Aspects of the communication and feeding behaviour of captive leopards *(Panthera pardus)*

by

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For my heavenly Father,
parents Charl and Hettie van Wyk,
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Chapter 1

Introduction

The leopard (*Panthera pardus*) is the most widespread of all the world's large cats and also the only one that managed to survive in reasonable numbers outside conservation areas. This was achieved despite the long history of conflict between the leopard and livestock farmers, which resulted in intense prosecution. Its ability to survive can be ascribed to its secretive, solitary and largely nocturnal habits, as well as its ability to adapt to a wide range of environments. However, despite the leopard being more resilient than other carnivore species, there is concern with regard to its future welfare.

With the recent expansion of the game ranching industry in South Africa the leopard is receiving increased attention. In the Limpopo Province it is estimated that about 2 300 farms have already been fenced with game proof fences, of which 83% with exemption. This represents an area of 3.6 million ha (26% of the total area of the province) (Van der Waal & Dekker 2000). The shift towards game ranching has benefited the leopard in expanding habitat availability and increased availability of prey animals. With game fetching record prices at game auctions at an average countrywide increase of 15% per annum for the period 1992-2003, losses due to leopard predation is often viewed by landowners in a more serious light than stock losses. This is especially true in the case of rare game species like roan (*Hippotragus equinus*) and sable (*Hippotragus niger*) antelope. This result in an increased prosecution of the leopard.

Viewing the leopard as a problem animal is in sharp contrast to its status as one of the "Big 5" and tourism's "Big 7". In view of the expanding eco-tourism industry in South Africa the leopard, remains one of the most sought after tourist attractions. Due to its secretive habits, any sighting of a leopard in its natural environment remains to those privileged enough to experience such a sighting, a highlight rivaled by no other species. Yet, very few tourists have experienced the privilege of spotting a leopard in the wild.

From the above discussion it is clear that the leopard is viewed by some as a problem animal that must be eradicated at all cost, and by others as an animal of great value, worthy of protection. A partial solution to this conflict may lie in the isolation of leopards

by restricting their movement to suitable areas where they are wanted, thus protecting them from prosecution in areas where they are viewed as problem animals.

Finding long-term solutions to the conservation of leopards and their management as problem animals will only be possible through a thorough understanding of their social and feeding behaviour. Communication of leopards is regarded as an integral component of their social behaviour. Subsequently the objectives of this study were to study the communication and feeding behaviour of captive leopards within a natural environment. However, it is also envisaged that the knowledge gained from this research will be applicable to free ranging leopards and the potential conflict between free-ranging leopards and game and livestock-farmers. In addition, this information will also be of benefit to the eco-tourism industry which relies on leopards as a tourist attraction.

Chapter 2
Literature review

2.1 Introduction

In sharp contrast to the 130 references to the lion in the Bible, there are only 8 references to the leopard (Hebrew = n~m-r). The leopard is more secretive and quiet, and thus not nearly as well known to the Hebrew society as the lion (Schmid 1997).

In early records the leopard was known mostly by its Dutch name "tijger" or "tyger", (often used in its English form "tiger"). The name gradually evolved to the Afrikaans name "tier", but currently the leopard is known by the Afrikaans name "luiperd". In the diary entry for 30 March 1654, Van Riebeeck wrote of domestic sheep grazing in the table valley, "Many are also carried away and devoured every day by leopards, lions and jackals...". A more poignant entry for 2 May 1655 read: "Last night the tigers killed six of our Dutch sheep in the enclosure, and that in the presence of two persons keeping watch. In the evening the tigers had also been in the hen house, killing the only three geese we had left, and biting a certain person severely on the arm when he tried to scare them away. It seems as if the wild animals will again be worrying us..." (Skead 1980).

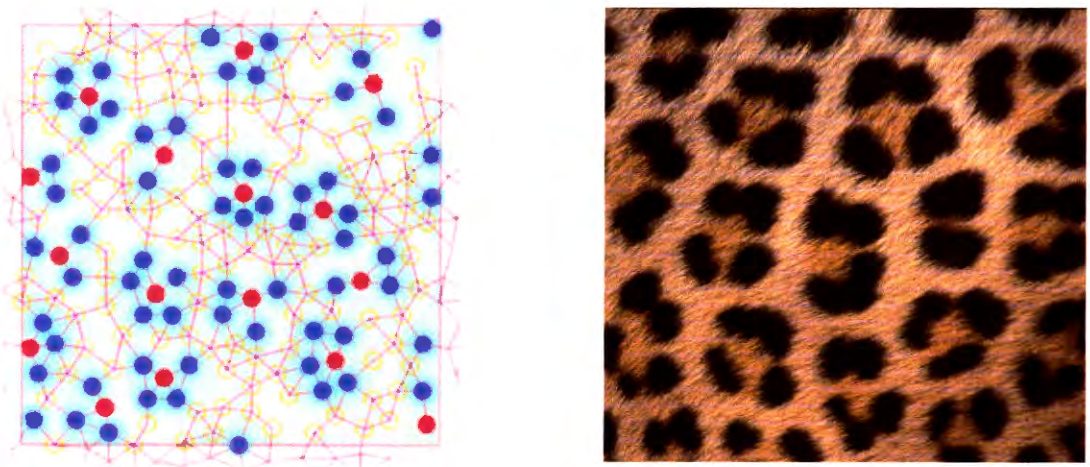
Through ages the leopard was and still is a mysterious and secretive animal to man. Because of their nocturnal and unknown behaviour it is feared in many ways, in either loss of livestock (food) or one's life. Based on current information it is evident from a broad overview of the literature that there are still large gaps in our knowledge of leopards.

2.2 Description

2.2.1 Body colouration

Like human fingerprints, each individual leopard's spots are unique. No two leopards are alike, either in the markings or the base colour. But in general they tend to have black spots on the limbs, flanks, hindquarters and head with rosettes on the remainder of the body.

The leopard's spots were posed and solved by Turing (1952) (Figure 2.1). Turing's solution involved a diffusion-reaction mechanism on a regularly arranged continuum of cells. The dynamics of diffusion-reaction is described and proved in terms of differential equations (Turing 1952, Murray 1989).



(a) (b)

Figure 2.1 A global pattern of cell-states in a spot like pattern (a) (Turing 1952), creating and structuring the pelage and rosettes of the leopard (b).

In Figure 2.1a, vertices represent cells, edges represent cell-cell communication and colour represents cell states. A spot is a single red cell totally surrounded by a minimal set of blue cells. As a group, the red-blue configuration is surrounded by a set of yellow cells, which keeps the spots from touching and is minimal (Turing 1952).

Variation in pelage has been the main basis for the description of numerous subspecies of leopard, from 13 (Skinner & Smithers 1990) to 24 in sub-Saharan Africa alone (Smithers 1975). However, Miththapala (1992), using molecular analysis and cranial measurements, concluded that sub-Saharan African leopards show too little difference

to warrant sub-specific division and proposed that the 10 sub-Saharan subspecies examined should be subsumed into *Panthera pardus pardus*, the name originally applied to the North African leopard.

The total length of a leopard can be two meters, of which the tail contributes approximately 80 cm (Yosef, 1998). This is more than half the combined length of the head and body (Skinner & Smithers 1990). When moving the tip of the female's tail is curved upwards, revealing its white underside which may act as a guide to the young in tall grass (Bertram 1978). The revealed white tip thus serves as a marker for cubs to follow, known as the "follow-me" signal (Estes 1999).

Black leopards (the so-called "black panthers") occur most frequently in humid forest habitats (Kingdon 1977), but are merely a colour variation, not a subspecies. Pocock (1932) found the following trends in colouration for leopard in Africa:

(i) Savanna leopard – rufous to ochraeceus in colour,

(ii) Desert leopards – pale cream to yellow-brown in colour, with those from cooler regions being more grey,

(iii) Rainforest leopards – dark, deep gold in colour and

(iv) High mountain leopards – even darker in colour than (iii).

2.2.2 Morphological and physiological trends

Exceptionally large leopard males weighing over 91 kg have been reported from the Kruger National Park (Turnbull-Kemp 1967), but the average weight of adults is 58 kg for males (n=3) and 37.5 kg for females (n=5) (Bailey 1993). Male leopards from the coastal mountains of South Africa's Western Cape Province are much smaller, with an average body mass of 31 kg (n=27) (Stuart 1981). Norton (1984) suggests that this is because prey species are smaller in these mountains. So far the largest individual measured from tip of snout to tip of tail was 2.92 m, but any leopard over 2.3 m can be considered large (Skinner & Smithers 1990).

As seen above, males are generally bigger than females and therefore their skulls are correspondingly larger. Male skulls have a distinct sagittal crest, whereas at maximum development it is represented as a low ridge in females. When viewed from above, the

postorbital constriction in males is narrower than the interorbital. In females this relationship is reversed. The zygomatic arches are broad and heavy to accommodate the powerful masseter muscles, which swing outward to the back to give room to the temporalis muscles. Together with the masseter this provides for the powerful action of the lower jaw. The lower jaw is heavily built with a broad, high coronoid process giving ample attachment for the temporalis muscles. The posterior end of the lower jaw is deeply excavated to allow a broad attachment of the masseter. The glenoid articulation allows just sufficient side-to-side action of the lower jaw to ensure cutting action of the carnassials. The upper second premolars are usually present in the leopard. The canines are sharp-pointed, heavily built and slightly flattened on the inner sides. The cheek-teeth, which include the carnassials, are clearly adapted to slicing. The upper first molars are tiny and hardly functional (Skinner & Smithers 1990).

Equally important than the specialised teeth is the leopard tongue. Like a common domestic cat (*Felis catus*), the leopard has a rough tongue covered with hook shaped structures called papillae. However, whereas the domestic cat's tongue feels merely scratchy or rough, the leopard's tongue can literally peel off the fur and skin of its prey.

The quard hair is shortest on the face and head where it is merely 3-4 mm long, about 10 mm on top of the shoulders and 15 mm on the hindquarters. Increasing in length on the flanks, it may reach a length of 25-30 mm on the under parts. On the back it has a harsh feel, but the hair on the under parts is silky and softer. The light-coloured hair under the tail may reach a length of 30 mm and is particularly thick and woolly towards the tip. The leopard's whiskers are particularly long and there are often several extra long hairs in the eyebrows, protecting the eyes and assisting movement through vegetation in darkness (Skinner & Smithers 1990).

Females have two pairs of mammae on the belly (Skinner & Smithers 1990).

With soft padded paws, the leopard is a digitigrade walker; only the five digits on the front feet and four on the hind feet touch the ground. Curved claws in a medium-sized specimen measured up to 30 mm across the curve and can be protractile at will. The claw of the first digit on the front feet, the dew claw, lies to the back of the plantar pad,

and is put to good use in holding larger prey. The claws and first digit on the front feet do not mark in the spoor (Skinner & Smithers 1990).

The scapula is adapted for the attachment of powerful muscles that raise the thorax, enhancing its ability to climb trees (Hopwood 1947).

2.3 Population and protection status

2.3.1 Population status

The status of the leopard in sub-Saharan Africa has been a matter of controversy since 1973, when it was first listed in CITES Appendix I due to fear about the impact of the then considerable international trade in leopard skins. Six attempts have since been made to determine the leopard's status (Myers 1976; Teer & Swank 1977; Eaton 1978; Hamilton 1981; Martin & De Meulenaer 1988; Shoemaker 1993). The first four relied mainly on interviews and questionnaires, but Hamilton's (1981) work was more intensive, supplemented by the author's own field studies, and focused wholly on Kenya as a microcosm of the forces impacting leopard populations throughout the continent. Martin & De Meulenaer (1988) also carried out wide ranging interviews, but carried the process one step further by developing a population model for the leopard, which they used in combination with a regression linking leopard densities with annual rainfall to predict numbers of leopard in the region. More recently, Shoemaker (1993) conducted an extensive literature review and global correspondence to summarise the status of the leopard throughout its entire world range.

The first five studies were criticised from different viewpoints (e.g., Hamilton 1981; Martin & De Meulenaer 1988; Jackson 1989; Norton 1990), with the debate focusing chiefly on the accuracy of various population estimates, namely:

(i) The model's failure to account adequately for persecution and reduction of wild prey as factors lowering leopard density.

(ii) The universality of the correlation between leopard density and rainfall.

(iii) The desirability or not of re-opening commercial trade in leopard skins.

Bailey (1993) argues that while the link between herbivore density and rainfall may be generally valid, a herbivore biomass could be in the form of very large species (elephant, buffalo, hippopotamus) or herd-forming species (zebra and wildebeest), which provide little food for leopards.

Despite the controversy, there appears to be general agreement that the leopard is not currently endangered in sub-Saharan Africa, but that it is subject to local depletion through exploitation and loss of habitat. Overall, Martin & De Meulenaer (1988) estimated the sub-Saharan population to number 714 000, based on their density/rainfall regression. Although this figure is generally considered to be an overestimate (Jackson 1989; Norton 1990), it represents the most practical and quantitative attempt to date to estimate potential cat numbers across a large geographic area. Its accuracy should be tested and improved by continuing investigation into leopard densities in key habitats, including tropical rainforests.

All biologists working in the central African rainforest describe the leopard as a common sight. The rainfall/density regression suggests that Zaire would hold some 33% of sub-Saharan African leopards, a figure resulting from presumed very high densities in tropical rainforest (up to 40 leopards, including young and transients, per 100 km²). However, Bailey (1993) is one of several authorities who have argued that since terrestrial mammalian prey biomass is lower in rainforests than in savanna environments, as the bulk of productivity is locked up in the tree canopy, the leopard density should be correspondingly lower in rainforests.

Martin & De Meulenaer (1988) estimated 40 leopards per 100 km² suggested by their rainfall/density regression. Schaller (1972) estimated 3.5 and Cavallo (1993) 4.7 leopards per 100 km² for the Seronera woodland area of Tanzania's Serengeti National Park, which are among the greater densities on the rainfall/densities regression if the rainforest estimates are excluded. In South Africa's Kruger National Park, Bailey (1993) estimated the average leopard density at 3.5 adults per 100 km², with much higher densities (up to 30.3 per 100 km²) in the riparian forest zones with high prey density. Leopard densities are lowest in arid environments (Martin & De Meulenaer 1988): for example, 1.25 adults per 100 km² in South Africa's Kgalagadi National Park (formerly known as the Kalahari Gemsbok National Park) (Bothma & Le Riche 1984). Hamilton

(1981) and Cavallo (1993) found that multiplying the number of adult residents by 1.7 accurately accounted for the total number of known animals in their study areas.

Leopards appear to be least numerous in West Africa, possibly due to high levels of hunting for their skins, and depletion of prey due to the trade in bush meat (Myers 1976; Martin & De Meulenaer 1988). A severe reduction in abundance of leopards was reported from the West African rainforest zone (Martin & De Meulenaer 1988). Also, in South Africa, the leopard has been extirpated from many areas (Stuart, Macdonald & Mills 1985; Norton 1986; Rowe-Rowe 1992).

The size of leopard home ranges as determined by radio telemetry, vary between an average of 30 – 78 km² (males) and 15 – 16 km² (females) in protected areas (Tsavo National Park: Hamilton 1981; Kruger National Park: Bailey 1993; Serengeti National Park: Bertram 1982; Cedarberg Wilderness Area: Norton & Henley 1987). However, long-term observations of individual female leopard indicated larger home range sizes in protected areas: 23 – 33 km² (Le Roux & Skinner 1989) and 37 – 38 km² (Cavallo 1993). Bailey (1993) found the ranges of adult females were centered near the most prey-rich habitat (riparian vegetation), while the larger male ranges included lower quality habitat. In mountainous terrain interspersed with farms and ranches, Norton & Lawson (1985) found home ranges of 338 km² for a male and 487 km² for a female, which indicate both severely reduced prey availability and low leopard density. On a Kenyan cattle ranch, which maintained wild ungulates, Mizutani (1993) found female leopard home ranges to average 18 km² (n=4) and those of males 55 km² (n=4).

2.3.2 Protection status

The leopard being considered a problem animal from as early as 1654, Jan van Riebeeck introduced a regulation placing rewards on the killing of beasts of prey, including the leopard. Subsequently, on 19 July 1656 a leopard was shot at Rondebosch and the forest worker was rewarded with three reals of eight in cash according to the resolution adopted on 17 June 1656, less than a month before. For the year 1664 several encounters with leopards were recorded. Leibrandt 1901 quoted an entry for 21 May 1664 which states: "This morning two leopards, the worst destroyers and murderers of the sheep, were shot and brought to the Fort. Later, a large leopard was shot in Table

Valley on 16 June 1664, and two others were shot below Windber, now known as Devil's Peak, on 23 October and 2 November 1664." During 1679 a new tendency of fur trade in leopard skins came to the fore. Skins were taken to Mittleburg and sold (Skead, 1980).

(Skead, 1980) quoted a certain O.F. Mentzel who during the late 1730's and early 1740's said: "We have already mentioned that the Company formerly paid 10 Rixdollars without exception for a dead tiger (leopard); but at present, since it is too difficult for the killers to obtain an affidavit that the animal was not killed by a gun-trap, and since tigers (leopards) are no longer to be found near the City, it is not worth while for the inhabitants to undertake a long journey to deliver a tiger-skin for the sake of 10 Rixdollards."

Since those early years the leopards have rapidly declined in numbers. This is evident from a statement by a certain Barnaba Shaw who said on 25 July 1838 that leopards were far from common and that they preyed on baboons and smaller animals (Skead 1980).

During the 1960's and 1970's the fur trade was a major threat to the leopard in some areas. Responding to the conservation crisis, 21 countries came together in 1973 to sign CITES, the Convention on International Trade in Endangered Species. CITES came into force in 1975, and South Africa joined the Convention that same year. CITES established three levels of protection of wild species (EWT 1994);

(i) Appendix I

Species thought to be in danger of extinction due to international trade, including the leopard, *Panthera pardus*. International trade was banned and import and export permits were required,

(ii) Appendix II

Species that might be threatened by international trade if the trade was not properly controlled. Export permits were required and import permits are required in some cases,

(iii) Appendix III

Indigenous species were listed in this appendix in order to help with the enforcement of national trade controls.

There was a peak during 1944, when in Uganda alone 2 344 permits for skins were sold. Hamilton (1981) reported that poaching for the fur trade substantially reduced the leopard population in Kenya, and he considered the species to be particularly vulnerable to baited trapping, as leopards patrol small home ranges along regularly used trails. The use of poisoned bait is also an important threat (Myers 1976). Martin & De Meulenaar (1988) simulated the effects of high harvests on leopards in East Africa during this period (they estimated that 30 000 leopards were killed between 1968 – 1969), and concurred with Hamilton's (1981) finding that hunting contributed to the severaly depressed populations. However, their model also indicated that even very high off-takes, in the order of 61 000 animals per year, had produced only a slight decline in the total Sub-Saharan population.

Statistics are:

Panthera pardus pardus:	African leopard	500 000 in wild
Panthera pardus nimr :	Middle Eastern	Nearly extinct
Panthera pardus jarvisi:	Middle Eastern	Nearly extinct
Panthera pardus saxicolor :	Persian leopard	Nearly extinct
Panthera pardus orientalis:	Amur leopard	30 – 50 in wild

A system by which selected countries accept an annual quota for the export of legitimate sport hunting trophies and skins has been in place since 1983. As from 1994, the quotas have been as follows: Botswana (130), Central African Republic (40), Ethiopia (500), Kenya (80), Malawi (50), Namibia (100), Mozambique (60), South Africa (75), Tanzania (250), Zambia (300), Zimbabwe (500). Killing of "problem" animals, either by landowners or government authorities, is generally permitted.

Hunting of leopards is prohibited or restricted to the killing of "problem/dangerous" animals in the following countries: Angola, Benin, Burkina Faso, Cameroon, Congo, Djibouti, Equatorial Guinea, Gabon, Ghana, Guinea Bissau, Ivory Coast, Liberia, Mali, Mauritania, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, Sudan, Togo, Uganda and Zaire.

Although the leopard appears tolerant to habitat modification and occurs in the vicinity of settled areas, density is certainly reduced in modified habitats when compared to its

occurrence in natural habitats, possibly to a level as low as 1/10 or even 1/100 of the potential population, as estimated by Martin & De Meulenaer (1988). The leopard subsequently becomes more vulnerable to exploitation and population fragmentation.

Martin & De Meulenaer (1988) argue that the re-opening of the fur trade with appropriate controls under CITES would significantly benefit conservation of the leopard by allowing local people to derive economic value from the species, which is seldom possible under current tourism and sport hunting practices of most countries. At present, rural people are responsible for the continuing decline of leopards in the region, through degradation of habitat where their livestock graze and persecution of the leopard as a threat to these animals. Development of options enabling local people to obtain income from leopards, could encourage them to refrain from eradicating the leopards in their vicinity. Without considering such options, Cobb (1981) could not foresee a future for the leopard in Africa outside protected areas. In 1986, protected habitat comprised only 13% of the potential leopard range (MacKinnon & MacKinnon 1986; Martin & De Meulenaer 1988).

In the Sariska Tiger Reserve, leopards are the main predator of livestock, and prey mostly on smaller livestock such as goats, sheep and subadult cows. Leopards travel to areas outside the Reserve to avoid competition with other predators, and break into livestock sheds. Livestock become especially vulnerable to predation due to their reduced escape abilities in comparison to wild herbivores (Mishra 1997). Now that poison provides the stockman with a cheap and convenient way to eliminate predators, the leopard as a species is threatened (Myers 1976). It was therefore important to reduce the leopard-stock farming conflict to the point where farmers have little need or excuse to kill leopards (Orban 2000).

The provincial fencing requirements as described in the ordinance of the Limpopo Province, South Africa, have not changed since its conception in 1983. Because of the high cost involved in erecting a fence according to the ordinance specifications, the need for a more effective fence existed for those ranchers wishing to keep leopards either inside their property, or out to protect their livestock. With specific placement of electrified wires on a normal, 2.4 m game fence, hand reared leopards were successfully contained (Orban 2000). Final testing was done with a wild female leopard in an experimental enclosure prepared according to the established criteria (Orban 2000). The

female leopard that was used in the experiment did not succeed in escaping from the enclosure, despite several attempts at doing so. The developed electrified game fence thus proved effective in constraining a wild leopard (Du Plessis & Smit 2002). Although the leopard proof game fence proved successful in a small (1.5 ha) enclosure, the effectiveness on larger areas still needs to be tested.

2.4 Habitat and distribution

2.4.1 Distribution

The leopard has the largest distributional range of any of the larger felids, occurring from the southern parts of the African continent through the Middle East to the Far East, northwards to Siberia and south to Sri Lanka and Malaysia (Skinner & Smithers 1990).

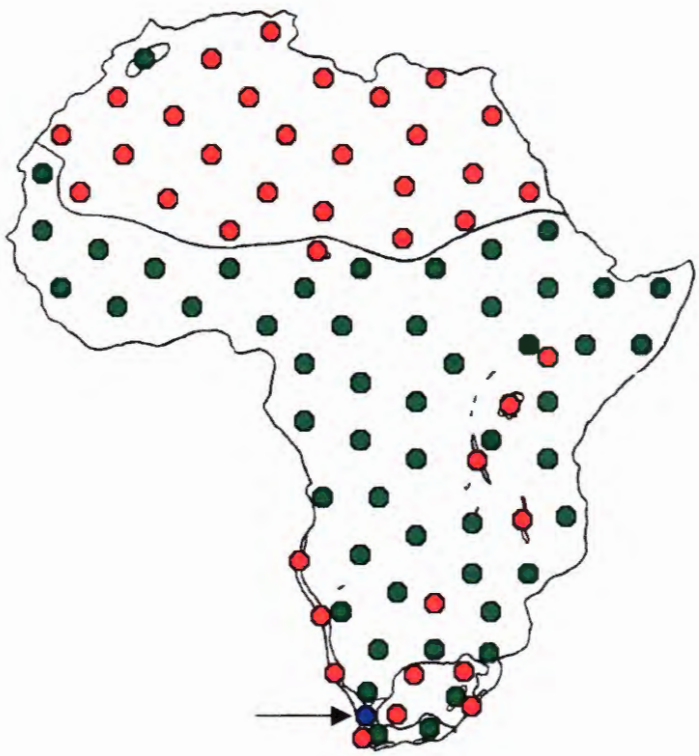


Figure 2.2 Distribution of the leopard in Africa (red octagon - absent; green octagon - present; blue octagon - uncertain). (See text for literature sources used).

The green octagons in Figure 2.1 represent areas where leopards still occur and the red octagons areas where they are absent. It is unclear from the literature (Burger 2000; Apps 1996; Skinner & Smithers 1990), if leopards still occur in the areas indicated with blue octagons. A male leopard was found in Delmas (Van Niekerk 2001), which is on the plato of South Africa where they are generally thought not to occur. A possible explanation for their occurrence in the so called "absent areas", could the conflict between farmers and leopards, driving these animals into new, unknown areas.

2.4.2 Habitat

Leopards have a wide habitat tolerance and while generally associated with such areas as rocky koppies, rocky hills, mountain ranges and forests, they also occur in semi-deserts. In desert areas they utilise watercourses and rocky outcrops where sufficient prey occurs (Skinner & Smithers 1990). They are found in all habitats with an annual rainfall above 50 mm (Monod 1965), and can penetrate areas with less than this amount of rainfall along river courses: e.g., leopards are found along the Orange River in the Richtersveld National Park, South Africa, which lies at the southern most extension of the Namib Desert (Stuart & Stuart 1989). Of all the African cats, the leopard is the only species which occupies both rainforest and arid desert habitats. Leopard habitat ranges exceptionally, up to 5 700 m above sea level where a carcass was discovered on the rim of Mt. Kilimanjaro's Kibo Crater in 1926 (Guggisberg 1975).

In the absence of intense persecution, the leopard appears to be very successful at adapting to altered natural habitats and settled environments. There are many records of their presence near major cities (e.g., Thunbull-Kemp 1967; Guggisberg 1975; Tello 1986; Martin & De Meulenaer 1988). Hamilton (1986) reports their occurrence in western Kenya in extensively cultivated districts with more than 150 persons per km², the largest livestock populations in the country, little natural habitat and prey, and where 20 years ago they had been considered extirpated. However, leopards appear to have become rare throughout much of West Africa (Martin & De Meulenaer 1988).

2.5 Biology and social behaviour

Reproduction of the leopard is probably year-around, but Bailey (1993) found a peak in leopard births during the lambing season of impala, the main prey species. Le Roux & Skinner (1989) found no evidence of seasonality in the reproductive pattern. A female leopard's oestrus lasts an average of seven days and the oestrus cycle is an average of 46 days with a gestation period of 96 (10-105) days (Hemmer 1976). The average litter size is 1.65 (range 1-4; n=59) (Eaton 1977). First year mortality of cubs is estimated at 41% (Martin & De Meulenaer 1988).

Average annual mortality of sub-adults (1.5-3.5 years old) was estimated at 32% (females 40% and males 25%) in the Kruger National Park. It is nearly twice as high as that of adults and can probably be ascribed to poorer hunting success. The interbirth interval is an average of 17 months (n=3) (Skinner & Smithers 1990) and 15 months (Martin & De Meulenaer 1988).

From the age of 13-18 months the sub-adults become independent (Bailey 1993; Skinner & Smithers 1990). Siblings may remain together for 2-3 months before separating (Skinner & Smithers 1990). Dispersal may be delayed in areas where prey is abundant, especially if adjacent habitat is occupied by resident leopards (Bailey 1993).

Female leopards become reproductive after 33 months (range 30-36) (Weiss 1952); 35 months (n=8) (Martin & De Meulenaer 1988) and males after 2-3 years. Bailey (1993) reported that the average proportion of adult females producing young each year in his Kruger National Park study area was 28%, while noting that in some years no females gave birth, whereas in others up to half of the females produced young. The sex ratio of resident adults is 1 male against 1.8 females (Hamilton 1981; Bailey 1993). At one zoo the average age of last reproduction was 8.5 years (females) (Eaton 1977).

In the Kruger National Park adult mortality averaged 19% for adult leopards (old males 33%, prime males 17%, old females 17%, prime females 10%). The proportion of deaths attributable to starvation was 64% (Bailey 1993). The normal lifespan of a leopard is 10-15 years (Turnbull-Kemp 1967; Martin & De Meulenaer 1988).

Leopards are solitary animals, except during the mating season or when juveniles accompany a female (Skinner & Smithers 1990). Schaller (1972) reported that long after the siblings became independent, affectionate reunions between mother and offspring might take place. Van Lawick (1977) also observed similar reunions, as well as playfulness between members of the litter. Leopards are territorial in that both males and females defend territories against conspecifics of the same sex (Hamilton 1976; Bertram 1982). Communication with members of their own species is done through scent marking and roaring, but normally they are silent and difficult to observe (Skinner & Smithers 1990).

2.6 Parasites and viral infections

2.6.1 Parasites

The most important diseases of leopards are cat flu, pheunomia, stomach blockages, deficiency diseases and endoparasites (Fourie 1980). Young (1975) listed some of the diseases and parasites found in lions in the Kruger National Park, but those occurring in leopards are largely unknown. Parasites on the leopard currently known are listed below (Boomker, Penzhorn & Horak 1997):

(i)	Protazoan (7)	(South Africa=4, Rest of Africa=5),
(ii)	Helminth:	
	a. Trematoda (1)	(South Africa=0, Rest of Africa=1),
	b. Cestoda (7)	(South Africa=2, Rest of Africa=6),
	c. Nematoda (16)	(South Africa=2, Rest of Africa=16),
(iii)	Arthropod, and	
	a. Flies (2)	(South Africa=2, Rest of Africa=0),
	b. Fleas (3)	(South Africa=3, Rest of Africa=0),
	c. Ticks (33)	(South Africa=3, Rest of Africa=30),
(iv)	Pentastomid (1)	(South Africa=1, Rest of Africa=0),

(v) Acanthocephalan (2) (South Africa=0, Rest of Africa=2)

The total number of parasites found on leopards is 17 in South Africa and 60 in Africa. It is a small diversity when compared to the number of parasites occurring in ruminants. The few records on parasites in South Africa are an indication that a lot of work still needs to be done as far as the parasites on these carnivores are concerned (Boomker *et al.* 1997).

2.6.2 Viral infections

The occurrence of catastrophic virus-induced diseases in free-ranging and captive carnivores in a number of countries during the last decade, stimulated renewed interest in the potential pathogenicity of viruses for these animals. Seven Kruger National Park leopards were found seronegative for the herpes virus, and one of two Botswana leopards was found seropositive. One of nine leopards tested positive for feline panleukopenia and corona viruses. Three of nine leopards tested positive for canine distemper virus antibodies. During the period 1938 - 1992 rabies was found in two leopards in Namibia and one leopard in Botswana. Between 1950 and 1992 two confirmed cases of rabies in leopards were reported in Zimbabwe (Van Vuuren, Stylianides & Du Rand 1997).

2.7 Diet selection and feeding preferences

The scat of predators provides valuable information about the type as well as the quality of the prey they have consumed. Indigestible remains such as hair, bone, teeth, nails and feathers can be used to identify the prey species if the scat is located, before it is consumed by other scavengers or broken down through insects or secondary microbial activity. Keratinous material such as hair, hooves, nails and feathers as well as hardened epidermal footpads are well preserved in scats (Norton *et al.* 1987). The order of excretion is proportional to the order of intake if the same type of diet is fed (Theron 2003).

The known prey of the leopard ranges from dung beetles (Fey 1964) to adult male eland (*Taurotragus oryx*) (Kingdon 1977), which can reach 900 kg (Stuart & Stuart 1992). Bailey (1993) listed at least 92 prey species that have been documented in the leopard's diet in sub-Saharan Africa. Grobler & Wilson (1972) identified 294 prey species through scat analysis in the Rhodes Matopos National Park. The flexibility of the diet is illustrated by Hamilton's (1976) analysis of leopard scats from Kenya's Tsavo West National Park, of which 35% contained rodents, 27% birds, 27% small antelopes, 12% large antelopes, 10% hyraxes and hares and 18% arthropods. Seidensticker (1991) and Bailey (1993) reviewed the literature, and concluded that leopards generally focus their hunting activity on locally abundant medium-sized ungulate species in the 20-80 kg range. Analysis of leopard scats from a Kruger National Park study area found that 67% contained ungulate remains, of which 60% were impala (*Aepyceros melampus*), the most abundant antelope, with adult weighing between of 40-60 kg. Small mammal remains were found most often in scats of sub-adult leopards, especially females (Bailey 1993).

The leopard has an exceptional ability to adapt to changes in prey availability, and has a very broad diet. Where large ungulates are less common, small prey such as mice and birds are killed by swatting with the paw. These are eaten on the spot (Skinner & Smithers 1990). Grobler & Wilson (1972) and Norton (1986) analysed leopard scats taken from Zimbabwe's Matopos National Park and the mountains of the south-western Cape province. Rock hyraxes (*Procavia capensis*) which are common in the study areas were found to be the most frequently taken prey. In the central African rainforest, Jenny (1993) found the diet to consist mainly of duikers and small primates. Jenny (1993) also noted that some individual leopards had shown a strong preference for pangolins (*Manis temminckii*) and porcupines (*Hystrix africaeaustralis*). A long-term study conducted in the Ivory Coast's Tai National Park on chimpanzees (*Pan troglodytes*), determined that leopard predation was the major cause of chimp mortality (Boesch 1991).

In the interior areas of South Africa's Kgalagadi National Park, where springbuck (*Antidorcas marsupialis*) are less abundant, Bothma & Le Riche (1984) found that 80% of leopard kills (n=30) weighed less than 20kg, but 37% of all kills still consisted of ungulates. By using the tracking method, they found that on average male leopards killed every three days, and females with cubs every 1.5 days. Child (1965) reported that at an altitude of 3 900 m in the Kilimanjaro Mountains of Tanzania, the leopard's diet

consists mainly of rodents, while Fey (1964) described how a leopard stranded on an island in the wake of the Kariba Dam, subsisted primarily on fish, even though impala and common duiker (*Sylvicapra grimmia*) were present in low numbers. Power (2002) found that leopards in the Soutpansberg area, South Africa, are non-selective, but show a preference for the medium-sized bushbuck (*Tragelaphus scriptus*). A tendency toward bushbuck selection occurs where the density of small and medium sized ungulates is beyond 10 animals/km^2.

The leopard shows several behavioural adaptations which permit it to compete successfully with other large predators. The first adaptation is its dietary flexibility. Bertram (1982) studied radio-collared lions (*Panthera leo*) and leopards in the same area in the northern Serengeti and found that, while their ranges overlapped, leopard preyed on a wider range of animals than lions did, and there was little overlap between their diets. Secondly, leopards often cache large kills in trees. Great strength is required and there have been several observations of leopards hauling carcasses of young giraffe (*Giraffa camelopardalis*), estimated to weigh up to 125 kg (2-3 times the weight of the leopard) up to 5.7 m into trees (Hamilton 1976; Scheepers & Gilchrist 1991). This behaviour is more common in areas where competing carnivores are numerous (Schaller 1972; Bothma & Le Riche 1984). In the absence of competing predators, leopards may still drag the carcasses of large prey into dense vegetation or a rock crevice some hundred meters from the killing site (Smith 1977).

Leopards may also retreat up a tree in the face of direct aggression from other large carnivores. In addition, leopards have been seen to either kill or prey on small competitors, e.g., black-backed jackal (*Canis mesomelas*) (Estes 1967), African Wild Cat (*Felis lybica*) (Mills 1990) and the cubs of large competitors such as lion, African wild dogs (*Lycaon pictus*), cheetah (*Acinonyx jubatus*) and spotted hyaenas (*Crocuta crocuta*) (Bertram 1982). According to (Bennet 1999) a male leopard killed two leopard cubs and ate the one. Leopards have also been observed to ambush terrestrial prey by leaping down from tree branches, although this behaviour is apparently opportunistic and relatively uncommon (Kruuk & Turner 1967). Leopards, like other cats, probably generally prefer to get their footing on the ground before launching the actual attack (Leyhausen 1979). While the diet of rainforest leopards may include arboreal animals (40% of scats from the Taï National Park included seven species of primates (Hoppe-

Dominik 1984), they are unlikely to forage much in trees. Estes (1967) has observed them using watercourses or dunes to bring them close to prey. Kingdon (1977) recorded the use of vehicles or even dust devils as screens in stalking.

Leopards are generally most active between sunset and sunrise, and kill more prey at this time (Hamilton 1976; Bailey 1993). In the Kruger National Park, Bailey (1993) found that males and female leopards with cubs were relatively more active at night than solitary females. The highest rates of daytime activity were recorded for leopards using thorn thickets during the wet season, when impala also used them (Bailey 1993).

2.8 Nutritional requirements and prey utilisation sequence

2.8.1 Nutritional requirements

Dietary and nutritional studies are important management tools to ensure optimal feeding habits (Theron 2003). Barbiers, Vosburgh, Ku & Ulrey (1982) determined the digestive efficiencies and maintenance energy requirements of captive Felidae, including the leopard. Daily food consumed by a male leopard (53.8 kg ± 2.4 kg) averaged 1.5 kg with digestible energy intake of 15.128 MJ. A female leopard (41.1 kg ± 3.3 kg) consumed an average of 1.1 kg food a day with digestible energy intake of 11.319 MJ.

Bailey (1993) estimated average daily consumption rates at 3.5 kg for adult males and 2.8 kg for adult females. A leopard will feed for several days on larger carcasses, consuming approximately 3.5 kg of meat per day (Bothma 1997). In Namibia it has been documented that females with cubs eat 2.5 kg, females 1.6 kg and males 3.3 kg meat per day (Bothma & Walker 1999). Male leopards are said to require 3.5 kg/day whereas cubs require less (Bothma & Le Riche 1986). It was proposed by Mizutani (1999) that a leopard requires 35g meat per kg body weight per day.

Food intake and digestibility studies have been conducted on captive leopards (Bloemfontein zoo, South Africa) showing an apparent digestibility of 94.5%. The mean fresh food intake per feeding three times a week was 5.691 kg for the male and 3.497 kg for the female. Only the large bones of fed carcasses (donkey or horse) were left

uneaten. The mean fresh food intake per feeding comprised 10.7% and 10.0% of the body weight of the male and female respectively. The low mean faecal lipid content of 21.952 g/kg shows the large extent to which lipids are digested and absorbed in the digestive tract (Borstlap 2002).

Analyses on apparent digestibility coefficients of fresh food are (0.954 ± 0.0014) and for dry matter (0.939 ± 0.0263), crude protein (0.955 ± 0.0253), lipid (0.993 ± 0.0012), mineral (0.715 ± 0.1361) and gross energy (0.952 ± 0.0189). The digestibility coefficients are very high for all the nutrients (Borstlap 2002).

The water content may account for 85% of the total mass of prey animal bodies (Green, Anderson & Whateley 1984). Predators may therefore obtain sufficient water from the blood and soft tissue of prey animals. Estimated mean water intake as a percentage of body weight is 7.7 for males and 7.2% for females (Borstlap 2002).

It is very difficult, if not impossible, to estimate the exact food intake of free-ranging predators. However, if the apparent digestibility of a particular food source is known and it is possible to collect the faeces of the predator, the intake of the animal can be estimated by using the following equation (Borstlap 2002):

FFI = (TFC) / (1-ADC), where
FFI = Fresh food intake (kg)
TFC= Total fresh faeces excreted (and collected) (kg)
ADC= Apparent digestibility coefficient

This is a much more accurate way of determining food intake than simply estimating the intake of predators. The disadvantages of using this suggested procedure are that a particular animal must be observed and tracked to be able to record feedings and subsequent dropping of faeces. All the faeces of a particular animal must be collected in order to make an accurate intake calculation, bearing in mind the varying rate of water evaporation from the faeces during the time of deposition (Borstlap 2002).

2.8.2 Prey utilisation sequence

A leopard usually starts feeding on the buttocks. Occasionally, it starts on the chest or shoulder. The muzzle, feet, viscera and part of the cranium of prey are seldom eaten (Bothma 1997).

2.9 Nutrients

2.9.1 Fat

The high energy of fat is widely known. The energy value for fat - 9.4 kcal g^{-1} (39.3 kJ g^{-1}) - is in huge contrast to the energy value of protein - 4.3 kcal g^{-1} (18.0 kJ g^{-1}) (Schmidt-Nielsen 1998). Lipids range from fats and oils to complex sterols. Fat yields about 39 MJ of metabolisable energy (ME) per kg dry material when oxidised in the cell, compared to about 17 MJ ME per kg dry material for a typical carbohydrate or protein. In addition to its major function of supplying energy, stored fat is important as a thermal insulator (HO de Waal 2003, Unpublished lecturing material, University of the Free State).

2.9.2 Proteins

When an animal grows, protein is continually synthesised and added to the organism. In the adult the protein remains much the same throughout life. It might therefore seem that once an organism has reached its adult size, dietary protein would be less important. This is not true: An inadequate supply of protein leads to serious malnutrition. In adults, proteins are incorporated into an organ and remain part of the permanent structure. Body proteins are constantly broken down and resynthesised (Schmidt-Nielsen 1998). Structurally, proteins have important functions as components of muscle, cell membranes, skin, hair and hooves. Metabolically important proteins are the blood serum proteins, enzymes, hormones and immune antibodies which all have specialised functions in the body (HO de Waal 2003, Unpublished lecturing material, University of the Free State).

2.9.3 Vitamins

Vitamins are required in small amounts for normal growth and maintenance of animal life. As a result of microbial activity within the reticulo-rumen of ruminants, the micro-organisms synthesise most of the essential water-soluble B vitamins and vitamin K. Vitamin C is synthesized in the tissue of all animals. Most vitamins are destroyed by oxidation, a process sped up by the action of heat, light and certain metals such as iron (HO de Waal 2003, Unpublished lecturing material, University of the Free State). Microbial activity is absent in all predators, subsequently all vitamins are gained from prey species' hind intestines (HO de Waal 2003, personal communication).

2.9.4 Minerals (ash)

About 40 minerals or elements occur regularly in animal tissue. Bone is the primary site for many of the essential elements including Ca, P, Mg, K, Na, Mn, Mo and Zn. Some organs, particularly the liver, kidney and spleen, serve as major storages for Mg, Co, Cu, Fe, Mn, Mo, Ni, Se and Zn (HO De Waal 2003, Unpublished lecturing material). Blood plasma has a high calcium content (McDonald, Edwards, Greenhalgh & Morgan, 1995).

Chapter 3

Study area

3.1 Geographical location

The study was conducted on the farm Masequa situated approximately 30 km north of Mukhado (formerly known as Louis-Trichardt) in the Soutpansberg district of the Limpopo Province of South Africa. The farm lies between 22°21'36" and 22°52'48" East and 29°53'19" and 29°56'28" South at an elevation of 760 m to 1 210 m above sea level. The geology of the area is mainly sandstone and conglomerates of the Wyliespoort formation (Soutpansberg group).

3.2 Vegetation and soil

The savanna vegetation is described as Soutpansberg Arid Mountain Bushveld (Low & Rebelo 1996) (Figure 3.1). The tree layer is diverse with a prominence of *Acacia* species, especially *Acacia tortilis* (umbrella thorn) and *Acacia nigrescens* (knob thorn), as well as broad-leaf species like *Combretum, Commiphora* and *Grewia* species. The *Acacia* species are dominant on the lower slopes whereas the broad-leaved species are on the higher ground. The most important grass species are *Aristida* spp., *Cenchrus ciliaris* (foxtail buffalo grass), *Digitaria eriantha* (common finger grass) and *Panicum maximum* (guinea grass). The soil varies from sandy-loam to shallow rocky outcrops on dry, hot, northern slopes. The area represents prime leopard habitat and free-roaming leopards still occur in the area.

Figure 3.1 View of the study area in autumn, illustrating the vegetation and topography.

3.3 Climate

The rainy season usually extends from October to March, inclusive, but rainfall is irregularly distributed and unpredictable. Average rainfall is 423 mm per year and the average summer temperature is 31.6°C, but can reach up to 42°C. The area experiences moderate winter temperatures with an average minimum of 7.9 °C.

3.4 Experimental animals

The study was conducted on five leopards. A vehicle on the road between Mukhado and Mussina had killed a lactating female, leaving her four young cubs to fend for themselves. The cubs were found on 18 June 1997 at an age of approximately three days and they were subsequently hand-reared. One of the cubs did not survive the trauma and another cub subsequently died during 1998.

The two surviving cubs, both females, grew to maturity. For the purpose of this study they are named females A and D, respectively. They were kept in a camp with an electrified fence, but during December 1998, after a severe storm that damaged the

fence, a wild male managed to enter the camp and female A subsequently became pregnant. She later gave birth to three cubs (April 1999), two females and one male. The cubs were also hand-reared. They have since matured and are currently kept separately from the two adult females. The two younger females are named females C and S, respectively. Because these animals have little fear for humans, close monitoring could be accomplished, which would have been impossible with wild leopards.

During the study the five leopards were kept in four adjacent camps (Figure 3.2) that varied in size from 1.5 ha to 33 ha and were fenced with an electrified leopard proof game fence. The leopards were separated as follows: the male in camp III (25 ha), females A and D in camp II (33 ha) and the other two females, C and S, in camp I (1.5 ha) (Figure 3.2). These three camps were adjoining, and some fences were shared. The electrified game fence allowed all five leopards to see and hear one another. After four years and nine months, female A was moved to camp IV (8 ha). Camps I, III and IV were adjacent, but camp II was some distance away and not adjacent to camp IV.

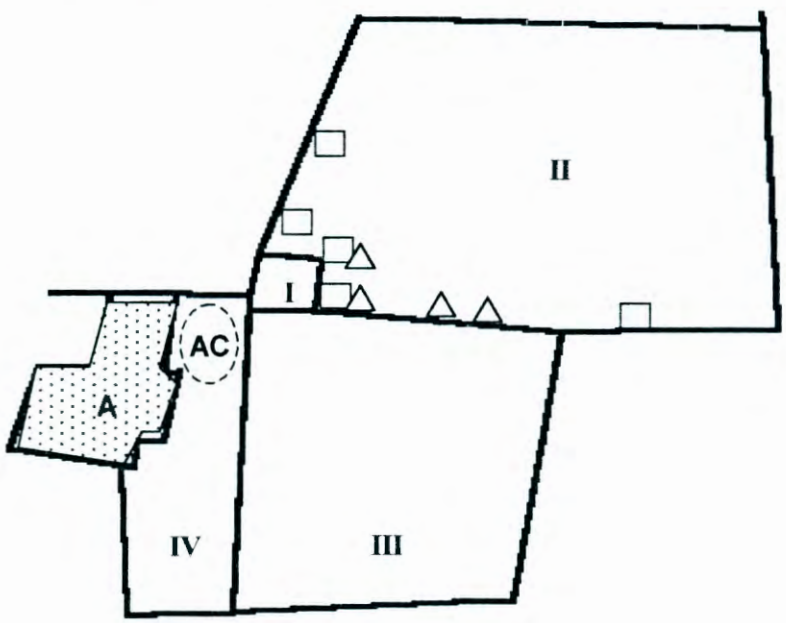


Figure 3.2 Study area on the farm Masequa illustrating the location of the farmstead (A) and the electrified leopard proof enclosures (I – IV). The locations of resting trees (△), scratch trees (□) and activity center (AC) in camp IV are also indicated (see text).

Chapter 4

Communication in leopards

4.1 Introduction

Communication is the passage of information (a representation of something) from one animal to another through messages or signals. A precise definition of communication is difficult and has received much discussion in the literature. Grieg (1984), stated:

Communication is usually treated as synonymous with social behaviour. If we accept "communication" as equivalent to "social behaviour," then we do not need the term "communication".

Without communication there can be no social behaviour and it is thus not surprising that mammals are intensely communicative, sending messages that are received through all five of the senses (Apps & Du Toit 2000).

The basic general characteristics of the common concept of communication include a signal (coded information or "message"), a sender, and a receiver. Other attributes include the following:

(i) Normally, but not always, both sender and receiver belong to the same species.

(ii) The process is in some way adaptive to either or both sender and receiver.

(iii) The sender and receiver must possess the appropriate structures to respectively send and receive the message. This does not imply that the sending or receiving is conscious, voluntary or even neutral (Grieg 1984).

Mammals have structural characteristics which permit them to show a greater range of expressions than other vertebrate species. Their ears are mobile, the shape of the mouth, eyes and nostrils can be altered by muscular action, the hair can be erected or sleeked down, the angle at which the head and neck are held can be varied, the articulation of the limbs is such as to permit the carriage to change from stiffly erect to a low crouch and the tail can be moved in all directions. The changes in demeanour, which

can thus be made, are not irrelevant incidentals to more important activities; many of them can be shown to constitute an important part of social communication behaviour (Ewer 1968). Since all senses are used during communication, it is thus clear that communication is not restricted to vocal communication only.

Despite a solitary lifestyle, the leopard displays an array of communication methods, which include visual, olfactory and auditory signals. Leopards are secretive, normally silent and very difficult to observe. Their most characteristic vocalisation is a rasping cough (sawing), repeated at intervals. Such a call is often answered if another individual is in the vicinity and may be repeated between them as they move. During encounters between territorial males, grunting and growling may reach a high level of intensity. Both males and females use scent marking by spraying urine (Skinner & Smithers 1990).

It is suspected that *P. pardus* is able to communicate in more ways than those that are currently documented in the literature. The fact that communication and social behaviour can be seen as synonymous to each other, implies that a better understanding of communication will also explain much about the social behaviour of the leopard. The objective of this study was to study the visual, olfactory and vocal communication of the captive leopards in relation to specific behavioural patterns.

4.2 Procedures

Observations were conducted on the communication pattern of the five captive semi-tamed experimental leopards for a period of 10 months (January - October 2002) (1 232 observation hours). During this period the animals became so accustomed to the presence of the same observer that they displayed their normal behaviour without showing any signs of discomfort or stress.

4.2.1 Visual communication

All communication methods were observed during field studies which included day as well as night observations. A Canon SLR camera with 28 x 90 mm and 75 x 300 mm lenses was used to record visual displays, which included different body, ear and tail

positions. These were verified amongst the experimental leopards, and compared with a range of leopard videos and photographs of other leopards. Behaviour was recorded before, during and after a specific action in order to establish a distinctive pattern that can be linked to the specific action.

4.2.2 Auditory communication

A cassette recorder system was used to record leopard vocalisations during field studies. Vocalisations were recorded with a Sony TC-D5 PRO capstan servo control stereo cassette recorder, using a Sony ECM-969 electrets condenser microphone mounted on a Sony PBR-330 parabolic reflector.

Being nocturnal animals, leopards are most active at sunrise and sunset with the result that most of the vocalisations also occurred during these periods. Approximately an hour before sunset the leopards regularly gathered at an area where the camps allowed visual contact among all the leopards. All vocalisations among the interacting animals were recorded and a presence was maintained until the leopards separated again. During recording sessions all behaviour was observed before, during and after a specific vocalisation was made. Twenty-four hour studies were also conducted to determine the interval and frequency of the various sounds.

Sonograms were obtained using the computer program "Visit SASLAB Light" to determine the duration, intervals and frequency of each sound. For editing, "Cool Edit" was used from the company Syntrillium Software Corporation. Sonogram images were prepared for printing using Adobe Photoshop 6.0.

4.2.3 Olfactory communication

Faeces of leopards are also used as a communication method. Defecation sites within the various camps of the leopards were recorded using a GARMIN eTrex Vista GPS. All the faecal co-ordinates and other GPS recordings were plotted on a "Micro Positioning System", a computer program based on a geographic information system that stores, generates and retrieves variables. A 1:50 000 aerial photograph of the farm Masequa with the borders of the leopard camps indicated, served as background so that any GPS

co-ordinates typed in could be plotted directly onto the aerial map. Sites of gland secretions, scratching trees, urination and scuffing were also recorded.

4.3 Results

4.3.1 Visual communication

Thirteen body-tail positions (Figure 4.3) and eleven facial expressions (Figure 4.4) that indicate specific moods, actions and actions to come, were identified. Neutral behaviour is not typified by any characteristic body posture. The ears are continuously turned forward or sideways (Table 4.2b) with the tail hanging down (Figure 4.3a).

4.3.1.1 Body colouration

The appearance of the leopard is unmistakable (Figures 4.1 & 4.2). The black markings on the face and chest are markedly in contrast to the general colour (Figure 4.1). The area surrounding the eyes is black (Figure 4.1b), which probably serves to accentuate the eyes during direct eye contact, accompanied by dominant behaviour. The area around the mouth is shiny-black (Figure 4.1d) due to the glittering saliva. When growling a black spot appears on the gum above the top incisors (Figure 4.1i) and the black whiskers' cups on the side of the snout form a black area (Figure 4.1h). In addition three black dots on top of the snout form a dark line towards the eyes (Figure 4.1c). The nose is normally black, but pink colouration of noses is not uncommon. During intense aggression the nose is rippled (Figure 4.1g) and the pupils are enlarged (Figure 4.1f).

The front of the lower jaw is white (Figure 4.1j), hereby contrasting and accentuating the black markings. On the medial side of the external ear, a black triangle (Figure 4.1e) again contrasts the profuse covering of long, fine, light coloured hair. This black triangle is visible when the leopard is facing one or displaying aggression. Black horisontal stripes on the external ear vary in number and thickness (Figure 4.1a). A black collar between the chest and neck (Figure 4.1k) is formed by a row of black spots. It is clearly visible when the head is held high during dominant displays, but is concealed during submissive behaviour when the head is lowered.

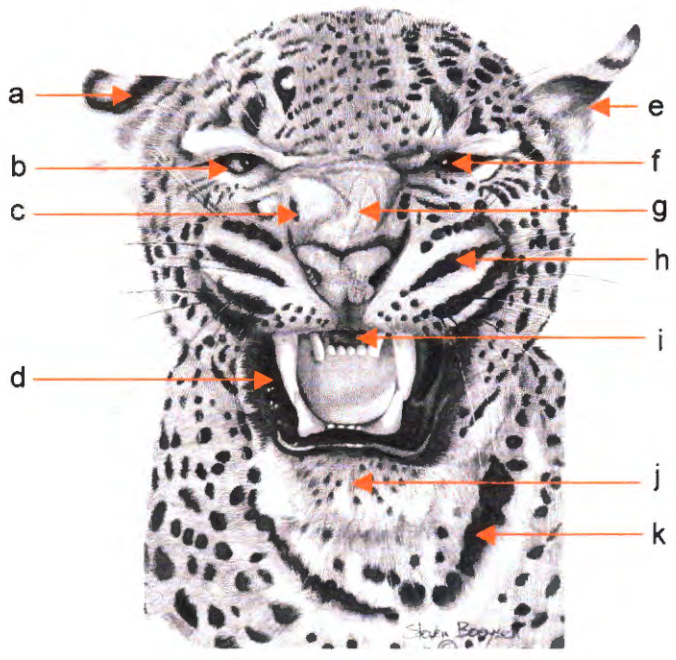


Figure 4.1 Facial and chest markings of the leopard as used in visual communication. (See text for explanation of a – k).

As shown in Figure 4.2, black spots are limited to the head, flanks, limbs and hindquarters (Figure 4.2d) of the leopard, while rosettes occur on the remainder of the body (Figure 4.2c). Blackish zones on the fore- and hind feet indicate the presence of glands, used when scratching or scuffing (Figure 4.2g). The rounded ears appear small for the size of the animal (Figure 4.2a). Along the complete length of the body the dorsal side (Figure 4.2b) seems darker than the ventral areas (Figure 4.2h). The twist in the tip of the tail occurs exactly where the rosettes end and the lines start (Figure 4.2f) ending with a white tip (Figure 4.2e).

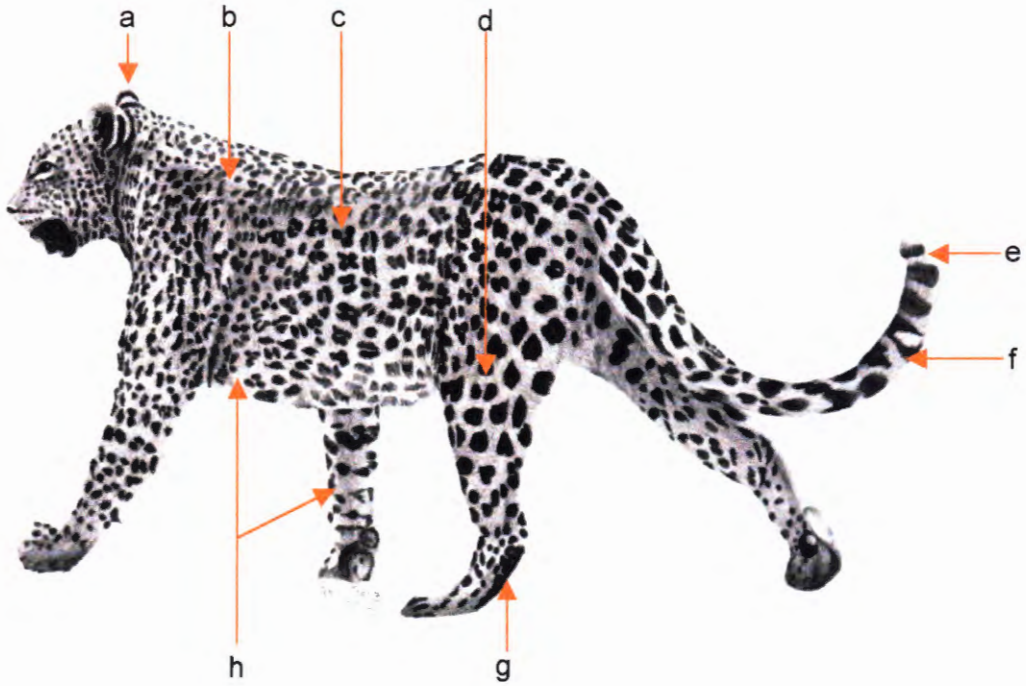


Figure 4.2 Body markings of the leopard that are used during visual communication. (See text for explanation of a – k).

4.3.1.2 Tail positions

Thirteen tail positions were identified, which are divided into four motivational categories namely dominant, submissive, hunting and reproductive behaviour (Figure 4.3).

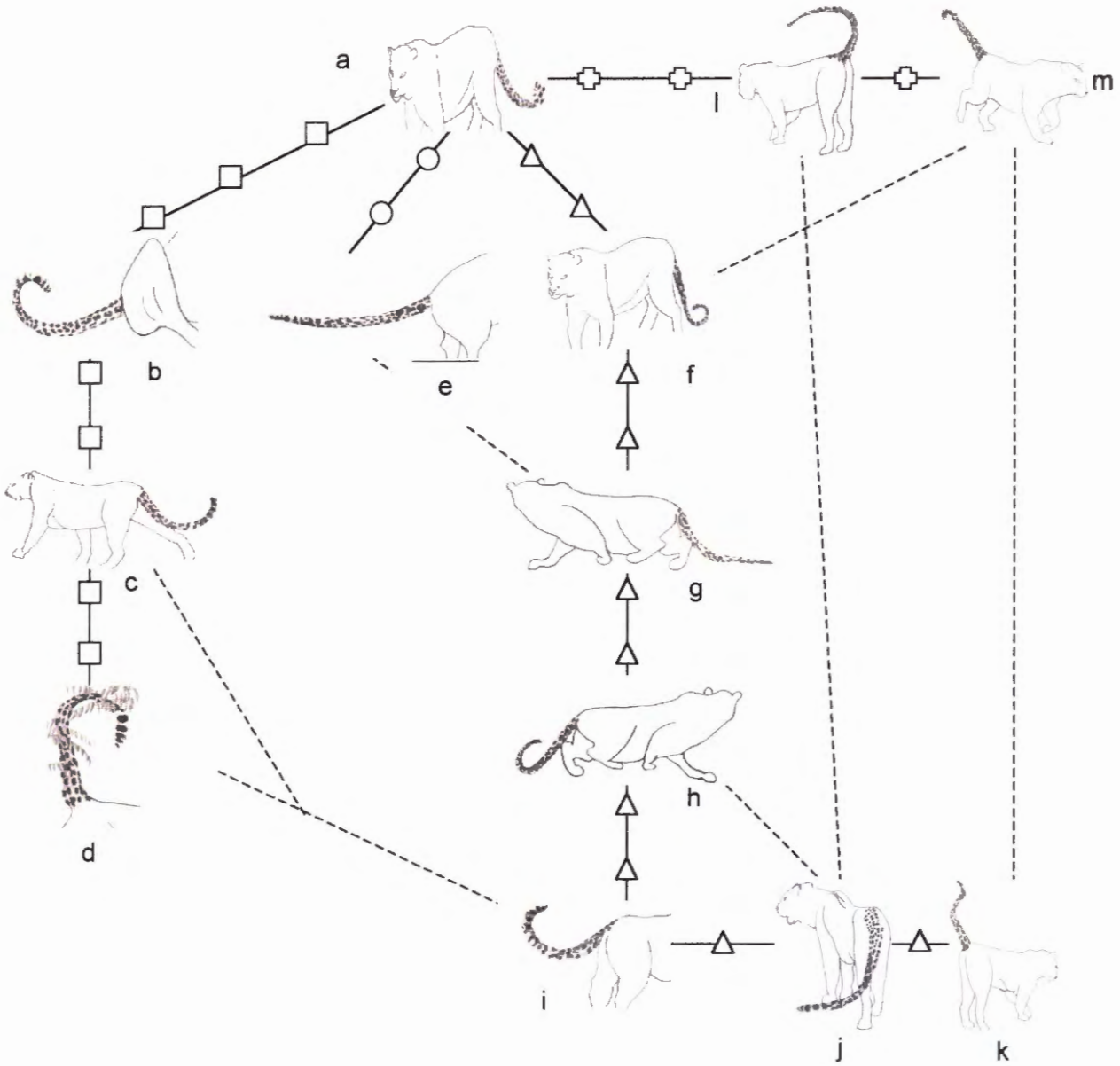


Figure 4.3 Variation in the tail position of the leopard: dominance (□); submission (○); hunting (△); reproduction (✣) (see also Table 4.1)

Table 4.1 Behavioural context of the different tail positions as distinguished in the experimental leopards.

Tail position (Figure 4.3)	Behavioural context	Female		Male	
		n	%	n	%
a	Normal position	-	-	-	-
b	Dominant sit urination; marking territory	762	24.8	190	20.5
b	Scuffing	251	8.2	295	31.9
c	Dominant walk; marking territory	448	14.6	113	12.2
d	Dominant spray urination; marking territory	1 010	32.8	254	27.4
e	Submission	123	4.0	2	0.2
f	Excitement	58	1.9	16	1.7
g	Stalking prey	48	1.6	16	1.7
h	Distraction to shift prey's attention: hunting	32	1.0	12	1.3
i	Sign of success, intimidation	28	0.9	14	1.5
j	Irritation, frustration	12	0.4	6	0.6
k	Curiosity	6	0.2	8	0.9
l	Oestrus, show receptiveness for mating	132	4.3	-	-
m	Oestrus, draw male's attention	167	5.4	-	-
	Total	**3 077**	**100.1**	**926**	**99.9**

4.3.1.2.1 Dominance

The lower tail is bent upwards when the dominant leopard squats or scuffs, (Figure 4.3b). While patrolling its territory early in the morning and/or late in the afternoon, the tail is carried with half a loop held at a level between the foot and heel (Figure 4.3c). When the dominant leopard urinates against bushes or trees, the tail is held straight up with the twisted tip pointing down towards the back (Figure 4.3d). The latter tail position was the most prominent and common position of the female leopards (Table 4.1).

4.3.1.2.2 Submission

The tail of the submissive leopard, by contrast, was held horisontally to the ground at a level between of the heel and the feet (Figure 4.3e). The submissive leopard never raised its tail above the heel, except in the case of a female in oestrus in which case the tail was bent over the back (Figures 4.3l & m).

4.3.1.2.3 Hunting

Six different tail positions related to hunting behaviour were observed. The moment potential prey was spotted, the tip of the tail quickly moved sideways with the rest of the tail held low down (Figure 4.3f). When the stalking distance had been reached, the tail was lowered and held horisontally at a level between the heel and foot (Figure 4.3g). While the leopard was stalking its prey, the tail was held absolutely still and all available cover was used.

Prey species have different flight distances and when a potential predator or enemy approaches beyond that distance, the prey will immediately take to flight. When the prey spotted a stalking leopard at that specific distance, the leopard responded by moving its tail sideways with a twist in the middle of the tail (Figure 4.3h). This movement probably serves as distraction to shift the prey's attention from the head (closest to the specific flight distance) to the tail up to 2 m further away, thereby increasing the leopard's chance of a successful hunt.

In cases where the hunt was successful, the tail was again raised upwards (Figure 4.3i). The latter tail position was also used to intimidate other animals. Whenever the hunt was unsuccessful or the prey moved out of reach, "frustration" was clearly displayed by sideways tail movements (Figure 4.3j). The latter was performed in exactly the same fashion than that described for distracting the prey's attention (Figure 4.3h), except that the leopard did not stalk the prey, but only used it to display its mood. The last hunting variation is very interesting in the sense that the shape of the tail may vary, even though it is held still in one position. When exploring strange objects for instance, the tail was twisted at different angles and the more the leopard was interested, the more prominent the twists became (Figure 4.3k).

4.3.1.2.4 Reproduction

Five to six days prior to the oestrus peak, the tail of the female was bent over her rump and back (Figure 4.3l). This bending consisted of an average of 2.3 bends during a movement interval and was only performed when the male approached the female or *vice versa*. This behaviour was displayed throughout the oestrus cycle.

When the male was near the female (within a distance of 2 - 15 m, depending on the habitat), the female's tail was held exactly at a 45° angle with a sideward twist at the tip, forming a hook (Figure 4.3m). The raised and hooked tail not only served as a method of visual communication, but was also used to create sound. By dragging the tail against objects such as twigs, branches and leaves, a rustling noise was produced which immediately attracted the male's attention.

As soon as the male looked in the direction of the female, she rolled onto her back (known as heat role), which also forms part of olfactory communication. In the presence of a male, the female never displayed a dominant tail position. The tail, when not bending over the back or held at a 45° angle, was either carried in a submissive (Figure 4.3e) or neutral (Figure 4.3a) tail position.

4.3.1.3 Ear positions, facial expressions and head movement

Eleven facial expressions of leopard were identified of which four behavioural categories namely observation, aggression, defensive/offensive threat and submission can be recognised (Figure 4.4).

4.3.1.3.1 Observation

When a leopard was focused on something in front of it, the ears were held straight up and pointed to the front, with the eyes wide open and staring at the subject (Figure 4.4a). The head was also lifted to gain height for a better view, except when aggressive or in the event of a pending hunt. When hunting the ears were pointed forward with a slight bend sideways which hid the ears. The head was lowered while the stalk proceeded.

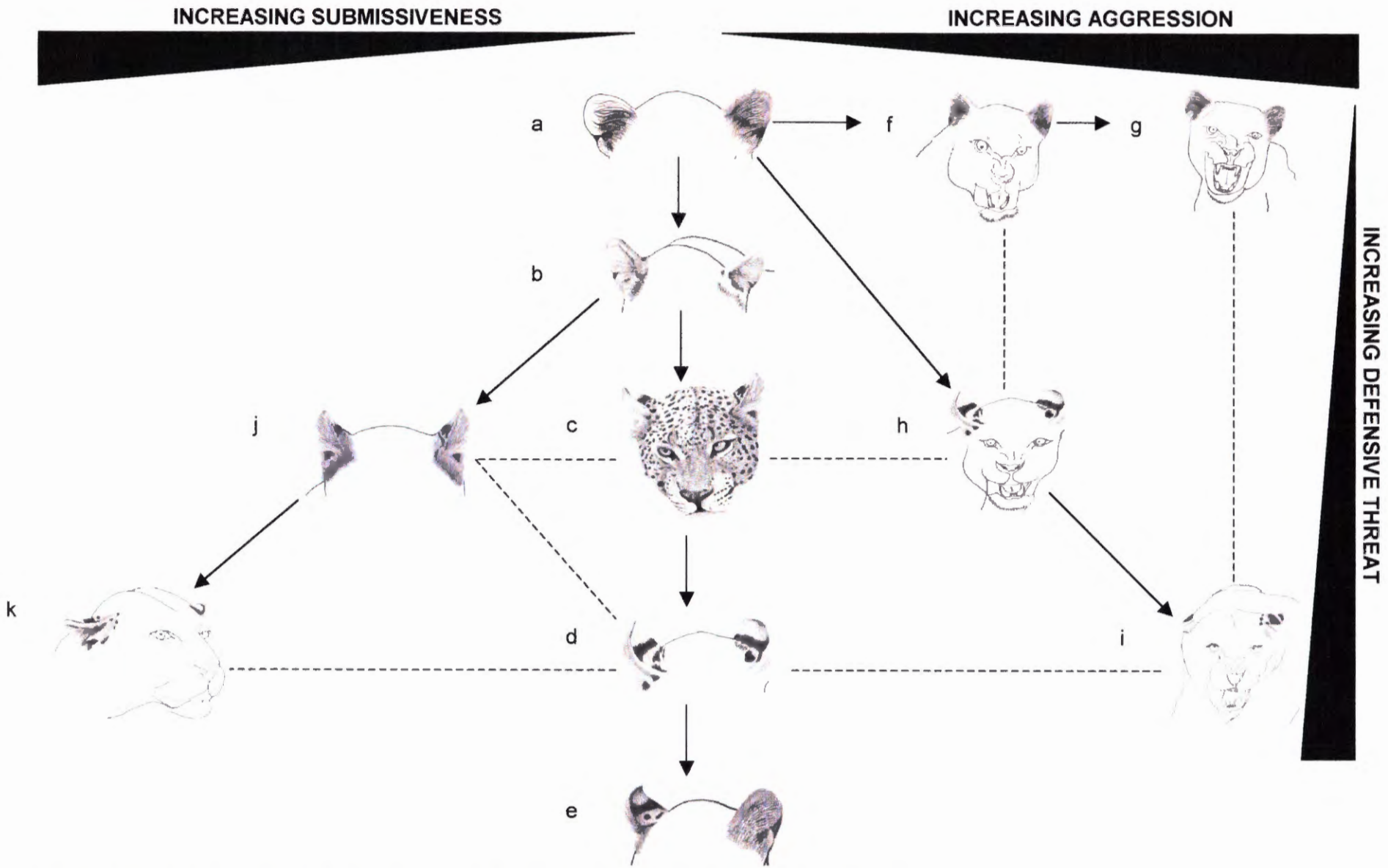


Figure 4.4 Variation of the facial expressions of the leopard. (See text for explanation of a – k).

Table 4.2 Behavioural context of the different ear positions distinguished in leopards.

Ear position (Figure 4.4)	**Behavioural context**	**Female**		**Male**	
	Relative occurrence for observation	**n***	**%**	**n***	**%**
a	Observation 1	-	25	-	25
b	Observation; neutral behaviour 2	-	35	-	35
c	Observation 3	-	25	-	25
d	Observation 4	-	10	-	10
e	Observation 5	-	5	-	5
	Total		**100**		**100**
f	Aggression	16	4.6	5	5.7
g	Aggression	17	4.9	6	6.9
h	Defensive threat	123	35.4	27	31
i	Defensive threat	86	24.8	35	40.2
j	Submissiveness	25	7.2	8	9.2
k	Submissiveness	80	23.1	6	6.9
	Total	**347**	**100**	**87**	**99.9**

* Due to uneven and continuous ear observation positions, it was impossible to get any n-values. Relative occurrences were therefore allocated on a percentage basis.

Ear observation postures two (Figure 4.4b) and three (Figure 4.4c) were very similar and served the same purpose, and thus can be seen as variations of each other. Many of the other ear position combinations also originate from observation posture two (Figure 4.4b). While resting or sleeping, the ears were in one of the above positions to listen for possible danger. Along with this ear position the eyes were usually closed or half-closed, but if a disturbance occurred in the vicinity, the eyes were opened fully and the ears moved to an observation one position while turning the head in the direction from which the noise came.

The fourth ear observation position was characterised by the ears being held flat and pointed backwards with the eyes open (Figure 4.4d). This ear position was only displayed when the leopard's attention was directed to something in front of it and the

noise or disturbance from behind was negligible. During such observation the eyes stayed fixed to the front, but if the disturbance from behind changed in such a way that the leopard felt threatened, it immediately turned its head while displaying observation one ear position (Figure 4.4a).

Ear observation position five (Figure 4.4e) is a further modification to this behaviour and can also be described as a scan-position with the eyes wide open. This ear position was adopted when a leopard was at its prey or busy eating, especially on the ground. Continuous movement of the ears was used to secure the area.

4.3.1.3.2 Aggression

Aggression was especially evident when the dominant leopard intimidated the submissive one, as well as when the dominant individual chased the intruder out of its territory. Aggression may also originate from observation posture one (Figure 4.4a) when the leopard was intensively focused on something.

Prior to the occurrence of phase one aggression, other aggressive behaviour, which can be considered a forerunner to phase one, was observed. Without any vocalisation, the upper lip was lifted on the one side, only baring its canine to the potential threat or challenger. The first phase of aggression was where the leopard pulled its upper lip back a little to display its teeth, thereby intimidating the other animal (Figure 4.4f). The ears stayed in the upward position, pointing towards the opponent, with eyes that narrowed a little. As a result of the withdrawal of the upper lip, a few wrinkles appeared on the nose which were usually accompanied by specific vocalisation that will be discussed later.

The second phase of aggressive behaviour represented intense aggression with the possibility of an imminent attack if the challenger did not show submissive behaviour or flee. The lips were fully withdrawn with narrowed eyes and many wrinkles were visible on the nose (Figure 4.4g). This coincided with the vocalisation illustrated in (Figure 4.5a) and can lead to a hoarse bark (Figure 4.5b), which serves as a challenge from the dominant individual.

4.3.1.3.3 Defensive / offensive threat

A moderately high intensity defensive threat normally followed from the observation one ear position. The ears are half drawn backwards, eyes are narrowed a little with a few wrinkles visible on the nose as a result of the withdrawal of the lips (Figure 4.4h). This was combined with vocalisation (Figure 4.5a), but of a low intensity.

A high intensity defensive threat usually developed from an initially moderately high intensity threat. The ears are drawn back fully, which almost represents observation four ear position, with eyes almost closed. The lips are fully withdrawn, displaying the teeth with the head facing the opponent (Figure 4.4i). Vocalisation (Figure 4.5a) also formed part of this combination but was much more intense than the previous defensive threat and it held a substantial threat for the opponent. It can thus be classified as an offensive threat.

4.3.1.3.4 Submission

Whenever the dominant leopard approached a submissive leopard at a distance of 8 to 20 m, the latter flattened its ears (Figure 4.4j). When the dominant individual moved closer, the submissive animal would flatten its ears further and lower the head with a sideways turn (Figure 4.4k). Under normal circumstances such submissive behaviour was adequate for the dominant one to accept the situation. When the dominant leopard growled or snarled at the submissive one, the latter totally flattened its ears while lowering the head as close as possible to the ground and uttering a specific sound (Figure 4.5g). The submissive one would remain in this position until the dominant leopard walked away or until there was a reduction in the dominant animal's aggression. Furthermore, the submissive animal looked down, not making any eye contact, as such behaviour could be seen as a challenge. When the male approached any female, the female displayed submissive behaviour towards the male by lowering her head with flattened ears. When a female approached the male, however, she would only flatten her ears to an intermediary position before lowering her head when she reached the immediate vicinity of the male.

4.3.2 Auditory communication

The sonograms of the different vocalisations as recorded during this study are presented in Figures 4.5 and 4.6. Similar to the previously discussed communication methods, the fourteen vocalisations were used in the context of aggression, submission (Figure 4.5), social interaction and mating (Figure 4.6).

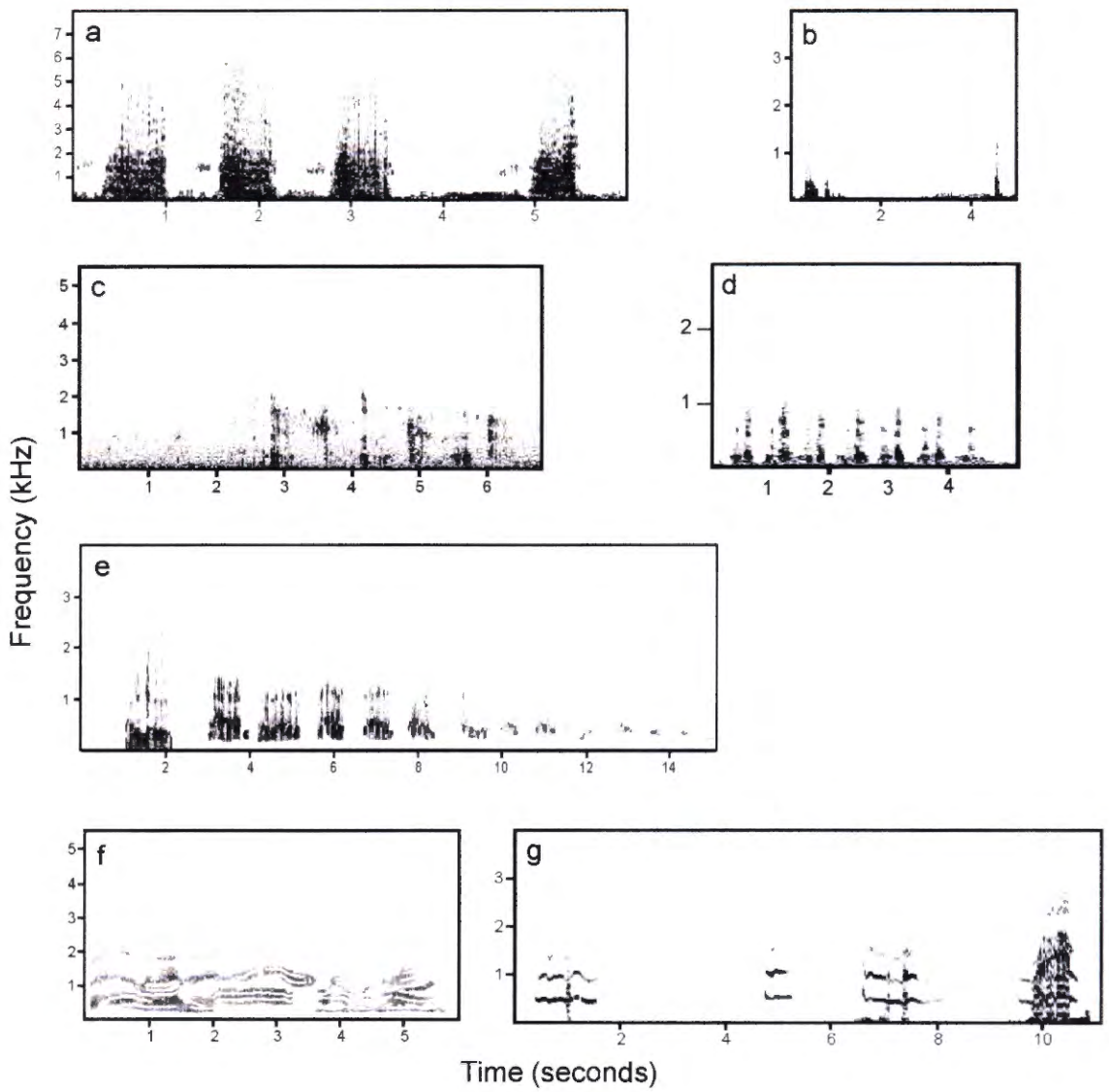


Figure 4.5 Sonograms of aggressive (a - e) and submissive (f - g) vocalisations of leopards. (a - hiss; b - hoarse bark; c - growl; d - rasp; e – bark-rumble; f - miaowowo; g - miaow).

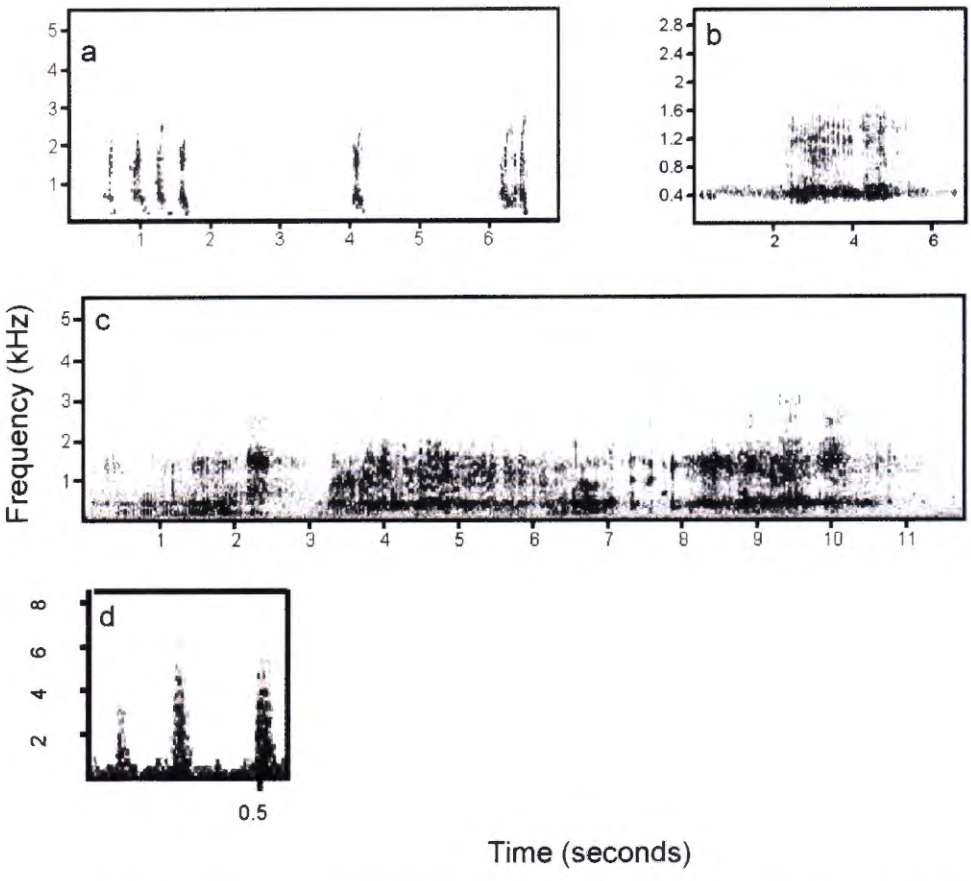


Figure 4.6 Sonograms of leopard vocalisations related to mating behaviour (a - c) and social interaction (d). (a - pre-mating call; b - mating call; c - intermediate mating call; d - snuffing).

4.3.2.1 Aggression

Hissing (Figure 4.5a) was a typical defensive threat and can be considered a forerunner to more intensive threat situations. The moment a dominant leopard, especially the male, noticed or became aware of another leopard in its territory, hoarse barking (Figure 4.5b) commenced.

Although growling (Figure 4.5c) consists of only one sound, it was used either as a sign of aggressiveness (Figure 4.4g) or as a defensive threat (Figure 4.4i) and it was produced after the hissing sound. As seen in Figure 4.5c, growling is a low pitched and continuous sound. This type of communication was most notable when a dominant

leopard approached a submissive one. The vocalisation was used to intimidate another leopard to display submissive behaviour accompanied by the "miaowowo" sound (Figure 4.5g).

As seen in Table 4.3, rasping is the most common vocalisation of leopards with 3 223 rasps recorded during the study period. During continuous 24-hour observation sessions it was found that the leopards' rasping activity were the highest in the late afternoon (Figure 4.7).

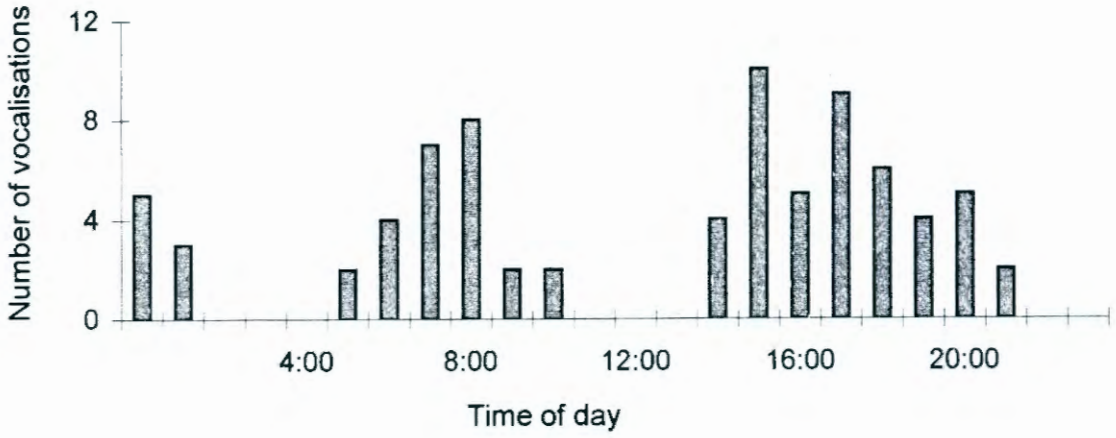


Figure 4.7 Temporal variation of vocalisations (rasping sound) by a female leopard in oestrus over a period of 24 hours.

Depending on the habitat, the sound is audible up to two kilometers away by human ear on cold, quiet nights. The male uttered more strokes per call ($\bar{\chi}$ = 8), compared to those of the females ($\bar{\chi}$ = 4). In the male the intervals between strokes were also found to be much quicker than those of the females. Being irregularly distributed, the male used this as a territory defense call.

Table 4.3 Summary of the auditory communication of leopards as recorded during the study period.

Vocalisation (Figure 4.5)	Male n	Male %	Female n	Female %	Situation	Loudness*	Duration (sec.) Avg. (min. – max)	Frequency kHz
Hiss (a)	35	4.9	86	1.2	Defensive threat, intimidating opponent	S – M	0.645 (0.61 – 0.66)	1 - 6
Hoarse bark (b)	23	3.2	47	0.7	Aggression; territorial marking and defence	L	0.33 (0.30 – 0.40)	0.4 – 1
Growl (c)	10	1.4	21	0.3	Aggression, intimidation	M	Continuous sound 7 sec.	1 - 2
Rasping (d)	435	60.4	3 223	46.3	Female in oestrus, calling male. Male territorial marking	L	0.32 (0.15 – 0.35)	0.2 – 1
Bark-rumble (e)	0	0	3	0.04	Submission towards dominant	M – L	0.506 (0.15 – 0.92)	0.5 – 1
Miaowowo (f)	0	0	972	14	Submissive female towards dominant female; female towards male	S – M	Continuous sound 6 sec.	1 – 3
Miaow-calling (g)	5	0.7	768	11	Female, calling male; male attention	M – L	1.138 (0.70 – 1.35)	0.5 – 2

continue...

Table 4.3 continued

Vocalisation	**Male**		**Female**		**Situation**	**Loudness***	**Average duration (s)**	**Frequency**
(Figure 4.6)	**n**	**%**	**n**	**%**			**Avg. (min. – max)**	**kHz**
Pre-mating call (a)	0	0	8	0.1	Dominant female towards male, assumed just before mating	S – M	0.157 (0.14 – 0.28)	1 – 3
Mating call (b)	3	0.4	3	0.04	Copulation	M – L	Continuous sound 7 sec.	♂ : 0.4 ♀ : 0.4 – 1,7
Intermediate mating call (c)	1	0.1	1	0.01	Early stages of mating; copulation	M – L	Continuous sound 12 sec.	♂ : 0.4 ♀ : 0.4 – 1,7
Snuffing (d)	138	19.2	1 682	24.2	Greeting; peaceful approach	S – M	0.058 (0.041 – 0.067)	5 – 6
Purring	67	9.3	132	1.9	Social interaction; sound of pleasure	S	Not analysed	-
Umf	3	0.4	8	0.1	Social interaction; satisfaction	S	Not analysed	-
Pinpointing	0	0	2	0.03	Pinpoint location	L	Not analysed	-
Total	**720**	**100**	**6 956**	**99.92**				

*Loudness at distance intervals: S = 0-1m, M = 1-10m & L = 10-20m.

As seen in Figure 4.7, during the female oestrus period, rasping intervals were very high with peaks in the early morning, afternoon and midnight. Rasping is the number of rasps performed during a specific hour with an average of four rasps performed during one single rasping effort. The use of rasping for the purpose of seeking a mating partner was more prominent than its use as a territory-defense or an awareness call. But when the females were not in oestrus, rasping by both sexes occurred when another leopard in the vicinity rasped.

The last type of vocalisation (Figure 4.6a) represents merely an intermediate phase uttered just before mating. The fact that aggression accompanies mating (exposed teeth of the female with ears straight up) suggests that this sound can be classified under the aggression category. This was the only time, except during copulation under normal circumstances, that females exposed their teeth to the male.

Pre-mating calls (Figure 4.6a) were normally uttered immediately after a series of social interactions between the sexes. Only dominant females that were in the peak of their oestrus period uttered this sound and then only towards the male. This behaviour was observed in different situations during the study. When leopard A was with leopard D, the latter was the dominant female. During lecpard D's oestrus period, she produced this sound towards the male after a series of forerunning social interactions including visual, olfactory, tactile and acoustic communication. Leopard A also came in oestrus as expected, but as she was the submissive one of the two, she never produced this type of acoustic communication towards the male. However, when leopard A developed dominant and territorial characteristics after being moved to a separate camp, she also communicated with the male using the pre-mating call. In camp I where female C was dominant over female S, the former regularly used the pre-mating vocalisation towards the male, but the latter never did.

Since the male was separated from the females by the fence, actual mating never took place, but the assumption can be made that mating would have followed under normal circumstances.

4.3.2.2 Submission

On occasion when one of the experimental leopards tried to hunt in another individual's territory, the territorial owner aggressively chased the intruder, whereupon the fleeing intruder uttered a bark-rumble (Figure 4.5e) while running with the head held low and the ears flattened. Immediately afterwards the territorial owner displayed aggressive behaviour, using all communication modalities (visual, olfactory and acoustic). The intruder then displayed visual and acoustic submissive behaviour, even though it was at the border of its own territory. On other occasions the dominant or territorial leopard allowed another individual to pass through its territory to drink water as long as the latter did not display any dominant behaviour or tried to hunt.

There were considerable variations in frequency, duration and form of the "miaowowo" vocalisation (Figure 4.5f), between individuals. This performance is an acoustic indication of submissiveness of a female towards the male or of one female towards a more dominant one.

4.3.2.3 Social interaction

Five distinct vocalisations involved in the social interaction of leopards have been identified, of which two were analysed on a sonogram. Of these, "Miaowing" (Figure 4.5g) can be considered a variation of the "miaowowo" sound used in submissive behaviour. Whenever the female saw the male at distances between 10 to 20 m, she uttered a "miaow", apparently to attract the male's attention. The moment the male came closer, intending to have contact with the female, the "miaow" was transferred into a "miaowowo" and the female displayed submissive behaviour.

During a series of "miaowing" and "miaowowoing" vocalisations, snuffing (Figure 4.6d) frequently occurred. At a distance of 15 m the female already started snuffing at the male. Snuffing was also produced during interaction between females. Snuffing occurred in series of two to three phases, with the intensity of the sound increasing towards the end.

Purring was often heard during social interactions between opposite sexes. When a female in oestrus saw the male, she started purring very loudly, regardless of the distance from the male. When the male lost interest in the female and walked away, the female stopped purring. Purring was also very prominent during feeding.

After social interaction between the male and a female standing next to each other on either side of the fence, both sexes produced an "umf" sound while walking away. This has been interpreted as an expression of "satisfaction".

When both leopards A and D were present in camp II, a rare but very interesting vocalisation occurred between the two females. Leopard A created a sound that started at a low frequency but ended a little bit higher. Moments later, leopard D produced exactly the same sound, but neither of the two searched for each other. This vocalisation can probably be interpreted as a contact call or pinpointing the location of the other individual.

4.3.2.4 Mating

Rasping, pre-mating and intermediate mating (Figure 4.6c) calls occurred as forerunners to true mating. It was especially noticeable when female A in camp IV and female D in camp II were simultaneously in oestrus. When female A rasped at the male, female D immediately followed suit, probably because the latter regarded female A as competition. But when the females were not in oestrus, rasping by both sexes re-occurred whenever another leopard in the vicinity rasped, suggesting that rasping can also be classified as a defensive territory call.

Both intermediate and full mating calls could not be recorded during the present study, but were analysed from external sources. The pre-mating sound (Figure 4.6a) produced by a dominant female in oestrus achieved a high frequency of 2.5 kHz. The assumption can be made that in Figure 4.6b the low frequency (0.4 kHz) would be that of the male and the higher frequency (0.4 - 1.7 kHz) that of the female.

4.3.3 Olfactory communication

Leopards made use of three different olfactory communication methods, which included urine marking, faecal defecation and glandular secretions.

4.3.3.1 Urine

The use of urine is prominent in the marking of territories. As a dominant leopard walked along the boundary of its territory, normally on an existing path, it urinated against all prominent bushes and tufts of grasses, marking its territory by spraying or squatting small volumes of highly concentrated urine.

Four types of urination by both sexes were observed:

(i) Copious urination by spraying the most abundant plant species while marking its territory.

(ii) Squirt urination on grass tufts and the ground after scuffing with the hind feet.

(iii) Backward directed spray onto densely leafed branches of shrubs, especially *Combretum apiculatum* (Red bushwillow) during the wet season - as will be discussed.

(iv) Backward directed spray onto trunks of larger trees, especially *Boscia albitrunca* (Shepherd's tree) and *Kirkia acuminata* (White syringa).

No plant species preference with regard to urine marking was observed in the study area. However, the *C. apiculatum* was most frequently marked, the reason simply being that it was the most abundant woody species in the study area.

Apparently the physical characteristics of the plant are more important than the species itself. Plants with dense leaves were normally preferred for marking purposes. When urinating, the abdomen was normally held as close as possible to the object, thereby limiting urine loss through the influence of wind. Because the *C. apiculatum* is a deciduous species, during the drier months of the year, leopards more frequently squat-urinated on the ground or spray urinated against *B. albitrunca*.

Squatting differed from spraying because of the scuffing movements immediately prior to urination. As the dust from scuffing settled down, it was likely that the urine mixed with the soil, aiding the transfer of the urine scent. A dominant individual displayed its dominance with a raised tail when urinating.

4.3.3.2 Faeces

The positions of leopard defecation sites in camp IV were plotted with the aid of a GPS (Figure 4.8). At the time of the count, female A occupied camp IV for three and a half months. The faecal deposits totaled 79, which represents a mean interval of 1.34 days between defecations.

A high concentration of faeces was found next to the fence on the side closest to the other leopards, as well as around a feeding tree and nearby paths, which formed the leopard's activity center (Figure 4.8), where the leopard spent most of its time. The distribution of faeces next to the fence, away from the adjacent camps was sparser but was clearly used to demarcate her home range.

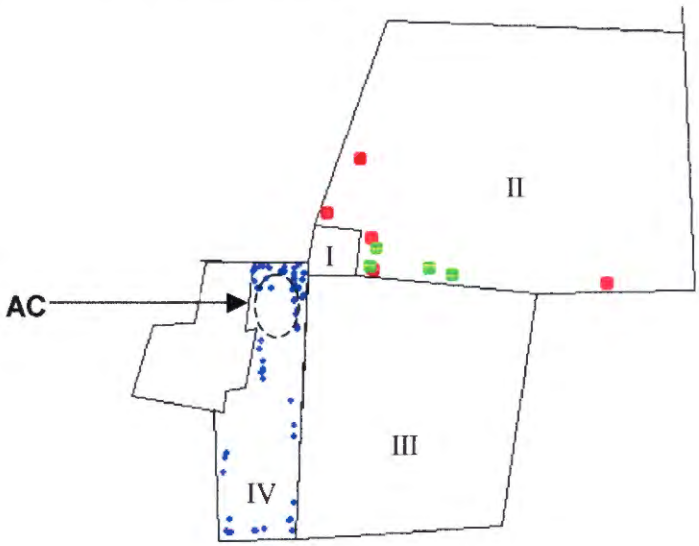


Figure 4.8 Position of defecation sites (blue dots) concentrated along the fences and around the activity center (AC) in camp IV. Resting trees are indicated with red dots and scratching trees with green dots.

Similar to urination, the faeces were excreted either in existing paths, roads or open areas and were left uncovered. None was found in long grass or underneath thick bushes. Faeces that were 106 days old, were still clearly visible due to a high concentration of hair.

4.3.3.3 Glandular secretions

Leopards often scraped substrates such as the trunk of trees, logs and the ground without urinating or defecating at the same time. Scraping against trees was visually very prominent, especially at the territory's edge next to another leopards' territory (Figure 4.9).

Figure 4.9 Scratching marks by a female leopard on the trunk of a *K. acuminata*.

No tree species preference was found, but 50% consisted of *K. acuminata*, 25% *Cassia abbreviata* (Sjambok pod) and 25% *B. albitrunca*. Trees used for scratching are often very prominent, usually standing alone and not in thick or dense bush. Such features apparently enhance the visibility of the scrape markings. In addition, all scratching trees seem to have hard bark as the scrapings are not very deep but more limited to the surface (Figure 4.9). Trees used for scratching purposes were not used to rest in and *vice versa*.

Head rubbing, possibly involving glandular secretion, was often performed by both sexes against bushes on which they subsequently urinated. During the oestrus period of the females, head rubbing on the ground commonly occurred, but such behaviour was never recorded from the male.

Females performed the heat-roll in front of the male, preferring longer grass to do so. On average 19 heat-rolls were performed during one hour, with a decline in rolls after 30 minutes. As shown in Figure 4.10, 14 rolls occurred during the first half an hour of observation with only 5 heat-rolls in the next. Whenever the male should show special interest in the female (indicated by arrows in the graph), the latter immediately responded by increasing the number of heat-rolls and object rubbing.

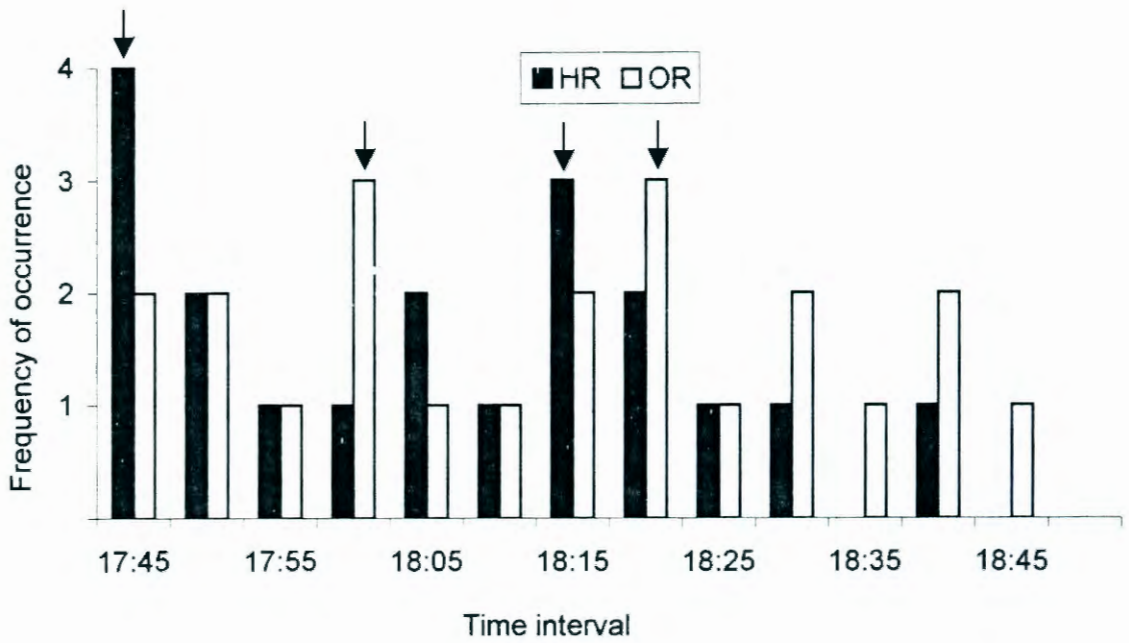


Figure 4.10 Oestrus related behaviour performed by a female leopard in front of a male during a one hour observation period (HR – heat roll; OR – object rubbing; arrow – male interest).

4.3.4 Touch

Physical contact between individuals is an indispensable component of courtship behaviour amongst animals. In the leopards observed during the study, the female and male often greeted each other by touching their noses through the fence, especially during a female's oestrus period. Before and after the touch, sexual displays involving all communication methods were prominently displayed.

4.4 Discussion

The successful functioning of a society is entirely dependent on its communicatory system (Schaller 1972). Communication is not only vital for an orderly social structure to be maintained between individuals, but is also essential in ensuring a very specific distribution of individuals which prevents overpopulation and subsequent over-utilisation of prey with subsequent starvation. Even though leopards are solitary animals, they possess an extensive and complex array of visual, acoustic and olfactory communication methods for intra and interspecies communication. These are often combined with specific behavioural patterns and must be regarded as communication units.

4.4.1 Visual communication

The conspicuous black and white colouration of the body plays and important role in visual communication, as it serves to focus attention on specific body parts. The total length of a leopard can be up to two meters of which the tail contributes approximately 80 cm (Yosef 1998). Apart from balance, the tail plays an integral role in visual communication, and not only to express different levels of excitement. Of the thirteen positions identified, each one is distinctive, although there is a degree of variation of the same position.

Ear positions and facial expressions were found to be reliable indicators of specific behavioural and activity patterns. It is important to bear in mind that specific behaviour is mostly indicated by a combination of ear positions and facial expressions and not by a single factor alone. Because leopards are solitary animals (Skinner & Smithers 1990), special ear positions have been developed to enhance their chances of survival. Ear

observation position four with the ears held backwards (Figure 4.4d), while securing an area which the leopard can't actually see, is a good illustration of adaptation to their solitary lifestyle. Due to the number of individuals involved, social animals need not perfect this ear position.

By using facial expressions alone it is possible to distinguish between offensive and defensive threats. The former carries a message equivalent to "if you don't retreat, I will attack"; while the latter means, "I am not about to launch an attack, but if you take the offensive, I will retaliate".

4.4.2 Auditory communication

A close relationship between behaviour and vocalisation of leopards was established. Considering the few vocalisations previously described, namely rasping (Apps 1996), hoarse barking (Burger 2000), "urr-urr-urr" contact call from cubs to the mother (Estes 1999) and growling and purring (Skinner & Smithers 1990), it is surprising that an additional eleven distinctive vocalisations were identified during this study. Quite clearly, leopards are more vocal than has been previously realised.

In potential conflict situations a leopard will lie down on the ground as flat as possible and use camouflage to hide itself. If undetected, the leopard will stay put, but if not, a hissing sound will be produced. In other circumstances, however, a leopard will attack without any acoustic warning, especially during a hunt when silence is of the utmost importance or when a female has cubs to protect.

Snuffing is not used in communication, but in detecting pheromones secreted by other individuals of both sexes. Purring can be considered an expression of pleasure (Turner & Bateson 2000), often recorded during social interactions. Since members of the genus *Panthera* have an incomplete ossified hyoid apparatus with an elastic cartilaginous band replacing the bony structure found in the genus *Felis,* purring is limited to times of exhaling. By contrast, members of the genus *Felis* can purr both when exhaling and inhaling (Grzimek 1975). The elastic ligament in the hyoidean apparatus allows roaring (known as rasping) and is one of the distinct modifying characteristics between the genera *Panthera* and *Felis* (Skinner & Smithers 1990).

Purring is generated by a sudden build-up and release of pressure as the glottis is closed and then opened, resulting in a sudden separation of the vocal fold, which produces the sound. The laryngeal muscles, which move the glottis, are driven by a free-running neural oscillator, generating a cycle of contraction and release every 30-40 milliseconds. Adult leopards may purr when in contact with a familiar partner and during tactile stimulation with inanimate objects, such as when rolling or rubbing (Turner & Bateson 2000).

The low frequency vocalisation of the male during mating, can possibly serve three functions:

(i) As a warning to other males that the mating male will not tolerate interference.

(ii) To create awareness of the presence of the male to other females that are ready for mating.

(iii) The long duration is presumably also designed to convey the size and the strength of the animal (Turner & Bateson 2000).

4.4.3 Olfactory communication

Olfactory signals are long lasting and would therefore be expected to play an important part in communication between both social and solitary members of the Felidae. Urination occurred where it is likely to persist and where it can be noticed. The use of urination in territorial behaviour in the arid bushveld was found to be similar to that of leopards in the desert. Bothma & Le Riche (1984) found that leopards in the Kalahari displayed four types of urination in marking their territories.

According to Turner & Bateson (2000) defecation sites of the Canadian lynx (*Felis lynx*) and the European wildcat (*Felis silvertris*) are localised and covered within territories, but left uncovered in prominent mating rendezvous sites between territories in the case of the lynx. With regard to leopards it was only observed in two females with small cubs that they occasionally scraped sand over their faeces. In both cases the cubs were younger than three months old and the females only covered their own faeces when defecating in the immediate vicinity of the cubs (Bothma & Le Riche 1984). Thus, by implication, leopards normally leave their faeces uncovered and exposed to serve as a means of communication.

The observed mean interval of 1.3 days between defecation of individual leopards closely corresponds with the mean interval of 1.2 days for a female leopard as reported by Bothma & Le Riche (1994). The order of excretion is proportional to the order of intake if the same type of diet is fed (Theron 2003).

As was the case with urination, defecation sites normally occurred in existing paths, roads or open patches. Faeces were never found in long grass or underneath thick bushes. Since faeces contain lipid pheromones, which act as a component of communication, it is important not to sample all faeces excreted for scat analysis. A minimum of twenty hairs taken at random from each scat will be enough for purposes of prey identification. Otherwise, a communication symbol is removed that can influence or disturb the leopard and may even result in abnormal behaviour.

According to Bothma (1997) rubbing is presumably more likely a grooming than a communication action. The fact that only females displayed such behaviour (particularly head-rubbing) during their oestrus period in the presence of a male is, however, a clear indication that it also serves as a communication method (Wolhuter 2001).

Along with rubbing, heat-rolling was a very prominent activity performed in front of the male. As the behaviour peaked during the initial stages of intersexual interaction, it can be assumed that copulation would have occurred were it not for the fence that separated the individuals. Physical touch is an inevitable pre-requisite for mating. Mating starts off by a bite from the male to the nape of the female's neck, presumably to pacify and physically control the female before and during copulation. As they mate, touch receptors in the female's genitals send messages to her brain, triggering the hormonal changes that result in ova being released for fertilisation. To ensure that the message is received and "understood", the male's penis is armed with tiny, backward pointing spines (Apps & Du Toit 2000). Aggressive reaction by the female at this time is probably in response to the pain caused by the male's penis when withdrawing (Wolhuter 2001).

Chapter 5

Feeding behaviour

5.1 Introduction

As observed in the literature review, very little is known about the feeding behaviour, daily fresh food intake and nutritional requirements of leopards. In contrast, prey selection has been well documented. With the expanding wildlife industry in southern Africa, knowledge of the diet selection and feeding preference of different predator species (in this case the leopard) is thus essential. More importantly it is essential to be able to quantify the ecological and economical impact of the leopard as a predator in the ecosystem.

To date no standard quantification has been set for daily food intake of leopards. Close monitoring was done on feeding sequences, day-to-day utilisation of prey and general feeding behaviour of the experimental animals.

The objectives of the study were to:

(i) describe the capacity of available prey species (species and numbers) to support a leopard,

(ii) establish the average daily food requirements of a leopard in relation to its size and sex, and

(iii) quantify the ecological and economical sustainability of a leopard within a specific environment.

5.2 Procedure

5.2.1 Body condition scoring

Hamilton, Buskirk & Buskirk (1977) devised a system to quantify the apparent relative physical condition of gemsbok (*Oryx gazella*). Subsequent grades in defining physical condition were made by three observers. Their average estimates were comparable and

differed less than 0.2 grades regarding 50 gemsbok. The same principle was used to score the body condition of the leopards. However, due to the quick change in physical appearance of the leopard, a simplified approach was used (Figure 5.1).

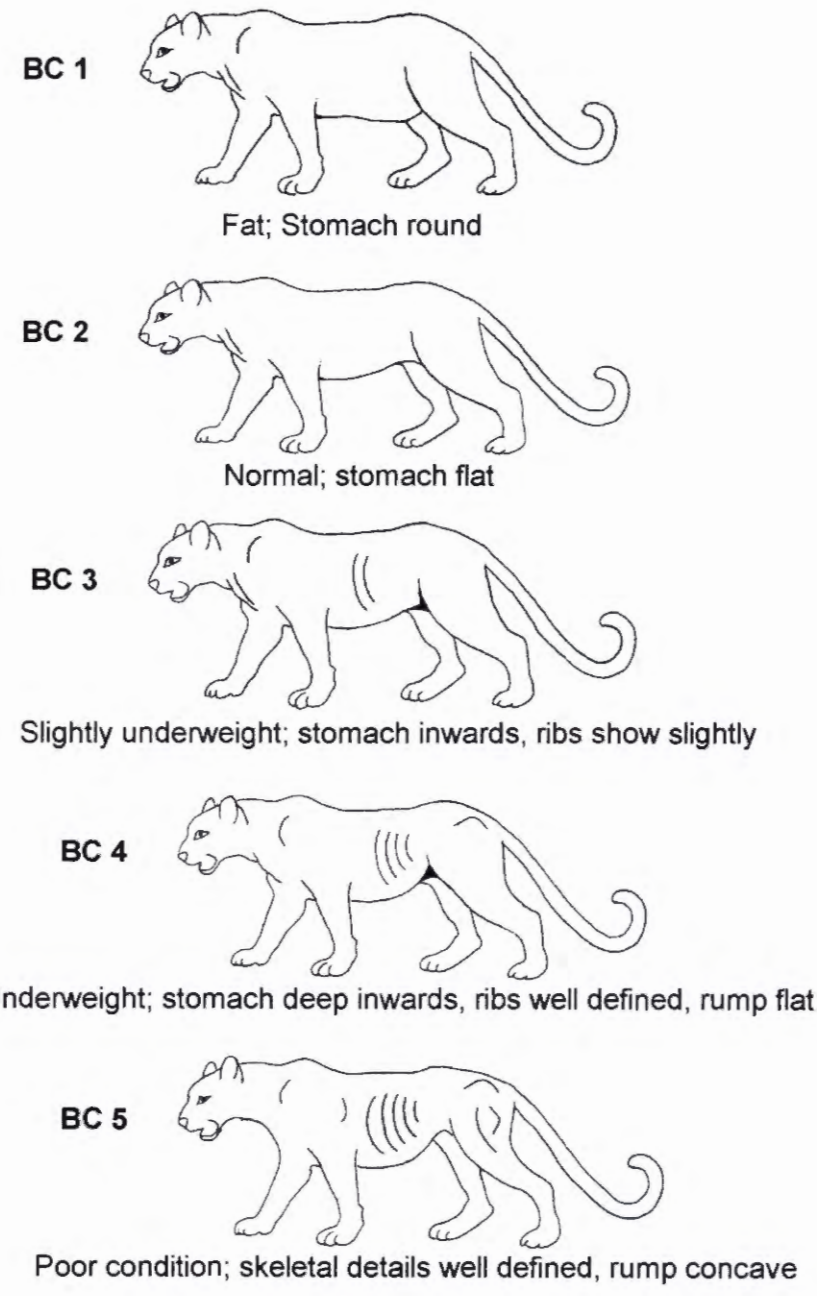


Figure 5.1 Schematic illustration of the visual criteria used for the scoring of body-condition (BC) of the leopard.

5.2.2 Prey utilisation

In order to determine the utilisation of different potential prey species, carcasses of various prey species were offered to the leopards from 20 March 2002 until 14 October 2002 (Table 5.2).

Prey was harvested in such a way as to cause as little damage to the carcass as possible. The carcasses of the prey were offered to a leopard as soon as possible after harvesting. The physical condition of the leopard was scored as discussed, and a leopard only received a carcass when it was in body condition 2 to 3. Because leopards normally hunt early morning or late afternoon until midnight, prey was given during these times to simulate normal hunting behaviour. All prey were weighed (whole carcass) before being fed to a leopard.

The prey's neck was tied with steel wire as close as possible (10 cm or less) to a tree in the vicinity where the leopards normally feed. This prevented the leopard from dragging its prey into thicker bush, thus preventing accurate observation of prey utilisation. The prey was tied up in a position that was deemed an ideal feeding spot, taking into consideration all weather conditions. Shade was an important factor because leopards usually drag their kill into thick bush or trees with high leave density to obtain maximum shade.

Monitoring of the utilisation of each carcass was conducted at 24 hour intervals at 07:30 each morning. During each observation session, it was recorded what part of the carcass had been utilised during the past 24 hours. Observations also included an estimate of the body condition of the leopard. Field observations determined that under normal conditions a leopard would hunt again when it was in a body condition 2 to 3. The observation cycle started when a carcass was offered to the leopard and ended when:

(i) the carcass was 100% utilised except for inedible remains (discussed later),

(ii) the leopard stopped feeding on the carcass or utilised only a small amount, or

(iii) the leopard started hunting other game.

In all cases the leopard had to be in body condition 2 to 3 before any supplementary feeding resumed.

The three leopards used for this research were weighed on a portable Trutest Economy plus Mod. 700 scale (Figure 5.2).

Figure 5.2 Female leopard being weighed on a portable scale.

After the scale was leveled and stabilised, it was zeroed with meat on it. The body mass of each leopard in body condition 2 was measured as they climbed onto the scale to take the meat during their routine feeding. Leopard A was wary of the scale and it was not possible to obtain an accurate measurement of her mass. Her mass was subsequently estimated (Table 5.1).

Table 5.1 Body mass of three selected semi-tame leopards.

Date	Leopard	Sex	Mass (kg)	Body condition
16-10-2002	B	♂	60.5	2
17-10-2002	D	♀	36	2
17-10-2002	A	♀	39 (Estimated)	2

5.2.3 Carcass analysis

Through observations a certain pattern of carcass utilisation by leopards was identified. It was hypothesized that the order of utilisation correlates with a decreasing fat-content distributed in the carcass and that a leopard deliberately selects such a diet. Due to this feeding behaviour, an impala carcass was analysed to determine fat distribution. An impala was selected because from literature (Bailey 1993) and common knowledge it is known that impala forms a high prey-selection percentage of the leopard's diet.

5.2.3.1 Carcass segments (CS)

In order to identify and quantify specific patterns and preferences in the order that a prey's carcass ≥5 kg was utilised, each carcass was divided into eight carcass segments (Figure 5.3):

(i) Head (c),
(ii) Neck (d),
(iii) Left fore limb (b),
(iv) Left rib cage and flank (g),
(v) Spinal column and tail (f),
(vi) Left hind limb (a),
(vii) Fore intestines,
(viii) Hind intestines.

For practical reasons the rumen, reticulum, omasum, abomasums and small and large intestines were grouped, named as "hind intestines". The heart, lungs, liver and kidneys were grouped as "fore intestines".

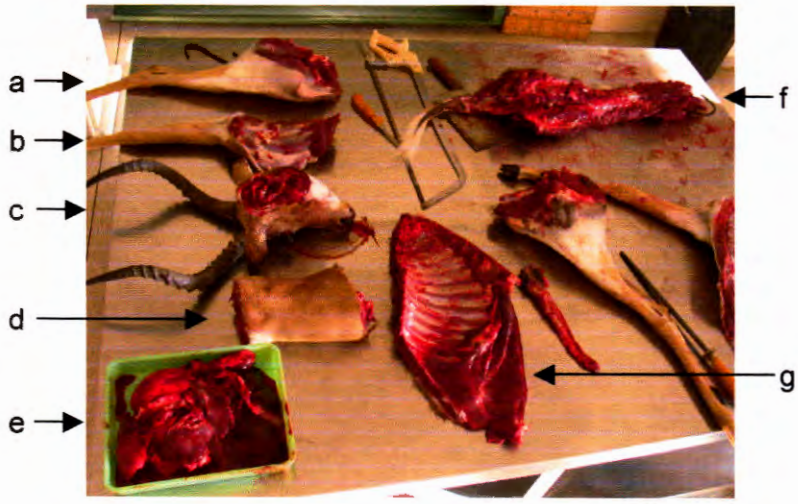


Figure 5.3 Carcass segments of an impala excluding the hind intestines. ((a), hind limb; (b), fore limb; (c) head; (d) neck; (e) fore intestines; (f), spinal column and tail; (g) rib cage and flank.)

5.2.3.2 Separation of the carcass segments

An adult impala was separated into the different carcass segments as discussed in paragraph 5.2.3.1. With close monitoring of the feeding behaviour of the leopards, it was possible to record for each carcass segments what the leopards consumed and what was left, the latter known as the remains. Based on this knowledge the eight carcass segments were subsequently further separated into edible and inedible parts (Figure 5.4), mimicking as closely as possible the observed feeding behaviour of the leopard.

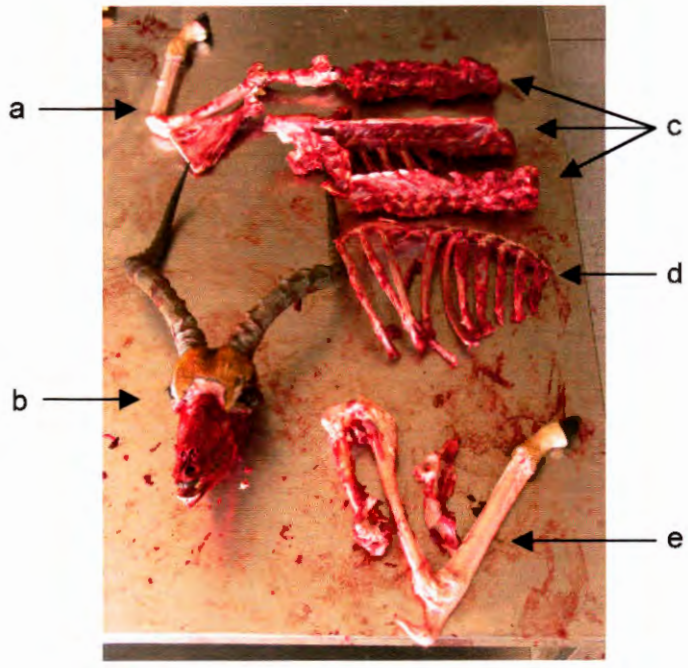


Figure 5.4 Remains of each carcass segment that is not generally eaten by a leopard. ((a), fore limb; (b), head; (c), spinal column and tail; (d), rib cage and flank; (e), hind limb.)

A rock hyrax, opportunistically obtained, was also included in the analysis. Since a leopard will consume such a small prey completely (except excretions in intestines) within one feeding, the carcass was not divided into the different carcass segments.

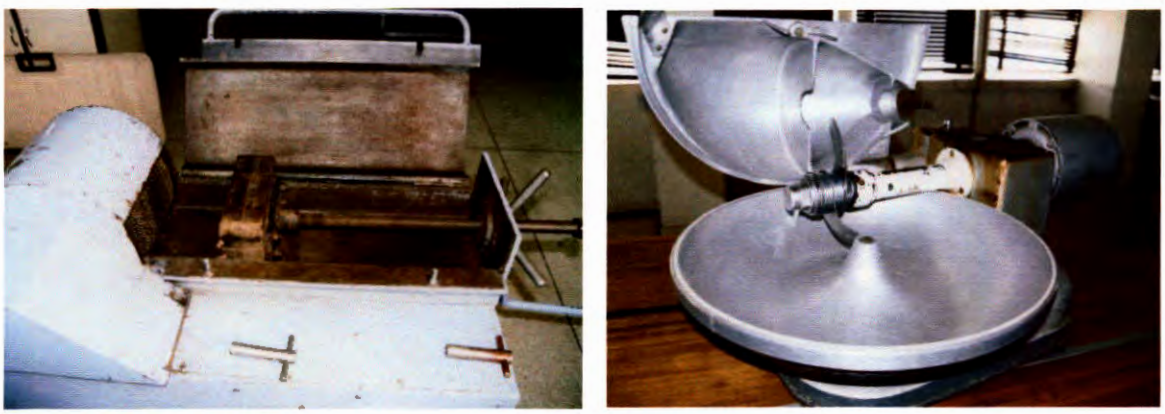
A sub-adult male kudu (*Tragelaphus strepsiceros*) was also analysed. Separation into the nine carcass segments did not take place in a lab, but there is a relatively close percentage mass correlation between the carcass segments of the impala ram and that of the kudu, except for the hind intestines and spinal column and tail (Table 5.6).

5.2.3.3 Grinding of the carcass segments

The frozen carcass segments of an impala and a complete rock hyrax were ground through a heavy duty carcass grinder (Figure 5.5a). The carcass grinder is equipped with 57 circular saw-toothed blades, each with a diameter of 300 mm. The blades are fitted 3 mm apart onto a single axle propelled by two fan belts pulled by a 10 HP electric motor. While the carcass segments were manually propelled through the blades, a steel lid prevented pieces of the carcass being flung from the grinder. The ground carcass

segments were collected in plastic bags. All small pieces of the carcass segments adhering to the grinder were carefully removed by hand to prevent any losses. The mass of every carcass segment was taken before and after every action (Table 5.4). The ground carcass segments were subsequently frozen again.

Before the frozen carcass segments were ground for a second time, large pieces of skin that were not ground the first time, were cut into smaller pieces with a meat saw. After the second grinding, the carcass segments were collected and transferred to a commercial bowl processed meat mixer (Figure 5.5b) and thoroughly mixed. A representative sample of 400 g was taken of each impala carcass segment and complete rock hyrax.



a b

Figure 5.5 Heavy-duty carcass grinder (a) and commercial bowl meat mixer (b).

5.2.3.4 Drying of the samples

The ground samples were dried in a force draught oven at 100°C for 24 hours. The samples were then put back into the freezer for another 24 hours.

5.2.3.5 Milling of samples

The dried samples were mixed with crushed dry ice in a 1:1 volume ratio and milled through a 0.75 mm sieve in a conventional Wiley mill. The dry ice kept the samples cold and prevented the fat from smearing too much during the milling process. All samples were placed in plastic containers with screw-on lids and stored at -10°C.

5.2.3.6 Nutrient analysis

The dry mass (DM) of each carcass segment sample was determined after the drying period of 24 hours at 100°C. All nutrient analyses were done in duplicate.

5.2.3.6.1 Crude protein (CP)

The crude protein content of the carcass segments was determined on a dry material basis with a Leco ® nitrogen (N) analyzer (Leco ® Corporation, 2001). A factor of 6.25 was used to convert the N content of samples to CP content.

5.2.3.6.2 Lipids

The lipid content of the carcass segments was determined in a soxhlet apparatus by using the hexane method (AOAC 2000). Lipid content caused smearing of fat onto the glass apparatus. Sample bottles were dried overnight to rectify any moisture gain while in the bottles. The mass difference between an empty and smeared glass apparatus resulted in the lipid content of each carcass segment and the complete rock hyrax.

5.2.3.6.3 Minerals (ash)

The mineral (ash) content was determined on a dry matter basis by ashing the samples in porcelain crucibles for four hours in a muffle furnace at 600°C (AOAC 2000).

5.3 Results

5.3.1 Prey utilisation

The prey offered to leopards of both sexes is listed in (Table 5.2). Each species mass and edibility is presented, as well as the total number of days the leopard fed on it and the average daily consumption of the leopard. Prior to feeding to the leopard, the body condition of prey was scored using the Hamilton, Buskirk & Buskirk (1977) system.

From the results in Table 5.2, it was possible to draw a graph (Figure 6.3) from which the exact day-support of a carcass can be determined. Day-support represents the total number of days that one carcass can sustain a leopard depending on the season, insect

activity and other environmental factors. The results presented in Figure 6.3 and the principle of day-support will be discussed in detail in chapter 6.

5.3.1.1 Utilisation sequence and feeding behaviour

A distinct feeding pattern of the leopard was observed, independent of the prey species, except on one occasion when an eland calf of 104.2 kg was consumed. In Table 5.3 the feeding sequence of the various carcass segments is numerically given. Observations of the feeding sequence indicated that the carcass is eaten in the following order: (i) hind intestines, (ii) fore intestines, (iii) hind limb, (iv) fore limb, (v) rib cage and flank, (vi) spinal column and tail, (vii) neck and (viii) head. Although this was the general feeding pattern, random utilisation of carcass segments occasionally occurred.

5.3.2. Carcass analysis

5.3.2.1 Carcass segments

The fresh intact impala weighed 48.947 kg and the rock hyrax 2.196 kg. Due to the cutting and grinding, a water loss of 9.27% was calculated for the impala (Table 5.4). After the impala was cut into the nine carcass segments and the remains separated, all segments were weighed again (Table 5.5).

Table 5.2 Different prey species offered and utilisation by the experimental leopards.

Nr	Date	L	Prey species	Sex	Class of prey	Mass of prey (kg)	Prey Edibility	Days fed on	Average kg / day live mass available	Average kg /day edible	% Utilised	% Unutilised
1	20/05/02	D	*S. grimmia*	♂	1	16.68	**13.01**	4	4.17	**3.25**	100	0
2	20/05/02	A	*S. grimmia*	♀	1	17.02	**13.27**	4	4.26	**3.32**	100	0
3	24/05/02	D	*P. africanus*	♂	1	50.36	**39.28**	11	4.58	**3.57**	100	0
4	24/05/02	A	*P. africanus*	♂	1	49.00	**38.22**	11	4.45	**3.47**	100	0
5	30/06/02	D	*A. melampus*	♂	1	65.00	**50.70**	16	4.06	**3.17**	100	0
6	2/7/02	**B	*A. melampus*	♂	1	59.40	**44.55**	8	7.43	**5.57**	100	0
7	24/07/02	D	*P. ursinus*	♂	1	18.80	**14.66**	6	3.13	**2.44**	100	0
8	21/08/02	D	*A. melampus*	♀	1	45.60	**35.57**	12	3.80	**2.96**	100	0
9	24/08/02	A	**P. africanus*	♂	1	52.40	**39.30**	0	0	**0.00**	0	100
10	24/08/02	**B	**C. mesomelas*	♂	1	7.60	**5.93**	0	0	**0.00**	0	100
11	26/08/02	**B	**T. strepsiceros*	♂	2.5	220.00	**154.00**	0	0	**0.00**	0	100
12	26/09/02	**B	*P. ursinus*	♂	1	30.00	**23.40**	4	7.50	**5.85**	100	0
13	26/09/02	D	**P. ursinus*	♂	1	27.20	**21.21**	5	3.08	**3.08**	72.61	27.39
14	26/09/02	A	**P. ursinus*	♂	1	28.40	**22.15**	0	0	**0.00**	0	100
15	28/09/02	A	**T. scriptus*	♂	1.5	28.60	**22.31**	0	0	**0.00**	0	100
16	1/10/02	A	*Goat*	♂	1	30.60	**23.87**	8	3.83	**2.98**	100	0
17	4/10/02	**B	*Fetus of cattle*		1	25.20	**19.65**	5	5.04	**3.93**	100	0
18	9/10/02	**B	*Goat*	♂	1	32.20	**25.11**	6	5.37	**4.19**	100	0
19	9/10/02	A	*Fetus of cattle*		1	19.80	**15.44**	6	3.30	**2.57**	100	0
20	11/10/02	D	**T. oryx*	♂	2	104.20	**78.15**	9	3.08	**3.08**	35.59	64.41
21	14/10/02	**B	**T. strepsiceros*	♂	2.5	156.90	**109.83**	2	5.25	**5.25**	9.56	90.41

*Explanation of symbols: (**) - male leopard; (*) - prey 100% unutilised; (*) - prey partly utilised; (L) – experimental leopard.

Table 5.3. Feeding sequence of the experimental leopards on different prey species. First number (bold) of each group indicates the carcass segment utilised the day after the prey was offered to a leopard and the second number after the back slash the utilisation of each carcass segment in each day.

		Carcass segments							
Nr.	**Species**	**Head**	**Neck**	**Fore limb**	**Rib cage & flank**	**Spinal column & tail**	**Hind limb**	**Fore intestines**	**Hind intestines**
1	*S. grimmia*	**4**/0	**3**/3	**3**/1	**2**/3	**3**/2	**1**/2 **2**/2	**1**/1	**2**/1
2	*S. grimmia*	**4**/2	**4**/1	**2**/3	**1**/2 **2**/2	**3**/2	**2**/1 **3**/1	**1**/1	**1**/3
3	*P. africanus*	**10**/2	**10**/1	**2**/1 **3**/1 **8**/2	**3**/2 **6**/1 **7**/2 **8**/1	**9**/1	**1**/1 **4**/1 **7**/1	**4**/2	**1**/2
4	*P. africanus*	**10**/2	**10**/1	**7**/7 **8**/1 **9**/1	**4**/2 **6**/1 **7**/2	**9**/2	**1**/1 **2**/1 **3**/1	**4**/1	**3**/1
5	*A. melampus*	**15**/2	**12**/1 **13**/1 **14**/1 **15**/1	**5**/1 **6**/1 **10**/1 **12**/2	**4**/1 **6**/2 **7**/1 **8**/1	**7**/2 **9**/1 **11**/1 **12**/3	**1**/1 **2**/1 **3**/1 **4**/2	**5**/2	**2**/2 **3**/2
6	***A. melampus*	**7**/2	**6**/1 **7**/1	**3**/1 **4**/2 **5**/2	**3**/2 **4**/1	**5**/1	**1**/1 **5**/3	**2**/1	**2**/2
7	*P. ursinus*	**5**/1	**4**/2	**3**/1	**3**/2	**4**/1	**2**/1	**1**/2	**1**/1
8	*A. melampus*	**10**/2	**8**/1 **10**/1 **11**/1	**5**/1 **6**/1 **7**/1	**4**/1 **6**/3 **7**/2 **8**/2 **9**/1 **11**/3	**5**/1 **6**/2 **7**/2 **11**/2	**1**/1 **2**/1 **3**/2	**4**/1	**2**/2 **3**/1
9	**P. ursinus*	-	-	-	-	-	-	-	-
10	**C. mesomelas*	-	-	-	-	-	-	-	-
11	**T. strepsiceros*	-	-	-	-	-	-	-	-
12	***P. ursinus*	**4**/2	**4**/1	**2**/2	**1**/3 **2**/3	**3**/1	**1**/1	**2**/1	**1**/2
13	**P. ursinus*	-	-	**4**/1	**3**/1	**4**/2	**1**/1 **2**/2	-	**2**/1
14	**P. ursinus*	-	-	-	-	-	-	-	-
15	**T. scriptus*	-	-	-	-	-	-	-	-
16	*Goat*	**6**/2	**6**/1 **7**/1	**4**/1 **5**/1	**2**/3 **3**/1	**4**/1 **5**/2 **7**/2	**1**/1 **2**/1	**2**/2	**1**/2
17	***Fetus of cattle*	**4**/3	**4**/2	**3**/2	**3**/3	**4**/1	**1**/1 **2**/2	**3**/1	**2**/1

continue...

Table 5.3 continued

Nr.	Species	Head	Neck	Fore limb	Rib cage & flank	Spinal column & tail	Hind limb	Fore intestines	Hind intestines
18	**Goat	5/3	5/2	3/1 5/1	3/2 4/2	4/1	1/2 2/1	2/2	1/1
19	Fetus of cattle	5/2	5/1	3/2 4/1	3/1	4/2	2/1	1/2	1/1
20	*T. oryx	-	-	1/2 5/1 8/1	5/2 5/2 6/2 7/1	6/1	1/1 2/1 3/1 4/1	3/2	-
21	***T. strepsiceros	-	1/1 2/1	-	-	-	-	-	-

*Explanation of symbols: (**) - male leopard; (*) - prey 100% unutilised; (*) - prey partly utilised.

Table 5.4 Mass of the Impala ram carcass segments (CS) and complete carcass of the rock hyrax before and after each of the two grinding procedures.

Impala

		13 June 2003	18 June 2003			20 June 2003			
Carcass section	**CS (g)**	**Before**	**After**	**Difference**		**Before**	**After**	**Difference**	
				g	**%**			**g**	**%**
Left hind limb	5 492	5 505	5 173	332	6.03	5 172	5 010	162	3.13
Left fore limb	2 561	2 562	2 214	348	13.58	2 213	2 114	99	4.47
Left rib cage & flank	2 446	2 446	2 132	314	12.84	2 132	2 030	102	4.78
Spinal column & tail	7 331	7 328	6 717	611	8.34	6 715	6 577	138	2.06
Neck	2 435	2 434	2 104	330	13.56	2 103	2 066	37	1.76
Head	996	993	851	142	14.30	852	837	15	1.76
Fore intestines	3 057	3 049	2 743	306	10.04	2 742	-	-	-
Stomach	1 974	1 974	1 754	220	11.14	1 754	-	-	-
Small & Large intestine	1 394	1 393	1 368	25	1.80	1 368	-	-	-
Rock hyrax									
Complete carcass		2 196	1 971	225	10.25				

Table 5.5 Wet weight of the various carcass segments of a male impala with a live mass of 48.947 kg.

Carcass section	Fresh mass (g)	Edible mass (g)	Inedible mass (g)	Total	Difference	
					g	%
Left hind limb	6 590	5 492	1 071	6 563	27	0.41
Left fore limb	3 450	2 561	873	3 434	16	0.46
Left rib cage & flank	2 890	2 446	436	2 882	8	0.28
Spinal column & tail	9 286	7 331	1 921	9 252	34	0.37
Neck	3 375	2 435	929	3 364	11	0.33
Head	4 174	996	3 162	4 158	16	0.38
Fore intestines	3 057	3 057	0	3 057	0	0
Stomach	1 974	1 974	0	1 974	0	0
Small & Large intestine	1 394	1 394	0	1 394	0	0

Although eight carcass segments were used, the hind intestines were divided into the stomach and the small and large intestines. These eight carcass segments were separated into edible and inedible parts known as the remains (Figure 5.4). The mirror images of the right hind limb with testis and right fore limb, each (6 638g) and (6 120g), respectively, were not included in the analyses. The remains of the impala ram, which will on estimate not be consumed by a leopard, totalled 10.772 kg.

Table 5.6 Comparison of carcass segments (CS) of an adult male impala and a sub-adult male kudu.

	Male impala (48.947 kg)			Male kudu (120.880 kg)		
Carcass section	CS kg	% mass	% section	CS kg	% mass	% section
Head	4.174	8.528	0	6.28	5.195	0
Neck	3.375	6.895	0	7.24	5.989	0
Fore intestines	3.057	6.246	0	4.16	3.438	0
Stomach	1.974	4.033	0	0	0	0
Small & large intestines	1.394	2.848	0	22.78	18.845	0
Spinal column & tail	9.286	18.972	0	11.44	9.463	0
Fore limbs	3.45	14.097	7.048	9.330	15.436	7.718
Rib cages & flanks	2.89	11.809	5.904	8.320	13.764	6.882
Hind limbs	6.59	26.927	13.464	16.840	27.862	13.931

5.3.2.2 Nutritional values

The results of the analyses of the fat, crude protein and ash of the various carcass sections are presented in Table 5.7. The complete data set of the analyses are presented in Appendix A – D.

Table 5.7 Percentage values of carcass segments of the male impala and rock hyrax (CP - crude protein; F - fat; A - ash; DM - dry material).

Carcass section	CP %	F %	A %	DM %
Head	80.53	16.15	6.29	98.85
Neck	92.97	5.55	4.90	99.18
Fore intestines	76.81	17.15	4.70	99.45
Stomach	67.42	13.95	8.84	99.36
Small & large intestines	42.27	41.75	6.06	99.10
Spinal column & tail	89.84	6.85	4.62	99.97
Fore limb	91.42	6.60	4.31	99.55
Rib cage & flank	88.41	10.30	4.89	99.29
Hind limb	91.05	5.45	4.75	99.98
Rock hyrax	69.735	6.80	14.71	98.84

5.4 Discussion

It is well known that leopards drag their prey up into a tree or under a bush, depending on the presence of natural enemies like lion or scavengers like spotted hyaenas. By doing this the leopard achieves the following benefits:

(i) The area where the actual hunt took place is abandoned and in doing so it minimises the risk of attracting scavengers.

(ii) The carcass is secured in a tree. It limits the feeding of vultures and other scavengers.

(iii) Under thick bush and densely leafed trees a high percentage of shade is present. In shade the carcass will not decompose as quickly as when in direct sun.

(iv) In addition to the shade in/under a tree, wind movement contributes to the cooling of the carcass.

By preserving food in the above way, the leopard ensures that it can feed for a longer period on the carcass, thereby preserving its energy by increasing the intervals between hunts.

5.4.1 Prey utilisations

From Table 5.2 it is evident that there were few prey species that were not utilised when offered to the experimental leopards. Carcasses of species indicated with a red asterisk were all two to three days old, lying in the sun with intestines intact. The leopards abandoned that specific prey, and did not even bother to lick or start eating it. Carcasses of those species marked with a green asterisks were not completely (100%) utilised due to decomposition and insect infestation. The baboon's (*Papio ursinus*) decomposition rate was very high due to abnormal high temperatures and soft rain that fell sporadically during that period. The eland was not completely utilised because of its size that result in decomposition before it was totally consumed. The head of the kudu (green asterisk) was cut off and all intestines were removed before it was fed to the male. The neck where the male started feeding, stayed well for two days, but the other open areas (body cavity) were exposed and insects took advantage of the situation.

From literature it is known that leopards start feeding at the hindquarters of the prey. Bothma (1997) stated that a leopard usually starts to feed on the buttocks. It is assumed that this feeding behaviour results from the high protein content in the buttocks. If the crude protein content of the various carcass segments (Table 5.7) is taken into consideration, bearing the above assumption in mind, then carnivores are supposed to start feeding at the neck followed by the shoulders.

It is clear from the feeding sequence observed in this study that the carcass is eaten in the following order: (i) hind intestines, (ii) fore intestines, (iii) hind limb, (iv) fore limb, (v) rib cage and flank, (vi) spinal column and tail, (vii) neck and (viii) head. This consumption pattern was verified (Figure 5.6) between leopards of both sexes and between captive hand-reared and wild free-roaming leopards on the farm "The Beacon" (approximately 15 km north of Gravelotte in the Limpopo Province).

a b

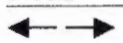
Figure 5.6 Feeding sequence on prey (impala) by captive (a) and wild free-roaming (b) leopards.

As can be seen from Figure 5.6, there is a similarity in the feeding sequence behaviour of the hand-reared captive leopards (a) and that of a wild leopard (b). Unfortunately the observations as depicted in Figure 5.6 were not on the same sequential day. In both cases the body cavity was opened and fed on first, but the impala illustrated in Figure 5.6b was longer fed on than the impala in Figure 5.6a and therefore already utilised up to the hind limbs. A leopard was observed biting a hole in one end of an intestine, whereupon the opening was turned away from the leopard and the contents of the intestine peeled by pulling the closed side through narrow-open incisors. By doing so almost all faecal content were squeezed out, where-after the intestine was consumed.

The hypothesis that the utilisation order correlates with a decreasing fat-content is supported by the data presented in Table 5.8. By comparing the fat content and the crude protein percentages of the various carcass segments to the feeding sequence, a close positive correlation was established (Table 5.8). This was especially the case with the fat content, which confirms the hypothesis that leopards deliberately select a diet with a high fat content.

Table 5.8 Feeding sequence compared to crude protein (CP) and fat content in each carcass segment (HF, highest fat percentage in CS). (numbers depict the feeding sequence and the fat and CP content from the highest to lowest)

Carcass	HF	Feeding sequence	CP
Small & large intestines	1	1	9
Stomach	4	2	8
Fore intestines	2	3	7
Hind limb	9	4	3
Fore limb	7	5	2
Rib cage and flank	5	6	5
Spinal column & tail	6	7	4
Neck	8	8	1
Head	3	9	6

 Illustrates the high correlation between feeding sequence and the fat percentages in each carcass segment.

 Compare the highest crude protein percentage in each carcass segment to the feeding sequence.

From the comparison in Table 5.8, it would be premature to conclude that protein does not play a role in the nutritional requirements of a leopard. From the literature review it is clear that proteins are vital for any organism, where-as fat is an important form of energy. An explanation for the buttock-theory (Bothma 1997) could be that it is the shortest way to the intestines and the flank is the softest part to cut through.

There could be a number of explanations for the observed feeding sequence:

(i) Leopards deliberately select specific carcass segments with a high percentage of fat.

(ii) Removal of the intestines before it contaminate the rest of the carcass and progressively speeds up the rotting process.

(iii) By eating the intestines first, essential vitamins are ingested before they are destroyed by oxidation as discussed in the literature review (2.9.3), and

(iv) it lessens the strong smell that can attract scavengers.

Chapter 6

Predator-prey units and predator carrying capacity

6.1 Predator carrying capacity

6.1.1 Trophic levels in an ecosystem

The principles of different trophic levels in an ecosystem, which include producers, primary, secondary, tertiary consumers and decomposing organisms, is well known (Figure 6.1).

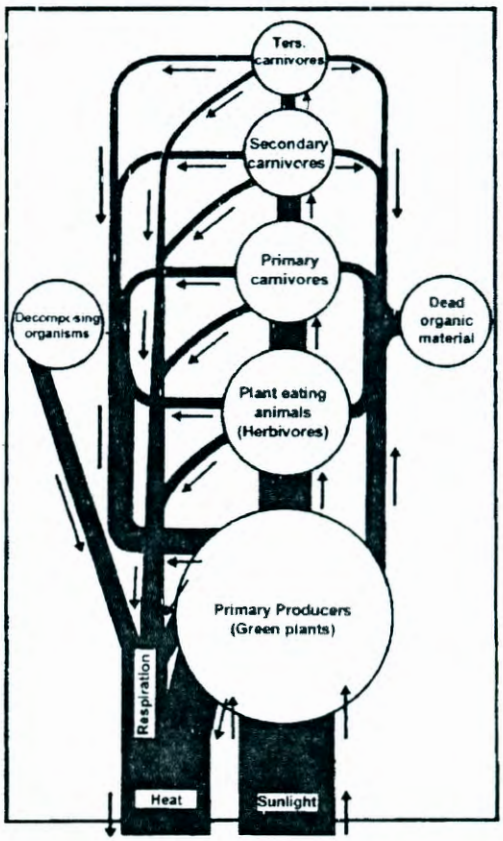


Figure 6.1 Diagrammatic presentation of trophic levels, energy flow and element circulation in an ecosystem (Ryke 1982).

The main objective of management of a game ranch with only herbivores is to ensure that the nutritional requirements of the herbivores are met in such a way that they maintain an acceptable level of productivity, while the productivity of the vegetation is also maintained or improved.

The addition of a predator into such a system establishes an additional trophic level in the food pyramid, however, the same principle of sustainability will apply. The given number of predators (leopards in this case) must be able to satisfy all their nutritional requirements by preying on the available prey species, but in such a way that the prey animals themselves are at least able to maintain their population size, or preferably be able to grow in numbers.

Each prey species has a total live mass of which only a certain part is edible for leopards (edible mass). From the results of the carcass analysis regarding the edibility of prey for leopards presented in chapter 5, as well information in literature, a list was compiled of the percentage of carcasses of different live mass sizes that will on average be consumed by leopard (Table 6.1).

Table 6.1 Estimated and calculated edible percentage of carcasses of prey species of different sizes for all leopards.

Live mass (kg)	Edible mass (%)
0 – 5	100
6 – 49	77.99
50 – 150	75*
151 – 250	70*
250 – 500	65*

* From Viljoen (1993)

The edible part of the carcass of a prey species consists of meat (heart, lungs, liver and kidneys), fore intestines, (rumen, reticulum, omasum, abomasum, small and large intestines) hind intestine, skin, cartilage and soft bone. The decline in edible mass with an increase in live mass of any given prey species is illustrated in Figure 6.2.

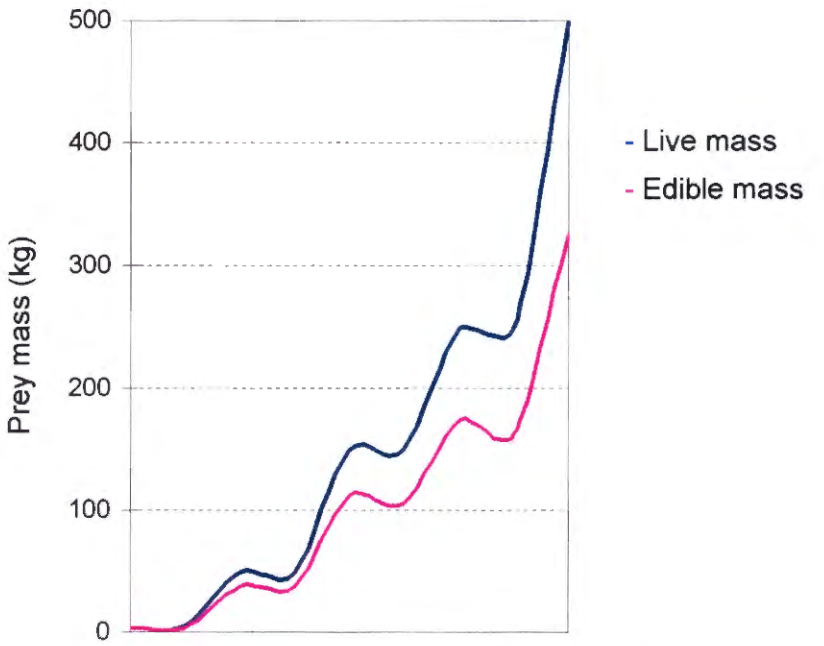


Figure 6.2 Relationship between edible mass of prey *versus* live mass of prey.

6.1.2 Calculations for leopard feeding behaviour

To manage a predator in a sustainable manner in a constrained area, nutritional requirements and the impact of leopards on herbivore biomass must be quantified.

Figure 6.3 is a visual illustration of the number of days a leopard will feed on a carcass by using the values from Table 5.2. The vertical line A represents the point of decomposition in summer at an average temperature of 31.2°C and line B that of in winter at an average temperature of 24.8°C. Decomposition values will vary according to environmental factors such as extreme heat, rain, wind etc. These average temperatures were determined with a minimum and maximum thermometer respectively in a Stevenson's screen on the study area during the study period.

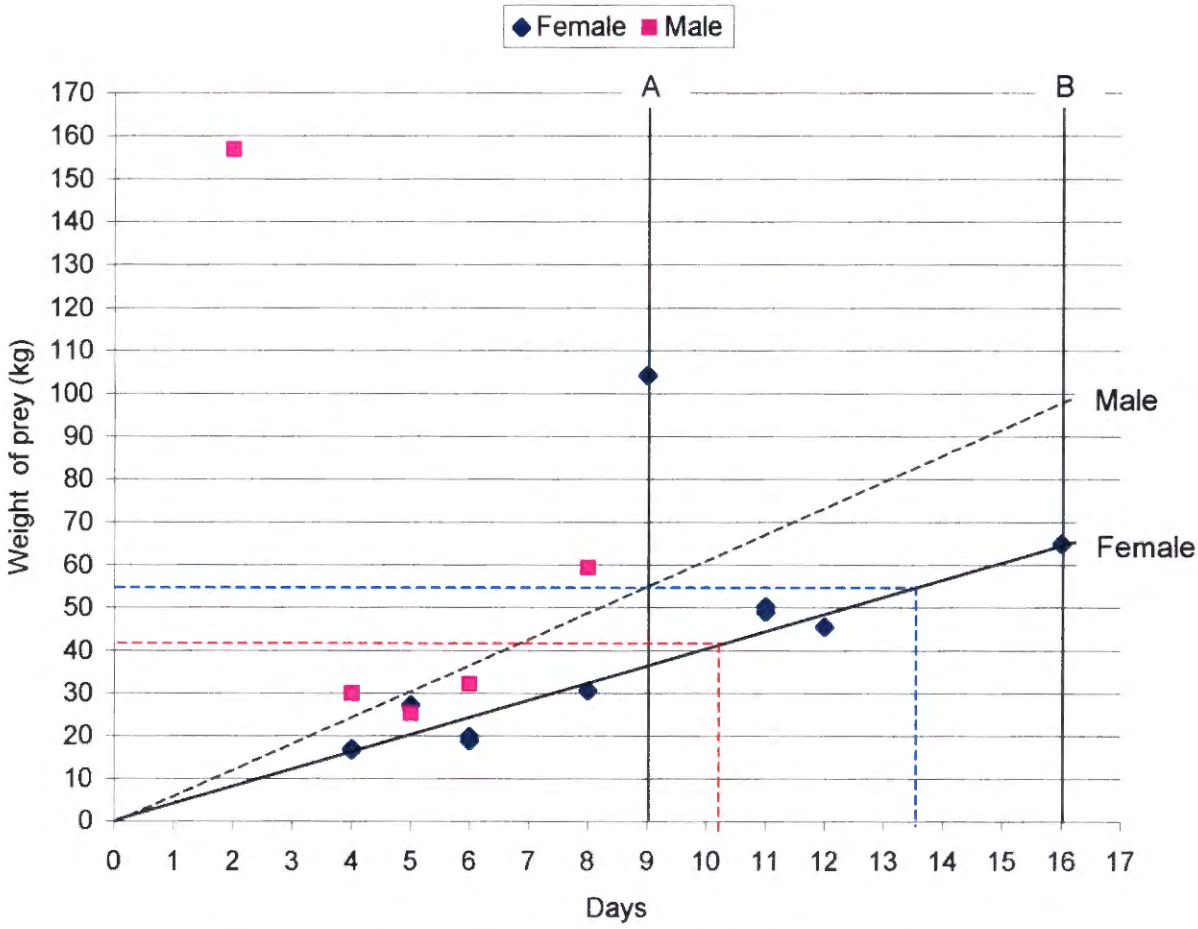


Figure 6.3 Illustration of the number of days that both a male and female leopard will feed on the carcasses of prey that vary in size, illustrating the difference between summer (A) and winter (B) with regard to decomposition and the abandoning of a carcass.

6.1.2.1 Feeding requirements of a leopard

Because lactating females (LF) have a higher nutritional requirement and thus a higher food intake, the increase in food intake of such a leopard can be calculated as: [1 + (%/100)]. The percentage represents the substitution value of the increase in daily food intake in kg for the lactating female. With this calculation, the determined value of (1 - 2), can be substituted in the feeding requirement equation. The minimum determined value is 1, which is representative of a non-lactating female with no additional nutritional requirements. The maximum value of 2 implies that a lactating female requires a 100%

higher food intake, thus double the normal daily requirements of a non-lactating female. For the calculation of the daily food intake of a male, the LF value can simply be substituted with 1.

The feeding requirements (FR) of a leopard per day can thus be calculated as follows:

$$FR = M \times SNF \times LF$$

where,

M = Mass of leopard in kg,

SNF = Sex Nutritional factor, based on sex (male or female)

LF = [1 + (%/100)] = (1 - 2), depending on it being a lactating female or not.

The nutritional factor is 8.56% and 8.07% of the body mass for females and males respectively. The above percentages are obtained by taking the total average kg / day edible consumption values (Table 5.2) for each sex for prey species that was completely utilised and dividing it by the mass of the experimental animal.

Sex Nutritional factor based on sex (SNF):

Female = 0.0856

Male = 0.0807

Example;

Male SNF = (4.885 / 60.5) x 100

= 8.07%

Example of two different female leopards' feeding requirements:

(i) An adult, non-lactating female leopard of 35 kg.

FR = M x SNF x LF

= 35 kg x 0.08558642 x [1 + (%/100)]

= 35 kg x 0.08558642 x [1 + (0/100)]

= 2.995524 kg

FR = 3.00 kg / day

(ii) A lactating female leopard of 35 kg.

FR = M x SNF x LF
= 35 kg x 0.08558642 x [1 + (%/100)]
= 35 kg x 0.08558642 x [1 + (56.25/100)]
= 35 kg x 0.08558642 x 1.5625
= 4.6805063 kg
FR = 4.68 kg / day

The 56.25% higher intake of a lactating female was calculated from the results of Bothma & Walker (1999). The latter authors found that a lactating female consumed 2.5 kg fresh food / day, compared to a non-lactating female consuming 1.6 kg fresh food / day.

With the former equation the daily fresh food intake of any leopard of a known weight can be calculated. An average female of 35 kg in the savanna biome thus requires an average of 1 093.37 kg fresh food / year and an average male of 65 kg 1 915.65 kg fresh food / year.

6.1.2.2 Impact of leopards on herbivore biomass

The impact of leopards on herbivore biomass (BI) in kg per year can be calculated as follows:

BI = M x HBV x Y x LF x SI

where,

M = Mass of leopard in kg,
HBV = Herbivore consumption value (0.105), (see explanation below)
Y = One year (365 days),
LF = [1 + (%/100)] = (1 - 2), depending on it being a lactating female or not,
SI = [1 + (X/365)] = (1 - 2), depending on impact of scavengers on prey,
X = Total days of scavenging or prey stolen from leopard.

Herbivores have a live and an edible mass as discussed. If a daily consumption value for a leopard is calculated based on the live mass, including both the edible component and remains, it will equal 10.5% of a leopard's body mass. Thus, the difference between the discussed daily feeding requirements percentage for a leopard and the above value is due to the edible mass of prey. Because the impact on herbivore biomass (edible and remains) is calculated, the live mass consumption percentage value of 0.105 is used.

A leopard does not need to hunt every day, but it must eat every day to fulfill its feeding requirements as discussed. If prey of a leopard is stolen 15 times per year, it results in 15 more hunts to resume feeding. The X-value is then substituted with 15, resulting in a higher impact of the leopard on the herbivore biomass. But, when scavengers steal a leopard's prey, there is not necessarily a loss in herbivore biomass, because another species (scavenger) in the ecosystem is now sustained. Without the food obtained by scavenging, the scavenger might have hunted the prey on its own.

Example;

The impact of a non-lactating female leopard of 35 kg on herbivore biomass without any scavenging:

$$BI = M \times HBV \times Y \times LF \times SI$$
$$= 35\ kg \times 0.105 \times 365 \times [1 + (\%/100)] \times [1 + (X/365)]$$
$$= 35\ kg \times 0.105 \times 365 \times [1 + (0/100)] \times [1 + (0/365)]$$
$$BI = 1\ 341.4\ kg / year$$

For a non-lactating female the FR was 1 093.4 kg / year and its BI = 1 341.4 kg / year. This represents an increase of 248 kg / year (18.49%) for the BI. This percentage increase closely corresponds with the edibility of carcasses (77.99 – 100%) in Table 6.1 of selected prey (1 – 49 kg) by leopard.

6.1.2.3 Number of days feeding on a carcass

Seasonal and daily temperatures determine the decomposing rate of a carcass. Subsequently substitution values for summer and winter at average temperatures of 31.2°C and 24.8°C respectively were calculated from the results in Figure 6.3 by dividing

the number of days feeding on a carcass that is being fully utilised, by the mass of the experimental leopard.

Example;

The amount of days feeding on a 55 kg male impala by an adult, non-lactating female leopard in summer,

NDF = MP x SN x SX x LF

= 55 kg x 0.2461538 x 1 x [1 + (%/100)]

NDF = 13.5 days

Above calculation can be verified from Figure 6.3 (blue line ----). The season values are 0.2721088 for winter and 0.2461538 for summer.

Adult male leopards are larger than adult female leopards. Therefore sex values were determined for the higher food intake by male leopards. These values are 1 and 0.5707559 for the female and male respectively.

The number of days feeding (NDF) on a carcass by a non-lactating female leopard of 35 kg in summer and winter:

NDF = MP x SN x SX x LF

where,

MP = Mass of prey in kg,

SN = Season value,

SX = Sex values,

LF = [1 + (%/100)] = (1 ≤ 2), depending on it being a lactating female or not.

6.2 Quantitative units and substitution values

6.2.1 Plant-herbivore production systems

The basic requirement of management systems for sustainable game production from veld is to balance the stocking rate of the various game species with the grazing and browsing capacity of the veld. The grazing capacity of the grazeable portion of a homogeneous unit of vegetation can be defined as the area of land required to maintain a single animal unit (AU) over an extended number of years without deterioration of the vegetation or soil (ha/AU) (Trollope *et al.* 1990). An animal unit (AU), also commonly referred to as a large stock unit (LSU), is defined as an animal with a mass of 450 kg, which gains 0.5 kg/day on forage with a digestible energy percentage of 55% (Trollope *et al.* 1990). The stocking rate can be defined as the area of land in the system of management, which the manager has allocated to each animal unit in the system, and is expressed per length of the grazeable period of the year (ha/AU) (Trollope *et al.* 1990).

The main difference, in practical terms, between the grazing capacity of the veld and the stocking rate, is thus that the grazing capacity refers to the true number of animals that the vegetation can sustain, and the stocking rate to the number of animals the manager perceived the vegetation can sustain.

The use and application of the Animal Unit (AU) or Large Stock Unit (LSU) originated from conventional agriculture and is based on the metabolic mass of the animals involved (mainly cattle and sheep in different age and sex classes). Comparison of different game species with the AU or LSU based on the metabolic mass, presents problems. The use of AU/LSU-values for herbivore game species does not allow for ecological separation, and thus overlooks the potential for using the specialised and complementary resource-use habits of wild ungulates to maximise veld utilisation.

In an attempt to find a system more suitable to multi-species systems, Dekker (1997) defined a grazer unit (GU) as the metabolic equivalent of a blue wildebeest (100% grazer) with a mean body mass of 180 kg. Similarly he defined a browser unit (BU) as the metabolic equivalent of a kudu (100%) browser unit with a mean body mass of 140 kg. The daily DM requirement of a GU will be 4.5 kg (2.5% of body mass for a blue

wildebeest) (Owen-Smith 1999) and the daily DM requirement of a BU will be 3.5 kg (2.5% of body mass for a kudu) (Owen-Smith 1999). Based on these definitions, substitution values of different game species in terms of GU and BU can be compiled.

6.2.2 Addition of a predator

With the addition of a predator (leopard) into a plant-herbivore system, an additional trophic level in the food pyramid is established. The given number of predators (leopards) must be able to satisfy all their nutritional requirements by preying on the available prey species, but in such a way that the prey animals themselves are able to, at least, maintain their population size, or preferably be able to grow in numbers. In order to achieve the goal of sustainability as set out above, some norms and terms regarding the predator and prey was developed.

In the savanna the average mass for female and male leopards is 35 kg and 65 kg respectively (Apps 1996). From this study it was established that a female leopard with an average weight of 35 kg consumes 3.00 kg fresh food / day and a male leopard with an average weight of 65 kg consumes 5.25 kg fresh food per day. Using these norms the following units are being proposed.

6.2.2.1 Predator Unit (PRU)

An adult, non-lactating female leopard (*Panthera pardus*) with an average mass of 35 kg and an average daily food consumption requirement of 3.00 kg / day is defined.

Males with an average weight of 65 kg will thus represent 1.75 Predator Units with an average food consumption of 5.25 kg / day. Females with cubs will represent a higher Predator Unit equivalent than non-lactating females.

Consumption values of other predators such as African wild dog (Bothma 1998); Cheetah (Borstlap 2002); lion (Viljoen 1993; Bothma 1998; Borstlap 2002; Power 2003); Spotted hyaena and Brown hyaena (*Hyaene brunnea*) (Mills 1990); Caracal (*Felis caracal*) (Skinner & Smithers 1990) were used to classify them as Predator Unit equivalents (Table 6.2).

Table 6.2 Substitution values of other large African predators in terms of Predator Units (PRU). (AW - average weight; DC - daily consumption; PRU – Predator Unit Equivalents; %BW - % daily consumption of body mass of predator).

Predator	Sex	AW (kg)	DC	% BW	PRU
Felidae					
Panthera leo	♂	190	9.35	4.92	3.12
	♀	130	7.43	5.72	2.48
Panthera pardus	♂	65	5.25	8.08	1.75
	♀	**35**	**3.00**	**8.57**	**1.00**
Acinonyx jubatus	♂	54	5.45	10.09	1.82
	♀	43	5.62	13.07	1.87
Felis caracal	♂	13	0.54	4.15	0.18
	♀	10	0.32	3.20	0.12
Hyaenidae					
Crocuta crocuta	♂	60	6.00	10.00	2.00
	♀	70	7.00	10.00	2.33
Hyaena brunnea	♂	47	3.29	7.00	1.10
	♀	42	2.94	7.00	0.98
Canidae					
Lycaon pictus	♂	25	3.55	14.20	1.18
	♀	25	3.55	14.20	1.18

6.2.2.2 Prey Unit (PU)

From literature and also commonly known, the impala forms a high prey-selection percentage of the leopard's diet. Scats of leopard were analysed in the Kruger National Park contained 60% impala (Bailey 1993). An average male impala has a live mass of 54.5 kg (47 – 66 kg) compared to the 41 kg (32 – 52 kg) of a female (Apps 1996). It is thus logical to use the impala as the norm to define a Prey Unit (PU).

Prey Unit (PU) is subsequently defined as a female impala (*Aepyceros melampus*) with an average live mass of 41 kg of which 30.75 kg is available for actual consumption.

Thus, one Prey Unit potentially supports one Predator Unit for 10.09 days. This is illustrated in Figure 6.3 with the red horisontal and vertical line (---) indicating a value of 41 kg live mass (y axis) that equals 10.09 days (x axis).

Other prey species are classified as Prey Unit equivalents (PU) (Table 6.3).

Table 6.3 Substitution values of other savanna game species in terms of Prey Units (1 PU = a female impala (*Aepyceros melampus*) with an average live mass of 41 kg of which 30.75 kg is available for actual consumption). (C% - consumption percentage of specie; Cons. Mass - consumption mass) (Live mass from, Apps 1996).

	Live mass			Cons. mass		Prey Unit Based on Live mass		Prey Unit Based on Cons. mass	
Species	**Female**	**Male**	**C %**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Giraffa camelopardalis	828	1200	0.65	538.2	780.00	20.20	29.27	13.13	19.02
Syncerus caffer	530	625	0.65	344.5	406.25	12.93	15.24	8.40	9.91
Taurotragus oryx	316	575	0.65	205.4	373.75	7.71	14.02	5.01	9.12
Equus burchelli	260	320	0.65	169.0	208.00	6.34	7.80	4.12	5.07
Hippotragus equinus	250	270	0.65	162.5	175.50	6.10	6.59	3.96	4.28
Equus zebra zebra	234	255	0.70	163.8	178.50	5.71	6.22	4.00	4.35
Kobus ellipsiprymnus	180	270	0.70	126.0	189.00	4.39	6.59	3.07	4.61
Oryx gazella	210	240	0.70	147.0	168.00	5.12	5.85	3.59	4.10
Hippotragus niger	210	230	0.70	147.0	161.00	5.12	5.61	3.59	3.93
Connochaetes taurinus	197	245	0.70	137.9	171.50	4.80	5.98	3.36	4.18
Tragelaphus strepsiceros	157	230	0.70	109.9	161.00	3.83	5.61	2.68	3.93
Connochaetes gnou	137	180	0.75	102.6	135.00	3.34	4.39	2.51	3.29
Sigmoceros lichtensteinii	140	170	0.75	105.0	127.50	3.41	4.15	2.56	3.11
Damaliscus lunatus	126	140	0.75	94.5	105.00	3.07	3.41	2.30	2.56
Alcelaphus buselaphus	120	152	0.70	84.0	106.40	2.93	3.71	2.05	2.60
Tragelaphus angasii	**62**	**107**	**0.75**	**46.5**	**80.25**	**1.51**	**2.61**	**1.13**	**1.96**
Damaliscus dorcas phillipsi	61	70	0.75	45.8	52.50	1.49	1.71	1.12	1.28
Damliscus dorcas dorcas	60	61	0.75	45.0	45.75	1.46	1.49	1.10	1.12
Potamochoerus larvatus	59	62	0.75	44.3	46.50	1.44	1.51	1.08	1.13
Phacochoerus africanus	56	80	0.75	42.0	60.00	1.37	1.95	1.02	1.46
Orycteropus afer	53	53	0.75	39.8	39.75	1.29	1.29	0.97	0.97
Aepyceros petersi	50.4	63	0.75	37.8	47.25	1.23	1.54	0.92	1.15
Aepyceros melampus	**41**	**54.5**	**0.7799**	**31.9**	**42.51**	**1.00**	**1.33**	**0.78**	**1.04**
Redunca arundinum	38.0	52	0.7799	29.6	40.56	0.93	1.27	0.72	0.99
Tragelaphus scriptus	28.0	42	0.7799	21.8	32.76	0.68	1.02	0.53	0.80
Redunca fulvorufula	28.0	30	0.7799	21.8	23.40	0.68	0.73	0.53	0.57
Antidorcas marsupialis	26.5	31.2	0.7799	20.7	24.33	0.65	0.76	0.50	0.59
Pelea capreolus	24.5	24.5	0.7799	19.1	19.11	0.60	0.60	0.47	0.47
Sylvicapra grimmia	20.7	18.7	0.7799	16.1	14.58	0.50	0.46	0.39	0.36
Papio ursinus	15.5	35	0.7799	12.1	27.30	0.38	0.85	0.29	0.67
Hystrix africaeaustralis	15.4	15.4	0.7799	12.1	12.01	0.38	0.38	0.29	0.29
Ourebia ourebi	14.1	14.1	0.7799	11.0	11.00	0.34	0.34	0.27	0.27
Oreotragus oreotragus	13.2	10.6	0.7799	10.3	8.27	0.32	0.26	0.25	0.20

continue...

Table 6.3 continued

	Live mass			Cons. mass		Prey Unit Based on Live mass		Prey Unit Based on Cons. mass	
Species	**Female**	**Male**	**C %**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Raphicerus camprestris	11.3	10.9	0.7799	8.81	8.50	0.28	0.27	0.21	0.21
Civettictis civetta	11.3	11.25	0.7799	8.77	8.77	0.27	0.27	0.21	0.21
Raphicerus melanotis	10.5	10.0	0.7799	8.19	7.80	0.26	0.24	0.20	0.19
Cephalophus natalensis	10.0	12.0	0.7799	7.80	9.36	0.24	0.29	0.19	0.23
Raphicerus sharpei	7.7	7.3	0.7799	6.01	5.69	0.19	0.18	0.15	0.14
Canis mesomelas	7.2	8.3	0.7799	5.62	6.47	0.18	0.20	0.14	0.16
Neotragus moschatus	5.4	5.0	0.7799	4.21	3.90	0.13	0.12	0.10	0.10
Cercopithecus mitis	4.9	9.3	0.7799	3.82	7.25	0.12	0.23	0.09	0.18
Cercopithecus aethiops	4.1	5.5	0.7799	3.20	4.29	0.10	0.13	0.08	0.10
Smaller mammals < 5kg	5	5	1	5	5	< 0.10	<0.12	< 0.08	<0.10

The nyala (*Tragelaphus angasii*) in bold in Table 6.2, represents prey with complete utilisation regarding consumption mass before decomposing. Prey larger than nyala will not be 100% utilised and thus be wasted.

6.3 Practical implications of leopard introductions

Since the presence of leopards on a game ranch has economical implications, the impact assessment of such a leopard must not only be based on ecological considerations, but also on economical considerations. From this point of view the food source of the leopard can be divided into the following three categories:

1. Prey with a direct commercial value (Table 6.4).
   This includes all ungulate game species, like impala, bushbuck, kudu, etc. with a direct economic value, either through live sales or hunting.
2. Prey with no direct commercial value.
   This includes all prey species, which do not normally have a direct economic value, like baboons, other small mammals (hares, rock hyraxes, rodents), birds, reptiles and insects.
3. Supplementary feeding.

Table 6.4 Potential prey species of a leopard. ALM - averages live mass from Skinner & Smithers (1990). (AEV - average economical values for game in Rand from Game & Hunt (June – November 2003). Total sp. – number of species to support one PRU for 1 year; NA - no prices available).

Species	Comm. val.	Value R	ALM	Specimens	AEV
Giraffa camelopardalis	Yes	17 000	1014	16	272 000
Syncerus caffer	Yes	122 500	557.5	16	1 960 000
Taurotragus oryx	Yes	4 517	445.5	16	72 272
Equus burchelli	Yes	4 469	290.0	16	71 504
Hippotragus equinus	Yes	150 000	260.0	16	2 400 000
Equus zebra zebra	Yes	22 500	244.5	16	360 000
Kobus ellipsiprymnus	Yes	6 200	225.0	16	99 200
Oryx gazella	Yes	4 098	225.0	16	65 568
Hippotragus niger	Yes	125 000	220.0	16	2 000 000
Connochaetes taurinus	Yes	1 892	221.0	16	30 272
Tragelaphus strepsiceros	Yes	2 980	193.5	16	47 680
Connochaetes gnou	Yes	2 500	158.5	16	40 000
Sigmoceros lichtensteinii	Yes	75 000	155.0	16	1 200 000
Damaliscus lunatus	Yes	16 500	133.0	16	264 000
Alcelaphus buselaphus	Yes	3 511	136.0	16	56 176
Tragelaphus angasii	**Yes**	**8 200**	**84.5**	**16**	**131 200**
Damaliscus dorcas phillipsi	Yes	792	65.5	20	15 840
Damliscus dorcas dorcas	Yes	7 083	60.5	22	155 826
Potamochoerus larvatus	Yes	440	60.5	22	9 680
Phacochoerus africanus	Yes	812	68.0	20	16 240
Orycteropus afer	No	0	53.0	25	0
Aepyceros petersi	Yes	750	56.7	24	18 000
Redunca arundinum	Yes	4 600	45.0	30	138 000
Aepyceros melampus	**Yes**	**620**	**41.0**	**32**	**19 840**
Tragelaphus scriptus	Yes	2 300	35.0	38	87 400
Redunca fulvorufula	Yes	4 150	29.0	46	190 900
Antidorcas marsupialis	Yes	800	28.9	46	36 800
Pelea capreolus	Yes	-	24.5	55	NA
Sylvicapra grimmia	Yes	1 200	19.7	68	81 600
Papio ursinus	No	0	25.3	53	0
Hystrix africaeaustralis	Yes	150	15.4	87	13 050
Ourebia ourebi	Yes	-	14.1	95	NA
Oreotragus oreotragus	Yes	-	11.9	113	NA
Raphicerus camprestris	Yes	800	11.1	121	96 800
Civettictis civetta	No	0	11.3	119	0
Raphicerus melanotis	Yes	2 400	10.3	131	314 400
Cephalophus natalensis	Yes	5 700	11.0	122	695 400
Raphicerus sharpei	Yes	1 000	7.8	179	179 000

continue...

Table 6.4 continued

Species	Comm. Val.	Value R	ALM	Total sp.	AEV
Canis mesomelas	No	0	7.8	173	0
Neotragus moschatus	Yes	4 333	5.2	258	1 117 914
Cercopithecus mitis	No	0	7.1	189	0
Cercopithecus aethiops	No	0	4.8	279	0
Smaller mammals < 5kg	No				0

The economical impact of a leopard that hypothetically fed on only a single species is illustrated in Table 6.4. Certain species such as impala are more preyed on, but non-commercial species are important in the leopard's diet. Prey selection is influenced by geographical location, habitat, environment and seasons. Hamilton (1976) found that birds comprised 27% and small mammals 10% of the diet of leopards, thus non-commercial species can contribute substantially to their diet. Available biomass/ha of small mammals will, however, influence their contribution to the leopard's diet.

The herbivore biomass impact (BI) of a non-lactating female of 35 kg is 1 341.38 kg / year. If 37% (496.31 kg) consists of non-commercial species, the biomass impact on commercial species will be 845.01 kg / year, reducing the economical impact more than one third. With supplementary feeding of say 20% of the initial herbivore biomass impact value of 1 341.38 kg, another 268.28 kg can be subtracted.

Non-commercial and supplementary feeding add up to 764.59 kg, equaling 57% of the BI value. The impact on prey with a commercial value is the difference of 43% (576.79kg). If impala comprised 100% of the selected prey with a commercial value, the economical impact would reduces from R19 840 to R9 114 / female leopard for impala.

6.3.1 Procedures for ecological sustainability

The following are required for the ecologically sustainable management of a game ranch.

(i) A vegetation map

A vegetation map should be the basis for any ecological planning. Every vegetation unit usually represents a unique management unit, which will be decisive in determining the habitat suitability for specific game species and also the number of the specific game species that can be kept.

(ii) Grazing and browsing capacity

The basic requirement of management systems for sustainable game ranching from veld is to balance game stocking rates with the grazing and browsing capacity.

If the amount of herbaceous dry mass per hectare is known, the grazing capacity can be calculated using for example the formula proposed by Moore *et al.* (1985), and again described by Moore & Odendaal (1987) and Moore (1989). For browsers a leaf quantification technique like BECVOL (Smit 1996) can be used to determine the leaf dry matter yield of woody plants on a species basis.

(iii) Game count

Different techniques can be used to determine game numbers and thus also available prey (species and numbers). However, the total biomass of game cannot be used, due to prey selection of the predator.

(iv) Predator information

The number, sex and mass of the predators must be known for substitution in the various equations to determine their nutritional requirements. Due to the differences in the habitat preferences of the specific prey species, prey selection, diet composition, habitat preferences and social behaviour of leopards are important factors that need be taken into consideration when determining the exact biomass impact on these species.

(v) Predator capacity

With objective criteria (like feeding requirements of a leopard, impact of leopard on herbivore biomass and days that they feed on a carcass)

established from this study, it was possible to define units such as the Predator Unit (PRU) and Prey Unit (PU). With substitution values that were compiled for all potential prey species, it is now possible to determine the predator-prey relationship in quantitative terms.

Taking into consideration all ecological components by following the previously discussed management steps, will ensure effective and sustainable game ranching of predators in the third trophic level.

6.3.2. Concluding remarks and recommendations

A game ranch or conservation area with predators should be managed in such a way that the number of Prey Units is sufficient to support the number of Predator Units in a sustainable way. This is a complex task with many other determinants that need be taken into account like predation by other predators, natural mortalities of game due to parasites, disease and droughts and an increasing problem of poaching.

Of the three categories of food sources, supplementary feeding is the most controllable, followed by the prey with a direct commercial value, while prey with no direct commercial value is the least controllable through management. Supplementary feeding can be considered as an opportunistic means to overcome a certain period of food scarcity or to alleviate pressure on prey species during critical periods like calving or lambing. Supplementary feeding should, however, never be used in such a way that the leopards can depend on that alone without the need to hunt.

It is recommended that the management model should be more refined regarding other predators. Research needs be done on the nutritional requirements and daily food intake of other predators in order to classify them more accurately in terms of Predator Unit equivalents.

Summary

The study on the captive leopards was conducted on the farm Masequa in the Soutpansberg district in the Soutpansberg Arid Mountain Bushveld. Field observations on five hand-reared leopards (*Panthera pardus*) were limited to four adjacent leopard proof enclosures of 1.5 to 33 ha in size located in prime leopard habitat.

An observational study on visual, auditory and olfactory communication of the leopards was conducted. Being a solitary animal, tactile communication is virtually absent in adult leopards, being mostly restricted to cub-cub and parent-cub interactions. Visual communication is discussed with regard to 11 facial expressions and 13 tail positions. A total of 14 vocalisations were identified (11 analysed on sonograms), that were used in the context of agonistic encounters, social interactions and mating behaviour. Olfactory signals apparently involve urine, faeces and glandular secretions. Combinations of all three communication methods are common. It was found that leopards possess an extensive and complex array of communication methods for intra and interspecies communication.

Five Body Conditions (BC) for leopards, divided in classes ranging from 1-5 were identified, where a rating 1 represented a good condition and 5 a poor condition. Selected prey species were offered to leopards in body condition 2 to 3 (hunting condition). The number of days they fed on the various carcasses as well as their behaviour and consumption were observed and values calculated. Carcasses were divided into nine carcass segments (CS) and the fat, crude protein, ash and dry material of a male impala divided into the various carcass segments classes, were determined.

Feeding sequence (FS), which started at the hind intestines, were correlated with the fat percentages of the different carcass segments. In contrast, the feeding sequence was not correlated with the decreasing crude protein content of the various carcass segments.

A Prey Unit (PU) was defined as a female impala (*Aepyceros melampus)* with an average live mass of 41 kg of which 30.75 kg is available for actual consumption. Similarly a Predator Unit (PRU) was defined as an adult, non-lactating female leopard

(*Panthera pardus*) of 35 kg with an average daily food consumption requirement of 3.0 kg per day. From these criteria, substitution values of other predator and prey species in terms of PRU and PU were calculated.

Equations were compiled from which the predator carrying capacity of a restricted area (e.g. game ranch) can be calculated for leopard. The daily feeding requirement in kg of a leopard can be calculated as follows: FR = M x SNF x LF. Explanation for symbols used: FR - feeding requirement of leopard; M - mass (kg) of leopard; SNF - sex nutritional factor based on sex with substitution values (0.0807) for male and (0.0855) for female; LF - consumption by lactating or non-lactating female, as determined by equation [1+(%/100)]. The percentage value is substituted with the difference in daily consumption (kg) of a lactating female as contrasted to a non-lactating female.

By means of equation BI = M x HBV x Y x LF x SI, the impact of leopard on herbivore biomass can be calculated. Explanation for symbols used: BI - impact of leopard on herbivore biomass; M - mass (kg) of leopard; HBV - herbivore consumption value substituting with 0.105; Y - 365 days; LF - lactating or non-lactating female as discussed above; SI - quantifies the impact of scavengers with equation [1 + (X/365)], where X represents the number of days prey was stolen from a leopard by scavengers.

Depending on environmental factors, the average number of days a leopard will feed on a carcass can be calculated with equation NDF = MP x SN x SX x LF. Explanation for symbols used: NDF - Number of days feeding; MP - mass (kg) of prey; SN - season values with summer (0.2461538) and winter (0.2721088); SX - sex values where a female represents (1) and a male (0.5707559); LF - lactating or non-lactating female as discussed above.

A management model for ecological sustainability in the third trophic level is introduced, which incorporates all ecological components consisting of grazer, browser, prey and predator units. With this model ecological and economical impact and sustainability can be calculated with the basic procedures discussed.

Opsomming

Die studie op luiperds in gevangenskap is uitgevoer op die plaas Masequa, Soutpansberg distrik in die Soutpansberg Ariede Berg Bosveld. Veldwaarneming op vyf handgrootgemaakte luiperds (*Panthera pardus*) was beperk tot vier aangrensende luiperdwerende kampe van 1.5 tot 33 ha, geleë in natuurlike luiperdhabitat.

Veldwaarnemings van visuele, akoestiese en olfaktoriese kommunikasie van die luiperd was gedoen. As alleenlopende dier is kommunikasie deur middel van fisiese aanraking feitlik afwesig in volwasse luiperds en beperk tot welpie-welpie en ouer-welpie wisselwerking. Visuele kommunikasie is bespreek met betrekking tot 11 gesigsuitdrukkings en 13 stertposisies. Altesaam 14 geluide was geïdentifiseer (11 geanaliseer met sonogramme), wat gebruik was in die konteks van antagonistiese ontmoetings, sosiale wisselwerking en paringsgedrag. Uriene, mis en klierafskeidings is blykbaar betrokke by olfaktoriese kommunikasie. Kombinasies van al drie kommunikasiemetodes kom algemeen voor. Luiperds beskik oor uitgebreide en komplekse kommunikasiemetodes vir intra- en interspesie kommunikasie.

Vyf Liggaamskondisies vir luiperds word beskryf en is verdeel in klasse van 1-5 waar 1 'n goeie kondisie en 5 'n swak liggaamskondisie verteenwoordig. Geselekteerde spesies is aangebied vir luiperds in liggaamskondisies 2 tot 3 (jagkondisie). Die aantal dae wat die luiperds op die verskillende karkasse gevoed het, asook hulle gedrag is waargeneem en waardes bereken. Karkasse is verdeel in nege karkas segmente en die vet, ru-proteïen, as en droë materiaal van 'n impala ram wat onderverdeel is in die verskillende segmente, is bereken.

Voedingsvolgorde beginnende by die derms, stem ooreen met dalende vet persentasies van die verskillende karkas segmente. In teenstelling het die voedingsvolgorde nie ooreengestem met die ru-proteïen inhoud van die verskillende karkas segmente nie.

'n Prooi Eenheid (PU) is gedefinieer as 'n rooibok ooi (*Aepyceros melampus*) met 'n lewendige massa van 41 kg waarvan 30.75 kg beskikbaar is vir benutting. Soortgelyk is 'n Predator Eenheid (PRU) gedefinieer as 'n volwasse, nie-sogende luiperdwyfie (*Panthera pardus*) van 35 kg met 'n gemiddelde daaglikse voedsel befhoefte inname van

3.0 kg per dag. Vanaf die gestelde normes, is vervangende waardes van ander predator en prooi spesies in terme van PRU en PU bereken.

Vergelykings is saamgestel waarvan die roofdier drakrag bereken kan word om 'n luiperd op 'n beperkte sisteem (bv. wildsplaas) te ondersteun.

Die voedingsbehoefte in kg van 'n luiperd per dag kan bereken word met die vergelyking FR = M x SNR x LF. Verduideliking van afkortings: FR - voedingsbehoefte van 'n luiperd; M – massa (kg) van luiperd; SNF - voedingsbehoefte gebasseer op geslag met waardes (0.0807) vir mannetjies en (0.0855) vir wyfies; LF - benutting van sogende of nie-sogende luiperdwyfie wat bereken word met vergelyking [1+(%/100)]. Die persentasie word vervang met die verskil in daaglikse voedsel inname (kg) van 'n lakterende wyfie teenoor 'n nie-lakterende wyfie.

Die impak van luiperds op die herbivore se biomassa kan bereken word met die vergelyking BI = M x HBV x Y x LF x SI. Verduideliking van afkortings: BI - impak van luiperds op die biomassa van herbivore; M - massa (kg) van luiperd; HBV - herbivoor benuttingswaarde met vervangingswaarde 0.105; Y - 365 dae; LF - vervanging van voedsel inname van 'n sogende of nie-sogende wyfie soos reeds bespreek; SI - kwantifisering van die impak van aasdiere met die vergelyking [1 + (X/365)] waar X die aantal dae voorstel wat aasdiere 'n luiperd se prooi steel.

Die gemiddelde aantal dae wat 'n luiperd op een karkas kan voed, afhangende van omgewingsfaktore, kan bereken word met die vergelyking NDF = MP x SN x SX x LF. Verduideliking van afkortings: NDF - aantal dae van voeding op karkas; MP - massa (kg) van prooi; SN - seisoenswaardes met somer (0.2461538) en winter (0.2721088); SX - geslag waardes waar 'n wyfie (1) en 'n mannetjie (0.5707559) verteenwoordig; LF - vervanging van voedsel inname van 'n sogende of nie-sogende wyfie soos reeds bespreek.

'n Bestuursmodel vir ekologiese volhoubaarheid in die derde trofiese vlak word voorgestel met inagneming van alle ekologiese komponente bestaande uit gras-, blaar-, prooi- en roofdier eenhede. Met bogenoemde model kan die ekologiese en ekonomiese impak van luiperds asook volhoubaarheid bereken word.

List of key words

Leopard (*Panthera pardus*)

Communication

Visual

Auditory

Olfactory

Feeding behaviour and sequence

Nutritional requirements

Prey and predator units

Predator capacity

Ecological and economical sustainability

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Appendix A. The fat content of each of the carcass sections of an impala ram and a complete rock hyrax as determined in a soxhlet apparatus using the hexane method (AOAC 2000).

Carcass section	Empty bottle (g)	Bottle with fat (g)	Difference (g)	Fat (g)	Fat (%)
Head	159.590	159.915	0.325	1.9997	16.252
	95.385	95.715	0.330	2.0665	15.969
Neck	95.450	95.565	0.115	2.0257	5.677
	87.430	87.540	0.110	2.0279	5.424
Fore intestines	107.325	107.665	0.340	2.0198	16.833
	167.650	168.010	0.360	2.0555	17.514
Stomach	88.985	89.275	0.290	2.0599	14.078
	91.5750	91.855	0.280	2.0353	13.757
Small & large	171.635	172.480	0.845	2.0218	41.794
intestines	136.630	137.480	0.850	2.0388	41.691
Spinal column & tail	140.010	140.145	0.135	2.0036	6.738
	161.395	161.540	0.145	2.0771	6.981
Fore limb	159.535	159.670	0.135	2.0625	6.545
	156.260	156.395	0.135	2.0105	6.715
Rib & flank	157.170	157.355	0.185	2.0538	9.008
	140.015	140.250	0.235	2.0265	11.596
Hind limb	163.470	163.575	0.105	2.0764	5.057
	111.805	111.925	0.120	2.0664	5.807
Rock hyrax	136.650	136.785	0.135	2.0148	6.700
	165.515	165.655	0.140	2.0169	6.941

Appendix B. The CP content of each of the carcass sections of an impala ram and a complete rock hyrax as determined on a dry material basis with a Leco ® nitrogen (N) analyzer (Leco ® Corporation 2001). A factor of 6.25 was used to convert the N content of samples to CP content.

Carcass section	Weight	% Protein	Calib.	Blank	A. Blk	Time	Moist	P-Fac
Head	0.1997	80.85	1.2826	0.401	0.25	169	0	6.25
	0.2004	80.20	1.2826	0.401	0.25	168	0	6.25
Neck	0.2004	92.89	1.2826	0.401	0.25	168	0	6.25
	0.2002	93.05	1.2826	0.401	0.25	168	0	6.25
Fore intestines	0.2005	76.82	1.2826	0.401	0.25	169	0	6.25
	0.2004	76.79	1.2826	0.401	0.25	168	0	6.25
Stomach	0.2003	67.78	1.2826	0.401	0.25	169	0	6.25
	0.2000	67.05	1.2826	0.401	0.25	168	0	6.25
Small & large	0.2006	42.47	1.2826	0.401	0.25	169	0	6.25
intestines	0.2006	42.07	1.2826	0.401	0.25	169	0	6.25
Spinal column & tail	0.2001	89.75	1.2826	0.401	0.25	168	0	6.25
	0.2007	89.93	1.2826	0.401	0.25	168	0	6.25
Fore limb	0.2008	91.45	1.2826	0.401	0.25	168	0	6.25
	0.2003	91.38	1.2826	0.401	0.25	168	0	6.25
Rib & flank	0.2014	88.22	1.2826	0.401	0.25	168	0	6.25
	0.2006	88.59	1.2826	0.401	0.25	169	0	6.25
Hind limb	0.2002	91.09	1.2826	0.401	0.25	168	0	6.25
	0.2000	91.00	1.2826	0.401	0.25	168	0	6.25
Rock hyrax	0.2004	70.11	1.2826	0.401	0.25	168	0	6.25
	0.2009	69.36	1.2826	0.401	0.25	168	0	6.25

Appendix C. The ash content of each of the carcass sections of an impala ram and complete rock hyrax as determined on a dry material basis by ashing the samples in duplicate in porcelain crucibles for four hours in a muffle furnace at 600°C (AOAC 2000).

Carcass section	Crucible (g)	Crucible & Ash (g)	Diff. (g)	Sample (g)	Ash (%)
Head	11.5786	11.7077	0.1291	2.0972	6.156
	10.6804	10.8145	0.1341	2.0851	6.431
Neck	10.3665	10.4610	0.0945	2.0463	4.618
	10.8132	10.9187	0.1055	2.0383	5.176
Fore intestines	9.98640	10.0856	0.0992	2.0998	4.724
	13.5938	13.6899	0.0961	2.0584	4.669
Stomach	11.0749	11.2556	0.1807	2.0435	8.843
	10.5606	10.7453	0.1847	2.0907	8.834
Small & large intestines	12.4493	12.5731	0.1238	2.0325	6.091
	13.1665	13.2916	0.1251	2.0763	6.025
Spinal column & tail	10.5559	10.6535	0.0976	2.0829	4.686
	14.2635	14.3568	0.0933	2.0531	4.544
Fore limb	14.2153	14.3020	0.0867	2.0151	4.303
	12.3541	12.4406	0.0865	2.0020	4.321
Rib & flank	12.5354	12.6382	0.1028	2.0867	4.926
	12.3647	12.4654	0.1007	2.0731	4.857
Hind limb	9.14810	9.24330	0.0952	2.0155	4.723
	12.6247	12.7208	0.0961	2.0117	4.777
Rock hyrax	9.85280	10.1522	0.2994	2.0178	14.838
	9.74080	10.0397	0.2989	2.0495	14.584

Appendix D. Dry material (DM) of each of the carcass sections of an impala ram and complete rock hyrax. The carcass sections were twice grinded with a heavy duty grinder and thoroughly mixed in a commercial bowl processed meat mixer. (MBG: Mass before grinding and MAG: Mass after grinding). Dry material was determined by drying the samples in a force draught oven at 100°C to determine the moisture content of each section.

Carcass section	Crucible (g)	MBG (g)	Sample (g)	MAG (g)	Sample (g)	Water loss (g)	Water loss (%)	Dm (%)
Head	13.6328	14.6366	1.0038	14.6255	0.9927	0.0111	1.1058	98.894
	8.5865	9.5976	1.0111	9.5855	0.999	0.0121	1.1967	98.803
Neck	11.0816	12.0917	1.0101	12.0829	1.0013	0.0088	0.8712	99.129
	11.0634	12.0792	1.0158	12.0714	1.008	0.0078	0.7679	99.232
Fore intestines	11.1895	12.2094	1.0199	12.2033	1.0138	0.0061	0.5981	99.402
	8.1793	9.1913	1.012	9.1862	1.0069	0.0051	0.5040	99.496
Stomach	10.9175	12.0119	1.0944	12.0045	1.087	0.0074	0.6762	99.324
	7.9359	8.9983	1.0624	8.9918	1.0559	0.0065	0.6118	99.388
Small & large	8.4522	9.5516	1.0994	9.5416	1.0894	0.0100	0.9096	99.090
intestines	11.147	12.1597	1.0127	12.1507	1.0037	0.0090	0.8887	99.111
Spinal column & tail	11.3095	12.3587	1.0492	12.3585	1.049	0.0002	0.0191	99.981
	10.9609	11.9714	1.0105	11.971	1.0101	0.0004	0.0396	99.960
Fore limb	11.0353	12.0972	1.0619	12.0926	1.0573	0.0046	0.4332	99.567
	11.1078	12.1636	1.0558	12.1587	1.0509	0.0049	0.4641	99.536
Rib & flank	11.0679	12.096	1.0281	12.0888	1.0209	0.0072	0.7003	99.300
	8.3324	9.353	1.0206	9.3457	1.0133	0.0073	0.7153	99.285
Hind limb	8.3453	9.3816	1.0363	9.3814	1.0361	0.0002	0.0193	99.981
	10.9191	11.9532	1.0341	11.953	1.0339	0.0002	0.0193	99.981
Rock hyrax	8.0098	9.0607	1.0509	9.0491	1.0393	0.0116	1.1038	98.896
	8.025	9.036	1.011	9.0238	0.9988	0.0122	1.2067	98.793