mean adult body mass of > 1 kg, and small prey weighing ≤ 1 kg (Table 1). In addition, those prey that left a visually faint or undetectable spoor were assumed to be small prey because the spoor of larger prey would be clearly visible and identifiable.

: *The mean body mass (kg) of the prey of caracals in the Kgalagadi Transfrontier Park from June 2000 to August 2002. Source: Skinner and Smithers (1990)*

Prey	Scientific name	Body mass	
		Males	Females
African wild cat	*Felis sylvestris*	4.90	3.70
Bat-eared fox	*Otocyon megalotis*	4.03	4.11
Black-backed jackal	*Canis mesomelas*	7.89	6.60
Brant's whistling rat	*Parotomys brantsii*	0.14	0.12
Cape fox	*Vulpes chama*	3.00	2.90
Ground squirrel	*Xerus inauris*	0.65	0.60
Kori bustard	*Ardeotis kori*	13.5 to 19.0	13.5 to 19.0
Scrub hare	*Lepus saxatilis*	2.20	2.60
Springhare	*Pedetes capensis*	3.13	2.83
Steenbok	*Raphicerus campestris*	10.90	11.30
Striped polecat	*Ictonyx striatus*	0.97	0.71
Yellow mongoose	*Cynictis penicillata*	0.59	0.55
Unidentifiable	~	~	~

~ no data relevant

Correspondence Analysis (SAS 1999) was used to model the sequence of hunting behaviours that was most likely to result in a kill. The behavioural components were weighted according to their ordered sequence leading up to an ultimate successful or unsuccessful hunt. For example, a hunting sequence for a successful hunt could be as follows: crouch-chase-pounce-kill. The weighting for the above sequence would then be: 16.6, 33.3 and 50.0 % for the crouch, chase and pounce components respectively. That behavioural component in this sequence that is theoretically furthest away spatially from a kill is the crouch, hence it receives the lowest weighting. Each hunting attempt was weighted independently. A kill would receive a weight of 1 and lack of success a weight of 0. Observations were weighted to represent an equal contribution of the successful and failed hunts because the successful hunts only contributed 10.1 % to the total number of hunts. Each behavioural component received its weighting independently for each hunt. The weighting was applied irrespective of whether the hunt was successful or unsuccessful.

By applying the Correspondence Analysis technique it is possible to plot the orientation of the data points relative to one another in a multi-dimensional space in an area with a restricted number of dimensions. The first three dimensions that were identified according to the Correspondence Analysis (SAS 1999) in this study, accounted for 78.0 % of the variation in the multi-dimensional space of the data (39.3, 21.2 and 17.5 % respectively), and were therefore used as an adequate representation of the data (Grimbeek pers.comm.)[1].

The weighted distances in a three-dimensional space were calculated according to the above dimensional weights between the points representing success and failure and the hunting behavioural components. These distances were then ordered, and

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the associated components of behaviour were interpreted as sequences leading up to a successful or unsuccessful hunt. The weightings positioned the behavioural components along a gradient relative to their likelihood of leading to a kill. Those components that were most likely to result in a successful hunt were positioned closest to the plotted success point, and those that were less likely to result in a success were oriented closer to the plotted unsuccessful hunting point.

RESULTS

Hunts

During the study 154 different sets of caracal tracks were followed for a total distance of 537.9 km. In all, 327 hunts were recorded at a rate of one hunt per 1.6 km. Seasonally, the hunting rate in the hot season was one hunt per 1.4 km, and one hunt per 1.9 km in the cold season. The hunting success rate was one kill per 16.3 km moved for the entire year. Seasonally it was 14.9 km per kill in the hot season and 17.7 km per kill in the cold season.

Of the 327 observed hunts, 166 and 161 hunts were recorded in the hot and cold seasons respectively. On 33 occasions the caracals killed the prey that they were hunting, giving an overall hunting success rate of 10.1 %. During the hot season the caracals killed 16 prey at a success rate of 9.6 % and in the cold season 17 prey at a success rate of 10.6 %. There is no significant difference in the frequency with which caracals hunt large or small prey between the hot and cold seasons (χ^2: 1.73, df: 1, $P > 0.05$).

The hunting success rates shows that caracals are more successful when hunting large than small prey. There is a significantly higher success rate for large than for small prey ($\chi^2 = 8.99$, df = 1, $P < 0.05$). When calculated for the entire year, 18.0 %

of the hunted large prey were killed, but only 7.5 % of the small prey. On a seasonal basis, 26.5 and 17.1 % of the large prey hunted were killed in the cold and hot seasons respectively. Of the small prey 7.5 and 7.4 % of the hunts were successful in the hot and cold seasons respectively.

The mean year-round distance over which all hunts took place was 18.0 m (SE = 2.2 m; range = 1 – 379 m). There is no significant difference between the mean distances over which caracals hunted in the hot and cold seasons (t = 0.9, df = 332, $P > 0.05$). On a seasonal basis the mean distance over which hunts took place was 22.5 m (SE = 3.1 m; range = 1.5 – 318 m) in the cold season, and 18.7 m (SE = 1.4 m; range = 1 – 379 m) in the hot season. There was no difference in the mean distances for successful and unsuccessful hunts on a year-round basis or in the cold season. However, in the hot season there was a significant difference between the distances of successful and unsuccessful hunts. In the hot season, there was a significant difference between the distances of caracals' successful and unsuccessful hunts. There is not a significant linear relationship between the success of a hunt and the distance over which a hunt took place (logistic regression, df = 1, $P = 0.87$) (Table 2).

On a year-round basis there is a significant difference between the hunting distances for large and small prey (t = 4.92, df = 71, $P < 0.05$). The mean hunting distance for large prey was 54.2 m (SE = 8.6 m; range = 1 – 379 m), while that for small prey was 11.6 m (SE = 0.8 m; range = 1 – 71 m). This is also true on a seasonal basis: hot season: t = 2.99, df = 30, $P \leq 0.05$ and cold season: t = 3.91, df = 40, $P < 0.05$. The mean hunting distances for large and small prey in the cold season was 54.1 m (SE = 10.7 m; range = 8 – 318 m) and 12.1 m (SE = 1.2 m, range = 1 – 54 m) respectively. In the hot season it was 54.3 m (SE = 14.3 m; range = 1 – 379 m) and 11.2 m (SE = 1.1 m; range = 1 – 71 m) respectively.

Table 2: *The mean hunting distances (m) of caracals for various components of hunting behaviour during successful and unsuccessful hunts in the Kgalagadi Transfrontier Park from June 2000 to August 2003*

Prey	Component	Period	Mean distance		Standard error of the mean		t-value	*P*-value	Degrees of freedom
			Successful	Unsuccessful	Successful	Unsuccessful			
All	Chase	Year-round	14.70	22.50	5.1	2.50	1.63	0.11	46
Large			25.00	62.50	7.8	10.70	2.83	0.0070 *	52
Small			5.80	12.70	1.2	0.80	4.96	<0.0001 *	26
All		Hot season	5.70	21.10	1.1	3.50	4.50	<0.0001 *	158
Large			6.60	63.00	1.8	16.40	3.42	0.0020 *	25
Small			5.30	12.50	1.3	1.10	4.28	0.0002 *	25
All		Cold season	25.20	24.00	16.1	3.70	0.14	0.89	16
Large			34.30	62.00	10.6	14.00	1.58	0.12	30
Small			7.10	12.90	2.6	1.10	-2.00	0.11	4
All	Pounce	Year-round	1.60	1.80	0.2	0.10	0.75	0.45	54
Large			2.30	1.80	0.2	0.50	1.23	0.27	5
Small			1.50	1.70	0.2	0.10	1.04	0.31	32
All		Hot season	1.70	1.80	0.2	0.10	0.58	0.57	28
Large			2.50	1.80	0.4	0.40	1.05	0.4	2
Small			1.60	1.70	0.2	0.10	0.55	0.59	17
All		Cold season	1.60	1.50	0.3	0.30	0.21	0.83	15
Large			~	~	~	~	~	~	~
Small			1.30	1.60	0.3	0.40	0.66	0.52	11
All	Stalk	Year-round	17.90	5.20	8.8	1.60	-1.43	0.2	6
Large			20.00	7.45	3.9	8.30	-0.90	0.43	3
Small			15.00	4.16	12.2	1.90	-0.89	0.47	2
All		Hot season	4.30	3.00	0	1.10	1.40	0.27	25
Large			~	~	~	~	~	~	~
Small			3.00	2.26	0	0.30	-2.72	0.0100 *	18
All		Cold season	23.80	7.50	11.5	5.40	1.33	0.24	5
Large			20.00	3.50	13.8	0.60	-1.20	0.32	3
Small									

Table 2: *Continued*

Prey	Component	Time-frame	Mean distance		Standard error of the mean		t-value	*P*-value	Degrees of freedom
			Successful	Unsuccessful	Successful	Unsuccessful			
All	Hunt	Year-round	16.38	20.98	3.70	2.40	1.08	0.29	65
Large			23.90	63.70	6.50	10.90	-3.16	0.0020 *	69
Small			8.90	11.80	2.20	0.90	-1.24	0.23	21
All		Hot season	7.26	19.75	1.00	3.30	-3.76	0.0002 *	175
Large			6.80	63.40	1.80	16.50	-3.40	0.0002 *	26
Small			7.50	11.50	1.50	1.20	-2.17	0.0390 *	25
All		Cold season	23.60	22.40	6.30	3.40	-0.17	0.86	32
Large			31.00	64.00	8.20	14.20	-1.98	0.055	38
Small			10.90	12.20	5.10	1.30	-0.25	0.81	7

* Significant difference within rows
~ Insufficient data

On a year-round basis there was no significant difference between the mean distances of successful and unsuccessful hunts for all prey. When the data for large and small prey are separated, unsuccessful hunts for large prey take place over significantly longer distances than successful ones. However, hunts not ending in a kill are not significantly longer than those ending in a kill when hunting small prey on a year-round basis. In the hot season, unsuccessful hunts take place over significantly longer distances than successful ones. This is true for all prey combined and for both large and small prey independently. In the cold season, the hunting distances for successful and unsuccessful hunts were similar. This is true for hunts for all prey combined and for hunts for large and small prey independently (Table 2).

On a year-round basis, both successful and unsuccessful hunts for large prey take place over significantly longer distances than hunts for small prey. There was no significant difference between the distances over which successful hunts for either large or small prey took place in either the hot or cold season. However, in both the hot and the cold seasons, unsuccessful hunts for large prey took place over significantly longer distances than unsuccessful ones for small prey (Table 3).

The hunting technique of the caracals in the Kgalagadi Transfrontier Park is highly varied. In the present study, 43 different behavioural sequences were identified as part of hunting. The traditional stalk, chase and kill sequence that has been described by Schaller (1972), was only observed once during this study (Table 4). The most frequently used hunting tactic involved a sequence of behaviours that began with a crouch, to be followed by a powerful take-off that culminated in a chase. Of the 327 observed hunts, 146 (44.6 %) began with this behavioural sequence. Another 73 (22.3 %) hunts started with a take-off followed by a chase. Only 31 (9.5 %) of the hunting sequences began with a stalk and 11 (3.4%) began and ended with

Table 3: *The mean hunting distances (m), comparing the distances of caracals hunting large and small prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Season	Hunting success	Mean		Standard error		t-value	*P*-value	Degrees of freedom
		Large prey	Small prey	Large prey	Small prey			
Year-round	Yes	23.90	8.90	6.50	2.20	2.20	0.0400	20.00
Year-round	No	63.70	11.80	10.90	0.86	4.80	< 0.0001	54.00
Hot season	Yes	6.80	7.50	1.80	1.50	-0.31	0.7600	9.00
Hot season	No	63.40	11.50	16.50	1.20	3.14	0.0040	25.00
Cold season	Yes	30.90	10.90	8.20	5.10	2.06	0.0550	16.00
Cold season	No	64.00	12.20	14.20	1.30	3.56	0.0010	27.00

a pounce with no other preliminary behaviour. Five (1.5 %) of the hunts began with a crouch, followed directly by a pounce and four (1.2 %) of the hunts began with a caracal crawling to begin the hunting sequence (Table 4).

The number of behavioural components that form a hunt is highly variable. A hunt could also consist of only one behavioural component. The highest number of consecutive distinct behavioural components that comprised a single hunt was 11. The most successful strategy seems to be a sequence of five behavioural components starting with a stalk, followed by a crouch, a take-off, a chase and a pounce. This sequence had a success rate of 66.7 %. A sequence of four behavioural components starting with a crouch, followed by a take-off, a chase and a pounce resulted in 10 kills in 19 attempts at a success rate of 52.6 %. On three occasions a single repetition of a distinct behavioural sequence resulted in a kill. In these cases no success ratio was calculated because of the inadequate sample sizes involved. The least successful strategy involved three behavioural components that had a success rate of 2.2 % (Table 4).

Hypothetically, the behavioural sequence that is most likely to end in a kill is the crawl - stalk - crouch - take-off - chase - pounce sequence. However, no behaviour sequence starting with a crawl was successful. When plotted along a gradient from failure to success, the crawl and stalk components are orientated closer to failure on a gradient of success. The crouch, take-off and chase components, however, are orientated more centrally between success and failure on the gradient, while the pounce is orientated closest to the kill because it usually preceded the kill immediately. The behavioural components that are most closely associated with one another are the take-off and chase. The crouch behaviour is also associated with the take-off and chase, but not as closely related as are the take-off and chase with one another.

e 4: *Hunting sequences of caracals in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Number of components	Number of repetitions	Sequence of components*	Number of successful hunts	Number of unsuccessful hunts	Percentage hunting success
1	9	6	3	6	33.3
1	29	5	3	26	10.3
1	6	2	1	5	16.7
1	7	3	0	7	0.0
1	5	4	1	4	20.0
2	1	6-6	1	0	100.0
2	1	6-5	1	0	100.0
2	1	5-6	1	0	100.0
2	4	2-6	3	1	75.0
2	1	2-5	0	1	0.0
2	1	2-3	0	1	0.0
2	4	3-6	0	4	0.0
2	1	3-3	0	1	0.0
2	7	3-4	0	7	0.0
2	1	3-1	0	1	0.0
2	1	4-6	0	1	0.0
2	61	4-5	4	57	6.6
2	1	1-1	0	1	0.0
3	1	2-4-6	0	1	0.0
3	1	2-4-5	0	1	0.0
3	126	3-4-5	1	125	0.8
3	1	3-4-6	0	1	0.0
3	1	3-1-3	0	1	0.0
3	5	4-5-6	2	3	40.0
3	1	4-5-5	0	1	0.0
3	1	1-4-5	0	1	0.0
4	1	2-3-4-5	0	1	0.0
4	8	2-3-4-5	0	8	0.0
4	1	3-6-4-5	0	1	0.0
4	2	3-2-4-5	0	2	0.0
4	19	3-4-5-6	10	9	52.6
4	1	3-4-5-4	0	1	0.0
4	1	4-5-4-5	0	1	0.0
5	3	2-3-4-5-6	2	1	66.7
5	1	3-4-5-4-5	0	1	0.0
5	4	4-5-3-4-5	0	4	0.0
6	1	2-3-3-3-4-5	0	1	0.0
6	1	3-3-4-5-4-5	0	1	0.0
6	1	4-5-2-3-4-5	0	1	0.0
7	1	2-2-2-3-4-5-6	0	1	0.0
7	1	1-1-3-4-5-4-5	0	1	0.0
8	1	1-2-2-2-3-4-5-6	0	1	0.0
10	1	3-4-5-6-3-4-5-3-4-5	0	1	0.0
11	1	2-3-4-5-4-5-4-5-3-4-5	0	1	0.0

*1: crawl 2: stalk 3: crouch 4: take-off 5: chase 6: pounce

Stalks

A stalk is a behavioural component that is found in a number of hunting sequences. On 39 occasions stalking was observed in relation to hunting. During a specific hunt, a caracal can stalk more than once, and on two occasions, stalking occurred three times during a single hunt. In all the other instances, stalking was recorded only once in a specific hunting sequence. Stalking was a component of seven (21.2 %) of 33 hunts that ended in a kill. Moreover, successful hunts never included more than one stalking sequence. Of the 39 stalks that were recorded, 13 were recorded in the cold season and 26 in the hot season. Stalking took place in 34 (10.4 %) of all 327 hunts (Table 4).

Caracals stalk their prey over variable distances. They also stalk them over significantly longer distances in the cold season than in the hot one (Fischer's exact test = 0.023, df = 1, $P \leq 0.05$). In the hot season the longest stalking distance was 27 m, but in the cold season it was 61 m. The mean stalking distance in the cold season was 12.9 m (SE = 5.5 m; range = 3 – 61 m) and 4.2 m (SE = 1.1 m; range = 1 – 27 m) in the hot season. Caracals stalk small prey significantly more often than large prey ($\chi^2 = 5.56$, df = 1, $P < 0.05$) (Table 5).

Caracals do not stalk large prey over significantly longer distances than small prey or vice versa, either on a year-round (t = 1.21, df = 22, $P > 0.05$) or a seasonal basis (hot season: t = 2.13, df = 6, $P > 0.05$; cold season: t = -0.24, df = 13, $P > 0.05$) (Table 5).

Chase

The chase is an integral component of most hunts, and during the present study 293 chases were recorded. Although chases were not recorded in every hunting

Table 5: *The mean ± standard error of the stalking distances (m) of caracals when hunting different types of prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002*

Prey	Season	Stalks ending in kills			Stalks not ending in kills			All stalks			
		Number	Mean	Standard error	Number	Mean	Standard error	Maximum distance	Minimum distance	Mean	Standard error
Bat-eared fox	Cold	1	10.0	0.0	1	2.5	0.0	10	2.5	6.3	3.8
	Hot	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
Brant's whistling rat	Cold	0	0.0	0.0	1	4.0	0.0	4	4.0	4.0	0.0
	Hot	2	3.0	0.0	5	2.5	0.8	5	1.0	4.3	2.2
Cape fox	Cold	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
	Hot	0	0.0	0.0	3	18.0	4.5	27	13.0	18.0	4.5
Kori bustard	Cold	2	31.0	29.1	0	0.0	0.0	61	3.0	31.0	29.1
	Hot	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
Scrub hare	Cold	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
	Hot	0	0.0	0.0	1	2.0	0.0	2	2.0	2.0	0.0
Springhare	Cold	0	0.0	0.0	3	3.8	0.6	5	3.0	3.8	0.6
	Hot	0	0.0	0.0	2	2.5	0.5	3	2.0	2.5	0.5
Steenbok	Cold	1	6.0	0.0	0	0.0	0.0	6	6.0	6.0	0.0
	Hot	0	0.0	0.0	1	7.0	0.0	7	7.0	7.0	0.0
Striped polecat	Cold	1	39.0	0.0	0	0.0	0.0	39	39.0	39.0	0.0
	Hot	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0
Unidentifiable	Cold	0	0.0	0.0	3	19.0	15.8	50	1.0	19.0	15.8
	Hot	0	0.0	0.0	14	2.2	0.2	3	1.0	2.2	0.2
All small prey	Hot	2	3.0	0.0	19	2.3	0.3	5	1.0	2.3	0.2
	Cold	1	39.0	0.0	6	10.2	8.2	61	2.5	12.9	7.6
	Both	3	15.0	12.2	25	4.2	1.9	61	1.0	5.3	2.1
All large prey	Hot	0	0.0	0.0	7	9.7	3.5	27	2.0	9.7	3.5
	Cold	4	20.0	13.8	4	3.5	0.6	61	2.5	11.8	7.2
	Both	4	20.0	13.8	11	7.5	2.4	61	2.0	10.8	3.9
All prey	Cold	5	19.1	11.5	8	9.4	5.9	61	3.0	14.9	5.7
	Hot	2	3.0	0.0	26	4.3	1.1	27	1.0	4.2	1.0
	Both	7	17.9	8.8	34	5.2	1.6	61	1.0	7.2	2.0

sequence, at least one chase was recorded in 270 (82.6 %) of the 327 hunts. In 10 (3.1 %) of 327 hunts more than one chase was recorded per hunt. The distances over which caracals chased their prey varied greatly, and there was no significant seasonal difference in these distances ($t = -0.94$, $df = 286$, $P > 0.05$). The mean chase distances for large and small prey and for individual prey species appear in Table 6. Of the 293 chases, 134 (45.7 %) were recorded in the cold season. There was no significant preference for chasing small prey rather than large prey ($\chi^2 = 2.9$, $df = 1$, $P > 0.05$).

Caracals chased large prey over significantly longer distances than small ones, both year- round ($t = 4.83$, $df = 66$, $P < 0.05$) and seasonally (hot season: $t = 2.97$, $df = 28$, $P < 0.05$; cold season: $t = 3.80$, $df = 37$, $P < 0.05$). The mean chase distances reflect this trend (Table 6).

On a year-round basis the distances of chases ending in kills and those that did not do so for the combined prey data set were similar. However, when the prey data are divided into small and large prey, chases ending in kills take place over significantly shorter distances than unsuccessful ones. In the cold season there is no significant difference between the distances of successful and unsuccessful chases, but in the hot season the chases ending in kills are significantly shorter than unsuccessful ones (Table 2).

Pouncing

During the present study pouncing was observed on 58 occasions occurring in 55 (16.8 %) of the observed hunts. On two occasions more than one pounce was recorded in a single hunt. Caracals pounced in similar frequencies when trying to catch small and large prey, doing so in 15.9 % of their attempts to catch small prey

Table 6: *The chase distances (m) of caracals when hunting different types of prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002*

Prey	Season	All chases				Chases ending in kills			Chases not ending in kills		
		Mean	Standard error	Maximum	Minimum	Number	Mean	Standard error	Number	Mean	Standard error
African wild cat	Hot	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cold	35.00	32.50	38.00	32.00	1.00	32.00	0.00	1.00	38.00	0.00
Bat-eared fox	Hot	24.50	17.80	56.00	5.50	1.00	5.50	0.00	2.00	34.00	22.20
	Cold	47.50	18.90	97.00	12.00	0.00	0.00	0.00	4.00	47.50	18.90
Black-backed jackal	Hot	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cold	302.00	0.00	302.00	302.00	0.00	0.00	0.00	1.00	302.00	0.00
Brant's whistling rat	Hot	7.00	1.20	18.00	1.00	5.00	7.60	1.60	12.00	6.75	1.50
	Cold	9.83	3.20	23.00	3.00	2.00	11.50	1.50	4.00	9.00	4.80
Cape fox	Hot	82.63	45.60	379.00	4.00	2.00	8.50	3.60	6.00	107.33	58.70
	Cold	318.00	0.00	318.00	318.00	0.00	0.00	0.00	1.00	318.00	0.00
Ground squirrel	Hot	22.50	18.70	41.00	4.00	0.00	0.00	0.00	2.00	22.50	18.70
	Cold	15.00	10.10	25.00	5.00	0.00	0.00	0.00	2.00	15.00	10.10
Scrub hare	Hot	63.00	24.80	125.00	16.00	0.00	0.00	0.00	4.00	63.00	24.80
	Cold	60.00	15.00	122.00	0.50	0.00	0.00	0.00	8.00	60.00	14.96
Springhare	Hot	51.50	19.20	181.00	4.00	1.00	4.00	0.00	9.00	56.78	20.90
	Cold	43.13	9.50	111.00	12.00	1.00	107.00	0.00	11.00	37.32	8.50
Steenbok	Hot	22.80	18.70	64.00	9.00	0.00	0.00	0.00	3.00	22.75	18.70
	Cold	17.50	2.50	20.00	15.00	0.00	0.00	0.00	2.00	17.50	2.50
Unidetifiable	Hot	12.53	1.10	52.00	1.00	4.00	3.50	1.90	101.00	12.89	1.21
	Cold	12.93	1.10	50.00	2.00	2.00	2.70	0.80	94.00	13.14	1.10
Yellow mongoose	Hot	1.00	0.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00
	Cold	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
All small prey	Hot	19.76	3.40	59.00	1.00	10.00	5.30	1.30	121.00	12.48	1.10
	Cold	12.67	1.00	50.00	2.00	4.00	7.13	2.60	99.00	12.89	1.10
	Both	12.30	0.70	59.00	1.00	14.00	5.80	1.20	220.00	12.60	0.80
All large prey	Hot	55.22	14.50	379.00	4.00	4.00	6.63	1.80	25.00	63.00	16.40
	Cold	56.01	11.30	318.00	8.50	8.00	7.13	1.90	29.00	62.02	14.00
	Both	55.70	9.00	379.00	4.00	12.00	25.00	7.80	54.00	62.50	10.70
All prey	Hot	19.78	3.20	379.00	1.00	14.00	5.68	1.10	133.00	21.13	3.50
	Cold	24.13	3.60	318.00	2.00	3.00	25.21	16.10	127.00	24.02	3.70
	Both	21.81	2.40	379.00	1.00	17.00	22.48	10.00	260.00	14.69	1.30

and 18.9 % of those to catch large prey. In the hot season 37 pounces were recorded as opposed to 21 in the cold season (Table 7).

Pouncing distances did not differ seasonally (t = 0.84, df = 32, *P* > 0.05) nor did they differ when hunting large or small prey year-round (t = 1.31, df = 20, *P* > 0.05) or seasonally (hot season: t = 1.33, df = 7, *P* > 0.05; cold season: t = 0.96, df = 14, *P* > 0.05) (Table 7).

Kills

Of the 327 hunts observed, 33 (10.1 %) ended in a kill. However, the method of killing could only be identified in those cases where the prey remains were found. It was assumed that for smaller prey, a throat-bite in conjunction with claw-raking was used, as was described by Leyhausen (1979). The only visual evidence that a small prey item had been killed was the visceral remains (n = 19 kills) that the caracals removed before eating the prey. In one case a caracal consumed a Brant's whistling rat *Parotomys brantsii* completely without evicerating it, and its identity was only confirmed because the caracal regurgitated the entire rat 10 m from where it had killed it. Caracals therefore do not always eviscerate smaller prey. In two cases where a caracal killed an African wild cat *Felis sylvestris*, two sets of teeth puncture marks were visible on each carcass, one set at the nape of the neck and one on the throat. The same killing method was used by caracals when killing two bat-eared foxes *Otocyon megalotis*, a scrub hare *Lepus saxatilis*, two springhares *Pedetes capensis*, a yellow mongoose *Cynictis penicillata*, two striped polecats *Ictonyx striatus*, a steenbok *Raphicerus campestris* and two Cape foxes *Vulpes chama*. On one occasion a caracal killed a Cape fox by biting it on the head, penetrating the skull with its canines. A caracal also killed two kori bustards *Ardeotis kori* by severing the spinal cord of each with a nape bite.

Table 7: *The distances (m) from which that caracals pounced on prey in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Prey animal	Season	Number of pounces			Distance of all pounces				Distance of pounces ending in kills			
		All	Ending in Kills	Not ending in kills	Maximum	Minimum	Mean	Standard error	Maximum	Minimum	Mean	Standard error
African wild cat	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	1	1	0	2.0	2.0	2.0	0.0	2.0	2.0	0.0	0.0
Bat-eared fox	Hot	1	1	0	2.0	2.0	2.0	0.0	2.0	2.0	0.0	0.0
	Cold	1	1	0	1.0	1.0	1.0	0.0	1.0	1.0	0.0	0.0
Brant's whistling rat	Hot	6	4	2	2.0	1.0	1.5	0.4	2.0	1.0	1.1	0.3
	Cold	3	2	1	2.0	1.0	1.7	0.4	2.0	1.5	1.8	0.2
Cape fox	Hot	2	1	1	2.0	2.0	2.0	0.0	2.0	2.0	2.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kori bustard	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	2	2	0	2.5	2.0	2.3	0.3	2.5	2.0	2.3	0.3
Scrub hare	Hot	2	1	1	3.0	1.0	2.0	1.4	1.0	1.0	1.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Springhare	Hot	1	1	0	2.5	2.5	2.5	0.0	2.5	2.5	2.5	0.0
	Cold	2	1	1	3.0	2.0	2.5	0.7	3.0	3.0	3.0	0.0
Steenbok	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	1	1	0	2.0	2.0	2.0	0.0	2.0	2.0	2.0	0.0
Striped polecat	Hot	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cold	2	2	0	2.0	1.0	1.5	0.5	2.0	1.0	1.5	0.5
Unidentifiable	Hot	23	4	19	3.0	1.0	1.7	0.1	2.0	1.0	1.4	0.3
	Cold	8	2	6	3.0	1.0	1.3	0.4	1.0	1.0	1.0	0.0
Yellow mongoose	Hot	2	2	0	3.0	2.0	2.5	0.5	3.0	2.0	2.5	0.5
	Cold	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
All small prey	Hot	31	10	21	3.0	1.0	1.7	0.1	3.0	1.0	1.6	0.2
	Cold	12	6	7	3.0	1.0	1.4	0.3	2.0	1.0	1.5	0.2
	Both	44	16	28	3.0	1.0	1.6	0.1	3.0	1.0	1.5	0.2
All large prey	Hot	6	4	2	3.0	1.0	2.1	0.3	3.0	2.0	2.5	0.4
	Cold	8	7	1	3.0	1.0	1.8	0.3	2.5	1.0	1.9	0.2
	Both	14	11	3	3.0	1.0	1.9	0.2	3.0	1.0	1.8	0.2
All prey	Hot	37	14	23	3.0	1.0	1.8	0.1	3.0	1.0	1.7	0.2
	Cold	19	8	11	3.0	1.0	1.7	0.2	3.0	1.0	1.8	0.2
	Both	56	26	30	3.0	1.0	1.7	0.1	3.0	1.0	1.7	0.1

Table 7: *Continued*

Prey animal	Season	Number of pounces			Distance of pounces not ending in kills			
		All	Ending in Kills	Not ending in kills	Maximum	Minimum	Mean	Standard error
African wild cat	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	1	1	0	0.0	0.0	0.0	0.0
Bat-eared fox	Hot	1	1	0	0.0	0.0	0.0	0.0
	Cold	1	1	0	0.0	0.0	0.0	0.0
Brants whistling rat	Hot	6	4	2	2.0	1.5	1.8	0.3
	Cold	3	2	1	2.0	2.0	2.0	0.0
Cape fox	Hot	2	1	1	2.0	2.0	2.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0
Kori bustard	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	2	2	0	0.0	0.0	0.0	0.0
Scrub hare	Hot	2	1	1	3.0	3.0	3.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0
Springhare	Hot	1	1	0	0.0	0.0	0.0	0.0
	Cold	2	1	1	2.0	2.0	2.0	0.0
Steenbok	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	1	1	0	0.0	0.0	0.0	0.0
Striped polecat	Hot	0	0	0	0.0	0.0	0.0	0.0
	Cold	2	2	0	0.0	0.0	0.0	0.0
Unidentifiable	Hot	23	4	19	3.0	1.0	1.7	0.2
	Cold	8	2	6	3.0	1.0	2.0	0.4
Yellow mongoose	Hot	2	2	0	0.0	0.0	0.0	0.0
	Cold	0	0	0	0.0	0.0	0.0	0.0
All small prey	Hot	31	10	21	3.0	1.0	1.7	0.1
	Cold	12	6	7	3.0	1.0	1.8	0.3
	Both	44	16	28	3.0	1.0	1.7	0.1
All large prey	Hot	6	4	2	2.0	2.0	2.0	0.0
	Cold	8	7	1	3.0	3.0	3.0	0.0
	Both	14	11	3	3.0	1.0	2.3	0.4
All prey	Hot	37	14	23	3.0	1.0	1.8	0.1
	Cold	19	8	11	3.0	1.0	1.9	0.2
	Both	56	26	30	3.0	1.0	1.8	0.1

Caracals often cached the carcasses of large prey. After the caracals had killed the kori bustards, bat-eared foxes, scrub hare and the steenbok, the prey were cached under a dense bush. In all these cases the caracal came back to where it had cached its kill to feed even after it had been disturbed, by the tracking.

DISCUSSION

Hunting variation

All hunts consist of a sequence of behavioural components that aim at a kill. These behavioural components do not necessarily follow a specific sequence. Traditionally, hunts by large wild cats are regarded to consist of either a combination of a stalk, a chase and a kill (Schaller 1972, Eltringham 1979, Bothma & Le Riche 1984). Caro (1994) extended this behavioural combination in cheetahs *Acinonyx jubatus* to include trotting, crouching and rushing. Because of the further inclusion of pouncing, take-off and crouching in the combination of behavioural components of hunting used here, the variability of the hunting sequences is high when compared with other types of cat. A caracal's hunting sequence does not necessarily consist of the repetition of any one behavioural sequence. The potential for variation of a behavioural sequence that could consist of six different behavioural components and any number of repetitions of these components, suggests a huge potential for adaptation of the hunting strategy of a caracal to specific situations. This potential supports the conclusion that caracals also use an adaptable hunting strategy, as was found by Schaller (1972) and Mc Bride (1990) for lions, and for leopards *Panthera pardus* by Bothma & Le Riche (1989). Mc Bride (1990) goes so far as to suggest that the hunting tactics of lions are so varied that they defy classification.

Moolman (1986) identified two distinct hunting strategies that were displayed by captive caracals in the Mountain Zebra National Park. The most frequently observed strategy involved the caracal stalking the prey to within 5 m, and then chasing it.

Grobler (1981) observed the same stalking technique in a captive caracal. The second, and less frequently observed, hunting strategy involved the caracal lying hidden in ambush of the prey, and then chasing it down from behind. In the Kgalagadi Transfrontier Park, the most frequently applied hunting strategy was an adaptation of the ambushing technique that was described above, and 44.5 % of the hunts that were recorded involved a caracal waiting in a crouched position in ambush and then chasing its prey. The stalking strategy was used less frequently than was reported by Moolman (1986).

Unlike the hunting behaviour of lions as reported by Schaller (1972) and Elliot *et al.* (1976), stalking does not appear to be the most important component of the hunting strategy of caracals in the Kgalagadi Transfrontier Park. Stalking was only used in 10.1 % of the observed hunts, and of these only 21.2 % ended in kills. This success rate is even less than that reported by Bothma & Le Riche (1984) for male leopards and for females without cubs. There does not seem to be any difference between the distances stalked when hunting large or small prey, but there is a trend towards stalking all prey over longer distances in the cold season when compared with the hot season. This may be a response by caracals to optimise their chances of killing prey in times when prey availability is more limiting (Nel *et al.* 1984, Begg 2001), and when energy conservation may be more important. Caracals were never observed to stalk either specific prey or any prey size group over excessively long distances. There is therefore no evidence of caracals using optimal positioning for specific prey that are difficult to hunt in the manner that Bothma & Le Riche (1989) described for some prey of leopards.

Caracals expend proportionally more energy on failed hunts in the hot season than in the cold season (Table 2). This suggests that in the hot season there is sufficient prey available to allow caracals to expend energy on extravagantly long hunts in the hope of killing large prey. This is surprising because the hot season is a time of relatively high prey abundance in the Kgalagadi Transfrontier Park (Begg 2001). Under these conditions it was expected that caracals would abandon long hunts in the hot season because there are enough other hunting opportunities, and theoretically excessive energy expenditure should be avoided.

It appears that although the available food resource is more limiting for caracals in the cold than the hot season, the seasonal energy expended whilst chasing prey is higher in the cold than in the hot season, based on mean hunting distances (Table 2). This is not surprising because it is expected that caracals would expend more energy in attempting to kill prey in the cold than in the hot season because of the lower prey abundance. It was also expected that the higher maintenance energy requirements of a caracal in the cold season, would induce them to expend more energy on attempts at killing large prey that would provide greater energetic gains per kill, especially in the cold season.

Caracals in the Kgalagadi Transfrontier Park seem to expend considerable amounts of energy on unsuccessful hunts of large prey, especially in the hot season. This situation is similar to that found by Mills (1990) for spotted hyaenas *Crocuta crocuta* in the Kalahari. Bothma & Le Riche (1984) reported that leopards in the Kalahari chase large prey more frequently than small ones, but there is no evidence caracals doing this.

Caracals chase large prey over longer distances than small prey in both seasons, as was also observed for leopards in the Kalahari (Bothma & Le Riche 1984). This supports the optimal foraging theory that stipulates that energy expenditure in acquiring a particular type of prey should be proportional to the expected energy gained from that prey item (Begon *et al.* 1990, Smith 1990, Brewer 1994). It also indicates an adaptation in hunting behaviour when hunting large prey. The importance of the potential energetic gain from hunting large prey is highlighted further by the fact that caracals tend to chase large prey over relatively long distances before giving up the chase, especially in the hot season.

It appears that caracals often surprise their prey, in a similar manner to that described by Bothma & Le Riche (1984) for leopards and Geertsema (1985) for serval, because only 9.4 % of all chases were preceded by stalks in which caracals could be regarded to be premeditating a potential hunting opportunity.

Hunting success

Burton (1962) contended that predators are unlikely to succeed in killing more than 50.0 % of the prey animals that they chase. The results of the present study support this conclusion. The overall hunting success rate of caracals in the Kgalagadi Transfrontier Park was 10.1 %. This is considerably lower than the success rate recorded for most other predators in this area. Bothma and Le Riche (1986) found that male leopards in the Kalahari kill 18.5 % of the animals that they hunted, while females killed 21.8 % of the animals that they hunted, for a mean hunting success rate of 20.2 % for both sexes. Eloff (1984) found that lions in the Kalahari had a hunting success of 38.5 %. Mills (1990) found that spotted hyaenas hunt with a success rate that varies between types of prey, as did Bothma and Coertze (2004) for leopards in the Kalahari.

Schaller (1972) and Kruuk (1986) suggested that hunting success in lions was reliant on sufficient cover. Lions tend to be most successful in areas of dense cover where they can stalk to within a close striking distance of the prey. Bothma *et al.* (1997) suggest that the ability of a male leopard to stalk certain prey is less than that of a female because of size differences and the general lack of large cover in the southern Kalahari. This is unlikely to be the case for caracals because they are small in stature and there is sufficient vegetation of the required height to ensure that they can stalk efficiently. It is therefore suspected that the low hunting success of caracals in the Kgalagadi Transfrontier Park is due to factors other than a lack of cover.

Caracals are more successful when hunting large than small prey, killing 20.2 % of the large prey that they attempt to hunt. This rate is similar to the hunting success of leopards in the same region (Bothma & Le Riche 1984). The low hunting success of caracals when hunting small prey may in part be due to the strict protocol that was used in the present study for the verification of a kill. In areas such as the Kgalagadi Transfrontier Park, where there is a low abundance of prey, the hunting efficiency of a leopard is influenced by the availability of its prey (Bothma & Le Riche 1986). It was expected that a similar hunting success for small prey would be recorded as that for other predators that utilise small mammals as a food resource elsewhere. However, Geertsema (1985) found that servals in the prey-rich Ngorongoro Crater in Tanzania killed 48.6 % of the small mammals that they hunted. It is probable that prey distribution and abundance limit the hunting success of caracals in the Kalahari region. This would require the caracals in the Kgalagadi Transfrontier Park to hunt more often than in prey-rich environments to satisfy their energy requirements. In the semi–arid southern Kalahari it therefore seems that a high level of energy expenditure is required by caracals per unit of energy gained.

Hunting model

A hunting model was developed here, based on the differential likelihood of a particular behavioural component resulting in a kill. It was hypothesised that behavioural components would have to occur in a specific sequence for the best hunting success rate. The gradient of success from no likelihood of a kill (failure) to high likelihood of a kill was plotted, as was the behavioural components that are associated with hunting.

Of the behavioural components of hunting, the crawl was least likely to be associated with a kill, and most often led to the failure of a hunt. The stalk was less likely to end in failure. However, the crawl and stalk components were not closely associated with one another. The take-off and chase components were closely and logically associated, no matter what behavioural component preceded the chase. This is logical because for a chase to develop from any other component of behaviour it has to be preceded by a take-off. The crouch was associated with both the take-off and chase components but not as closely as was the take-off with the chase. The crouch, take-off and chase components were all positioned centrally along a gradient from success to failure, suggesting that they did not dictate either the success or the failure of a hunt. The pounce was oriented close to the kill on the gradient because it often is part of the conclusion of a successful hunt.

It was indicated previously that the most successful hunting sequences contained five behavioural components, but any given sequence could repeatedly contain various behavioural components. Using the sequences that were modelled here, a commonly used five-component behavioural sequence would start with a stalk, followed by a crouch, then by a take-off, then by a chase and finally by a pounce. This was found to be the most successful hunting sequence that is used by caracals in the Kgalagadi Transfrontier Park (Table 4). The model does not dictate the number of behavioural components or the number of repetitions of a component within a sequence, but rather indicates that a certain sequence of behavioural components is most likely to result in a kill. Therefore the hunt does not have to begin with a crawl, and all the other behavioural components do not have to follow in a specific sequence to end in a kill. A hunting sequence could just as easily begin with a crouch and progress directly to a pounce without a chase. However, the model does confirm that a logical sequence of any number of goal-orientated behavioural components has the best chance of ending in a kill.

Killing prey

Caracals in the Kgalagadi Transfrontier Park kill their prey in a similar way as elsewhere. When killing large prey, caracals tend to subdue the prey first by capturing it and then applying a nape bite that is not fatal. A final throat bite is then used to suffocate the prey. This agrees with the killing method as described by Grobler (1981), Stuart (1981, 1982), Moolman (1986) and Stuart & Hickman (1991) for caracals elsewhere. In doing so, caracals kill their prey in much the same way as the other larger felids of Africa (Estes 1995). Pringle & Pringle (1978) and Skinner (1979) stated that caracals can kill large prey with a nape bite, but the only evidence of it happening in the Kgalagadi Transfrontier Park was when two kori bustards were killed in this way. These birds were each despatched by a bite to the nape of the neck that appeared to sever the spinal cord. This is much more easy to do with a bird with a slender and fragile neck than with a mammal, and could be a further indication of prey-specific hunting behaviour.

The method of killing a small prey such as a rodent could not be examined in the present study because of the method of observation. However, it is likely that caracals in the Kgalagadi Transfrontier Park use the same methods to kill small prey as were reported in other caracal studies (Grobler 1981, Stuart 1981, 1982, Moolman 1986, Stuart & Hickman 1991).

Pringle and Pringle (1978) indicated that caracals do not usually return to their kills for a second feeding bout once they have moved off or have been disturbed, but Grobler (1981), Stuart (1982), Moolman (1986) and Stuart & Hickman (1991) all found that caracals would return to a kill, provided that it was still fresh. In the present study the caracals also returned to fresh kills of large prey to feed again. This may be especially important in terms of energy balance in prey-poor areas where the use of the prey resource must be optimised (Bothma & Le Riche 1989). Small prey was usually consumed too quickly and completely to allow a second feeding bout. Even in areas in the vicinity of the Namibian border, where the caracals are often persecuted by farmers, they regularly returned to fresh kills to feed again after having been disturbed.

Caracals in the present study regularly cached remains of 42 % of larger kills under dense bushes such as *Boscia albitrunca* and *Acacia mellifera*, as was also described for leopards by Bothma & Le Riche (1986). This supports the observations of Grobler (1981) and Stuart (1982) that caracals do cache their kills. Mills (pers. comm.)[2] also observed caracals to cache prey remains, and on one occasion he observed that a caracal carried the carcass of a springhare up a tree. However, no evidence of caracals caching kills in trees was found in the present study, and it seems to be a rare event. When it does happen, it is likely to be in response to an immediate threat from a competing predator for the kill. In areas where the density of predators is high and the likelihood of interspecific competition is higher than in the Kgalagadi Transfrontier Park, leopards also take their prey into trees more frequently than in the more prey-poor Kalahari (Bothma & Le Riche 1984).

On a number of occasions the caracals carried their kills from the killing site to areas of more dense cover. The distance over which the caracals did so was highly variable, with the longest distance being a scrub hare that was carried for 160 m. The behaviour of carrying kills has also been recorded by Grobler (1981) for

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[2] Dr. M.G.L. Mills. Specialist Scientist, Kruger National Park, Private bag X402, Skukuza 1350, South Africa.

caracals. It probably happens to prevent other predators, including raptors, from spotting and competing for the kills.

CONCLUSIONS

Although a hunt is often interpreted as a single activity for African predators generally, it is not a single behaviour in a caracal. Rather it is a sequence of behavioural components that are adapted to the prevailing conditions and the prey target. There is no strict sequence of behavioural components that comprises a hunt. Hunting behaviour in a caracal is therefore a fluid situation without a pre-ordained sequence. It is a constant adaptation to a specific situation and type of prey, with the sequence developing as a specific hunt unfolds. As for other felids in the Kgalagadi Transfrontier Park, opportunism is an important component of hunting. In the caracal, hunting behaviour is therefore both flexible and adaptable.

When caracals hunt large prey, they do so with a greater intensity and expend more energy in the hunting process than when hunting small prey. The relatively high hunting success rate of caracals when hunting large prey might justify the increased effort because of the greater amount of energy gained, although more energy is expended when hunting large prey than small ones as is revealed by the longer mean hunt distances for the large prey. Moreover, more effort is required to overpower large prey than small ones. There also is an increased likelihood of a caracal being injured when killing a large prey.

The sequence of behavioural components that forms a hunt, varies. Yet, the hunting behavioural components follow a logical order, ending in a kill, although not all the components appear in all the hunts. A hunting model for a caracal therefore should rather emphasizes the sequence in which the various behavioural components must occur for a kill, and not the full complement of each sequence. Nevertheless, there is an ideal sequence of behavioural components for the best kill rate. The overall killing technique of caracals when hunting large prey supports what has been found in other studies elsewhere.

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CHAPTER 8

PREY SELECTION BY CARACAL IN THE KGALAGADI TRANSFRONTIER PARK

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ABSTRACT

In the Kgalagadi Transfrontier Park, 116 caracal *Caracal caracal* scat samples were collected and 327 attempted hunts were reconstructed from spoor-tracking. The data were analysed to establish the prey-use of caracals in the Kgalagadi Transfrontier Park, and to study the extent to which caracals use small stock by moving into the adjacent farming land in Namibia. It was found that the primary prey resource was small mammals, the vast majority of which were rodents, including springhare *Pedetes capensis*. Larger prey animals included steenbok *Raphicerus campestris* and smaller carnivores up to the size of a black-backed jackal *Canis mesomelas*. Birds were an abundant prey resource, especially the larger ground-roosting species. Invertebrate remains were found in a large proportion of the scats, indicating that they are commonly used as a source of food. Domestic livestock remains were identified in eight of the scat samples and the temporal distribution of these indicates an increased use of domestic livestock by caracals in the cold season.

Keywords: Caracal, Felidae, scat analysis, spoor-tracking, small mammals, livestock

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INTRODUCTION

The survival of any predator is directly related to the quality and quantity of its diet. Predatory strategies have evolved to maximise the nutrient intake within a certain habitat. For this reason prey selection determines the spacing patterns and structure of predator social patterns (Sunquist & Sunquist 1989). Of the terrestrial carnivore families, the Felidae are the least dependent on vegetable and invertebrate food sources. Felids also tend to feed on prey species commensurate with their own body size. Despite being highly specialised predators, felids display certain levels of intra-specific prey preference that could include the habitual depredation on domestic livestock (Kruuk 1982).

The caracal *Caracal caracal* is known to be a predator of small domestic livestock throughout southern Africa (Pringle & Pringle 1978, Grobler 1981, Roberts 1986, Stuart 1986, Palmer & Fairall 1988, Stuart & Wilson 1988, Stuart & Hickman 1991). Responses to questionnaires conducted during this study indicate that this is the case in the Kalahari region, especially in areas where domestic livestock is farmed on the border of proclaimed conservation areas. One such area of conflict is the South African border with Namibia, where stock farms border on the Kgalagadi Transfrontier Park. Although widely condemned as a problem animal, caracals contribute to controlling populations of small mammals that eat natural forage upon which domestic livestock depend (Grobler 1981, Stuart 1982, Moolman 1986, Palmer & Fairall 1988, Stuart & Hickman 1991).

Most studies indicate that mammals contribute the primary component of the diet of caracals (Grobler 1981, Stuart 1982, Moolman 1986). In terms of absolute numbers, rodents contribute the largest percentage to this diet, but in terms of biomass domestic livestock and antelope make the greatest contribution towards the diet (Stuart 1982). In the Karoo National Park, Palmer and Fairall (1988) found that caracals killed large mammalian prey such as springbok *Antidorcas marsupialis*, grey rhebok *Pelea capreolus,* klipsringer *Oreotragus oreotragus* and mountain reedbuck *Redunca fulvorufula*. They hypothesised that this was due to a decrease in hyrax *Procavia capensis* and rodent populations as a result of drought conditions.

Aspects of caracal hunting behaviour have been discussed elsewhere (Melville unpublished data). The caracal fills the top predator niche in many areas of its range in South Africa (Estes 1991, Avenant & Nel 1998). In the Kgalagadi Transfrontier Park, however, it falls lower down the predator hierarchy. This study investigates what prey resources the caracals use, and whether they prey on small livestock that occur on farms outside the park in the vicinity of the Namibian border.

STUDY AREA

This study was conducted along the Namibian border near Mata-Mata in the southwestern portion of the Kgalagadi Transfrontier Park, in an area that extended 60 km north from the Mata-Mata rest camp to O'Kuip windmill and approximately 20 km into the interior of the Park.

The Mata-Mata area lies in the Shrubby Kalahari Dune Bushveld of the Savanna Biome (Low & Rebelo 1996). This is an arid savanna with temperatures varying from –10° C to 45° C in the shade with an annual mean rainfall of 182 mm that occurs mainly in the summer. The landscape is one of undulating dunes with sparse vegetation, and altitudes varying from 1000 to 1100 m above sea level (Low & Rebelo 1996).

The vegetation is characterised by *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca* trees, with a shrub layer of *Grewia retinervis* and *Rhus tenuinervis* and a well-developed grass layer consisting mainly of *Stipagrostis amabilis*, *Eragrostis lehmanniana*, *Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996). There is little variation in the soil forms because the area is predominantly covered by aeolian sand overlying calcrete (Low & Rebelo 1996).

METHODS

Two methods were used to assess the diet of caracals. One hundred and sixteen fresh scats were collected whilst spoor-tracking caracals. Scats were placed in paper bags, labelled and air-dried. Each scat was then sewn into a separate nylon sachet, numbered for future identification and washed until only insoluble, macroscopically identifiable material remained in each sachet (Merriwether & Johnson 1980). The individual sachets were then oven-dried (Bowland & Perrin 1993). Teeth and jaw fragments were compared with available keys or references (De Graaff 1981, Bowland & Bowland 1989). Hair was examined microscopically, including hair cuticle scale patterns and cross-section patterns (Dreyer 1966, Perrin & Campbell 1979, Keogh 1983, Keogh 1985). To ensure that no prey items were missed, imprints of a minimum of 20 hairs from each scat were made (Mukherjee *et al.* 1994).

Gelatine imprints of hair cuticle patterns were made according to the method of Dreyer (1966). The resultant impressions were compared with existing reference keys (Keogh 1985, Keogh 1983, Perrin & Campbell 1979; Dreyer 1966). Additionally imprints of reference cuticle scale patterns, of known prey, were made according to the same method. The benefit of this was that the reference samples could be viewed under the same conditions and at the same magnification as the hair samples from the scats. The prey identified in each scat, according to the cuticle patterns, were then recorded.

Cross sections of hair were made by adapting the method of Douglas (1989) for both the reference samples of hair and hair from the scats. The method involved embedding bundles of hair in a molten mixture of 25 % depilatory wax and 75 % paraffin wax (Kaunda 1998). Identification of prey was based on the appearance of a combination of hairs of various cross-sectional structures, sizes and colours rather than on the identification of single hairs (Henschel & Skinner 1990).

Results obtained through scat analysis are prone to certain biases due to the variable digestion rates and travel time of certain food items through the gut (Putman 1984, Hiscocks & Bowland 1989, Bothma & Le Riche 1994). In absence of baseline data relating faecal volume to food intake, it was decided to concentrate on the analysis of the prey diversity that caracals used (Bothma & Le Riche 1994; Putman 1984). Diagnostic parts of an individual prey might be present in more than one scat, and as a scat is seen as a sampling unit, the number of individual prey detected might exceed the number consumed (Weaver & Hoffman 1978).

Where caracal hair was found in a scat, it was assumed that its inclusion was due to grooming behaviour (Bowland & Perrin 1993) and not due to cannibalism (Stuart & Hickman 1991). As such, the occurrence of caracal hair was not regarded as food for analytical purposes, but as further substantiation of the origin of a scat (Avenant &

Nel 1997; Bowland & Perrin 1993).

The contribution of various components in the scats are presented in Table 1 where the following guidelines of Avenant & Nel (1997) were used;

1. Percentage occurrence in the scat sample:

   (Number of scats containing a particular prey item ÷ total number of scats) X 100

2. Percentage of the total number of prey units;

   {Number of incidences of a prey type ÷ (incidence of all ingesta – plant material)} X 100

3. Percentage occurrence of the total number of ingesta;

   (Number of incidences of a particular prey type ÷ incidence of all ingesta) X 100

A large proportion of the study comprised the investigation of caracal predation by tracking spoor. Experienced Kalahari San trackers assisted in following and interpreting fresh caracal tracks, over a distance of 537 km, as has been done in a number of studies in the Kalahari (Bothma & Le Riche 1984, Eloff 1984, Mills 1990, Stander *et al.* 1997). All hunting attempts interpreted as such by the tracker were recorded whether successful or not and where possible the type of prey targeted was identified. The pre-requisite for hunting success was the discovery of prey remains. This might underestimate the number of successful hunts because caracals are known to consume smaller prey entirely (Stuart & Hickman 1991). In many instances the target prey could therefore not be identified from spoor and were recorded as unknown prey. To investigate prey selection, only the data relating to identified prey that caracal targeted during hunts has been included here.

The results from spoor-tracking were compared with those compiled from scat analysis (Table 1). It was expected that the results from spoor-tracking would

Table 1: *The prey used by the caracal in the Kgalagadi Transfrontier Park from June 2000 to July 2002, based on scat analysis and evidence from hunts*

Prey	Scat analysis				Spoor tracking			
	Occurrences of prey in 116 scats	Percentage of scats in which prey occurs	Percentage contribution of prey to carcal diet relative to total number of prey	Percentage contribution of all ingesta compared with total number of ingesta	Occurrences in 327 hunts	Percentage of total hunts	Percentage of hunts with identifiable prey	Number of hunting successes
Lagomorpha								
Lepus saxatilis : scrub hare	11	9.5	4.9	3.9	14	4.3	18.9	1
Rodentia								
Pedetidae								
Pedetes capensis : springhare	43	37.1	19.1	15.2	23	7.0	31.0	2
Sciuridae								
Xerus inauris : ground squirrel	*	*	*	*	4	1.2	5.4	0
Muridae								
Parotomys brantsii : Brant's whistling rat	26	22.4	11.6	9.2	*	*	*	*
Rhabdomys pumilio : striped mouse	23	19.8	10.2	8.1	*	*	*	*
Aethomys namaquensis : Namaqua rock mouse	1	0.9	0.4	0.4	*	*	*	*
Desmodillus auricularis : short-tailed gerbil	3	2.6	1.3	1.1	*	*	*	*
Gerbillurus paeba : hairy-footed gerbil	4	3.5	1.8	1.4	*	*	*	*
Tatera brantsii : Highveld gerbil	37	31.9	16.4	13.1	*	*	*	*
Carnivora								
Felidae								
Felis silvestris : African wild cat	4	3.5	1.8	1.4	2	0.6	2.7	1
Canidae								
Canis mesomelas : black-backed jackal					1	0.3	1.4	0
Otocyon megalotis : bat-eared fox	6	5.2	2.7	2.1	8	2.4	10.8	2
Vulpes chama : Cape fox	5	4.3	2.2	1.8	10	3.1	13.5	2
Mustelidae								
Ictonyx striatus : striped polecat	3	2.6	1.3	1.1	2	0.6	2.7	1
Cynictis penicillata : yellow mongoose	6	5.2	2.7	2.1	1	0.3	1.4	1
Artiodactyla								
Raphicerus campestris : steenbok	3	2.6	1.3	1.1	7	2.1	9.5	
Ovis aries : dorper sheep	8	6.9	3.6	2.8	*	*	*	

Table 1: *Continued*

Prey	Scat analysis				Spoor tracking			
	Occurrences of prey in 116 scats	Percentage of scats in which prey occurs	Percentage contribution of prey to carcal diet relative to total number of prey	Percentage contribution of all ingesta compared with total number of ingesta	Occurrences in 327 hunts	Percentage of total hunts	Percentage of hunts with identifiable prey	Number of hunting successes
Aves								
Gruiformes								
Ardeotis kori : kori bustard	5	4.3	2.2	1.8	2	0.6	2.7	2
Eupodotis ruficrista : redcrested korhaan	3	2.6	1.3	1.1	*	*	*	*
*U*nidentified	7	6.0	3.1	2.5	*	*	*	*
Insecta								
Coleoptera : unidentified	27	23.3	12.0	9.5	*	*	*	*
Plants								
Mimosaceae								
Acacia erioloba : camel thorn	2	2.6	na	0.7	*	*	*	*
Acacia haematoxylon : grey camel thorn	1	0.9	na	0.4	*	*	*	*
Acacia meliferac : black thorn	1	0.9	na	0.4	*	*	*	*
Scrophulariaceae					*	*	*	*
Aptosimum elongatum	4	3.5	na	1.4	*	*	*	*
Cucurbitaceae					*	*	*	*
Citrullus lanatus : tsamma melon	3	2.6	na	1.1	*	*	*	*
Poaceae					*	*	*	*
Schmitia Kalihariensis	45	38.8	na	15.9	*	*	*	*
					*	*	*	*
Unidentifiable plant material	2	1.7	na	0.7	*	*	*	*
Unknown	*	*	*	*	253	77.5	na	15
Total	283	na	100	100	327	100	100	27

* no data for these categories

underestimate the contribution of small mammals to the diet of caracals (Grobler 1981).

RESULTS

Of the 37 suitable mammalian prey species available to caracals in the study area, 16 were used by them. Rodents, including the springhare *Pedetes capensis,* comprised 60.9 % of the total number of individual prey items identified. Springhares alone contributing 31.4 % of the total number of rodents identified. Carnivora constituted 10,7 % of total prey identified, whereas larger artiodactyls such as the steenbok *Raphicerus campestris* featured infrequently in the scats (Table 1).

Wool from sheep *Ovis aries* was found in eight (6.9 %) of the scats. The scats that contained wool were not limited to regions of the Kgalagadi Transfrontier Park that border directly with Namibia. Three of these scats were found in the vicinity of the border, the others were found further than 13 km from the Namibian border in the interior of the Kgalagadi Transfrontier Park. One was found approximately 23 km away from the border.

Remains of avian prey occurred in 13.0 % of the scats, the identified ones being kori bustard *Ardeotis kori* and redcrested korhaan *Eupodotis ruficrista* (Table 1). As a group, birds contributed 6.7 % to the total number of prey identified in the scats.

Of the invertebrates carapaces were found in 23.3 % of the scats (Table 1). No reptilian remains were found in any of the scat samples, neither were hunting attempts on reptiles recorded while spoor tracking.

Plant material formed 20.5 % of total number of ingested items that were identified, but probably only seeds from the tsama melon were taken in as food. Once a caracal being tracked also apparently ate a tsama. Kalahari sour grass *Schmidtia kalihariensis* leaves or seeds were found in 38.8 % of the scats (Table 1).

Tracking

During the study 327 hunts were recorded from spoor (Table 1) but in only 74 (22.6 %) of the cases could the target prey be identified. According to spoor tracking, caracals achieved a 10.1 % hunting success. Hunting attempts on two prey species not found with scat analysis, black-backed jackal *Canis mesomelas* and the ground squirrel *Xerus inauris,* were recorded while tracking, although none were successful.

From spoor-tracking, the most frequently recorded prey were springhare Cape fox *Vulpes chama* and a *Lepus* species. These animals were hunted on 23, 11 and 15 occassions respectively with two of the springhare hunts, three of the fox hunts and one of the *Lepus* species hunts being successful. Twenty-three of the 74 (31.1 %) recorded hunts, involved attempts to catch other carnivores of which seven were successful involving six species (Table 1). Although the relative importance of small rodents in the diet could not be determined from spoor tracking, it is likely that most of the unidentified hunts were on rodents.

DISCUSSION

Many studies have been conducted into the minimum sample size required to estimate the diet of predators (Bothma *et al.* 1976, Windberg and Mitchell 1990, Mukherjee *et al.* 1994). Based on a comparison with the sample sizes in these studies, it is likely that the sample (116 scats) used here should give a reliable first order indication of the diet of caracals in the Kgalagadi Transfrontier Park and this is augmented with data from tracking spoor. The sample size is still too small, however, to give an accurate estimation of the seasonal prey use by caracals. Scat analysis shows that the remains of more than one prey is often included in a single scat (Mukherjee *et al.* 1994). Therefore a large enough hair sample should be taken from each scat to include all prey that may occur in that scat.

General mammalian prey

The most abundant prey for caracals during this study were rodents which were found in 60.9% of scats. This is likely to be due to increased rodent recruitment in response to two seasons of good rain in the study area (Nel *et al.* 1984). Like other predators, the caracal is an opportunist (Bothma & Walker 1999; Bothma 1998) and uses suitable prey that is most abundant and consequently most frequently encountered while hunting. When compared with other studies in southern Africa, the only study that found a higher percentage of rodent use than that of the Kgalagadi Transfrontier Park, was in the arid West Coast National Park, where rodent remains were found in 89.1 % of the scats (Avenant and Nel 1997). Other studies revealed rodents to vary in percentage occurrence from 5.3 % to 50.0 % (Table 2).

Most caracal diets elsewhere include a larger proportion of artiodactyls with a body mass of ≥10 kg than in the Kagalagadi Transfrontier Park (Tables 2 and 3). Only the study of one male caracal in the desert of Saudi Arabia recorded a lower incidence of large mammals in the diet of a caracal than the present study. The collared male caracal in Saudi Arabia was observed feeding on the carcasses of dead camels *Camelus dromedarius* and sand gazelles *Gazella subgutturosa* (Van Heezik & Seddon 1998). Although these are large prey it is likely that the caracal was scavenging on the carcasses of these animals. In an arid area such as the northern

Table 2: *Synopsis of the relative percentage contributions of major prey sources from the Kgalagadi Transfrontier Park compared with those from previous studies, based on scat analysis.*

Prey	Region and source of data						
	Kgalagadi Transfrontier Park: current study	West Coast National Park Avenant & Nel (1997)	Southwestern and eastern Cape: Stuart & Hickman (1991)	Karoo National Park: Palmer & Fairall (1988)	Mountain Zebra National Park: Moolman (1986)	Farm land in the eastern Cape: Moolman (1986)	Mountain Zebra National Park: Grobler (1981)
Mammals	81.3	69.8	94.8	85.2	94.9	96.9	93.7
Lagomorpha	4.9	1.3	5.2	14.7	15.3	9.4	10.6
Rodentia	60.9	57.4	50	30.2	8.5	24	5.3
Hyracoidea	na	1.2	9	17.1	52.5	30.3	53.3
Carnivora	10.7	1.2	2.9	1.6	5.1	na	0.9
Artiodactyla	1.3	4.2	10.9	21.7	13.5	10.3	23.6
Insectivora	na	4.5	na	na	na	na	na
Domestic stock	3.6	na	16.8	na	na	22.9	na
Birds	6.7	11.5	5.2	1.6	4.3	2.1	5.3
Reptiles	na	7.9	na	na	0.8	1	0.9
Invertebrates	12.0	10.8	na	13.2	na	na	na

Table 3: *Mean body mass of various animals that caracals preyed on in the Kgalagadi Transfrontier Park from June 2000 to July 2002 (Skinner Smithers 1990)*

Prey	Scientific name	Body mass	
		Males	Females
African wild cat	*Felis sylvestris*	4.9	3.7
Bat-eared fox	*Otocyon megalotis*	4.0	4.1
Black-backed jackal	*Canis mesomelas*	7.9	6.6
Brant's whistling rat	*Parotomys brantsii*	0.1	0.1
Caracal	*Caracal caracal*	11.8 *	8.6 *
Cape fox	*Vulpes chama*	3.0	2.9
Ground squirrel	*Xerus inauris*	0.7	0.6
Kori bustard	*Ardeotis kori*	13.5 to 19.0	13.5 to 19.0
Scrub hare	*Lepus saxatilis*	2.2	2.6
Springhare	*Pedetes capensis*	3.1	2.8
Steenbok	*Raphicerus campestris*	10.9	11.3
Striped polecat	*Ictonyx striatus*	1.0	0.7
Yellow mongoose	*Cynictis penicillata*	0.6	0.6
Unidentifiable	~	~	~

* Based on the body masses of caracals captured in the Kgalagadi Transfrontier Park

steppe desert of Saudi Arabia, where prey are not abundant, opportunistic feeding behaviour dictates that caracals use whatever food resources are available.

The most important prey animal in the diet of caracals in the Kgalagadi Transfrontier Park is the springhare. Springhare remains were found in 37.1 % of the scats collected and made up 6.1 % of kills recorded (Table 1). The importance of the springhare in the diet of caracals is due to its abundance and large size relative to other prey. In the Kgalagadi Transfrontier Park the springhare probably fills the same prey niche, in terms of degree of use (Table 2) and mean body mass (Table 3), as the rock dassie *Procavia capensis* does in other areas (Skinner & Smithers 1990).

Carnivore prey

Although the use of carnivores as prey is not uncommon (Bothma & Walker 1999, Mills 1990), a prominent feature of the diet of caracals in the Kgalagadi Transfrontier Park is the high proportion and diversity of carnivores used as prey. In the present study five species of carnivore contributed 10.7 % of the total number of prey identified in the scats. This is more than twice the number of carnivores recorded by Moolman (1986), in the Mountain Zebra National Park (Table 2). Other studies recorded a variation in contribution of carnivores to caracal diets (Table 2). Of the prey that could be positively identified from spoor-tracking, 32.4% were carnivores and 22.5 % were killed.

Previous studies have shown that the carnivores preyed upon by the caracal weigh <1 kg (Skinner & Smithers 1990), with the exception of water mongooses *Atilax paludinosus,* that weigh 3.4 kg, in the southwestern Cape (Stuart & Hickman 1991). Four of the six carnivore species preyed upon by caracals in the Kgalagadi Transfrontier Park weigh from 2.5 to 8.0 kg (Table 3). In most areas the risk of preying on larger carnivores is probably not ameliorated by the energetic benefits gained from utilising them. In the southern Kalahari the energetic benefit provided by larger prey may outweigh the risks involved in preying upon larger carnivores (Sunquist & Sunquist 1989). The low density of smaller artiodactyls, except for steenbok, in the Kgalagadi Transfrontier Park, creates the opportunity for smaller carnivores to fill this medium to large prey category for caracals. The low density of leopards *Panthera pardus* and cheetahs *Acinonyx jubatus* in this area may increase the availability of such small predators to caracal. This is further evidence of the opportunism and adaptation displayed by the caracal in its predatory behaviour.

Diurnal prey

Predation on diurnal animals including Brant's whistling rat *Parotomys brantsii*, ground squirrels, and yellow mongooses indicates that caracals in the Kgalagadi Transfrontier Park display some diurnal behaviour. This is supported by observations in the present study of caracal activity during daylight hours, especially in the cooler winter months, as well as by observations of Avenant & Nel (1988) in West Coast National Park.

Domestic livestock

It is clear that caracals living in the vicinity of the border of the park with Namibia do occassionally feed on small livestock. Four of the six scats that contained wool were found during the cold season (April to September) when the livestock lamb. This is supported by the observations of Namibian farmers who indicate that the majority of sheep losses occur in the cold period. The furthest distance from the park border that small livestock remains were found in a caracal scat was 23.3 km. This suggests that caracals with a good proportion of their foraging range within the park, do transgress into the neighbouring farming areas.

Avian prey

The occurrence of avian prey in the diet of caracal in the Kgalagadi Transfrontier Park is higher than recorded for most other areas, except in West Coast National Park (Table 2). It was surprising that birds did not contribute more to the diet of caracals in the Kgalagadi Transfrontier Park. Kori bustards and korhaans seem to be ideal prey because of their relatively large size and ground-nesting habits (Maclean 1985). On two occasions a caracal stalked and killed kori bustards that were roosting on the ground.

Invertebrate prey

Invertebrate prey, made up exclusively of Coleopterans, was found in 23.3 % of the caracal scats. Because of their low individual biomass, their contribution to the diet of the caracal is limited, but they probably supplement the diet when taken opportunistically. Coleopterans form an integral component of the insect fauna in the semi-arid regions of southern Africa (Palmer & Fairall 1988). Moolman (1986) found scorpion remains in a small percentage of the caracal scats that he analysed. Stuart and Hickman (1991) suggest that insects do not contribute to the diets of caracals, however, the current data supports the results of Palmer and Fairall (1988) that at least in some areas they do. Perhaps in the more arid areas where prey abundance is low, opportunism dictates that caracals use items not taken under other conditions.

Vegetable matter

The occurrence of plant material in caracal scats has also been recorded in other studies (Palmer & Fairall 1988, Stuart & Hickman 1991, Avenant & Nel 1997). Caracals probably usually ingest vegetable matter accidentally while grooming or while consuming other food. Tsamma melon seeds were found in three scats in the present study. Caracals were also recorded to eat tsamma melons based on spoor evidence. This confirms that caracals, like other carnivores, use these plants in the Kgalagadi Transfrontier Park (Eloff 1984, Mills 1990, Bothma & Le Riche 1994). This habit probably supplements the moisture intake of carnivores in the southern Kalahari (Bothma 1998).

Comparison of methods

As discussed by Mills and Mills (1978) both methods have advantages and disadvantages that to an extent augment each other. Scat analysis reveals small items such as insects and small rodents not recorded when tracking spoor and tracking spoor gives an indication of hunting success and type of prey hunted.

CONCLUSIONS

The primary prey resource used by caracals in the Kgalagadi Transfrontier Park is rodents, of which the springhare is especially important. Smaller carnivores form an important component of the diet and seem to replace the artiodactyls as a larger prey resource for caracals as eaten in other areas. The use of small livestock seems to take place on an opportunistic basis when there is an increase in vulnerability due to the birth of lambs.

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CHAPTER 9

POSSIBLE OPTIMAL FORAGING FOR BRANT'S WHISTLING RATS BY THE CARACAL IN THE KGALAGADI TRANSFRONTIER PARK

H.I.A.S. Melville, J. du P. Bothma & M.G.L. Mills

Optimal foraging in caracals has never been substantiated. The foraging pattern relative to a common prey animal can give an insight into the optimality of hunting behaviour. Foraging behaviour in caracals relative to Brant's whistling rats was investigated in the southern Kalahari. It showed that in the cold season no optimal foraging for these rats occurred, but in the hot season it did occur.

Keywords : Caracal, optimal foraging, Brant's whistling rat, Kalahari

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Little is known about optimal foraging behaviour in carnivores. Several attempts have been made to test the optimal foraging theory for predators consuming sedentary prey (Brown *et al.* 1999). Here, Brant's whistling rat *Parotomys brantsii*, a common prey of the caracal *Caracal caracal*, is used as a measure of optimal foraging in caracals in the semi-arid savanna environment of the Kgalagadi Transfrontier Park.

Traditionally it is assumed that natural selection dictates that animals have to optimise their behavioural patterns to ensure their survival (Ollason & Lamb 1995), but the currently accepted view is that optimality is merely a convenient framework within which to describe animal behaviour (Krebs *et al.* 1984). In predators, optimal foraging can be described as minimising the total path length required to survey areas of varying prey density so as to maximise hunting opportunities (Gelenbe *et al.* 1997). Stated differently, predators select routes that maximise their opportunities of encountering prey that are suitable for hunting.

Brant's whistling rats were chosen in this study because they are an abundant prey resource and they were found to contribute to the diet of caracals in the southern Kalahari (Melville *et al.* 2004). Brant's whistling rats contributed 11.6 % of the total number prey items found in caracal scats (Table 1), with no apparent seasonal variation.

To investigate whether caracals in the Kgalagadi Transfrontier Park adopted an optimal search strategy for Brant's whistling rats, the likelihood of encountering Brant's whistling rat colonies if moving randomly, was compared with the frequency in which caracals passed close to or through Brant's whistling rat colonies while foraging.

To estimate the likelihood of encountering Brant's whistling rat colonies, a vehicle was used to survey 20 straight-line randomly spaced transects of 10 km each in the study area. Ten transects were surveyed in the hot season (October to March) and 10 in the cold season (April to September). Observations on the presence or absence of Brant's whistling rat colonies were made at 0.5 km intervals along the length of each transect. A total of 400 observations were made, of which 200 were made in the hot season and 200 in the cold season.

To establish whether the observed rat colonies were occupied, each colony within a 10 m radius of the vehicle was checked for evidence of fresh rat activity. If no colony was

Table 1: *The incidence of active Brant's whistling rat colonies at 0.5 km intervals along randomly chosen transects and on caracal spoor in the Kgalagadi Transfrontier Park from June 2000 to August 2002.*

Item	Cold season		Hot season		Total	
	Present	Absent	Present	Absent	Present	Absent
Transects	158	177	128	74	286	251
Spoor	112	88	108	92	220	180
Total	270	265	236	166	506	431

present, or if there was no evidence of current activity in a colony, it was recorded as being inactive. This survey provided baseline data of the expected occurrence of active Brant's whistling rat colonies in the study area. The incidence of active Brant's whistling rat colonies along known movement paths of the caracals, were then compared with these baseline data.

The spoor-tracking method of Bothma & Le Riche (1984), Eloff (1984) and Stander *et al.* (1997) was used to track caracal movements. To determine a comparable frequency of occurrence of rat colonies along the caracal movement paths, the same observations were made on the spoor-tracking paths of caracals as were done for the baseline data. Therefore, observations of the occurrence of active Brant's whistling rat colonies were made every 0.5 km along each set of caracal tracks. This resulted in a total of 537 observations, 335 of which were in the cold season and 202 in the hot season.

The data were transformed to give those obtained from surveying the random transects and those obtained while spoor-tracking an equal weighting. This was done to ensure that both the data sets contributed equal proportions to the combined data set. This data transformation was done in four stages:

- The sum of all the observations from the transects and the spoor-tracking was calculated first.
- This total number of observations was then divided by the number of observations from the transects and from the spoor individually,
- The results from the above calculations were then multiplied by 0.5 to give an applicable ratio for both the transect and the spoor data.

- The total number of observations for the spoor tracking data and the transect data were then multiplied by the applicable ratio from the above process.

The above transformation ensured that the straight-line transect survey data and that of the spoor-tracking data contributed equally to the total number of observations in the data set. The transformation of the data also improved the comparability of the component data sets.

The CATMOD procedure of SAS (1999) was then applied to the transformed data. Logit modelling was then applied to determine whether the odds ratio of encountering a Brant's whistling rat colony was greater while tracking caracal spoor than on the randomly selected control transects. The results of this procedure generated confidence intervals at the 95 % level. When analysed for the whole year (df = 1, confidence interval [0.7, 1.22], *P* = 0.57) and for the cold season only (df = 1, confidence interval [0.5, 1.08], *P* = 0.12) there was no significant difference between the chances of encountering a Brant's whistling rat colony on the control transects or while tracking from spoor. However, for the hot season (df = 1, confidence interval [1.30, 3.38], *P* = 0.0023) there was a significantly higher likelihood of finding Brant's whistling rat colonies along the caracal spoor than on the control transects.

These results indicate that during the cold season, caracals do not forage optimally with regard to Brant's whistling rats. However, in the hot season they do seem to follow paths that include a high incidence of Brant's whistling rat colonies. This implies that a caracal may have a tendency to optimise its movements in terms of search time, encounter rate and energy expenditure (Sunquist & Sunquist 1989) in relation to Brant's whistling rat colonies in the hot season, and hence to optimise the number of opportunities to hunt these rats then.

It seems that caracals follow different foraging strategies for Brant's whistling rats seasonally. In the cold season when Brant's whistling rats are less abundant, caracals may well employ a random search strategy. However, in the hot season when these rats are more abundant and there is more overlap between their diurnal and nocturnal activity patterns (Nel & Rautenbach 1974; Skinner & Smithers 1990), caracals seem to choose paths that include a high number of Brant's whistling rat colonies.

Caracals probably optimise their foraging strategy based on the prevalence of other food resources too (Table 2). However, to substantiate this it would be necessary to investigate the optimality of foraging behaviour in caracals relative to other prey individually. It would also be necessary to establish whether optimal foraging by caracals is species-specific, or whether it includes their entire prey spectrum, and whether any such selection is based on the variation in seasonal abundance of the total prey resources.

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Table 2: *The seasonal occurrence of Brant's whistling rat remains in caracal scats in the Kgalagadi Transfrontier Parkfrom June 2000 to August 2002 .*

Prey	Hot season		Cold season		Total	
	Incidence	Percentage	Incidence	Percentage	Incidence	Percentage
Brant's whistling rat	7	11.5	19	11.6	26	11.6
Other	54	88.5	145	88.4	199	88.4
Total	61	100.0	164	100.0	225	100.0

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CHAPTER 10

THE EFFECT OF SMALL STOCK FARMING IN NAMIBIA ON CARACAL DENSITY IN THE NEIGHBOURING KGALAGADI TRANSFRONTIER PARK.

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Abstract

A spoor count was done to determine whether caracal spoor densities in the vicinity of the border of the Kgalagadi Transfrontier Park differed from those in the interior of the Park. The objective was to compare caracal densities close to the agricultural land with those deeper in a national park. Two long-distance transects, one along the Namibian border and one diverging from the Namibian border into the interior of the Park, were surveyed on a monthly basis. Spoor density, discrete track set distances and orientation of spoor to the road were recorded and analysed to establish use patterns for three distinct zones in the Park. The hypothesis tested was that increased spoor counts along the border should result from an attraction to the adjacent agricultural (cattle and sheep production) land. It is shown that caracals avoid the areas near the Namibian border during the hot season but increased their utilisation in this region in the cold season. This implies that under conditions of low prey availability (cold season) caracals may move to the border and cross onto agricultural land to prey on small livestock, there.

Keywords: Spoor-counts, caracal, *Caracal caracal*, Namibia, Kalahari.

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Introduction

In southern Africa, the caracal *Caracal caracal* (Schreber, 1776) is regarded and legislated as a problem animal (URL: http://lynx.uio.no/catfolk/ssacr101.htm) due to their habitual depredations on small livestock (Stuart & Wilson 1988). Problem animals have broadly been described as wild animals that persistently and seriously detract from the achievement of man's agricultural endeavours (Thomson 1992). Several studies have confirmed that caracals do prey on small domestic livestock to varying degrees (Stuart 1982, Moolman 1986, Stuart & Wilson 1988, Stuart & Hickman 1991, Bothma & Walker 1999, Melville *et al.* 2004). In areas where domestic livestock production occurs on land adjacent to conservation areas, there is a definite polarisation between agriculturalists and conservationists into two antagonistic camps (Thomson 1992). This polarisation is largely due to the differing attitudes of the two groups to problem animals and their management, especially where larger predators are involved. This antagonistic relationship also exists in the southern Kalahari, where a number of Namibian small livestock production units share boundaries with the western parts of the vast Kgalagadi Transfrontier Park.

From the responses to questionnaires used in this study, it was clear that the agricultural community believes that predators from the Kgalagadi Transfrontier Park regularly move across the border onto their land to prey on small livestock. If this were the case, then it would be expected that there would be a higher population density of caracals along the western border of the Kgalagadi Transfrontier Park than in the adjacent interior parts of this Park. This general hypothesis is tested in the present study. To do so, the following key questions were examined:

- Is caracal spoor density significantly higher along the border areas than in the interior of the Park?
- Is the intensity of use of roads along the border similar to that of the roads in the interior of the Park?

Study area

This study was done in an area along the Namibian border near Mata-Mata in the southwestern portion of the Kgalagadi Transfrontier Park. For logistic reasons it was decided to confine the research to an area that extended 60 km north from the Mata-Mata rest camp along the Namibian border (20° 00' E longitude) to approximately 20 km into the interior of the Kgalagadi Transfrontier Park.

The Kalahari Gemsbok National Park was proclaimed in 1931, but it only became a reality in 1935 when a number of farms along the southern bank of the Aoub River were acquired. Today, the Park exists in much the same ecological state as it was then (Van Wyk & Le Riche 1984). An agreement to formally combine the Kalahari Gemsbok National Park (South Africa) with the bordering Gemsbok National Park (Botswana) to form the Kgalagadi Transfrontier Park was signed by representatives of the governments of South Africa and Botswana in 1999. This agreement was ratified at an amalgamation ceremony that was held on the 12 May 2000 (Donaldson 2000).

The Mata-Mata area lies in the Shrubby Kalahari Dune Bushveld of the Savanna Biome (Low & Rebelo 1996). This area is an arid savanna with temperatures varying from –10° C to 45° C in the shade with an annual mean rainfall of 153.5 mm occurring mainly in the hot season. The landscape is one of undulating dunes with sparse vegetation at altitudes varying from 1000 to 1100 m above sea level (Low & Rebelo 1996).

The vegetation is characterised by the trees *Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca*, a shrub layer of *Grewia retinervis* and *Rhus tenuinervis,* and a well-developed grass layer consisting mainly of *Stipagrostis amabilis*, *Eragrostis lehmanniana, Aristida meridionalis, Schmidtia kalihariensis* and *Centropodia glauca* (Low & Rebelo 1996). There is little variation in the soil forms because the area is predominantly covered by aeolian sand overlying calcrete (Low & Rebelo 1996).

The Kgalagadi Transfrontier Park forms the southern part of the greater Kalahari ecosystem. Because of the arid nature of the area, many of the plants there are ephemeral. After sufficient rain, these plants germinate quickly to complete their life cycle in a short time (Eloff 1984).

Because of the harshness of the environment, the southern Kalahari is an area that is only sparsely inhabited by humans. This above any other factor contributes to the uniqueness of the area, and it enhances the value of the area for field research in wildlife management and conservation.

Methods

It is difficult to obtain reliable indices of density for animals that are nocturnal, camouflaged and cryptic as are most solitary mammalian carnivores (Mahon, Banks & Dickman 1998). Direct sampling, where density estimates are made based on sightings of animals, is too time-consuming and costly to be seriously considered for monitoring purposes (Smallwood & Fitzhugh 1994). For the purposes of the present study it was also not relevant to establish the exact number of individual caracals. Rather, the aim was to gauge the relative density of caracals in different parts of the Park.

The most frequently used methods for monitoring carnivore densities are, spotlight counts, spoor counts, scent-post visitation rates and bait-use rates (Mahon, Banks & Dickman 1998). Spoor counts are an efficient and relatively low-cost method of estimating species richness and abundance (Litvaitis, Sherburne & Bissonette 1985, Smallwood & Fitzhugh 1994, Stander 1998, Silveira, Jacomo & Diniz-Filho 2003). Because of the ease with which caracal spoor can be found and counted on the sandy substrate of the Kalahari, spoor counts were used in the present study to monitor the relative abundance of caracals in various parts of the western Kgalagadi Transfrontier Park. Moreover, there is a direct relationship between the frequency of spoor and the density in which the animals occur (Tyson 1959, van Dyke, Brocke & Shaw 1986, Stander 1998, Thompson *et al.* 1998, Funston *et al.* 2001).

In this study it was necessary to use terminology with definitions specific to the circumstances in which they were used. The following is a list of terms and definitions as they were applied to this study:

- Spoor density : the mean number of sets of caracal tracks per 100 km.
- Spoor ratio : the relative frequency of caracal spoor per 100 km of tracking over successive counts along the same transect.
- Discrete track sets : a continuous set of caracal tracks along or across a transect.

Field study

Spoor counts were done along the management roads in the study area because the soft sand was eminently suitable for the detection of spoor (Funston *et al*. 2001). Transects were done by vehicle on a monthly basis from June 2001 to July 2002, with the assistance of experienced Kalahari San trackers. These trackers are known to be highly accurate and reliable when identifying and interpreting animal tracks (Stander *et al*. 1997). The study was structured so that one of the routes lay directly along the Namibian border. The route in the interior, against which data from the border route were compared, started 5 km inland from the border, then it converged to intersect briefly with the border before it progressively swung away again from the border (Fig. 1). At its furthest point the road was 30 km away from the border. The route along the border was 114.6 km long and that in the interior portions 138.5 km long. Long transects are better suited to detect variation in population densities of caracal than short transects, because they are likely to include the ranges of more caracals than shorter routes (Van Sickle & Lindzey 1991). The transects were surveyed intermittently at monthly intervals for a total of 26 surveys over a total distance of 3290.4 km.

The roads were scanned by the tracker who was seated on a specially designed tracking chair mounted on the front bumper of the slowly moving research vehicle, as was done by Funston *et al.* (2001) when working with lions *Panthera leo*. To ensure that spoor was not missed, the transects were travelled at a constant speed of 12 km per hour. Due to the

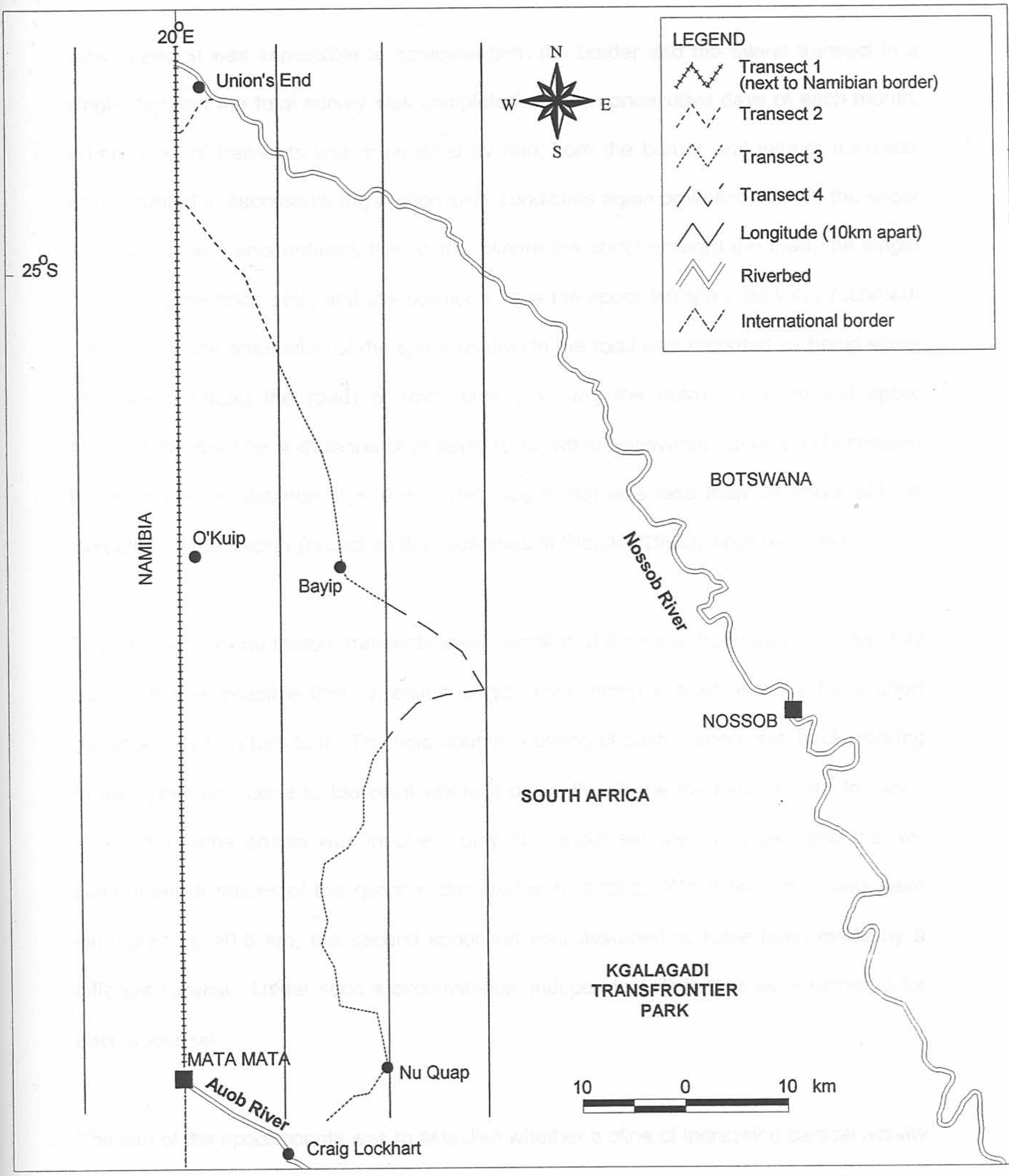

Figure 1: Transects used for determining the relative caracal spoor density along the Namibian border and the interior of the Kgalagadi Transfrontier Park from June 2001 to July 2002.

slow speed, it was impossible to complete both the border and the inland transect in a single day, but the total survey was completed on two consecutive days of each month. When a set of transects was interrupted by rain, both the border and interior transects were counted in successive days when ideal conditions again prevailed. When the spoor of a caracal was encountered, the position where the spoor entered the road, the length of the discrete track sets, and the position where the spoor left the road were recorded. Additionally, the orientation of the spoor relative to the road was recorded as being either longitudinal (along the road) or transverse (crossing the road). Longitudinal spoor followed the road for a distance of at least 10 m, while transverse spoor simply crossed the road over a distance of <10 m. Only spoor that was less than 24 hours old, as indicated by the tracker (based on the guidelines of Stander 1998), were recorded.

Both the border and interior transects were sampled at an equal frequency on a monthly basis. It was possible that an animal might move along a road, leave it for a short distance only to return to it. To avoid double-counting of such a spoor set, back-tracking of the spoor was done to the point where it originally left the transect or not. In cases where the same animal was involved, only one spoor set was recorded, and the two component distances of the spoor in the road were added. When two spoor sets were separated by >0.5 km, the second spoor set was assumed to have been made by a different caracal. Under such a circumstance, independent distances were recorded for each spoor set.

The aim of the spoor counts was to establish whether a cline of increasing caracal activity occurred as was expected, as a road from the interior approached a border road. Therefore the roads that diverged from the border into the interior were stratified into three separate components based on the perpendicular distance of each component away from three separate components based on the perpendicular distance of each component away from the Namibian border. The result was that four distinct survey areas were identified within the following distance intervals relative to the road along the Namibian border: transect 1 was along the Namibian border (114.59 km); transect 2 was from 0 – 10 km from the Namibian border (33.52 km), transect 3 was >10 - 20 km from the Namibian border (79.74 km), and transect 4 was >20 - 30 km from the Namibian border (25.26 km). Caracal spoor density was expressed as the frequency of spoor per 100 km of road surveyed, and was calculated for each of the four transects. The length of each discrete track set and the orientation of the track sets were also recorded. Spoor density, spoor orientation and the discrete track set length were calculated seasonally for a hot season from October to March and a cold season from April to September.

To ensure that the integrity of the comparisons between the data that were collected along the border and those that were collected in the interior was maintained, the data were collected in a standardised manner (Thompson *et al.* 1998), with no variation from the set protocol (Smallwood & Fitzhugh 1995).

Data analysis

Standard t-tests and least square means tests were used to compare the mean spoor density along the border transect with that along the transects in the interior, and to compare the mean spoor densities of the transects in the interior with one another (Table 1). Chi-squared tests were used to compare the spoor ratio along the border transect with that on each of the transects in the interior. The spoor data from the transects in the interior were also compared with one another. The longitudinal and transverse movement patterns were compared by using chi-squared tests to determine whether caracals tended to use the roads as corridors (Mahon *et al.* 1998) or whether

Table 1: *Chi-squared tests to compare caracal spoor ratio and standard t-tests and least square mean tests comparing mean spoor density between seasons and transects in the Kgalagadi Transfrontier Park from June 2001 to July 2002*

Transects compared	Season	χ2 - test			t-tests		Least square mean test		
		χ^2 –value	Degrees of freedom	*P* -value	t-value	*P* -value	Mean	Standard Error	*P* - value
1 and 2	Both	16.61	12	NS	-1.27	0.220	4.94	1.24	0.250
1 and 3	Both	18.71	12	NS	-2.54	0.020	4.94	1.24	0.040 *
1 and 4	Both	18.12	12	NS	-3.45	0.003	4.94	1.24	0.003 *
2 and 3	Both	22.31	12	$\leq$ 0.05	-0.92	0.360	6.98	1.24	0.320
2 and 4	Both	28.22	12	$\leq$ 0.05	-1.68	0.110	6.98	1.24	0.051
3 and 4	Both	6.97	12	NS	-0.81	0.430	8.74	1.24	0.320
1 and 2	Hot	15.18	3	$\leq$ 0.05	-1.49	0.190	3.48	2.06	0.390
1 and 3	Hot	21.53	3	$\leq$ 0.05	-3.25	0.023	3.48	2.06	0.120
1 and 4	Hot	26.57	3	$\leq$ 0.05	-3.31	0.021	3.48	2.06	0.010 *
2 and 3	Hot	6.11	3	NS	-1.49	0.200	6.00	2.06	0.460
2 and 4	Hot	15.30	3	$\leq$ 0.05	-2.17	0.080	6.00	2.06	0.100
3 and 4	Hot	2.63	3	NS	-1.33	0.260	8.15	2.06	0.350
1 and 2	Cold	16.01	8	$\leq$ 0.05	-0.82	0.430	6.40	1.37	0.430
1 and 3	Cold	15.43	8	NS	-1.61	0.140	6.40	1.37	0.140
1 and 4	Cold	10.70	8	NS	-2.11	0.058	6.40	1.37	0.060
2 and 3	Cold	27.82	8	$\leq$ 0.05	-0.56	0.580	7.96	1.37	0.480
2 and 4	Cold	31.98	8	$\leq$ 0.05	-0.89	0.390	7.96	1.37	0.270
3 and 4	Cold	8.27	8	NS	-0.33	0.750	9.33	1.37	0.690

* Significant values for results of least square means tests

NS: No significant difference for the comparison.

they simply crossed them in their daily movements. These data were analysed seasonally and year-round on an inter-transect basis.

Analysis of variance (ANOVA) was applied to the discrete track set distance data to establish whether the caracals moved greater distances along the roads in the interior than along the Namibian border transect. The variance was calculated across the four road strips simultaneously, on a seasonal and year-round basis. To establish the nature and cause of any variance, t-tests were done to compare the border data with those of each of the interior transects. Additionally the mean discrete track set distances between transects in the interior were compared by using t-tests (Table 2).

Results

The spoor density varied seasonally and between the various transects (Table 3). On a year-round basis and for the hot season only there is a significantly higher mean spoor density per 100 km in the interior on transects 3 and 4 than in transect 1 (Table1). However, there is no difference in the mean spoor density between transects 1 and 2 in this period (Table 1). In the cold season there is no difference between the spoor density along the border and any of the interior transects (Table 1). There also is no seasonal difference between the mean spoor density on any of the transects in the interior (Table 1).

On a year-round basis there also was no difference between the spoor ratio on transects 1, 2, 3 and 4. The spoor ratio on transect 1 was significantly different from that on transects 2, 3 and 4 in the hot season. In the cold season the spoor ratio on transect 1 was significantly different from that on transect 2, whereas that on transects 3 and 4 did le 2: *t-Test results comparing the mean discrete caracal track set length in each spoor count transect in the Kgalagadi Transfrontier Park from June 2001 to July 2002.*

Transects compared	Season	t-test		Mean discrete track length (km)			
		t-value	*P*-value	Transect 1	Transect 2	Transect 3	Transect 4
1 and 2	all	1.65	0.10	1.2	0.85	~	~
1 and 3	all	3.61	0.01	1.2	~	0.68	~
1 and 4	all	1.70	0.09	1.2	~	~	0.83
2 and 3	all	0.93	0.36	~	0.85	0.68	~
2 and 4	all	0.11	0.91	~	0.85	~	0.83
3 and 4	all	-0.72	0.47	~	~	0.68	0.83
1 and 2	cold	1.30	0.20	1.24	0.93	~	~
1 and 3	cold	3.62	0.01	1.24	~	0.64	~
1 and 4	cold	1.04	0.30	1.24	~	~	0.92
2 and 3	cold	1.44	0.16	~	0.93	0.64	~
2 and 4	cold	0.26	0.79	~	0.93	~	0.85
3 and 4	cold	-0.83	0.41	~	~	0.64	0.85
1 and 2	hot	0.84	0.41	1.04	0.68	~	~
1 and 3	hot	0.92	0.36	1.04	~	0.79	~
1 and 4	hot	0.79	0.44	1.04	~	~	0.77
2 and 3	hot	-0.28	0.79	~	0.68	0.79	~
2 and 4	hot	-0.19	0.85	~	0.68	~	0.77
3 and 4	hot	0.07	0.94	~	~	0.79	0.77

~ Data not relevant to this comparison

Table 3: *Spoor density and mean spoor length of caracal tracks on management roads in the Kgalagadi Transfrontier Park from June 2001 to July 2002.*

			Track set distance (km)	
Route	Season	Spoor density per 100 km	Mean length	Standard error
1	Hot	3.39	1.04	0.22
	Cold	6.40	1.24	0.14
	All	5.50	1.19	1.13
2	Hot	8.20	0.68	0.36
	Cold	7.95	0.93	0.19
	All	6.60	0.70	0.14
3	Hot	8.15	0.79	0.16
	Cold	9.48	0.64	0.08
	All	9.07	0.68	0.07
4	Hot	10.89	0.77	0.26
	Cold	10.12	0.85	0.24
	All	10.35	0.83	0.19

not differ significantly from transect 1. There is no seasonal difference between the relative frequencies of spoor along any of the transects ($\chi^2 = 2.79$, df = 3, $P > 0.05$) (Table 1).

On a year-round basis there is a significant difference between the mean length of discrete caracal track sets on all the transects (ANOVA: $F_{2,64} = 4.35$, $P < 0.01$). In the hot season there is no difference (ANOVA: $F_{2,75} = 0.41$, $P = 0.74$), but in the cold season, there again is a significant difference (ANOVA: $F_{2,65} = 4.27$, $P < 0.01$). There was no seasonal difference between the mean lengths of discrete track sets along any of the transects. There also was no seasonal difference between the mean length of discrete track sets across all transects ($t = -0.71$, df = 122, $P = 0.48$) (Table 4).

The relative incidence of caracals moving along the transects, as opposed to crossing the transects is highly variable (Table 5). On a year-round basis caracals tend to move along transect 1 and 2 more often than along transects 3 and 4. Caracals therefore tended to use the transects in the interior less often as corridors for movement than the transects close to the Namibian border. In the hot season, caracals used all the transects as corridors of movement to a similar extent. However, in the cold season it appears that the interior transects are used less often than the transects close to the Namibian border (Table 5). The ratio of longitudinal spoor to transverse spoor over all the routes is 20.3 : 1 in the hot season and 8.1 : 1 in the cold season. There is no significant difference between the frequency of longitudinal movements among the transects on a seasonal basis ($\chi^2 = 3.48$, df = 3, $P > 0.05$). However, there is a significant seasonal difference between the frequency of transverse movements among the transects ($\chi^2 = 62.85$, df = 3, $P < 0.05$).

able 4: *Standard t-tests comparing the seasonal variation in the mean length of discrete caracal track sets along spoor count transects in the Kgalagadi Transfrontier Park from June 2001 to july 2002*

Transect	Cold season		Hot season		t-value	*P*-value
	Mean length of discrete track sets (km)	Standard error	Mean length of discrete track sets (km)	Standard error		
1	1.24	0.15	1.04	0.22	0.77	0.45
2	0.68	0.19	0.93	0.59	-0.62	0.55
3	0.79	0.08	0.64	0.16	0.84	0.40
4	0.77	0.23	0.85	0.26	-0.24	0.81
Total	0.83	0.07	0.92	0.11	-0.71	0.48

Table 5: *Chi-squared tests comparing the ratio of caracals moving along the transects to those crossing the transects, during transect counts in the Kgalagadi Transfrontier Park from June 2001 to July 2002.*

Transects compared	Hot season		Cold season		Year-round	
	χ^2–value	P- value	χ^2–value	P- value	χ^2–value	P- value
1 and 2	7.90	≥ 0.05	9.53	≥ 0.05	1.19	< 0.05
1 and 3	3.92	≥ 0.05	2.56	≥ 0.05	1.93	< 0.05
1 and 4	9.54	≥ 0.05	8.02	≥ 0.05	4.35	≥ 0.05
2 and 3	2.34	< 0.05	15.88	≥ 0.05	5.79	≥ 0.05
2 and 4	0.00	< 0.05	24.40	≥ 0.05	9.27	≥ 0.05
3 and 4	2.27	< 0.05	1.66	< 0.05	0.53	< 0.05

The mean distance over which caracals travel along the transects does not vary either on a year-round basis or seasonally, based on the proximity of the transect to the Namibian border (Table 2).

Discussion

Track counts are often the most efficient and rapid method for detecting the relative abundance of wild animals. Climatic conditions and ground conditions are limitations to the detectability and identification of the tracks (Silveira *et al*. 2003). Funston *et al*. (2001) also indicated that population estimates based on spoor counts of small carnivores are unreliable because of the difficulty in detecting the spoor of these animals. However, provided that the detectability of the spoor remains similar in all areas, the same level of error in track detection can be expected (Burnham & Anderson 1984). Hence estimates of population size and trends that are based on relative spoor densities are appropriate. For the caracal, such spoor counts are of great value to detect relative area use.

Mooty and Karns (1984) and Strayer (1999) concluded that presence-absence surveys should be used with caution when trying to detect population trends. Due to their relative insensitivity to small variations, spoor counts may be susceptible to Type 2 statistical errors and may tend to overestimate abundance because spoor sets from the same animal can be counted more than once in a single survey (Silveira *et al*. 2003). Great care, through back-tracking, was taken to ensure that this type of overestimate did not occur in the present study.

To determine whether caracals specifically moved into the adjacent agricultural area from the Park would require evidence of a cline of increased caracal activity and density from the interior of the Kgalagadi Transfrontier Park towards the Namibian border. If caracals were moving towards or were concentrating along the border to cross it into Namibia, then the incidence of caracals moving along transect 1 next to the border would be significantly less than that along the interior transects because the fence would prove to be no obstacle. Conversely, if the border fence acted as a barrier to movement, it can be expected that the caracals would move for longer distances along the border road (transect 1) than along the interior ones, while searching for holes in the fence through which to move or suitable fence posts over which to climb.

In the hot season, there is a low caracal spoor density along the border road relative to that found in all the interior transects, where spoor densities were at least twice that of transect 1. Transect 4, that was furthest away from the border, had the highest spoor density in the hot season but not in the cold season (Table 3). This may indicate that during the hot season caracals do not concentrate near the border areas, but in the cold season they do so despite human activity that should cause them to avoid the border. This in turn may indicate that there may be a higher degree of use of the border areas, in the cold season, possibly because of reduced natural prey availability in the interior then (Begg 2001). This seasonal prey variation may cause caracals to extend their search for prey to the border areas where sheep production units are situated. That the caracals travel distances along all the roads that are similar to those travelled along the border road indicates that there is an equal use intensity of all the roads (Mahon *et al.* 1998).

No observations were made of caracals moving across the border road into or out of Namibia in the hot season. However, in the cold season when natural prey are less abundant (Begg 2001), crossings of the border road did occur, and then caracals may target small livestock on the Namibian side of the fence. This is further supported by the overall increased frequency of movement on all the roads in the cold season, indicating a more intense use of their range in search of prey.

It has been argued by many authors that spoor counts are only useful to detect large changes in population density (Kendall *et al.* 1992, Beier & Cunningham 1996, Strayer 1999). The seasonal changes in caracal spoor density and road use that was found in the present study confirm these arguments. Caracal spoor increases in density along the Namibian border in the cold season. These changes in intensity of road use are probably a natural response to seasonal changes in the abundance and distribution of natural prey (Begg 2001). Moreover, the sheep that are present on the Namibian side of the fence lamb in the winter and create an additional abundant prey resource for caracals then, which may attract them to the border areas.

Conclusions

It is likely that caracals vary their range use in the Kgalagadi Transfrontier Park along its borders with Namibia on a seasonal basis, with an increased intensity of use of the border area in the cold season. There also seems to be an increased incidence of border road crossings in the cold season into Namibia. This may reflect changes in the prey abundance within the Park and a concomitant increase in prey abundance in Namibia due to small stock lambing. However, there is no change in the mean length of discrete track sets along any of the transects in either season, suggesting that caracals use the roads with similar intensity year round, irrespective of their proximity to the Parks border with Namibia.

Due to the small data set, it is possible that the results may be affected by Type 1 errors (Beier & Cunningham 1996) with the hypothesis that caracal density may vary seasonally along the Namibian border being incorrectly rejected (Samuels 1991). Any management strategies that are implemented based on these conclusions should therefore be applied with circumspection. It is therefore recommended that a long-term monitoring system of road track counts of caracal and other larger predators be implemented along the border of the Kgalagadi Transfrontier Park with Namibia, and in the immediate interior region of the Park.

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CHAPTER 11

GENERAL DISCUSSION

The aims of this project were to investigate the behavioural ecology of free-ranging caracals in the Kgalagadi Transfrontier Park, and to try to establish whether the caracals from the Park impacted on the small stock farming industry in Namibia. To accomplish these aims it was necessary to complete a number of parallel studies to investigate various components of caracal behaviour that might have a bearing on the impact of caracals on the small stock farming industry. The results from each component study will therefore now be briefly discussed.

Capture, collaring, care and release

To conduct any study that requires radio-telemetry, it is first necessary to capture the research animals. To ensure that such a study is successful it is essential that the research animals be released in the same or better condition to that in which they were captured.

The two factors that have the greatest bearing on the success of any wild predator capture programme are the efficiency and selectivity of trapping (Boddicker 1999). To accomplish these goals in relation to the capture of caracals it was necessary to use box traps that were specifically designed for caracals. Therefore the cages that were used here were of a size that ensured that predators such as lions, brown hyaenas and spotted hyaenas could not enter the traps. To prevent smaller animals from tripping the caracal traps, the treadle can be set to release the trap door only after a specific pressure was applied (Boddicker 1999). However, this approach was not ideal because of the possibility of setting the treadle too coarsely and thus missing the capture of some caracals. Positioning the traps in areas of known caracal activity is the most effective method of improving the selectivity of such trapping.

Due to logistic, ecological and ethical considerations, live baits could not be used in the present study. Several combinations of bait and lure were therefore used in this study, the most effective and most frequently used bait and lure combination being fresh frozen chicken bait in conjunction with a shiny lure of tinfoil.

The low, (1.4 %) trapping success rate achieved in this study, compares well with that of previous studies on caracal (Stuart 1982, Norton & Lawson 1985, Moolman 1986, Avenant & Nel 1998). It emphasises the fact that caracals are inherently difficult to capture alive. The best way to improve the rate of capture is to saturate the study area with box traps. The only proviso is that each cage trap must be checked, cleared and reset on a daily basis.

To fit caracals with radio-collars and to measure and weigh them, it is necessary to immobilise them (Brand 1993). Of the methods that are available, the most effective and humane one to administer the immobilising drugs to a captured caracal was by physically restraining the animal with a crush plate that is inserted into the cage, before administering the drugs with a hand-held syringe.

McKenzie & Burroughs (1993) suggested that caracals be immobilised with a dose of 3 to 4 mg of Zoletil per kg of body mass. It was found that under field conditions it was preferable to prepare a standard dose of 50 mg of Zoletil for the immobilisation of wild caracals in box traps. All caracals captured were successfully immobilised with this dose, and no top-up dose was required whilst working on any of the animals. The estimation of body mass upon which to base the dose of Zoletil caused unnecessary stress to the captive animals and was often found to be inaccurate. Therefore it was discarded as an option.

To ensure that caracals remain cool whilst recovering from the narcosis, they were placed in the box traps in a cool, shaded place for the duration of their recovery. Once the caracals had recovered fully, the box traps were opened and the animals were released.

Range use by the caracal in the Kgalagadi Transfrontier Park

The ranges of the radio-collared caracals varied greatly. A female and two male caracals generated sufficient data to allow meaningful statistical analyses of the results. The range of male 1 was larger than that of male 2. It is likely that this discrepancy is due to male 1 being a dominant adult whose range encompasses the ranges of a number of females, whereas male 2 was a young subdominant animal. The range of female 1 was smaller than that of either male 1 or male 2. These results agree with the theory that female predators generally have ranges that are limited by the availability of prey and refuge sites, whereas males have range sizes that are dictated by their dominance status and the distribution of females (Sandell 1989). Two other caracals were collared and estimates of their range sizes were based on the available data. However, due to the small number of data points for each of these individuals, the ranges are not considered reliable. Male 3 was a young caracal that was tracked over a considerable distance before being killed in Namibia, probably while dispersing from his natal range. Female 2 was an older caracal that died of natural causes after having been collared for a month. During the period for which she was collared she remained in the vicinity of the Nu Quap windmill, in the interior of the Kgalagadi Transfrontier Park.

The ranges of the caracals in the Kgalagadi Transfrontier Park are larger than those that were found for caracals in other southern African studies (Stuart 1982, Norton & Lawson 1984, Moolman 1986, Avenant & Nel 1998). Bothma & Le Riche (1994) calculated the range size of a single male caracal in the southern Kalahari at 308 km^2, and in Saudi Arabia a single male caracal had a range of 1116 km^2 (Van Heezik & Seddon 1998). It is clear from these results and comparisons that caracal range sizes increase with increased aridity and reduced prey availability.

Habitat selection

The contribution of dune crests, dune slopes and dune streets to the Shrubby Kalahari Dune Bushveld (Low & Rebelo 1996) was calculated with the non-mapping method of Marcum & Loftsgaarden (1980). It was clear that caracals preferentially used the dune crests and dune slopes, probably because the elevation of the dune crests and slopes provides vantage points from which caracals can locate prey and other predators (Leyhausen 1979, Bothma & Le Riche 1989).

The suitability of the habitat for hunting seems to be a driving force behind the habitat selection of a caracal. A high density of *Rhigozum trichotomum* bushes, and of the annual grass *Schmidtia kalihariensis* that occur in these dune streets, and it inhibits the vision and movement of caracals in the dune streets. Caracals may also avoid areas of high *Schmidtia kalihariensis* density because the acidic exudates that this grass produces affects the animals negatively (Van Rooyen 2001).

Various authors have suggested that caracals prefer habitats that support large prey populations (Moolman 1986, Van Heezik & Seddon 1998). Preference for dune slopes is probably due to rodents occurring in higher densities there than on dune crests (Nel *et al.* 1984). The southwest facing dune slopes are generally steeper than the northeast facing ones (Van der Walt & Le Riche 1999). The sheer nature of the southwest facing slopes may inhibit caracal movements. Rodents seldom build burrows on southwest facing dune slopes because the sand there is less compact than elsewhere and the burrows collapse easily (Nel pers. comm.)[1]. The combination of these factors probably creates a habitat preference by the caracals for the northeast facing dune slopes.

The method that was used for detecting plant associations and their preferences by caracals for various activities has limitations, especially when caracals utilise plant species that are not recorded in a step-point transect that was used to collect the base-line plant frequency data. However, caracals do utilise certain plant species preferentially when performing certain types of behaviour.

Hunting behaviour

All hunts consist of a sequence of behavioural components that aim to kill prey. There are six basic behavioural components (crawl, stalk, crouch, take-off, chase, pounce) that could possibly be included in a hunt ending in a kill. There is no specific sequence or frequency of these behavioural components that comprise a hunt. Therefore the hunting behaviour of a caracal is highly adaptable and variable.

Moolman (1986) identified two separate strategies that are used by a caracal when hunting. The most frequently used one involved a caracal stalking the prey to within

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5 m, and then chasing it. A less frequently used tactic was hunting from an ambush. In the Kgalagadi Transfrontier Park, caracals tended to ambush their prey more often than stalking until close to them. Therefore stalking is the less frequently used tactic while hunting.

The hunting success of the caracal in the Kgalagadi Transfrontier Park is lower than that of other felids there (Eloff 1984, Bothma & Le Riche 1984). This may be due, in part, to the strict protocol that was used in the present study to determine whether a hunt was successful or not. When no visible evidence of a kill was found, the hunt was considered to have been unsuccessful. In the case of small prey, this might underestimate the hunting success achieved because caracals sometimes eat such an entire prey animal without disembowelling it. The success achieved by caracals when hunting large prey is similar to that recorded for leopard by Bothma & Le Riche (1984). It is probable that the distribution and abundance of prey limit the hunting success of caracal in the Kgalagadi Transfrontier Park. Therefore it seems that a high level of energy expenditure is required per unit of energy gained for a caracal to survive.

A hunting model was developed that was based on the differential likelihood of particular behavioural components resulting in a kill. It was hypothesised that hunting components should occur in a specific sequence to optimise hunting success. From the data analysis, it seems that the most successful strategy consists of five components, starting with a stalk, and then followed in sequence by a crouch, a take-off, a chase and finally a pounce. There are no restrictions to the number of repetitions of the behavioural components in a hunt, nor to the sequence in which they are performed. However, the model confirms that a logical sequence of goal-orientated behavioural components has the best chance of resulting in a kill.

Caracals in the Kgalagadi Transfrontier Park adopt similar methods to kill prey as reported elsewhere. They subdue large prey by pouncing on the prey and applying a non-fatal nape bite, followed by a killing throat bite to suffocate the prey. This is similar to the strategy that is applied by other large felids in Africa (Estes 1995). It is likely that caracals in the Kgalagadi Transfrontier Park use the same method to subdue small prey as was recorded in other studies (Grobler 1981, Stuart 1981, 1982, Moolman 1986, Stuart & Hickman 1991).

As in other studies (Grobler 1981, Stuart 1981, 1982, Moolman 1986, Stuart & Hickman 1991) caracals in the present study usually returned to large kills for a second feeding bout. This tendency was even observed in the vicinity of the Namibian border where the farmers often persecute the caracals. It is likely that in prey-poor environments caracals are found to return to their kills, even in areas of human activity.

Caracals cached the remains of larger kills under dense bushes, as was described by Bothma & Le Riche (1986) for leopards. However, caracals were never observed to cache kills in trees in the present study. Caracals often carried kills from the killing site to areas of more dense cover. This was probably done to prevent other predators spotting and competing for the kills.

Prey selection

The analysis of the diet of a predator should be representative of the diet of the population in that area. This means that the sample analysed should be large enough to include all possible prey. This part of the study was based on a sample of 116 scats, which is considered to be sufficient to give a reliable first order indication of the diet of caracals in the Kgalagadi Transfrontier Park. Rodents were the most abundant prey item for caracals in the present study, and they probably play a more significant role in the diet of caracals in the Kgalagadi Transfrontier Park than elsewhere in South Africa because of the low density of alternative prey (Avenant & Nel 1997). The tendency of using a high proportion of rodents was also observed for a single male caracal in Saudi Arabia (Van Heezik & Seddon 1998).

Springhares are the single most important prey item in the diet of caracals in the Kgalagadi Transfrontier Park. Although they are rodent too, they can be separated from the other rodent prey because of their large body size and concomitant high nutritional value to caracals.

Carnivores form a significant proportion of the diet of caracals in the Kgalagadi Transfrontier Park. The contribution of carnivores to the diet of caracals in the present study is higher than that recorded in other studies (Grobler 1981, Moolman 1986, Palmer & Fairall 1988, Stuart & Hickman 1991). It seems that the carnivores in the diet of caracals in the present study fill the medium to large prey category that is usually filled by small artiodactyls in other habitat types.

Predation on diurnal prey indicates that the caracals in the Kgalagadi Transfrontier Park display some level of diurnal activity. This supports the conclusions of Avenant & Nel (1998).

Wool from domestic sheep was found in eight of the 116 scats. Most (75 %) of the scats that contained wool were found in the cold season. It appears that caracal prey more upon domestic stock in the cold season when the abundance of natural prey is relatively low (Begg 2001) and the domestic stock are lambing to create a temporary potential prey peak.

Birds contribute less to the diet of caracal in the Kgalagadi Transfrontier Park than in the West Coast National Park (Avenant & Nel 1997). This low utilisation of avian prey is surprising because various birds, including the Kori bustards and korhaans that occur within the present study area, were thought to be ideal prey for a caracal.

Invertebrates do not contribute significantly to the diet of the caracal, due to their low individual biomass. Nevertheless coleopteran remains were found in a high proportion of the scats in the present study. This supports the findings of Palmer & Fairall (1988) that insects do contribute to the diet of caracals.

Caracals generally consume vegetable matter accidentally. The majority of the vegetable matter that was recovered from scats in the present study included grass, twigs and seeds. No scats that only contained plant material were found. No conclusive reason for the ingestion of plant material has been proposed. Most of the consumption is likely to be accidental. Tsamma melon seeds were found in three (2.6 %) of the scats. This confirms that caracals, like many other carnivores inhabiting this environment, do eat tsamma melons to supplement their moisture intake (Eloff 1984, Mills 1990, Bothma & Le Riche 1994).

Possible optimal foraging for Brant's whistling rats

It seems that the caracals display a level of optimal foraging when hunting for Brant's whistling rats in the hot season. In the cold season there is no evidence of optimal foraging. This is probably due to low relative abundance of Brant's whistling rats during the cold season. Caracals therefore follow a random search pattern in terms of Brant's whistling rats in the cold season, but in the hot season they follow paths that include a relatively high number of Brant's whistling rat colonies as part of optimal foraging.

The effect of small stock farming in Namibia on caracal density in the neighbouring Kgalagadi Transfrontier Park

Spoor density is an accurate index of animal density (Litvaitis *et al*. 1985, Smallwood & Fitzhugh 1994, Stander 1998, Jacomo & Diniz-Filho 2003). To determine whether caracals were actively moving on to Namibian small stock farms from the park, it was necessary to monitor whether the density of caracals in the interior of the Kgalagadi Transfrontier Park was identical with that along the Park's border with Namibia. If there were a cline of increasing spoor density from the interior towards the Namibian border, it would indicate that caracals were moving towards the stock farms.

Climatic factors and ground conditions influence the detectability of spoor along a track (Silveira *et al.* 2003). Provided that the detectability of spoor remains constant in all areas of the survey, the same level of error can be expected (Burnham & Anderson 1984). Hence, the error can be factored into the estimation of animal density.

It appears that in the hot season there is a low density of caracal spoor along the Namibian border in comparison with the interior of the Kgalagadi Transfrontier Park. In the cold season the spoor density in the interior and along the border are the same. Therefore it appears that caracals actively avoid the areas along the Namibian border in the hot season. However, in the cold season, when natural prey is more limiting, caracals utilise the areas along the Namibian border to the same extent as they use the interior of the park.

Because many authors feel that spoor counts are only useful for detecting moderate to large changes in population density (Kendall *et al.* 1992, Beier & Cunningham 1996, Strayer 1999) it is clear that there is a change in caracal density in the vicinity of the Namibian border between the hot and cold seasons. This further substantiates the theory that caracals move across the Namibian border more in the cold season when the abundance of natural prey is relatively low (Begg 2001) and the domestic stock are lambing to create a temporary potential prey peak.

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CHAPTER 12

MANAGEMENT RECOMMENDATIONS FOR CARACALS IN THE KGALAGADI TRANSFRONTIER PARK

Caracals that come from the Kgalagadi Transfrontier Park have an impact on small stock farming in Namibia, but it is not possible to quantify the extent of this impact objectively. From the results of a questionnaire survey that was done in Namibia, the perception is that caracals have a serious impact on small stock production. The estimated losses of small stock to predation vary from none to 40 %. The farmers believe that the vast majority of the problem animals come across the boundary fence from the Kgalagadi Transfrontier Park. There is no way to objectively quantify whether these estimates are accurate. To do this would require a long-term monitoring programme of caracal depredation on the small stock farms in Namibia. In addition, there is also the perception among the Namibian farmers that the officials of the Kgalagadi Transfrontier Park are apathetic to what happens on the Namibian farms that are adjacent to the Park. Additionally, the Park officials are viewed as being unhelpful when Namibian farmers report predator depredations.

It is obvious that even if the estimates of the level of the impact are exaggerated and incorrect, there is a perception that predators have a great impact on the small-stock farming enterprises in Namibia close to the Park. As long as this perception remains and the South African National Parks are regarded as being apathetic to the plight of the farmers (Botha 2000), the friction between the farmers and the conservation organisation will persist.

The ranges of caracals *Caracal caracal* do include both the Kgalagadi Transfrontier Park and Namibia in some places. The caracal population in South Africa is therefore contiguous with that of Namibia. The border fence is no obstruction to the movements of caracals (Moolman 1986) whether moving to or from Namibia. Although a new fence is currently being erected, it is unlikely that this fence will stop caracals from moving freely across it. The erection of a caracal-proof fence would be too costly to consider. Although a well maintained, electrified fence should be a deterrent to caracals that want to move across the border, and consequently will reduce the frequency of such border crossings, the environment and the animals that occur near the border fence will require it to be constantly maintained. A strict protocol of border patrols should be reinstated to ensure that the fence and its electrification system are properly maintained on a regular basis.

Some of the caracals that occur in areas of the Kgalagadi Transfrontier Park that are close to the Namibian border do prey on sheep (Melville *et al.* 2004). However, the extent of caracal utilisation of small stock in the Kalahari is less than what has been recorded elsewhere where a conservation area borders agricultural land (URL: http://lynx.uio.no/catfolk/ssacr101.htm). Moreover, the majority of the incidences of depredation on livestock in Namibia occur in the colder months (Melville *et al.* 2004). This is synchronous with the lambing season of the sheep and the reduced abundance of natural prey in the Park. The frequency of border patrols should therefore be increased during the cold months.

One of the common practices that was noted in the Kgalagadi Transfrontier Park was the capture of rogue animals that had crossed into Namibia. It is recommended that this practice only be retained in the case of large predators crossing the fence. In the case of caracals and other small predators, this practice will be too costly in terms of time, manpower and vehicle wear and tear. Additionally, the chance always exists that staff members could be injured in the process of tracking predators. Repatriating caracals to the Park is also often unsuccessful.

Spoor counts provide an effective and relatively low cost method to monitor predator populations (Funston *et al.* 2001). Spoor counts indicated an increase in caracal activity along the Namibian border in the cold season. A system of spoor counts should be used while doing the regular border patrols to confirm the pattern of increased use by caracals of the border area in the cold months. Additionally, the results of all the spoor counts should be communicated to the Namibian farmers so that they can identify possible high impact zones and periods.

The implementation of management strategies such as employing shepherds, running sheepdogs with the flocks and bringing the flocks in at night (Mazzolli *et al.* 2002) are not viable in the Namibian context. Not only is the viability of this strategy limited by the extensive farming system that is being used in Namibia, but also it is limited because dorper sheep are involved for mutton production in this area (Campher *et al.* 1998). Dorper sheep do not form flocks and they disperse throughout the camps, making regular control and monitoring of flocks impossible. This trait also increases the vulnerability of the sheep to predation.

Various methods of lethal predator control, including gin-trapping, box-trapping, poisoning, predator-calling, tracking, hunting and using packs of hounds are employed (Bowland *et al.* 1990), by the Namibian farmers, to eliminate problem animals. Most of these methods are unselective and therefore there is no guarantee that the predator responsible for killing livestock is the one that is killed during such control operations.

The most effective, and selective method of destroying a problem animal in the Kalahari is spoor-tracking. The benefit of this method is that, provided that the spoor is followed from the fresh sheep carcass onwards, there is a high likelihood that the animal responsible for killing the sheep will be found and destroyed. All predators will visit a carcass, and if the carcass is not fresh there is a high likelihood that other predator spoor will have obscured the spoor of the responsible predator. Where fresh carcasses are found in the veld it is normally possible to determine whether the animal was killed by a predator or had died of other causes.

Unselective extermination of predators is not the ideal solution to predator control. Predators such as the caracal are opportunists and utilise the most suitable available prey resource. Small stock depredation is a learned behaviour (Stahl *et al.* 2001), and once a predator has experienced killing small stock it is likely to continue doing so. The destabilisation of a predator population by random extermination simply promotes increased recruitment in these areas because there is a surplus of available space and the environment does not limit the predator population. Where possible, it is therefore preferable to eliminate the individual animal that is responsible for the killing of the stock (Stahl *et al.* 2001). In the case of caracals it is difficult to recognise individuals from a distance, and therefore most small stock farmers assume that all caracals are problem animals.

The most effective and selective method for controlling small predators such as caracals is the use of toxic collars (Bowland *et al.* 1990). The collars are fitted to particular sheep and the poison affects only animals that attack those sheep. The problems are the capital outlay that is required to acquire the collars initially, and the labour involved in putting the collars on the sheep. This method may be appropriate for use on high value stud animals, but whether it is justifiable to use it extensively on large flocks of dorper sheep is questionable.

The use of poison baits is generally unacceptable unless the implementation of such a strategy is closely supervised by an experienced person, because of its non-selective nature and the likelihood of secondary poisonings (Bowland *et al*. 1990).

Stuart (1982) suggested that methods such as aversive conditioning and chemosterilants be used. These methods may be effective in controlled intensive pasture systems or areas with relatively high predator densities, but it is questionable whether such methods would be effective in the open, arid spaces of the Kalahari.

The final alternative is to change the production system on the farms, either to an alternative breed of sheep, or to a combination of sheep and wild animals. Although perhaps not as profitable as the dorper sheep an alternative might be to change over to Damara sheep production. The Damara sheep is an indigenous breed that is known to protect its young aggressively from predators. This breed is also adapted to thrive in harsh environmental conditions (Campher, Hunlun & van Zyl 1998). An option that many farmers seem to be implementing currently is the introduction of wild animals as an additional source of revenue, either through tourism or through consumptive utilisation. The problem with such a switch in breed or livestock type is the initial financial loss that will inevitable.

There is no cheap, effective solution to the predation of small stock by caracals or any other predators along the Namibian border with the Kgalagadi Transfrontier Park. The method that is likely to reap the most immediate benefits is an increase in management effort from both the South African National Parks and the individual Namibian farmers. A joint but sincere effort by the farmers and the Parks officials should be made to maintain the fence. However, from various discussions with the Namibian farmers it was clear that they felt that the maintenance of the fence was not their problem. This attitude will have to change to the mutual benefit of both parties involved if they are serious about reducing stock losses to predators.

Where known problem animals can be identified, they should be eliminated. Such a strategy should be adopted with caution, however, because the removal of animals that do not prey on sheep will make space available for colonisation by another individual that might be more inclined towards preying on domestic stock than the one that was removed.

Communication between the South African National Parks and the Namibian farming community should be improved. An open exchange of ideas and information is the ideal. In doing so, the rationale behind the Park's management decisions should be communicated to the farmers. Ultimately an educational process has to take place to change the attitude amongst the farmers from the belief that all predators are problem animals to one that only some predators become problem animals, and must be dealt with.

Any active management programme for the control of predators on farmlands should be implemented with the economic viability of the endeavour in mind. If the control method is more costly than the value of the actual stock losses, there obviously is no profit in implementing such a management programme.

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BEHAVIOURAL ECOLOGY OF THE CARACAL IN THE KGALAGADI TRANSFRONTIER PARK, AND ITS IMPACT ON ADJACENT SMALL STOCK PRODUCTION UNITS

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Summary

A study was done on the behavioural ecology of caracals in the Kgalagadi Transfrontier Park, and their potential impact on the small stock-farming enterprises along the border of this park with Namibia.

To fit caracals with radio-collars it was necessary to capture animals by using the most humane and efficient methods. This required that the most effective bait and lure combination for use in box traps must be selected. The most effective bait and lure

combination in the present study was fresh chicken with a shiny foil lure that was suspended in the back of a single-door box trap. To further optimise selectivity of the capture technique, box traps that were too small for lions, brown and spotted hyaenas were positioned in areas of known caracal activity. Refinements to the cage design included the introduction of a crush plate to handle captured caracals. This crush plate limited the freedom of movement of the caracal by physically restraining it inside the box trap. The benefit of using the crush plate was that an accurate dose of the immobilising drug could be administered, with a hand-held syringe. Once the caracal had been collared, weighed and measured, it was returned to the box trap to recover. The box trap was placed in a cool area and the caracal was only released once it had fully recovered from the effects of the immobilising drugs.

To determine whether the ranges of caracals from the Kgalagadi Transfrontier Park extended beyond the border of the Park, caracals that had ranges in the vicinity of the Namibian border were captured and collared. The collared animals were located regularly with the aid of radio-telemetry. On all occasions the caracal's location were confirmed visually. The GPS position of each caracal location was recorded. Where appropriate, the ranges of the caracals were calculated by using two statistical and one non-parametric method with two current range estimation computer programs. This enhanced the comparability of the results of this study with future studies. Caracals in the Kgalagadi Transfrontier Park have larger ranges than caracals in other areas of southern Africa. The ranges of caracals from the Kgalagadi Transfrontier Park extend beyond the borders of the Park into Namibia. This indicates that the border fence does not hinder the caracal movements and that the caracal population in South Africa is contiguous with that of southern Namibia.

The Shrubby Kalahari Dune Bushveld is a homogeneous habitat but it does display repetitive and distinct vegetation stratification over a short distance. The habitat stratification is based on the position of the vegetation relative to the slope of the sand dunes. The three habitat components that were used were the dune streets, dune slopes and dune crests. The contribution of each of these components to the total habitat use was calculated by using a non-mapping method. The utilisation of the various habitat components by the caracals was based on spoor-tracking data for a number of individuals from June 2000 to July 2002. It was found that caracals utilised the dune slopes and dune crests in a higher proportion than that in which they occurred, but that they used the largest habitat type, the dune streets, less often than expected. In addition, the preferential utilisation of various plant species by the caracals in conjunction with specific types of behaviour was investigated. It was shown that caracals utilised specific plant species for specific stationary behaviours.

Hunting is a fundamental activity of any predator. A large proportion of the activity of a caracal is devoted to searching for and hunting of prey. To investigate the nature of the hunting behaviour of the caracal and to calculate their hunting success, caracal spoor was followed with the assistance of an experienced Kalahari San tracker. The tracker described the behaviour as it unfolded along the length of the spoor. Hunting behaviour was subdivided into six intrinsically linked behavioural components. From these observations it was clear that caracals adopted a tactic of lying in wait to ambush prey rather than trying to locate prey first and then stalking it. Further, an optimal hunting strategy for caracals was modelled based on the sequences of behavioural components that were recorded for all the hunts. It is clear that there is an optimal hunting strategy, but this strategy is variable and adaptable based on the situation and prey. Large prey was chased over longer distances than small prey. The hunting success rate of caracals in the Kgalagadi Transfrontier Park is low when compared to other predators in this region and with similar sized predators elsewhere. This is likely to be because of the relatively low prey density and the strict protocol that was used in the present study when identifying successful kills. Observations of the killing techniques that caracals used on larger prey could be seen from the bite marks on carcasses of prey. However, the killing technique that was used on small prey could not be observed because the method of observation that was used was indirect, and caracal often consume small prey totally. When caracals cached carcasses of large prey, they regularly returned to them for further feeding bouts.

Prey selection by caracals in the Kgalagadi Transfrontier Park was determined by using scat analysis and records of known prey that had been hunted. The prey consisted of a high proportion of rodents, but surprisingly few bird remains were found in the scats, even though there seems to be an abundance of birds that would be suitable as prey. Insect remains were found in a high proportion of the scats and this indicated that although insects might not contribute significantly to the total prey biomass, caracals do eat insects. Plant material was found in many of the scats, but in the majority of cases this is probably attributable to accidental ingestion whilst grooming or feeding. However, seeds of tsamma melons in the scats indicate that caracals may eat tsamma melons to supplement their moisture uptake, as do other predators in this area.

Many authors have proposed that animals may forage optimally, although whether this theory holds in the case of predators when hunting has not been substantiated yet. It is possible that caracals follow an optimal search pattern relative to Brant's whistling rats in the hot season. This was based on a comparison of the frequency of occurrence of

Brant's whistling rat colonies along randomly placed transects with the frequency of occurrence of colonies along caracal spoor.

Namibian farmers feel that caracals from the Kgalagadi Transfrontier Park actively move across the border, into Namibia, to prey upon small livestock. To investigate whether this was the case, spoor counts were used as an index of caracal density. The spoor density in the interior of the Park was compared with that along the Park's border with Namibia. If the spoor density were higher along the Namibian border than in the interior of the Park, it would indicate that caracals being attracted to the border areas. It was found that in the hot season there was a lower caracal spoor density along the border of the Park than in the interior. However, in the cold season there was an equal density of spoor along the border and in the interior. The results indicate that the caracals avoid the border areas in the hot season, but that they increase their utilisation of the border areas in the cold season when the natural prey are depleted and the small stock are lambing.

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